THE ECOLOGY OF LARGE HERBIVORES IN THE MIOMBO WOODLANDS OF SOUTH EAST TANZANIA

WILLIAM ALAN RODGERS

'A thesis submitted in fulfilment for the Degree
of Doctor of Philosophy in the University
of Nairobi

1972

This thesis is my original work and has not been presented for a degree in any other university

W.A Rodgers

W A Rodgers

This thesis has been submitted for examination with my approval as University Supervisor

John B. Sale

Dr J B Sale

This thesis is dedicated to the memory of the late

Constantine John Phillip Ionides

and to

Brian Dearnley Nicholson,

who, as Game Rangers in South East Tanzania from 1937 to 1973, created and developed the Selous Game Reserve, Africa's largest wildlife sanctuary.

and to

Bobbi, who shared the fun of the field work and the horrors of the writing.

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SUMMARY

The studies described in this thesis arose from an ecological survey of part of the eastern side of the Selous Game Reserve in south east Tanzania from 1967 to 1975. The intensive study area contained two major, ecologically distinct habitats, an area of tall grass miombo woodland and a smaller area of short grass scattered tree grassland. Several species of large grazing ungulate utilise these habitats, namely: buffalo, hartebeest, impala, sable, warthog, wildebeest and zebra. Seasonal changes in the environment such as the six month drought and widespread annual fires affect the pattern of habitat utilisation exhibited by each species. This thesis examines such utilisation and shows that each species has developed its own ecological and feeding strategies in order to maximise nutrient inputs and reproductive success in what is seasonally a harsh environment.

In many ways the miombo (Brachystegia) woodlands remain the least studied of the East African habitats. This lack of data on the miombo in general and the Selous Game Reserve in particular means much of the thesis is taken up by descriptions of the physical and biotic environment of the study area. Following an introductory chapter the thesis is divided into three parts. Part one, with three chapters, describes the physical environment: geology, soil, climate, water and prehistory; the vegetation: community description, distribution and species composition, floristics and vegetation dynamics; and range factors of productivity and forage nutrient content. Part two contains chapters on animal numbers, distribution patterns, feeding and nutrition and a chapter examining growth and reproduction as indices of population performance. Part three concludes the thesis with a chapter reviewing the miombo woodlands and the Selous as a wildlife habitat and a final chapter discussing management policy for the Selous Game Reserve.

The study area is low lying (100 - 700m asl) with a single rainy season from late November to early May (average 760mm p.a.). Despite a long hot dry season, surface water is relatively plentiful. Habitat distribution is primarily controlled by geology and soil type with major modifications by fires and past human activity. The upland Karoo and post karoo sandstones give rise to infertile acidic red sandy soils which carry a climax-thicket formation. These have been degraded into woodland by fire and settlement activity. Lower down the drainage slope the flat Pleistocene river terrace of grits and sands has produced a hard alkaline sodic soil carrying short grass scattered tree grassland. The drainage sump of recent alluvial clay carries tall floodplain grasses.

The vegetation is diverse, collections to date totalling over 1200 vascular plants including 150 grass species. The woodland vegetation shows strong affinities to the Zambezian flora, and the thicket, riverine and alkaline communities show affinities to the East African coastal flora. The thesis contains species lists and a vegetation community map. Fire has opened up the thickets producing

tall grass woodlands of various types. Grasses, mainly Andropogonae, are coarse tussock perennials with very low nutritive values when dry. No burning allows the spread of woody and climbing species which engulf the grass layer and rapidly reduce grazing values. Late dry season fires reduce woody elements and plant diversities and leave coarse grass growth thoughout the dry season. Cooler early dry season fires maintain mixed woodland communities and a mixture of grass species and, where water tables allow, rapidly produce a flush of nutritious regenerating grass growth. Crude protein content of such growth can reach 20% although standing crop is low.

The alkaline soils carry a short grass sward of mixed annual perennial species of high nutritive values in the rains. There is no flush after burning and dry season grazing values are low.

Chapter 5 discusses techniques of animal census in detail. A vehicular ground sample census using fixed systematically placed transects was used for common ungulates. Rainy season densities on the short grass habitats are as follows: Impala 28.7/km^2, wildebeest 27.2/km^2, zebra 16.2/km^2 and warthog 9.4/km^2. Wildebeest and impala densities have remained unchanged for six years, zebra and warthog densities have increased significantly. Less detailed data are given for other species. Distribution data have been collected at several different scales from Tanzania wide, to the Selous, to the study area, to the different facets of a miombo valley-ridge catenary system.

It is shown that sable and Lichtensteins hartebeest are restricted to tall grass woodland habitats, wildebeest and impala must have access to short grass areas in the rains and that buffalo, zebra and warthog, are more habitat tolerant but achieve higher densities on short grass habitats.

Within the study area virtually all impala, warthog, wildebeest and zebra concentrate on the short grass areas in the rains, moving into the woodlands following the onset of burning. Within the woodland habitat wildebeest and impala concentrate on the green flush of the valleys and avoid the unburnt areas and ridge tops. Sable and hartebeest are distributed throughout all categories and warthog and zebra are intermediate showing some selection of valley and green areas. The onset of the November rains signals a return to the short grasslands.

Studies of feeding behaviour showed buffalo, hartebeest and wildebeest to be total grazers whilst sable and impala took significant proportions of browse in the dry season and warthog diet changed to perennial monocot roots and rhizomes. Feeding studies concentrated on wildebeest and impala and much data was obtained from post mortem analysis. By assuming that extrapolation of data from other large ungulate studies was unlikely to cause large relative errors it was possible to make estimates of protein and energy intakes and of theoretical nutrient needs for these two species. During the rainy season both species had inputs greater than theoretical requirements for maintenance, i.e. they were in positive nutritional balance. As the dry season progressed both male and female wildebeest which remained on the dry short grass habit entered a period of negative nutritional balance. However wildebeest moving to fresh flush in the woodlands were shown (albeit on less evidence) to maintain a positive balance. Impala at the onset of the dry season changed their diet to nutrient rich browse components and so maintained a positive nutritional balance. These two strategies of habitat change and dietary change have resulted in peak nutritional inputs at different times of year. Impala have peak inputs in September and wildebeest in December. Onset of parturition coincides with these peak periods. The nutritional load of gestation is minimal compared to that of lactation. Calving season therefore allows lactation and weaning of calves at the nutritional optimum time of year. Other species show different strategies, which allow a separation of niche space reducing competition for food resources. Chapter eight shows that individual growth rate, body condition and fecundity rates are as high or higher than other populations in Africa, and that populations here are well adapted to the ecological conditions of this part of the Selous Game Reserve. This chapter discusses why the wildebeest population is stationary when nutrition is adequate, condition is good and fecundity is high. Predation by lion is put forward as a major limiting factor. The concluding chapters look at the miombo woodlands throughout Africa as wildlife reserves and suggest that only when tall grass woodlands are adjacent to other habitats

such as short grassland or floodplains do animal densities reach levels high enough to warrant major conservation inputs. The importance of fire in providing dry season graze is stressed and fire management polices for the Selous are discussed. Past, present and future human impacts on the wilderness values of the Selous are examined and a plea is made for definite land use policy statements for south east Tanzania and the reserve.

ACKNOWLEDGEMENTS

The studies contained within this thesis have been undertaken over a ten year period and in a very remote area of East Africa. I have been fortunate in that many people and institutions have given advice and assistance at all stages of my work. I trust I can remember them all!

The first six years were basically field work and I owe a great deal to my assistants and guides - the staff of the Selous Game Reserve and the Miombo Research Centre. both for making sure I am alive today and for teaching me much about the ecology of the miombo woodlands. Game Assistants Mohammed Athumani and Saidia Mwambezi took me on my first foot safaris. Field Assistants Marombe, Goryama, Daudi and Makonila were the mainstay before the Research Centre became a reality. Ali Makonila then became my driver until I left the Division. Memedi Menge, Saidi Mpapa, Mshamu Mkopoka and Hemedi Matali helped in the field and with post mortem studies. Alfred Mponda helped me wrestle with maps and air photographs. Wazee Mohammed Ligogi and Nchigagi Mfaume lived and hunted in what became the study area well before I was born. They still know more about this area of wilderness than I will ever learn. My two Senior Research Assistants helped in many ways, Rashidi Ludanga with botanical aspects and Henry Desuzo with post mortems, census work and data analysis. I will miss their companionship.

Gordon Matzke, Patrick Stobart, Franc Mes, Bob Gainer and Kaj Vollesen, biologists at the Centre all contributed to my studies, Kaj still does - thank you!

Wardens, Engineers and Administrators of the Game Division have helped me with my work, kept vehicles going, built roads and lightened my load of non research tasks. I too acted as warden, engineer and administrator during my service. Hemedi Mahinda OBE, John Capon and Raphael Jingu

Directors and Acting Director of Game approved my activities and gave considerable support in terms of finance, staff and equipment. Bakari Mbano who has replaced me as officer in charge of the M.R.C. (and as pilot!) was a welcome companion in the field office and the air.

C.J.P. (Iodine) Ionides, whom I had the privelege of knowing, provided inspiration; if he could live there for thirty years I could manage ten! Piet and Minnie Wessels taught me how to live in and enjoy the bush in my early years. Allen & Margaret Rees (Principal Game Warden & Ecologist in the Selous) themselves knowlegeable naturalists, gave much welcome assistance, advice and hospitality.

Brian Nicholson, my "boss" was heard to say that "he didn't want any schoolboy interfering in his reserve" when I was first posted to his range. I did interfere and we became friends. I trust this thesis justifies his support and enthusiasm. Brian has done more than any other person to protect the superb natural wilderness that is the Selous.

Then there were the students, nameless now, who helped during field courses, and their intructors from C.A.W.M. Mweka; Tony Mence, Les Robinette, John Kundaeli, Clive Spinage and especially Pat Hemingway. Pat and I have argued for years over census methodology, he in calculus and myself in rude English. I think he has the answer, but I cannot understand it.

Some biologists braved the wilds of the Selous, visited the M.R.C. and gave me much advice - some of which I took. To Anton de Vos, Ken Ashby, George Petrides, Hugh Lamprey, Ray Lawton, Colin Pernycuick, Bob Wingfield, Peter Jarman, Ron Skoog, Dennis Herlocker, Rudi Sachs, Hans Jacob and Pat Duncan, my thanks!

The Central Veterinary Laboratories undertook Chemical analysis and veterinary investigations. Laboratories in Tanga, Dar es Salaam, Ifakara and Kilosa analysed soils. Williamsons Diamonds supplied old aerial photographs and maps. The East African Herbarium and the Botany Department of the University of Dar es Salaam identified plants. Old men of Ngarambe village told me of the Selous in the good old days, when they lived there.

The East African Wildlife Society gave a generous grant in the early days of 1968, which provided the first of the permanent buildings at the M.R.C. The Government of Denmark gave a very large grant in 1969, this grant supported the study for the next five years and gave a lasting research base to the Tanzania Government.

Professor Prasad, Professor Jolly, Dr. Ian White and Dr. David Griffiths gave statistical advice. Staff of the Department of Botany at the University of Aberystwyth held my hand through the intricacies of computing and taught me much plant ecology. Drs David Griffiths, Kim Howell and Katherine Bulstrode read draft chapters and Professor Msangi encouraged the completion of thesis. Mrs Lena Guy and Miss Jennie Morris helped with drawings, Miss Erica Khuri with reproduction.

My supervisors, Dr. Brian Harris and Dr. Andrew Agnew gave assistance during the early stages of the study. Andrew Agnew gave me hospitality and organised my stay in Wales. Dr. John Sale remained patient and understanding for ten long years a supervisor. I owe him much, I don't think he expected me to complete the study.

My parents and my wife nagged for six years for me to finish the thesis. They were successful - it is done. Bobbi typed innumerable drafts for five years, I'm glad it is over for her sake.

CHAPTER ONE

INTRODUCTION

1.1 Aims of this study and Structure of the Thesis

Miombo (Brachystegia - Julbernardia)species woodland is estimated to cover half of Tanzania's land surface but until the last decade has been little studied from an ecological or agricultural view point. Despite the scale of wildlife resources within this ecological zone (which includes the 50,000 km^2 Selous Game Reserve and 25,000 km^2 Ruaha - Rungwa complex) there had been no intensive wildlife research input until this study commenced in 1967. This thesis has been compiled from data collected during my ten year ecological study of the eastern Selous, as Game Research Officer with the Tanzania Game Division.

The thesis examines the utilisation of the miombo woodland and associated grassland and floodplain communities by a spectrum of seven species of large grazing herbivore. The extremes of six month wet and dry seasons and the prevalence of dry season fires are responsible for great seasonal variation in the levels of forage production and nutrient content in the different habitats. In response to this variation the animal populations modify their utilisation patterns resulting in changed habitat occupance and feeding behaviour. Each species appears to have developed distinct strategies to obtain adequate nutritional inputs to allow for bodily maintenance and population growth. The evolution of these different strategies has resulted in a greater separation of niche space between sympatric herbivores at a time of scarce resources (Westoby 1974).

The objectives of this thesis are to demonstrate that such different strategies exist, to elucidate the reasons for the change in strategy and to measure the ecological benefits from such strategies. Such a task required the integration of several different lines of study, including:

(a) The detailed description of the environment and the different vegetation communities, and the seasonal change in the quantity and quality of their forage resources.

(b) The development of methods of animal census in woodland environments and the assessment of population density in each habitat in each season from year to year,

(c) The determination of animal population movements and habitat utilisation patterns, and the analysis of feeding activity and nutrient input in these habitats,

(d) The assessment of species performance in terms of population growth, body condition and reproductive activity,

(e) An attempt to relate the factors necessary for population success to the environment of the Selous Game Reserve and the miombo woodlands in general and to identify management inputs necessary to promote such success.

Thesis structure is detailed in the table of contents. The thesis contains nine chapters apart from this introduction and they are divided into a section describing the physical vegatation environments, a section describing the animal population and their use of the environments and a section reviewing the ecology and the management wildlife resources of the miombo woodlands and the Selous Game Reserve. There are ten appendices which either describe studies peripheral to the central theme of the thesis or contain extra details of methodolgoy or discussion to that of the main text.

Part One.

The physical environment is described in chapter two with sections on geology and geomorphology, soils, climate, water resources and past history. These topics have not been examined in depth but they do serve as relevant background information to the main study.

The vegetation is examined in much greater detail. Chapter three has sections on floristic affinities, vegeatation communities and distribution patterns, vegetation succession and dynamics, and vegetation diversity. The parameters of forage production and nutrient (mainly crude protein) content in relation to grazing pressure and annual fires are described in chapter four. The lack of previous descriptions of the vegetation of south east Tanzania and the complex role of fire in controlling woodland dynamics and forage parameters have meant this section is extremely lengthy.

Part Two.

This part commences with details of the animal census studies and shows change in numbers for four species (Wildebeest, zebra, impala and warthog) from 1968 to 1977, A discussion of the merits of the census technique is included in appendix 9. Chapter six discusses distribution patterns of the animal species on several different scales ranging from the whole of Tanzania, to the Selous Reserve, to the study area and to a small ridge slope valley catenary system in the miombo woodlands. The chapter concludes with a description of each species in terms of habitat occupance and compares this with other areas in Africa.

Details of feeding and nutritional studies are contained in chapter seven. Animal species are classified as to feeding type on the basis of their distribution, morphology and behaviour. The concept of selection in diet is discussed in some detail. Estimates of nutrient input are made for wildebeest and impala and these compared with theoretical requirements. Nutritional parameters are frequently taken from published studies on domestic stock. The use of such parameters is discussed in appendix 10. The chapter concludes with a discussion of the feeding strategies of the different herbivores.

Details of animal species population growth rates, reproductive parameters and condition levels are described in chapter eight. These values together with data on individual growth rates and disease-parasite levels are used to quantify "how well the populations are performing" in their habitats.

Part Three.

Part three brings together the conclusions of earlier chapters into a discussion of wildlife ecology in the miombo woodlands and the Selous Game Reserve, and the thesis finishes with a review of conservation, management and development options for the wildlife resources of the Selous Game Reserve.

1.2 THE SELOUS GAME RESERVE

The Selous is not only the largest but also one of the oldest wildife reserves in Africa, part being gazetted by the German Colonial Administration in 1905. Reserve boundaries are not static however, the latest additions being gazetted in 1976. Matzke (1975, 1977) describes the history of the reserve and Nicholson (1969) documents the development and utilisation of the resources of the Selous. Rodgers (1976 and appendix 2) describes past human occupance of the eastern part of the reserve and Rodgers (1977b) discusses the ecological values of the Selous in the light of plans for large scale hydro-electric dam development.

The reserve is situated on the coastal plains in South East Tanzania, ranging in altitude from 80 to 1300m (300 to 4,200 ft) and is included in four administrative regions and ten districts (Fig. 1.1). To coordinate development, the reserve is controlled directly from Division Headquarters in Dar es Salaam and not from each region.

The Selous is dissected by the large Rufiji River System, whose major tributaries, Great Ruaha, Kilombero, Luwegu and Mbarangandu flow across the reserve. The difficulties of access and communications caused by these rivers have been important in allowing such a large area (6% of Tanzania's land surface) to be retained as a wildlife sanctuary. Being a reserve the area has no human habitation or human rights of access. Before their evacuation in 1945-1947 (due to trypanosomiasis) Selous area inhabitants were shifting cultivators, hunters and fishermen, predominantly of the Wangindo, Wapogoro and Warufiji tribes. The area has no history of domestic livestock. The prolonged dry season, poor infertile soils and the ubiquitous tsetse fly (Glossina morsitans) have meant the area is little suited for agriculture, cattle or forestry.

In 1964, the Tanzania Government implemented a policy of long term development for the Selous Game Reserve involving revenue from tourist trophy hunting and game viewing. This development necessitated the creation of 7000 km of roads and tracks, plus airstrips, ferries and bridges. Such a policy of resource utilisation required information on the ecology of the Selous, and in particular, knowledge of the abundance and distribution of the large mammals. This was the reason for my posting to the Selous in September, 1976.

The reserve is largely covered with miombo woodland although as is to be expected in an area of this size there is considerable variation in climate, soils and topography which give rise to several different vegetation types. These types with an estimate of their relative cover are as follows:

Thicket-forest	5%
Woodland	85%
Miombo communities	50%
Combretum communities	35%
Wooded grassland	8%
Swamp-floodplain	2%

A description of the miombo woodlands of East Africa can be found in Burtt (1942), Gillman (1949), Russell (1962) Lind & Morrison (1974) and in chapter three of this thesis. Broad detail of vegetation cover of the Selous are shown in Fig. 6.2b. General features of the Selous Game Reserve are shown in plates 1 and2.

Table 1.1 lists large mammals found in the Selous Game Reserve and in the study area (see below). This table gives the scientific names for all mammal species mentioned in the text of the thesis. Preliminary estimates of large mammal population size for the Selous and immediate environs are given in table 1.2. These figures were obtained from a 3% aerial census of the Selous undertaken in 1976 by Douglas-Hamilton, Rodgers & Mbano (unpublished data).

1.3 THE STUDY AREA AND MIOMBO RESEARCH CENTRE

As it was clearly impossible to study the whole reserve in detail, especially before the impact of light aircraft on wildlife research in East Africa, a smaller study area was needed. A large area in the eastern Selous was found to be adequate (blocks LL1 & LL2, named after the Lukiliro River) in that it had relatively easy access, large wildlife populations and it contained examples of all major vegetation types. The fact that the vegetation types were arranged in a distinct sequential fashion across an east-west drainage basin made study very much easier. Animal populations move across the vegetation zonation and, with the exception of elephant, do not leave the study area in significant numbers. The study area therefore, can be thought to contain populations of finite size for the purposes of analysis and discussion. This block of some 1900 km^2, became the site for intensive ecological studies; less intensive surveys were made of other areas in the Selous The study area is shown in Fig. 1.2, the pattern of animal movement in fig. 1.3 and general features in plates 3-10.

In 1969, the Game Division benefited from a very generous grant from the Government of Denmark for the construction, equipping and running a wildlife research centre to investigate the miombo habitat and its fauna. This centre was built at Kingupira in the study area (38°30'E, 8°30'S). I administered the centre from its inception until 1975.

1.4 CONVENTIONS IN DATA PRESENTATION

(a) Within each chapter I have attempted to keep to a logical introduction - mehtods - results - discussion format. However, within very large chapters such as chapter three, or very diverse chapters such as chapter two I have resorted to the use of sub-chapters.

(b) Numerical data are given in metric units, imperial equivalents are given in the case of altitude and hydrological data.

(c) The numbering of diagrams and tables follows that of of the chapter they refer to; thus table 4.2 is the second table in chapter four. Pages are numbered within chapters and appendices, e.g. page 7.28 is page 28 in chapter seven, page A3.4 is page four in appendix 3.

(d) Most statistical analyses used standard techniques and, as such, few details are given in the text. Unusual analyses are explained more fully and source references given. The significance value of the results of statistical tests are starred in tables and in the text, according to the scale:

* = probability less than 0.05

** = probability less than 0.01

*** = probability less than 0.001

PART I

THE ENVIRONMENT

Chapter 2: The physical environment

Chapter 3: The vegetation

Chapter 4: Forage production and nutrient content.

CHAPTER TWO: THE PHYSICAL ENVIRONMENT

2.0 INTRODUCTION

This chapter gives a brief description of the physical features of the study area; covering the geology, geomorphology, soil types, climate and water distribution. The chapter finishes with an outline of the prehistory of the Miombo woodland formation in terms of past climates and human history. Appendices on the dynamics of water hole formation and a recent history of Wangindo settlement in the study area, (Rodgers 1976) add to the chapter content.

Descriptions are based on published material, field observations and measurements, and analyses undertaken by specialist institutes in Tanzania. This chapter does not go into detail on any of the topics, but as the environment of South East Tanzania is poorly known and documented, I do draw extensively on published material from elsewhere in Africa. This is considered essential for an understanding of the ecology of the study area. Plates 1-10 show general features of the Selous and the study area.

2.1 GEOLOGY AND GEOMORPHOLOGY

The geology of South East Tanzania and the area of the Selous Game Reserve in particular has been poorly documented.

Williamson's Diamond Mines, Mwadui, produced a small scale geological types map in 1975. Published descriptions are based on early exploratory traverses and a detailed survey of the Rufiji River basin in connection with proposed irrigation and hydro-electric schemes, (Haldemann 1968, and F.A.O. 1961). Rodgers (1969) gives a summary of the available geological information.

The oldest geological formation within the Selous is the Usagarian system of basement rocks, composed of quartzites, limestones, schists and gneisses. The most widespread formation is the Karoo sandstone system (Jurassic/Cretaceous) of which one bed, the Rufiji bed, is found in the study area. Surface rocks vary from coarse and fine sandstones to lime nodules, mud pellets, shales and mudstones. A fossil gymnosperm (probably Dadoxylon dantzii Potonii) is characteristic and widespread.

During the early Cainozoic era, degradation or base levelling reduced the Karoo formation to a smooth land surface with few pre-Karoo or Gondwanaland relict surfaces, Nandanga mountain (37°45'E, 8°25'S) in the central Selous is an example of such a relict surface. Later degradation further reduced the early Cainozoic surfaces, of which one example, the Libungani hills (800m) is found in the west of this study block. These surfaces are referred to as the Neogene or African surfaces, (King, 1967), and have led to "the very distinctive topographic features, flat topped mesas bounded by cliffs of friable cream coloured gravels", (Spence, 1957). Further degradational cycles are distinguished as Late Cainozoic 1 and 2 and a Recent cycle.

The first of these later cycles ended in the Miocene leaving an undulating landscape characteristic of much of southern and western Tanzanian miombo. The second cycle, which ended in the Pleistocene, is characterised by the deposition of alluvial grits and sands, found in many African river terraces eg. the Kafue and Luangwa valley systems in Zambia and the Ruvuma valley and this study area in Tanzania. The recent cycle has caused further deposits of alluvial clays in many river valleys. A scaled profile diagram of the study area is shown in figure 2.1 indicating land surfaces and basic geology.

Present erosion is accentuated by annual fires enabling severe surface run-off to occur early in the rainy season. As a result sand rivers are widening, and horse-shoe shaped erosion basins are cutting into the African land surface. The fact that the Rufiji river carries 13.5 million metric tons of sediment per year from a 155,000 km^2 basin is an indication of the extent of erosion, (F.A.O., 1961). The geological boundary of the Karoo sandstones and Pleistocene alluvial deposits is of importance in that it produces a line of permanent springs and seepages. This is discussed in appendix one.

Secondary to the major topography described above are a series of minor ridges and valleys, many of which are catenary. These catenary systems are discussed in chapter 2.2 and 3 as geomorphology, through its role in determining soil type and drainage patterns, plays a major part in the causation of vegetation distribution (Cole 1963).

This general correlation between geomorphology, soil and vegetation allows the delimitation of easily recognized landscape units suitable for land use planning and land scape mapping. This has been attempted in the Luangwa valley system in Zambia by Astle et al, (1969), and many of their landscape units are easily recognizable here. The similarity between the Luangwa system and this study area will be further demonstrated in this thesis (Chapters 3 and 9).

2.2. SOILS.

2.20 Introduction.

This section describes the soils of the study area in terms of their distribution, physical characteristics and chemical constituents. As the taxonomy of tropical soils is complex and controversial no attempt is made at classification. Soils are named by reference to their physical characters, following the system of Anderson, (1952, 1963). The section finishes with a discussion of some soil features of importance to vegetation growth and distribution: the soil nutrient content, the properties of alkaline-sodic soils and the soil catena within the Karoo system.

2.21 Methods.

Major soil types were immediately recognizable in the field by their colour, physical composition (sand, silt, clay) and from their drainage and site situation. Such soil types were tabulated for all vegetation communities, (see chapter 3.4). Soil pits were examined in each soil type, at first in collaboration with the Ministry of Agriculture/U.S. Peace Corps "land use and soil survey team" in 1968. Later soil samples from known depths were collected from other sites, e.g. smaller communities, topographic profiles, burning plots etc.

Soil samples were air dried and sent for analysis either to the Agricultural Research Centre at Ilonga, Kilosa; or to the Water Department's Soil Laboratories in Dar es Salaam. In 1971 soil samples from 10cm depth were collected from vegetation sample sites (chapter 3) and analysed for pH and clay content at the Department of Botany at the University of Dar es Salaam.

2.22. Results.

2.221. Soil types and distribution.

The following soils dominate the study area:

a) Non laterised red and yellow soils on sandstones.

b) Leached ferruginous soils in valley bottoms,

c) Alkaline-sodic soils (solonetz) with hard pan characteristics,

d) Alluvial clays on flood plains.

These may be described as follows:

a) Non laterised soils: these are zonal for much of the Karoo/Cretaceous systems of southern Tanzania. They are equivalent to the red latosals, tropical red earths or ferralitic soils of other classificatory systems. Sub surface soil colour varies from bright red through yellow browns to grey, depending on iron oxide content. Red soils dominate on drier sites on upper slopes and ridge tops. These soils are old, inherently infertile, well drained, acidic and very low in major nutrients; Nitrogen (N), Phosphorous (P), and Potassium (K), (tables 2.1 & 2.2). Organic matter content is low especially where sheet erosion and surface run off occur. Clay content, principally kaolinite, increases downslope.

These soils dominate the African land surface and the upper levels of the late Cainozoic surfaces in the study area. They are catenary with the ferruginous soils described below.

The soils have a poorly differentiated profile and no real structure or form. A stone line may occur at depth, and in areas of cliff erosion a thin iron concretionary layer may be seen.

b) Leached ferruginous soils: these soils do not reach their full development in this area and are similar to a) in many ways. They are distinguished by their situation in valley bottoms with poor or sluggish drainage, by iron staining of roots and surface puddles and by an increase in clay content. Colours range from red to chocolate brown. Clay content (kaolinite with some montmorillonite and illite) is variable. Structure and horizons are poorly differentiated.

c) Alkaline-sodic soils: these soils are typical of the Pleistocene alluvial/colluvial deposits of the river terrace. Calcium in the profile is replaced by sodium entering through ground water, sodium levels are high and soils are strongly alkaline. Calcium is lost by leaching and some is deposited lower down the profile as calcium carbonate concretions. The soils are predominantly sandy especially on the surface as the sodium causes clay dispersion through the profile giving the soil its black colour and hardness. This hardness makes the soil impervious to water and so the soil is poorly drained with considerable surface wash. In some areas the loose sandy top soil may be removed leaving a very hard cement like surface. This is characteristic of the southern part of the study area.

Crossing these deposits are low east to west ridges of more acidic sandy soils which are similar to the soils of 'a' above.

d) Alluvial clays: these are restricted to recently deposited flood plains (Lungonyo valley and Nangue). They resemble the tropical black earths of Anderson (1963) but here calcium is replaced by magnesium. Characteristically they are heavy black clays, exhibiting dry season cracking (to 3cm wide) and rainy season flooding. Clays are predominantly montmorillionite and illite and the profile exhibits a massive columnar structure. This soil type carries an edaphic perennial grassland. From the air a ridge furrow appearance is seen and it is thought this may be an ordered form of gilgai relief with annual flooding and water flow causing the symmetry. Ridges are about 3m apart and up to 10cm high.

2.222 Physical and chemical composition.

Physical and chemical analyses for three major soil types are shown in table 2.1. Horizons are not labelled but shown by depth. It must be stressed that horizon delimitation is not at all clear and the dimensions shown are very subjective.

Analyses for the major vegetation associations are shown in table 2.2. Here, data is averaged for all sites and horizons pertaining to each association and figures are to show differences between vegetation types. It is clear that the soils of the thicket and woodland associations are very similar. These similarities are discussed further in chapter 3.

Figure 2.2 illustrates some of the characteristics of the alkaline-sodic soils, and figure 2.3 is a traditional soil physical composition diagram used in naming soils into clay, loam and sand classes.

2.23. Discussion.

2.231. Nutrient status and fertility.

Major nutrient levels are low in all soil types and the area is classed as one of low fertility on the Tanzania Land Potential Map (Tanzania Survey Division, 1969).

The non lateritic red soils are old and highly weathered, their permeability and topography favours the leaching of soluble salts down profile and down slope, causing a deficit on high ground and an accumulation in the lower alluvial deposits (eg. sodium on the Pleistocene terrace). The high proportion of magnesium in the upland soils, table 2.2, is an indication of long term weathering and leaching (Black, 1968).

Nitrogen levels are low, in part a function of high temperatures (Black, 1957), and in part due to annual burning of the vegetation cover in which N is lost to the atmosphere. A dry season grass cover of 300gm/m^2 (dry matter) with a 4% protein content will release some 15-20 Kg per hectare of N to the atmosphere. Woody material will release another 5-10 Kg. To balance this is a possible input of up to 20Kg per hectare of N from rainfall (Eriksson, 1952), and further nitrogen may come from the nitrogen fixing bacteria of legume root nodules. Miombo woodland soils respond well to N fertilisation (Allen, 1965). Organic carbon is also lost through burning and the thicket soils (where fire is excluded) show a C content some 40% higher than adjacent woodland soils.

Potassium levels are low and continuous agricultural production requires fertilisation of most miombo soils. Phosphorus levels are low enough to cause P deficient forage in terms of animal husbandry. (Rodgers 1976 & appendix 5).

Subsistence agriculture in the miombo of East and Central Africa requires a system of shifting cultivation. A large part of the available nutrients are tied up in the vegetation layers (Nye and Greenland 1960 and Rodin and Bazilevitch, 1968), and their release through slashing and burning allows good crops for 3 to 5 years. On poor miombo soils a 30-50 year replenishment cycle is necessary before further agriculture (Allan 1965). .

2.232. The alkaline-sodic soils.

Soils with an exchangeable sodium content of over 15% of all exchangeable bases are classified as sodic. (Black, 1968; Russell, 1961). Figure 2.2 shows soils in this area to have sodium levels of up to 25%. These soils are found along the whole eastern boundary of the Selous from north of the Rufiji River southwards to the Matandu River. Hot springs, soda lakes, salt deposits and alkaline seepages are a feature of these areas. This soil type has a characteristic vegetation cover of a scattered tree grassland with short annual and perennial grasses. This association forms an important wet season animal concentration area with large mammal densities of up to 80 per km^2 (see chapter 5).

The combination of excess sodium and high alkalinity in the soil tends to inhibit phosphorus uptake in the plant and to a lesser degree calcium and magnesium. Vegetation on such soils appears as a more arid type than is normally associated with the rainfall. This may be due to two factors: firstly, the hard impervious nature of the soil causing excessive surface run off and, secondly, a decrease in water absorption by the plant due to changes in soil hydraulic conductivity and osmotic potentials.

Black (1968) and Russell (1961) discuss the chemical and physical properties of these soils in detail.

2.233. The soil catena of the Karoo system.

The concept of the catena or soil topo-sequence was first used by Milne (1947), who later used it as a term of mapping convenience for Tanzanian soils. Burtt (1942) described the importance of the catenary concept to miombo vegetation distribution in Tanzania. Stanley-Price (1974) gives a brief review of the water and particle movement characteristics of an East African catena.

Within the Karoo system of the Eastern Selous a soil catena with correlated vegetation changes is clearly seen. The vegetation aspects are discussed in chapter 3. Many of the soil characteristics can be briefly described as follows:

Soil	Catenary Position		
Character	Upper Slope	Lower Slope	Sump.
Soil colour	Red	Orange, Yellow, Grey	Black, Grey, Brown
Physical Composition	Sand	Loamy sand	Sandy clay loam
Clay type	Kaolinite (very little)	Kaolinite	Montmorillionite & Illite
Drainage	Free	Free	Impeded
Water table	Very Deep	Shallow	Shallow
Leaching	Severe	Little	Very little
Base status	Very Low	Low	Higher

Chapter six examines animal distribution with respect to slope position (water and grass availability) across a catenary sequence in the Nakilala valleys of the Karoo system.

2.3. CLIMATE.

2.31. Introduction.

The Selous Game Reserve and immediate surrounds has the lowest density of rainfall recording stations of any area in East Africa. Data for 23 years are available from the Steiglers Gorge water gauging station on the Rufiji River, for 8 years from the Miombo Research Centre and sporadic data from two other stations in the reserve and eight stations within 25 Km of the reserve boundary. Clearly quantitative climatic analysis of the complete reserve is not possible and this section merely examines data from the Miombo Research Centre in detail and from south east Tanzania (5°30'S to 12°S and 35° 30'E to 39° 30'E) in general terms. In broad climatic terms the area is classified on Thornthwaite's scale as "Dry Subhumid," (Sanson, 1954).

2.32. Rainfall.

The whole of the Selous falls within the unimodal rainfall belt of south Tanzania and central Africa, rainfall concentrating from late November to early May . with a partial drying up period in January or February.

Trend surface analysis (computerised production of isohyets) was attempted for 160 rainfall stations with data sets of 3 years or longer within the whole of south east Tanzania. This did not produce meaningful results due to the clumped distribution of recording stations and the great variation in mean annual rainfall, which varies from 500 mm in Mikumi National Park to 2400 mm in the Mahenge mountains to the west of the reserve. Visual examination of the data shows a trend of increasing rainfall from a low of some 700 mm p.a. on the eastern boundaries to a high of up to 1200 mm p.a. along the western boundary. This trend is supported by the preliminary isohyet maps for the Rufiji River Basin (F.A.O. 1961). It is possible that mountainous areas in the North West and South West may have rainfalls of up to 1600 mm p.a. Within the study area there is probably a slight increase in rainfall from the flat eastern area to the hills of the west.

Annual rainfall for the period 1924 to 1964 for Liwale (37° 5'E $9^{\circ}50$'S) is shown in figure 2.4. Data is shown in its raw form and after smoothing with a 4 by 4 smoothing function, (Lamb et al, 1966), where rainfall for year "x"

$$= \frac{1}{16} \times \left(1(x-3)+2(x-2)+3(x-1)+4x+3(x+1)+2(x+2)+1(x+3)\right)$$

The raw data suggest a 5-6 year cycle of successive peaks and troughs in annual rainfall but this trend disappears after smoothing. The smoothed data show some indication of a 10 year cycle in successive troughs.

I was fortunate in that I was able to subject long term rainfall data for eight stations in South East Tanzania to Fourier Analysis. This analysis (a form of harmonic or spectral analysis) is a rigorous statistical technique which evaluates cyclical phenomena on the basis of a series of sine wave harmonics. The analysis was undertaken at the University of Oxford computing centre by Dr. S. Cobb & Dr. L. Pennycuick. Data sets for the eight stations varied from 48 to 54 years, which is minimal for satisfactory analysis of long term cyclical phenomena (Cobb, pers. comm.). As the stations were scattered within a 100,000 km^2 area, data for individual stations were not amalgamated.

Fourier analysis results for these stations are shown in Figure 2.8 and whilst there are indications of cycles close to the 2.5, 5.5, 17 and 25-year wavelengths, these cycles differ from station to station and the variance content for each wavelength also differs from station to station. Detailed investigation of rainfall cycles must await longer term data. At present one can only conclude that a 5-6 year cycle appears prominent in the data sets.

Table 2.3 gives detailed monthly rainfall data for the Miombo Research Centre from 1968 to 1976, and mean monthly rainfall together with temperature is shown in a climatic diagram (as per Walter 1973) in figure 2.5. The intensity of rainfall can be high, some 40 mm falling in 20 minutes in January 1969, a total rainfall of 136 mm on January 28, 1969; and a total of 295 mm (some 40% of the annual mean) falling in 3 day consecutive days in February 1970.

2.33. Temperature and Humidity.

Temperatures in the eastern Selous are high, a maximum of 40.1°C being recorded in November 1970. Temperatures reach their highest in the early rains (November to February) and are lowest at the beginning of the dry season in May and June.

Mean monthly temperature data are shown in Table 2.4 and graphically in the climatic diagram of figure 2.5. A recording thermohygrograph was used from 1970 to 1974 to show daily changes in temperature and humidity in light shade at the research centre. Rainy season humidities reached 100% (R.H.) at night falling to 70% during the afternoons. Dry season humidities would reach 60% at night falling to 20% during the day.

Table 2.5 gives further climatic data for two long term agro-meteorological recording stations in south east

Tanzania. Whilst some distances from the study area these data serve to show the prevailing climatic pattern of the Selous Game Reserve.

2.4 WATER AVAILABILITY

2.40 Introduction

The Selous Game Reserve is extremely well-watered in comparison with other large game areas, despite a six-month annual dry season. Water is available in the form of major rivers, streams, water holes, seepages and from sub-surface flow in sand rivers. The study area, situated in the driest part of the game reserve has a water scarcity only at the end of an exceptionally dry season. Normally no area is more than eight km from available water. Typical mid-dry season water availability is shown in Figure 2.6.

2.41 Rivers

No permanent rivers flow in the study area. The Lungonyo shows a small flow for two km at the northern end of the flood plain (now dammed by the Research Centre) otherwise there are permanent pools only at Kingupira, Matawatawa and Nambule. The other major rivers: Lukiliro, Lihangwa, Namamba and Mwende, have sub-surface water available to elephant digging and occasional surface water (where clay or rock strata force the water level to rise) at Mpapule, Namatarawe and Narurai.

2.42 Streams and Seepages.

Many small valleys in the Karoo hills have a perennial water flow, if only for a few metres. Such a flow varies greatly from year to year, season to season and valley to valley. Examples include Nahomba, Nandindga, Namahema and Nakilala. Such streams may either originate in the valley bottom or on the lower slopes (at the so called "spring line" some 1/3 way up the slope see Howard 1974).

The line of seepages along the karoo-pleistocene geological boundary has been mentioned elsewhere, chapter 2.1 and appendix 1. Major examples in this study area are Chimbiriri, Malemba and Balani.

2.43 Waterholes.

Water holes, some temporary and some permanent, are found in topographic depressions in the Karoo system, e.g. at Nanuleo, Namatipi, Mkumbanyiko. Water holes or pans are much more frequent on the relatively flat surface of the pleistocene terrace, e.g. Kilunda and Kariokoo. These latter water holes appear to be dynamic and not permanent in nature, their development from small diggings to senescence by silting probably taking over 100 years. Details of their origin, growth and decay are discussed in detail in appendix 1.

2.44. Run Off and Watershed Management.

Run off maps for the eastern Selous, (FAO, 1961) show mean annual run off to be of the order of 200 acre feet per year ($98,500m^3/km^2$/p.a.) or some 15% of the total annual precipitation. Whilst this is low compared with the mountains to the west of the Selous ($995,000m^3/km^2$/p.a. or approximately 50% annual precipitation) the loss is more serious as the water deficit in the eastern Selous is much greater due to a 6 month drought, high temperatures and a consequent high potential evaporation.

Within the study area, the main water sheds are still forested and it is from these forested areas that flowing streams and seepages originate. It is probable that if forest cover decreases, run off will increase and permanent seepages disappear, (Colman 1968). The need for water shed conservation is discussed further in chapter 9.

2.5. PREHISTORY.

2.50. Introduction.

The prehistory of Africa with respect to past climate and palaeoecology is still poorly understood and a subject for controversy (Moreau, 1966; van Zinderen Bakker, 1966). However, the past historical record of climatic regimes, fire and human settlement is of considerable importance in understanding present vegetation and animal distribution in eastern and central Africa. This section outlines the major climatic influences of the past and discusses these influences and the history of man as they relate to the ecology of the Tanzanian miombo. A more recent historical study of human settlement in the eastern Selous Game Reserve is given in Appendix 2, (Rodgers, 1976b).

2.51. Past climates.

The concept of a series of pluvial and drier interpluvial periods in the Pleistocene period has dominated African prehistory for the past fifty years (Cole, 1954; Moreau, 1966). Four major pluvials have been postulated, although it has not been possible to correlate these periods with the temperate ice ages. As Sonia Cole (1954) said, "That there were times when the climate was definitely wetter than today, and other times when it was drier, is not disputed; it is the intensity and timing of these changes that is questionable." Evidence from geology, archaeology, palynology and botany point to a major pluvial period, peaking some 21,000 years before the present (B.P.). This is the Gamblian or last pluvial period to be recognized.

Moreau (1966) gives evidence that there was a 5-8°C temperature drop during the Gamblian and he suggests this could have resulted in a rainfall regime some 50% higher than at present. Moreau argues that under these climatic conditions montane and upland forests would have moved downwards to some 400m above present sea level. This would have meant an almost continuous forest cover from Ethiopia to Cape Province of South Africa. Wetter areas would bear montane or rain forest and drier areas would have deciduous forest or thickets.

At this time, two centres of arid conditions still existed: the horn of Africa around Somalia and the Kalahari Desert in Namibia. That these two centres have been in past contact during dry interpluvials is shown by strong botanical affinities (Wild, 1964; Moreau, 1962). Since the Gamblian period the climate has steadily ameliorated. Moreau (1966) discusses two further minor wet periods and one dry period, 12,000 BP, since the Gamblian. Most authorities view the Pleistocene as a dry period with occasional wetter periods, the pluvials, rather than vice versa.

More recent work in Uganda has cast doubt on the occurrence and the timing of the Pleistocene dry and wet phases. The work of Livingstone (1967), Kendall (1969) and Hamilton (in Lind and Morrison 1974, and pers. comm.) suggests that at the time of the Gamblian the climate was colder (by 6°C) but drier than at present. At sometime after 12,000 BP the climate became warmer and wetter culminating in a period of forest maxima at some 6,000 to 4,000 BP. Studies of fossil lake levels in Kenya (Richardson, 1966) give evidence of high lake levels at 8,000 and not 20,000 BP. Martin (1966) argues on faunal evidence for drought conditions around 12,000 BP.

Extensive deposits of Kalahari sands in the soil profile of southern Zaire tropical forests aged at some 12,000 BP is the only definite evidence of the events postulated for Uganda taking place further south as well. There is a dearth of detailed palynological or fossil climate studies from the woodland areas of East and Central Africa. Lawton's (1963) data appears to fit the Gamblian pluvial theory but could be reanalysed to agree with Hamilton. For the purposes of this thesis, the concept of a forest maximum around 6,000 BP is accepted. It is suggested that as a result of fire and vegetation clearing, especially in the last 2,000 years, the miombo woodlands have developed as a fire held disclimax from the preceding forest or thicket vegetation types. This premise is developed more fully in Chapter Three.

2.52 The history of man and fire

West (1965) and Phillips (1965) show that natural fires must have been a major ecological factor throughout the tertiary period. Hoffman (1974) mentions the early tertiary as the age of dominance of grasses and the rise of the ruminant artiodactyls at the expense of the non-ruminant perissodactyls. Such radiation of the grasslands must have occurred with the presence of fire.

Man in Africa has had the use of fire for at least 53,000 years (Phillips, 1965, quoting Clarke). Van Zinderen Bakker (1966) gives Carbon 14 dates of over 40,000 years for charcoal deposits associated with stone age cultures. Man the cultivator has developed since the Gamblian ice age in the last 10 - 20,000 years (Allen, 1965; Clarke, 1969; Martin, 1970). The practise of shifting cultivation would have necessitated the clearing and burning of large areas of climax forest. Hamilton (pers. comm.) considers that the major impact of man on vegetation has occurred in the last 2,000 years and Martin (1966 & 1970) states evidence on the basis of faunal extinctions that man in Africa has only recently had major effects on the ecology.

2.53 The effects on vegetation and animal distribution.

Since the forest maximum large areas of climax forest and thicket have been destroyed and fragmented by man's clearing and burning, coupled with a gradual change to a slightly drier climate. The continuous belt of forest is shown today by relict vegetation types in East and Central Africa, and pollen spore analysis from swamp sediments shows the botanical nature of previous forests. That these relict forests have been joined and fragmented several times in the past is shown by close botanical similarities and by the degree of endemism in both plants and animal species (Lawton 1963). Woodland formations (the miombo) adapted to frequent fires have replaced the climax forests. This is discussed in detail in chapter 3.

The arid areas of Somalia and Kalahari show considerable faunal similarities (Carcasson 1962, Wild 1964). These refuge areas provided centres of radiation for grassland animals, shown today by the great array of grazing mammals on the East African and South African plains. The presence of many allopatric species and subspecies pairs such as white rhino, oryx and spring hare show previous faunal connections. These grassland areas are separated by the miombo woodland formation of Central Africa, a zone with few large mammal endemics, notably sable and Lichtenstein's hartebeest.

Wildebeest, an animal of short grasslands, is an example of subspeciation in isolated grassland habitats. Their distribution can be shown as follows (after Sidney, 1965).

Species or Subspecies	Area	Notes
Black wildebeest	South African plains	Almost extinct
Blue wildebeest	Zambezi valley	Isolated valley grassland systems in Miombo woodland
Cooksons wildebeest	Luangwa valley	
Nyassa wildebeest	Rufiji & Ruvuma valleys	
White bearded wildebeest	East African plains	Races either side of the rift valley.
Eastern Wildebeest		

Figure 2.7 shows the extent of forest and thicket in Africa during the Gamblian, the present distribution of the miombo woodland formation separating the East and South African plains and the present distribution of wildebeest subspecies in their isolated grassland habitats.

2.54. Conclusions.

It is now accepted, if not proven, that the vast expanse of woodlands in Central Africa has developed from the forest and thicket formations by human agencies of fire and clearing, aided by a shift towards a more arid climate. This woodland formation separates the present day centres of grazing ungulate radiation, the East and South African plains. Within the woodlands can be found forest relics whose botanical composition in terms of floral similarities and degree of endemism indicate past cycles of fusion and isolation. Localised edaphic conditions have formed grassland islands in the woodlands which created areas of subspeciation for wildebeest along its range from East to South Africa.

CHAPTER THREE: THE VEGETATION

3.0. INTRODUCTION.

3.01. The Miombo woodlands of South East Tanzania.

This study area, and virtually the whole of the Selous Game Reserve, fall into the south-east Tanzania block of deciduous woodland or "miombo" (Gillman 1949, Russell 1961). This vegetation type covers large areas of East and Central Africa, from Rhodesia in the south through parts of Mozambique, Angola, Zaire and Zambia into south-western and eastern Tanzania. A physiognomically similar woodland exists in West Africa, the "Guinea savanna" (White 1965, Ramsay & Rose-Innes 1963). The distribution of the "miombo woodland" in Africa is shown in figure 2.6.

Within Tanzania this formation is estimated to cover almost 450,000 km^2 or just under half the total land surface. The south-eastern block is separated from the western areas by a drier zone running from the Rukwa valley to Dodoma. This dry belt had possible importance as part of a past link between the arid communities of Somalia and South West Africa, (Carcasson 1964, van Zinderen Bakker 1967). The south-eastern block differs from the more typical western Tanzania and Zambezian miombo floras by having fewer endemic miombo elements and by the inclusion of coastal elements, especially in the riverine and thicket communities. (Rodgers 1969, Hedberg 1966).

The miombo formation can be defined as follows: A deciduous unarmed woodland occurring in the unimodal rainfall areas of East and Central Africa on old, acid, sandy soils. It is characterised by Caesalpinaceous trees, especially species of Brachystegia and Julbernardia. The ground cover varies from a dense coarse grass growth to a sparse cover of herbs and small grasses. The shrub layer is variable in density and species composition, often dominated by Diplorhyncus condylocarpon and species of Combretum. The whole is maintained by periodic dry season fires.

As the vegetation of south east Tanzania has been poorly collected and described, this chapter is necessarily large. An understanding of the seasonal movement of grazing ungulates and the management of the study area depends on a knowledge of the plant cover, its dynamics and seasonal change. Consequently the vegetation is discussed at some length, and for ease of presentation, this chapter is split into six sections, viz:-

1) The vegetation communities and vegetation map
2) A computerised analysis of the ground layer communities.
3) Floristic composition and affinities
4) Vegetation and the environment
5) Succession and community dynamics and
6) The concepts of diversity, equitability and maturity.

Where possible each section is split into introduction, methods, results and discussion. In addition, three appendices dealing with vegetation are enclosed with this thesis. One contains the detailed annotated species list, the second contains a description of the computer analysis techniques and the third, already referred to in chapter two, discusses the effect of past settlement on the vegetation of the study area.

3.02. General Methods:

In order to be able to identify and name plants in the field a self-contained reference herbarium was initiated in 1967. The collection is maintained as a fully mounted and annotated herbarium and duplicate specimens kept at the East African Herbarium in Nairobi and the herbarium of the Department of Botany at the University of Dar es Salaam.

To date the collection contains over 4,000 specimens covering almost 1,100 species from this study area, in addition to collections from other parts of Tanzania. In 1975 a plant taxonomist was appointed to the Miombo Research Centre and he has maintained and revised the plant collections and species check list since then.

Using local assistants a Latin-vernacular dictionary for over 400 woody species has been prepared and checked in order to facilitate discussions on plant ecology and distribution with field staff.

Full aerial black and white photographic cover of the study area was available as follows:

1947 to 52	Occasional flight lines: R.A.F.	1:32,000
1965	Complete stereo cover: Tanzania Survey.	1:48,000
1970	Stereo cover of selected flight lines within the study area	1:10,000

Vegetation communities were recognized qualitatively over 4 years of field studies (1968 - 1972) and located and marked on aerial photographs. Such communities are shown in Plate 9 for a typical air photograph of the woodland karoo system.

Species lists and determinations of dominants were made for several sites within the different communities. This information and data from collected herbarium material were mounted on punch cards, cross referenced for habit, dominance, distribution, community and regional affinities. An example of such a card is shown in figure 3.1.

Fire plots and grazing exclosures were set up early in the study to monitor vegetation changes due to fire and grazing. This is discussed in detail in Chapter 4.

3.1. VEGETATION COMMUNITIES AND THE VEGETATION MAP.

3.11 Introduction.

No standardised procedure of hierarchical classification exists for African vegetation. The following procedure is adopted for this thesis. The miombo woodlands of Africa as a whole are referred to as a "formation type". The word formation is used to denote separate physiognomic vegetation categories, e.g. forest or grassland. These formations are divided into associations, which are frequently occurring vegetation groupings characterised by similar species dominance, physiognomy and ecology. Their terminology follows that described by Pratt, Greenway and Gwynne (1966), in their paper on the classification of East African rangeland. In this method, association names are compounded of dominant genera and physiognomic characteristics. In some cases, as in thickets, the choice of dominants is difficult, and I have resorted to geographical and ecological criteria. Two vernacular terms are partly retained in the terminology and text, both of which have extensive usage in East and Central Africa. These are "miombo", which now specifically refers to the Brachystegia/Julbernardia communities, and "chipya", a Zambian term used to describe the fierce fire woodland communities with dense grass cover. The terms "upper valley" and "lower valley" as defined by Trapnell (1953), are useful categories, and they are partly retained in association names. Their relevance is discussed in the text.

Five physiognomic formations are recognized. These are:

A) Forest - here defined as a closed stand of trees over 8 metres in height whose canopies interlock. There may or may not be an understory of shrubs or small trees. The ground layer, if present, is sparse.

B) Thicket - here defined as a closed vegetation type dominated by shrubs and trees of less than 8 metres. A sparse ground cover may be present.

C) Woodland - here defined as a vegetation type dominated by trees, but whose crowns are not touching and the ground layer is predominantly grass. An understory of trees or shrubs may or may not occur. Canopy cover is from 20 to 80%.

D) Scattered-Tree Grassland - defined as an open vegetation type, dominated by grassland, with occasional trees or groups of trees. Canopy cover is less than 20%.

E) Grassland - a completely open type with no, or very few, woody elements.

3.12. Methods:

Using field notes and marked aerial photographs 19 constant and discrete vegetation associations were recognized qualitatively. These were recognizable on the ground, on photographs (see Plate 9) and by listing dominant species.

By examining herbarium records and species data cards, the species dominating, frequently occurring in, or constant to, each association for each of the tree, shrub and grass layers were identified and used to form a brief description for each association.

Where an association showed several sub-types based on minor but real changes in species composition, these sub-types were also described as communities within the association.

A vegetation map at a scale of 1:125,000 was drawn onto a base map from the marked aerial photographs using a Zeiss Sketchmaster to reduce the photo scale of 1:48,000. A base map showing rivers was prepared by photographically reducing and tracing the published 1:50,000 survey maps for the study area.

This base map was overdrawn with the photo flight lines and photo centres. A geometric diagram of a scaled down photograph showing photo centre, photo limits, stereo overlap and diagonals was used to minimise edge distortion. A Casella mirror stereoscope was used to clarify vegetation boundaries (Howard 1970).

Vegetation mapping at this scale necessitated some sacrifice of detail for final visual clarity. In practice any vegetation unit of less than 2mm on the final map was not shown. This has meant some riverine communities could not be portrayed and the map shows only 16 of the 19 associations. Several vegetation boundaries were not discrete, and communities tended to merge rather than end abruptly; in such cases boundary lines were subjectively positioned after checking in the field. Final colouration of the map was chosen (within the limits of the printers) to show major physiognomic formations as well as individual associations (Kuchler 1967).

3.13. Results.

Nineteen associations were recognized. These are:

A) Forest Formation:

1. Ground Water Forest
2. Riverine Forest
3. Coastal Dry Evergreen Forest

B) Thicket Formation:

1. Riverine Thicket
2. *Brachystegia microphylla* Thicket
3. Coastal Dry Thicket on Alkaline Soils.
4. Coastal Dry Thicket on Sands

C) Woodland Formation:

1. *Brachystegia* Woodland (Miombo)
2. *Pterocarpus-Pseudolachnostylis* Woodland (Chipya)
3. *Pteleopsis-Millettia* Woodland (Chipya)
4. *Combretum-Terminalia sericea* Woodland
5. Upper Valley Mixed Woodland
6. Lower Valley *Combretum-Sclerocarya* Woodland

7. Shallow Soil Stunted Woodland

D) Scattered Tree Grassland Formation:

1. *Terminalia spinosa*–*Spirostachys* Wooded Grassland
2. *Acacia*–*Combretum* Shrub Short Grassland
3. *Cassia*–*Combretum* Shrub Medium Grassland

E) Grassland Formation:

1. Seasonally Flooded Tall Grass Swamp

F) Oddments:

1. Anthill Communities

Association descriptions, revised slightly from Rodgers and Ludanga (1973) follow. Many of the associations are shown in Plates 1 - 6.

A.1 Ground Water Forest:

This association occurs as a discrete 10 km^2 area at the northern end of the large Lungonyo flood plain, where there is permanent water seepage. The southern half of the forest consits largely of mature wild date palms, *Phoenix reclinata*, overlooking muddy swamp pools. The northern half, away from the water seepage, becomes more similar to riverine forest. The canopy cover is dense, but no well-defined layering exists. Forest trees have buttressed boles and lianes are common, but not epiphytes. A ground cover exists only where the canopy is broken. The whole area is criss-crossed by the trails of hippopotamus, for which the forest offers a dry season refuge. The edge is sharply defined by the action of fire. Several small alkaline streams enter from the east, and saline plant species occur - e.g. *Haplocoelum mombasense*, *Salvadora persica* and *Sporobolus virginicus*.

Common trees are *Phoenix reclinata*, *Hyphaene spp*, *Lepisanthes senegalensis*, *Alangium salviifolium*, *Balanites wilsoniana*, *Celtis wightii*, *Azanza garkeana*, *Sorendeia madagascariensis*, *Mimusops kummel* and *M. fruticosa*, *Calancoba* and *Memcylon spp*, which present a continual evergreen aspect.

The understory contains many *Rubiaceae* and *Celastraceae* eg. *Tarenna*, *Canthium*, *Coffea*, *Psychotria* and *Tricalysia*, and *Elaedendron*, *Salacia* and *Mystroxylon*. *Commiphoria* species are common.

Several small isolated forest clumps are scattered around the main forest edge. *Tamarindus indica*, *Afzelia quanzensis*, *Hyphaene* and *Euphorbia* species are common elements.

Grasses are mainly forest species - e.g. *Leptochloa* and *Eleusine*. *Cynodon dactylon* and *Chloris Gayana* are common in the clearings. These species indicate the alkaline nature of the forest.

A small area of ground water forest occurs to the north of the study area, at Maua ($38^{0}10'E$, $8^{0}20'S$), around a fresh water spring. Dominant species are Khaya nyassica, Ficus spp. and Sterculia appendiculata. Syzygium guineense and Majidea zanguebarica are common in the understory. This is more similar to the ground water forests of Zambia (Lawton, 1963; Wild, 1964).

A.2 Riverine Forest:

This is a varied association, occurring as true gallery forest along only two rivers - the Lungonyo and lower Lihangwa, and isolated patches occur on the Mwende river. In all these cases the forest is rapidly decreasing due to both fire and river bank encroachment.

The gallery forest varies from a few metres to over 100 metres in width, with discrete fire maintained edges and several game trails. Where the forest has been cleared, many such trails lead to severe erosion gulleys. Dominant trees are Pterocarpus holtzii, Diospyros kirkii and D. mespiliformis, Sterculia appendiculata and Terminalia sambesiaca. Albizia amara and A. zimmermanii are occasional elements. Common understory trees are *Garcinia livingstonei*, *Dalbergia arbutifolia*, *Erythroxylum emarginatum*, *Haplocoelum mombasense*, *Commiphora zanzibarica*, *Cleistochlamys kirkii*, and *Cola* species.

The shrub layer contains many species, especially *Rubiaceous* elements - e.g. *Lamprothamnus*, *Pavetta*, *Polysphaeria*, *Tricalysia* etc. Grasses such as *Leptochloa*, *Rottboelia*, *Heteropogon melanocarpus*, and *Oryza* are common in open glades.

Climbers such as *Artabotrys*, *Abrus*, *Monodora* and *Entada* are frequent. A fringe zone of shrubs such as the *Malvaceae* - *Thespesia*, *Urena* and *Hibiscus* species with *Deinbollia borbonica* and *Combretum goetzei* is a characteristic feature.

One small relict forest of primarily riverine species occurs on clay soils away from major rivers. Examination of air photographs from 1949 shows these patches were more frequent even twenty years ago. Dominant trees are *Diospyros*, *Mimusops*, *Sterculia* and *Afzelia*.

There are a very few forest patches in the upland areas on more sandy acid soils. Where they occur *Pterocarpus* *holtzii* is common as a riverine tree. Mention must be made of a small (one hectare) forest at Mpapule on alluvium by permanent water. This forest patch is dominated by tall *Trichilia emetica* trees, with *Ficus* spp. The understory is largely composed of *Markhamia acuminata*, *Vangueria acutiloba* and *Cleistochlamys*.

A.3 Coastal Dry Evergreen Forest:

This association is restricted to the higher areas (above 700 metres) of the western watershed, with an estimated rainfall of 1000 to 1200 mm per annum. The forest shows a dense stunted aspect on steep slopes with a closed shrub layer. Taller stands with a bare ground layer occur on deep soil ridge tops. *Usnea* is common, but other epiphytes are rarely seen. The soil shows a permanent litter/humus layer of up to 5 cm and the top soil is a rich sandy loam.

Common canopy trees are *Mimusops busseana*, *Albizia adianthifolia*, *Trachylobium*, *Brachylaena*, *Dracaena*, *Ricinodendron tomentellum*, *Ficus zanzibaricus*, *Manilkara discolor* and *M. sulcata*, *Pteleopsis*, *Strychnos* sp. and *Lannea* sp.

Sapium, Drypetes, Fagara chalybea, Byrsocarpus bovinianus, Calancoba gigantocarpa and Hymenocardia are common in the understory.

Typical thicket species occur on the slopes as a shrub layer - e.g. Croton pseudopulchellus, Grewia conocarpa Salacia senegalensis, Lingelsheimia, Memecylon, Maerua and Uvaria species.

Climbers such as Combretum trothae and C. padoides, Acacia brevispica and Schlecterina mitostemmatoides are frequent.

Polyneura squarrosa, a sparse creeping grass on the open floor is endemic to the sandy soil forests of south east Tanzania.

B.1 Riverine Thicket:

As with the gallery forest, analysis of photographs reveals a general decrease in extent since 1949. This formation occurs in several forms:

1. Degraded riverine forest, still with occasional emergents such as Pterocarpus holtzii. Dense groves of Lamprothamnus, Polysphaeria, Haplocoelum etc.

2. Flood plain, fringing the major channels - *Combretum constrictum* with small composite shrubs - e.g. *Pluchea dioscoridis*, *Vernonia exsertifolia*.
3. Drier areas on clay - *Maytenus putterlickiodes*, *Albizia anthelmintica*, *Capparis tomentosa*, *Harrisonia abyssinica*, *Dalbergia melanoxylon* and the occasional baobab - *Adansonia digitata*.
4. Wetter areas on clay - *Markhamia acuminata*, *Heinsia crinita*.
5. On deep alluvial sands, often in association with trees such as *Stereospermum*, *Trichilia*, *Kigelia* and *Dalbergia hochmii*. Typical shrub species are *Xylotheca glutinosa*, *Antidesma venosum*, *Psorospermum febrifugum*, *Canthium zanzibaricum*, *Dichrostachys cinerea* etc.
6. In miombo valleys where fire protected - *Ziziphus abyssinica*, *Dichrostachys*, *Harrisonia*, *Maytenus senegalensis* etc.

B.2 Brachystegia microphylla Thicket:

This is restricted to the steep upper slopes of major hill systems, on poor shallow soils. The canopy, which is light and feathery, is almost entirely composed of

B. microphylla and the occasional *Rhodognaphalon schumannianum*. On better sites such trees as *Cleistanthus*, *Afzelia*, *Cussonia zimmermanii*, *Albizia petersiana* and even *Tamarindus indica* have been seen as occasional emergents.

Common shrubs and small trees are *Gardenia resiniflua* and *Gardenia sp.* = *Mgaza 272* (both restricted to this association), *Hymenocardia ulmoides*, *Strychnos henningsii* and *S. panganensis*, *Maerua kirkii*, *Lingelsheimia*, *Croton*, *Paropsia braunii*, *Rothmannia engleriana*, *Vernonia zanzibarica*, *Acokanthera schimperi* and *Alchornea laxiflora*. *Usnea* is common, grasses are rare, the ground usually being covered by *B. microphylla* seedlings.

B.3 Coastal Thicket on Alkaline Soils:

This association occurs in small patches in this study area, but occupies a high proportion of the alkaline soil to the north. The soil is highly sodic (pH 9.0 with a high sodium content) and sets very hard in the dry season. The association is semi-deciduous and xeric in character.

Common emergents are *Spirostachys africana*, *Afzelia*, *Manilkara mochisia* and *M. sp.* (Muhike), *Tamarindus* and Millettia stuhlmannii. Diospyros cornii and D. bussei are common, as is Euphorbia candelabrum. Several shrub species occur, chiefly Cola species, Cleistochlamys, Commiphora, Suregada zanzibarensis, Erythroxylum emarginatum, Euphorbia grandicornis, Sansevieria species, Lamprothamnus, Teclea simplicifolia, Securinega virosa, Indigofera schimperi, Toddaliopsis, Dichapetalum, Croton and Harrisonia.

Several large seasonal water pans occur, often with hippopotamus, especially when fire produced open woodland areas are close.

B.4 Coastal Thicket on Sands:

This association occupies several large areas in the study area (totalling almost 150 km^2). It is nearly always restricted to ridge tops or the upper slopes on deep sandy soils. It is semi-deciduous, with a virtually bare ground layer and a sharp fire controlled edge.

Dominant emergents are Pteleopsis myrtifolia and Millettia stuhlmannii with occasional to common Commiphora serrata, Lannea sp. (Mumbo), Vitex species, Manilkara discolor and Oldfieldia somalensis. Understory trees are: Calancoba, Markhamia obtusifolia

Drypetes gerrardii, *Ochna holstii*, *Citropsis daweana*, *Cola microcarpa*, *Hymenocardia ulmoides*, *Memecylon* sp, *Fagara chalybea*, *Haplocoelum inopleum*, *Wrightia* sp, *Erythroxylum emarginatum* and *Strychnos henningsii*. Common shrubs are *Polyalthia* sp., *Uvaria acuminata*, *Salacia senegalensis*, *Dichapetalum* spp., *Croton pseudopulchellus*, *Grewia conocarpa*, *Lingelsheimia* sp., *Leptactina bussei*, *Strophanthus hispidus*, *Lindackeria* sp., *Alchornea laxiflora*, *Chassalia umbraticola*, *Clerodendrum* spp., *Pentas parvifolia* and *Mildbraedia carpinifolia*.

Climbers are common, viz: *Hugonia castaneifolia*, *Combretum trothae* and *C. padoides*, *Acacia brevispica* (sp. aff), *Schlecterina*, *Monodora junodii*, *Ancyclobothrys petersiana* and *Landolphia* sp.

Small ephemeral herbs appear in the ground layer - e.g. *Triumfetta kirkii*. Thicket grasses such as *Megastachya mucronata* and *Panicum heterostachyon* occur.

An occasional variant of this type is a thicket dominated by *Manilkara discolor* and *M. sulcata* often found just above the *Brachystegia microphylla* zone.

The thicket to the west of Balani is unusual in that it is completely deciduous and poor in species composition.

Pteleopsis and Millettia are complete dominants, and Leptactina bussei the commonest shrub. This community gives rise to the adjacent Pteleopsis, Millettia woodlands when opened up by fire.

Isolated thicket and pioneer thicket clumps are occasionally found. Landolphia spp., Markhamia obtusifolia, Grewia conocarpa, Monodora junodii, Hymenodictyon floribundum and Vernonia zanzibarica are amongst the earliest pioneer species.

On isolated steep scarps a drier variant occurs, composed almost entirely of Diospyros bussei, Croton pseudopulchellus and Strychnos henningsii.

C.1 Brachystegia Woodland (Miombo):

This association is the true "miombo" of Central Africa. It rarely reaches the height, density or species richness of the Zambian form, and often contains coastal elements. Here it is dominated by Brachystegia spiciformis and Julbernardia globifera, either together or separately. Julbernardia appears to dominate on poorer soils. The shrub layer is dominated by Diplorhynchus condylocarpon and Byrsocarpus orientalis;

occasional Xeromphis obovata, Tetracera masuiana, Ximenia caffra and Flacourtia indica occur. Hugonia busseana and Lonchocarpus eriocalyx are common understory trees. The ground layer is more open than the fierce fire woodland; rarely are dense, coarse stands of grass present. Herbs, sedges and suffrutices are common. Grasses are sweet, chiefly Panicum infestum, with several small species such as Sporobolus ioclados and Sporobolus subglobosus.

Other Brachystegia species are more restricted in their distribution. Mention has been made of B. microphylla, which can occur as a woodland dominant on steep, rocky soils, without a thicket understorey.

B. utilis is rare in this area, but can be found on steep slopes below the B. microphylla zone.

B. bussei is usually restricted to poor, steep slopes, but is occasionally found in dense groves in valley bottoms.

B. boehmii is common on lower slopes of higher clay content, often in poorly drained areas.

In deep shade, and usually fire protected, thicket pioneer clumps occur: Landolphia and Leptactina bussei are common.

Throughout this association, occasional trees of Afzelia, Ficus sp., Pterocarpus angolensis, Pteleopsis, Millettia stuhlmannii, Pseudolachnostylis and Strychnos innocua occur.

C.2 Pterocarpus-Pseudolachnostylis Woodland (Chipya):

Referred to as "chao" in this area, this is the basic fierce fire woodland, with a dense coarse grass cover. Dominant and common trees are Pseudolachnostylis, Pterocarpus angolensis, Pteleopsis myrtifolia, Millettia stuhlmannii, Combretum zeyheri and C. collinum, Strychnos innocua, Boscia salicifolia and Xeroderris stuhlmannii.

Shrubs are rare and subject to severe die back due to fierce annual fires. Terminalia sericea seedlings may be common. Grasses are sour and coarse, and dominated by Andropogon schirensis and Hyparrhenia spp. Sedges, small grasses and herbs are not common. Herbs, where they do occur, are semi-suffruticose, such as Crotalaria and Phyllanthus.

A richer form occurs, dominated by Burkea, Amblygonocarpus and Erythrophleum africanum. It is not known whether this is a successional series or edaphically controlled.

A related form occurs on the slopes of the Tundu Hills, which is dominated by Boscia salicifolia, Pseudolachnostylis and some Pterocarpus and Millettia. Grewia monticola is a common constituent of the shrub layer.

On the lower slopes of upland valleys, a woodland dominated by Pseudolachnostylis is common. The grass layer is dominated by Loudetia arundinacea and Tristachya bequartii. The lack of fire sensitive elements, and a dense grass layer, warrants its inclusion in this association.

C.3 Pteleopsis-Millettia Woodland (Chipya):

Possibly a variant of C.2 (above), but is discrete and readily identifiable. Trees are almost exclusively Millettia stuhlmannii and Pteleopsis, with a few Schrebera trichoclada. One occurrence of this community is adjacent to the deciduous thicket variant discussed under B.4. Markhamia obtusifolia and Millettia micans are dominant shrubs. Pseudolachnostylis has only been seen as a rare seedling and sapling.

C.4. Combretum-Terminalia Tall Grass Woodland:

As will be shown later, this is a successional stage following cultivation, and will proceed to a miombo or chipya form in time.

The woodland is dominated by trees of Terminalia sericea,, Combretum zeyheri, Pseudolachnostylis and Xeroderris. Suffrutices of T. sericea are very conspicuous in the ground layer. Grasses are predominantly tall and coarse, Andropogon schirensis, Loudetia simplex, Tristachya and Themeda are common.

Other trees found are Combretum collinum and C. molle, Lannea stuhlmannii, Lonchocarpus eriocalyx and Pterocarpus angolensis. Mature woodland contains more Pterocarpus, Burkea, Erythrophloem, Millettia and Afzelia. Shrubs are more common, especially Diplorhynchus, Byrsocarpus orientalis and Xeromphis. Saplings of B. spiciformis occur. The grass cover becomes more open and sweet, with Panicum infestum and several herbs.

Occasional copses of mature B. spiciformis occur.

C.5 Upper Valley Mixed Woodland:

A complex and heterogenous zone with many variants. They occur in the valley bottoms of all upland sandy alluvial valleys or "dambos". As such they are aptly described by the blanket association term "upper valley mixed woodland."

Type 1: Dominated by *Pericopsis angolensis*, *Vitex doniana* and *Hyphaene* species. *Albizia versicolor*, *A. harveyi* and *Acacia nigrescens* are common, with the occasional *Tamarindus*, *Dalbergia boehmi*, *Kigelia aethiopum* and *Cleistanthus*. *Tamarindus*, *Ziziphus* sp. and *Boscia angustifolia* are common on anthills. Grasses are tall and dense, and include *Panicum maximum*, *P. aphanoneurum*, *Cymbopogon giganteum* and the occasional *Setaria*.

Type 2: One more sandy soils. *Acacia sieberana*, *Piliostigma thonningii*, *Lonchocarpus capassa* and several *Combretum* species - e.g. *C. collinum*, *C. psidiodes*, *C. fragrans* and *C. molle*. *Annona senegalensis* is common. *Ricinodendron rautanenii* sometimes occurs.

Shrubs of *Xeromphis*, *Maytenus senegalensis*, *Mimosa pigra*, *Securinega*, *Dichrostachys* and *Ziziphus* are common to both forms.

C.6 Lower Valley. Combretum-Sclerocarya Woodland:

An equally heterogenous association found on the more extensive and gentle slopes of the lower valleys. It also shows sandy and clay communities. Soils are usually pale, and the community is an inter-zone between the woodland and scattered trees grassland.

Type 1: On more sandy soils of drainage lines such as Chimbiriri and Balenje, Sclerocarya caffra, Crossopteryx febrifuga, Combretum species, Manilkara mochisia and the occasional Brachystegia boehmi; Pseudolachnostylis and Xeroderris are common.

Type 2: On clay soils, drying hard and slightly alkaline, the following are common: Dalbergia melanoxylon, Acacia nigrescens, Albizia harveyi, Dobera glabra, Berchemia discolor, Sclerocarya caffra, Combretum species, Lonchocarpus capassa and L. eriocalyx; Combretum imberbe and Balanites aegyptiaca in some lower areas. Mimusops schliebenii, Manilkara mochisia and Tamarindus are common on anthills. The occasional water pan occurs with fringing thicket. The baobab and Sterculia africana are characteristic elements.

In both types the shrub layer is poorly developed. *Diospyros usumbarensis*, *Ziziphus* spp., *Turraea nilotica* and *Cassia auriculata* are common. *Acacia nilotica* and *A. robusta* occur.

Grasses vary from tall *Themeda*, *Hyparrhenia*, *Loudetia* communities to medium height *Hereropogon contortus* and *Digitaria milanjiana* on heavier soils. *Panicum infestum* is common in shade.

C.7 Stunted Woodland on Stony Slopes:

Common in other parts of the Selous, here restricted to small areas near Balenje and from Nunga to Mpapule. Stunted *Julbernardia* and *Brachystegia boehmi* occur. *Uapaca nitida* is restricted to this community in this area. *Diospyros bussei* and *Dalbergia melanoxylon* are common, as is *Acacia robusta*. *Alloteropsis semialata* is a characteristic grass species.

D.1 Terminalia spinosa-Spirostachys Wooded Short Grassland:

The dominant vegetation type on alkaline, poorly-drained, sandy clay soils in the absence of thicket.

Terminalia spinosa is the characteristic dominant, although in some areas it gives way to pure *Spirostachys africana*.

Other common trees are *Acacia nigrescens*, *Afzelia*, *Sterculia africana*, *Cassia abbreviata*, *Albizia harveyi*, *Sclerocarya caffra*, *Dobera glabra* and, on anthills, *Tamarindus*, *Euphorbia candelabrum*, *Mimusops schliebenii*, *Manilkara mochisia* and *Berchemia discolor*.

Common small trees and shrubs are *Diospyros usumbarensis*, *Cassia auriculata*, *Acacia senegal*, *A. zanzibarica*, *A. robusta* and *A. gerrardii*; *Dalbergia melanoxylon*, *Turraea nilotica*, *Markhamia acuminata* and *Combretum hereroense*.

The grass cover is short, usually less than 60 cms., and sweet. Common species are *Sporobolus ioclados*, *Digitaria milanjiana*, *Panicum infestum* and many annual species of *Eragrostis*, *Brachiaria*, *Dactyloctenium*, *Urochloa*, *Aristida* and *Chloris*. Sedges, especially *Mariscus mollipes*, are common. The herb layer is dominated by *Cyathula lanceolata*, *Heliotropium strigosum*, *Cassia mimosoides*, and *Tephrosia pumila*. Patches of ungrazed fire-resistant *Bothriochloa pertusa* are a characteristic feature of some areas.

To the south on harder soils, trees, especially *Terminalia spinosa*, become less conspicuous, although several dead stumps indicate greater densities in the past. The grass cover becomes more dense and dominated by *Heteropogon contortus* and *Digitaria milanjiana*.

Several permanent and semi-permanent water pans occur with a fringing thicket of *Markhania acuminata*, *Lamprothamnus* and *Polysphaeria*, and trees of *Mimusops* and *Tamarindus* and the occasional baobab.

D.2 Acacia-Combretum Shrub Short Grassland:

Small areas in the vicinity of the Miombo Research Centre headquarters show a community dominated by *Acacia robusta*, *A. senegal*, and *A. gerrardii*. *Combretum hereroense* and some *C. zeyheri* are present. Both *Terminala spinosa* and *Spirostachys africana* are absent.

D.3 Cassia-Combretum Shrub Medium Grassland:

Running across types D.1 and D.2 are low sandy ridges which bear a characteristic vegetation type. Both *Terminala spinosa* and *Spirostachys* are absent, and common trees are *Xeroderris*, *Sclerocarya* and the occasional *Pseudolachnostylis*, *Burkea*, *Lonchocarpus eriocalyx* and *Lannea stuhlmannii*. *Combretum zeyheri*, *C. molle* and *Cassia auriculata* dominate the shrub layer, with some *Diospyros usambarensis*, *Turraea nilotica* and both *Markhania acuminata* and *M. obtusifolia*.

Grasses are dense, and chiefly *Themeda*, *Heteropogon* and *Hyparrhenia* spp., with some *Panicum infestum* in shade. *Astripomoea malvacea* is dominant in the herb layer.

E.1 Seasonally Flooded Tall Grass Swamp:

Occurs in two major localities, the main flood plain of the upper Lungonyo River (c.125 km^2) and a smaller plain at Nangue (c. 25 km^2).

Nangue is dominated by *Setaria sphacelata*, *Echinochloa haploclada* and *Andropogon gayanus*. Several dead tree stumps (mainly *Dalbergia melanoxylon*) indicate a possible recent increase in area.

The Lungonyo flood plain is bordered by trees of *Combretum imberbe* and *Balanites aegyptiaca*. The larger channels are bordered by *Combretum constrictum*.

Grass dominants are *Echinochloa haploclada*, *Ischaemum afrum*, *Setaria sphacelata*, *Andropogon gayanus*, *Bothriochloa glabra* and *Vetiveria nigritana* and *V. zizaniodes*. The edges are characteristically *Echinochloa*, *Themeda* and *Digitaria milanjiana*, and tussock *Sporobolus* such as *S. pyramidalis*; *Imperata cylindrica* occurs in small areas.

There is a rich herb flora and occasional outcrops of Sesbania hirtistyla and Aeschynomene spp.

F.1 Ant Hill Communities:

These present a very diverse flora, only partially related to the surrounding community. In general, anthills provide a more alkaline, base rich habitat and this is reflected by the vegetation cover.

Tamarindus, Mimusops schliebenii and Manilkara mochisia have already been mentioned as common anthill trees. Smaller trees are Commiphora spp., Salvadora, Cleistochlamys, Ziziphus spp., including Z. pubescens, and Ehretia amoena and Cordia spp. Euphorbia candelabrum and several fleshy climbers are common, as are species of Pavetta and other Rubiceae. Grasses are often sweet, and include Leptochloa, Cynodon, Sporobolous and Chloris virgata.

3.2. COMPUTER ANALYSIS OF THE GROUND LAYER VEGETATION

3.20. Introduction.

During the course of the study the ground layer vegetation was analysed quantitatively in order to stimulate plant collecting, gather base line data for species composition change and to be able to describe and compare different plant communities and associations. Analysis was undertaken by random quadrats and assessing plant presence or absence and percentage frequency for each site. In 1970 I decided to extend these assessments into a grid coverage of the entire study area and to analyse such data by standard computer techniques (Kershaw 1973; Greig-Smith 1964). The analysis was intended to show ecological relationships between different species and different sites of the study area, and to compare the computer generated association map with the more subjective vegetation map on figure 3.2.

This section describes the field data collection, presents the computer analysis results and discusses the biological value of these results. Details of computer techniques, programmes, choice of methods and parameters etc are given in appendix 4.

3.21. Field Methods.

Data were collected at each mile post along the road transect system of the study area. This system was designed for animal census and is described in chapter 5. Five transects were used: Lihangwa, Kilunda, Chimbiriri, Malemba and Mwende with 30, 25, 18, 11 and 25 sites respectively, (total 109 sites). In addition 68 sites along a transect network in a miombo catenary system were analysed. Four transects of 20, 18, 18 and 12 sites, each 300m apart on transects 1000m apart were used. This transect system is described in chapter 6. Later in the study a transect of 33 sites across the Lungonyo floodplain and 6 additional sites in minor associations were analysed. This gave a total of 216 sites examined between 1970 and 1973 in the months of March and April when most grasses and herbs were flowering.

At each site 100 quadrats (25cm square) were thrown in a pattern of 25 quadrats per compass quadrant within 100m of the site central mile post or marker. Quadrats landing on bare soil, litter, trails, wallows etc were discarded. Each quadrat was examined for herbaceous species rooting within the square and each species was identified and tabulated. Data could be expressed as presence/absence for each site and as species percentage frequency for each site. In 1973 only 33 quadrats were thrown per site in the relatively homogenous vegetation along the woodland parts of Lihangwa transect and the floodplain transect.

Within the miombo catena system woody vegetation was analysed by tabulating all tree and shrub species over 25cm high within a 15m radius circle around the marker for each site. These plots were used only for presence/absence data. A total of 108 species (ignoring those occurring in less than 3 of the sites) were used for the ground layer analysis, and 42 woody species were used for the miombo catenary system.

3.22. Computer Analysis.

Data were analysed in late 1974 at the Botany Department of the University College of Wales, Aberystwyth, using prepared programme modules. Programmes were available for classification analysis (using only presence/absence data) and ordination analysis (using both presence/absence data and the quantitative data of percentage frequency). Details of these techniques and their application are described in appendix 4.

Classification programmes involved the use of association analysis in both the normal and inverse modes and also cluster or constellation analysis. Association analysis examines the levels of chi-square correlations between pairs of species or sites and in the normal mode produces groupings of sites with similar floral characteristics and in the inverse mode produces groupings of species with similar site characteristics. Cluster analysis involves the plotting of species chi-square correlations into a web or constellation of species linkages, a technique used by Welch (1960) in his study on the woodland vegetation of Morogoro, East Tanzania.

The complete data set was analysed first and this, as expected, split the data into separate formations; the floodplain, the wooded grassland and the woodland system. Following this the data for each formation, as determined by the computer, plus adjacent sites as "edge areas" were analysed separately. This technique was followed for normal and inverse analysis and cluster analysis. The miombo catena data were run separately and together with the woodland data from the grid transects.

The ordination technique chosen was principal component analysis, but due to data size limitations this was run for the woodland set, the miombo catena set and the flood plain set using percentage frequency data. The flood plain data was also analysed using presence/absence criteria. Principal component analysis examines the variance-covariance matrix of species or sites pairs and generates gradients of variation which can be portrayed linearly with the variables ranked along the gradient. Output is in the form of two dimensional (two gradients of variation) graph plots of either sites in normal analysis, or species in inverse analysis. The proximity of such species or sites on the plot is taken as an indication of their ecological similarity.

3.23 . Results.

3.231 Classification Techniques.

3.2311 The total data set.

The complete data matrix of 109 species and 216 sites was analysed. Normal analysis resulted in 12 associations or groups of sites of similar floristic composition. The first division was on Brachiaria leucranthra at a high level of total chi square and this split off 68 sites of the wooded grassland formation. The second division on Ischaemum afrum removed 12 flood plain sites and a later major division on Hyparrhenia divided the woodland formation into 49 valley sites and 71 upland sites. A dendrogram of the hierarchy of divisions is shown in figure 3.3A. The chi-square levels are scaled which tends to mask the high level of the primary division into alkaline soil sites and others. As there are no further divisions until a much lower level of chi-square, this grouping is relatively homogenous.

The spatial distribution of sites into the 12 associations is shown in figure 3.3B, and the associations can be classified as shown in table 3.1.

The inverse analysis produced 12 associations or groups of similar species. The first split at a very high level of chi square cut off a group of 8 woodland perennial grasses with no further division, indicating a high degree of similarity. The second split, also at high chi square level, cut off 16 alkaline terrace species but subdivided them at a low chi square level into 3 subgroups of little apparent ecological meaning. Further divisions at lower significance levels split off 2 floodplain groups, one from the centre and one from the edge, 2 *Combretum* ridge groups, 3 woodland forbs and short grasses groups and a large "noise" group of species of little information content.

The dendrogram of divisions is shown in figure 3.4 and group species composition in table 3.2.

The constellation diagram of species affinities as determined by cluster analysis is shown in figure 3.5.

Five major clusters of species are shown, one for the flood plain, three for the wooded grassland and one for the woodland habitat. These clusters are shown as circles in figure 3.5 and the letters in the circles refer to association groups as determined by inverse association analysis. A few major species are shown to characterise each grouping. The notation 'n' and 'd' under each circle indicates the number of species making up the cluster and the density of species linkages within the cluster. For example, if every single species of the cluster was significantly associated (a positive chi square level) with every other species then 'd' would equal 1.0; a 'd' of 0.8 indicates 80% of the possible linkages do occur. It is evident that the 3 grassland clusters have more species associations than the 2 woodland clusters.

Each cluster is related to other clusters by intermediate species which are shown in figure 3.5. The intermediate species have positive associations with species in both the adjoining clusters; for example Echinochloa haploclada is a constituent of both the flood plain and the wooded grasslands.

3.2312. The flood plain data set.

This data set contained 18 sites and 42 species. The sites were 12 designated as the floodplain unit under the total data set and 6 edge sites of the wooded grassland.

Normal association analysis produced 3 associations; a central floodplain community of 8 sites characterised by Andropogon gayanus, C; an edge community of 5 sites characterised by Mariscus mollipes, A; and an intermediate community of 5 sites, B.

Inverse analysis produced 7 groups of species, but ignoring divisions at low chi square levels 4 ecological groups of species can be picked out. These groupings are shown in table 3.3.

Cluster analysis (fig. 3.5) shows 3 groupings: a discrete edge community of wooded grassland species labelled D in the figure and in table 3.3, a group of herbs from the periphery of the flood plain, labelled C, and a central swamp group of grasses and herbs only roughly divisible into the A and B communities of inverse association analysis.

3.2313. The scattered tree grassland data set.

This data set consisted of 81 sites and 78 species. Normal analysis showed 9 groups of sites. The dendrogram of divisions is shown in figure 3.6 and a table of group characteristics in table 3.4. The first division splits off 18 sites which are ectonal with the woodland formation. *Borreria subvulgata*, a herb of *Combretum* ridges, is the divisive species. The second split removes 14 species without *Brachiaria leucrantha* as a "noise" grouping. These sites border the flood plain and include the *Hyparrhenia* communities to the south of the wooded grassland area. The third division separates 12 sites with *Indigofera* which resemble the *Borreria* sites and include the *Combretum* - *Cassia* ridge communities. The remaining 35 sites, equivalent to the D, E&F groups of the total data set are relatively homogenous and are split at lower chi square levels into 6 small communities.

Inverse analysis produced 13 groups of species classifiable as 4 ecological groups and one large noise group. The dendrogram is shown in figure 3.7 and the species groupings in table 3.5.

Cluster analysis, as shown in figure 3.5, produced 2 discrete constellations, relating to groups A-F and H-I of the association analysis and two lesser groups with affinities to the flood plain and woodland habitats.

3.2314. The woodland data set (including the miombo catena data).

The data set consisted of 132 quadrats and 78 species. Normal association analysis produced 6 groups of sites, with all divisions well above the minimum level of chi square. The first division, on Heliotropium strigosum split off 5 sites which are ecotonal to the wooded grasslands and the second division on Hyparrhenia virtually separated the miombo catena sites from the rest. Further subdivisions removed small groups of sites on rather uncommon species. The dendrogram is shown in figure 3.8 and the site groups tabulated in table 3.6.

Inverse association analysis was rather unsatisfactory due to the "chaining effect" in the divisions (see appendix 4). Ten groups of species were produced. The first group comprising the woodland tall grasses and sedges, split off at a chi square level nearly 4 times as high as the next split. It is of interest in that the woodland tall grasses are separated from the forbs and shorter grasses as was done in the total data set. The dendrogram is shown in figure 3.9 and species groups listed in table 3.7.

Cluster analysis produced a complex array of linkages with many negative and few very high positive associations. One tight cluster of 16 species is associated with the ridge communities of the wooded grassland and also with the 'valley' communities (Hyparrhenia, Heteropogon) of the woodlands. There is a diffuse grouping of tall grasses associated with two different groups of forbs, but linkage chi-square values are not high.

3.2315, The miombo catena: ground layer and woody species data sets.

This combined data set was composed of 68 sites and 90 species (42 woody species and 48 herbs). As woody and herbaceous data were collected by different methods and at different times inverse analysis was not attempted. Normal analysis produced 13 groups of sites, 7 groups (38 sites) with Brachystegia spiciformis, the first division species, and 6 groups (30 sites) without. Of the 12 division species only 3 were herbs. It was felt that the small quadrat size (710m^2), tended to exclude tree species and as such site classification on the basis of species presence or absence was not feasible. Many groups produced by association analysis were heterogenous.

Cluster analysis of the combined data set did produce data of value, although 35% of all associations were negative.

The constellation diagram is shown in figure 3.10; two separate groups are formed, a small 'valley' group and a much larger woodland group. The woodland group is dominated by a 'ring' of miombo species (n=11, d=0.51) with a thicket grouping to the right, Euclea and Markhania and a chipya group to the top with Andropogon, Tristachya etc.

Association analysis of the ground layer data set gave 10 site groups in the normal mode; the first split on Panicum infestum giving 12 valley sites and 56 upland sites. The dendrogram of divisions is shown in figure 3.11 and the site groups are classified in table 3.8. Inverse analysis was not run for this data set.

3.232. Principal Components Analysis (P.C.A)

Details of terminology and the basis of the PCA technique are given in appendix 4. Table 3.9 gives analytical data for all the PCA analyses described below.

3.2321. The floodplain data set.

This analysis utilised the same 18 sites and 42 species as the association analysis.

Normal P.C.A. clearly showed a separation of sites which gave general agreement with the sites separated by association analysis. The first axis contained over 35% of the data variance and for both the frequency and presence/absence analyses, the loading species for the first axis were a wooded grassland and a major floodplain grass species. Both analyses emphasised the difference of sites 1 and 2 which was not brought out in association analysis. The two analyses are shown in figure 3.12. The 3 groupings of the association analysis A, B and C are shown in the diagram.

Inverse P.C.A. using the presence/absence criteria worked well, separating species into groups readily identifiable with the groupings of inverse association analysis.

P.C.A. using % frequency data presented a problem, in that dominant grass species which have a high % frequency suppress the information of the rarer smaller grasses and herbs, which tend to cluster at the negative side of the graph plot axis origin. This tendency is repeated for the woodland and for the miombo catena data sets for inverse P.C.A. All graph plots raveal a characteristic pattern similar to a "proportional sign", with the arms including dominant grasses and the fulcrum all the small plants of low cover and low % frequency values.

Enlargement of the graph plot scale around the origin does show that species are grouped into ecological entities, but these are completely masked by the dominant grasses. Graph plots for both criteria are shown in figure 3.13.

For both normal mode P.C.A.s it is fairly obvious that the first component reflects the major ecological changes from the wooded grassland (sites 1 and 2) to the central floodplain, these changes being an increase in moisture and an increase in clay content. The second component is more difficult to assess and appears to differ between the P/A and the % frequency plots. Note from table 3.9 that the proportions of the variance explained by the first components are similar but differ for the second components for the P/A plot and the % frequency plot. Loading species for the second component are in both cases species from the central flood plain against species from the flood plain margin, so this component is not to do with the great disparity between flood plain and grassland communities.

For the inverse presence/absence plot the components are not readily identifiable in environmental terms, despite the first component accounting for 45% of the variance. Site loadings are positive on grassland sites and negative on the edge/central sites, but the species associated with the central sites are placed in an intermediate position.

The inverse % frequency plot appears to be dominated by species of high frequency of occurrence, and whilst species are ordered in groups identifiable with association analysis groups, it is not possible to pick out ecological criteria for the components.

3.2322. The woodland data set.

The restriction of data matrix size for P.C.A. resulted in the exclusion of all but 65 woodland sites, made up from Kilunda, Lihangwa, Chimbiri, Malemba and the first (out of four) of the miombo catena transects. 62 species were used.

Normal PCA resulted in a satisfactory spread of sites but beyond a separation of the miombo catena sites and a partial separation of valley sites, the sites are not sharply divided. The variance content of the first two axes is only 35% of the total and loading species are *Andropogon* and *Hyparrhenia* on the first axis and *Panicum* and *Andropogon* on the second, possibly showing an ordering into "dryness/wetness" and "miombo/chipya" respectively. The graph plot is shown in figure 3.14.

Inverse PCA showed the same trend as the floodplain plot in that 8 grasses and sedges dominate, leaving an extremely tight cluster of smaller plants at the negative side of the origin. The major grass species do show a dry trend and a wet trend with *Panicum maximum* in an intermediate position. It is of interest to note that the grasses with the highest value on the first axis, *Andropogon*, *Digitaria* and *Panicum* are not restricted to the woodland community but are commonly found in the alkaline wooded grassland as well. The graph plot is shown in figure 3.15.

3.2323, The miombo catena data set.

All 68 sites and 44 ground layer species were included for analysis (woody species had no % frequency data).

Normal PCA gave a good spread of sites but with little ecological meaning except a separation of valley sites. Variance content of the first two axes totalled 39% and species loadings were <u>Andropogon</u>/<u>Panicum</u> and <u>Panicum</u>/<u>Loudetia arundinacea</u> respectively showing a possible ordering into miombo/chipya and upland/valley sites.

Inverse PCA showed a domination by tall grasses and a near origin cluster of smaller grasses and forbs. The spread of grasses shows a separation of upland and valley species. Normal and inverse plots are shown in figures 3.16 and 3.17.

3.24. Discussion and Conclusions.

A discussion of the computer programmes and analytical techiques is contained in appendix 4. This section deals only with the results. Methods of classification and ordination undertake the "mathematical sorting" of biological data; as such the interpretation of results needs considerable care. Changes in the preset termination levels for analysis (number of species occurrences, chi square levels etc) can lead to considerable differences in the computer output of results.

As was expected the analysis of the total data set showed the study area vegetation to be highly stratified and classification produced little more than the major formations with their linkage or transitional species. This sharp stratification is shown clearly in the cluster analysis diagram of figure 3.5. The gross homogeneity of these formation clusters masked internal relationships at the total data set level.

Comparing the associations of sites produced by N.A.A. (fig 3.3B) with the subjective vegetation categories of the map in figure 3.2 shows a high similarity. Use of a simple matching coefficient, (Sokal and Sneath, 1963).

$$\text{where } S = \frac{\text{No. of agreements (+ve or -ve)}}{\text{No. of characters (sites)}} \times 100$$

gave a similarity of 72.4%. The similarity can only be partial as the vegetation was mapped mainly by reference to the woody vegetation and the computer analysis was confined to ground layer data.

Within the confines of the technique the wooded grassland formation proved the most complex system, showing a tenuous link with the floodplain communities through such species as Echinochloa and Eriochloa and a much stronger link to the woodland system through the *Combretum* ridge communities which are clearly ecotonal or transitional..The placing of *Themeda* and *Heteropogon* is of interest as these two species occur in two distinct habitats, the *Combretum* ridges (giving way to *Andropogon* closer to the woodlands) and the flat, hard, clay sands to the south of the study area.

The profusion of small associations from both NAA and IAA for the wooded grasslands is difficult to explain. One division appears to be the broad-leaved, more nutritious species of less disturbed (less grazing pressure?) or more fertile sites, eg. *Brachiaria*, *Sporobolus*, *Urochloa* (table 3.5), as opposed to the *Chloris*, *Cyathula*, *Euphorbia* group typical of highly grazed sites. The many groups typical of the *Combretum* ridges may represent a gradient or successionary series to the woodland communities.

The floodplain community is relatively simple (possibly due to less "noise" from a single transect at right angles to the gradient). The edge sites of the wooded grasslands are separated immediately by all analyses and the community boundary is very sharp. PCA further divides these grassland sites into 2 groups, a group of sites 1 and 2 and a group of sites 3, 4, 5 and 6.

The woodlands as analysed here have few internal groupings or relatively few positive associations in the cluster analysis. This may be attributable to:-

1) The dominance in real terms and by number of occurrences of five grass species: Andropogon, Tristachya, Schizachyrium, Panicium and Digitaria, these species tend to show only negative associations.
2) The low occurrence and seemingly random distribution of forbs and smaller grasses.
3) The low mean number of species per site (11.8 compared with 21.4 for the wooded grassland).
4) The relative homogeneity of the formation.

It is of interest that the inverse PCA produced axes of greater variance content than the normal PCA. Figures for each formation are shown in table 3.9. As the first axis is much greater than the second for inverse PCA, this seems to indicate that species may be responding heavily towards one environmental factor, whereas sites can only be characterised by several factors of less individual importance.

In conclusion it can be stated that the objective analysis of the herbaceous vegetation has revealed patterns that are understandable in ecological terms and are in agreement with the earlier more subjective survey and delimitation of vegetation associations. The apparent lack of internal communities within the large woodland formation and the close association of most species (figure 3.10) indicates the formation is a continuum of possibly several successional stages and not an assemblage of discrete communities separated by edaphic or topographic factors. This point is discussed in greater detail in later sections of this chapter.

SECTION 3.3. FLORISTIC COMPOSITION AND AFFINITIES

3.30. Introduction.

Plant collections in the Selous have shown the heterogeneity of the vegetation with elements of the Kenyan, Mozambican and Zambian floras common in certain habitats. It was considered of value to assess quantitatively the level of these inclusions and to show the degree of similarity and affinity with major floristic zones. As the Selous is close to the North eastern limit of miombo woodland such an analysis is necessary to describe the Selous flora in phyto-geographical terms.

This section also analyses the flora in terms of numbers and sizes of taxonomic units.

3.31. Methods.

The herbarium collection and plant species list was checked to provide data on botanical family and genus content and size. The checklist (appendix 3) and punch card sorting system (as illustrated in figure 3.1) was used to compare the woody element of this flora (as known in 1973, and including taxa identified to species level only) with the

Kenyan flora, Dale and Greenway (1961), and with the Zambian flora, White (1962), to show similarities or affinities in plant species composition. Similar comparisons were made with smaller area check lists from Zambia, Lawton (1963) and Fanshawe (1960-1969), and from Tanzania, Harris (1970).

It was not possible to carry out statistical analyses of affinity and similarity as described by Exell and Wild (1961) as no comparable species lists were available for areas of similar size to this study area. However, simple percentile similarity figures were obtained by using Sokal & Sneath's (1963) formula of:

$$S(\%) = \frac{N}{N + D} \times 100.$$

where S is coefficient of similarity, N is the number of shared species and D the number of different species.

White (1965) described phytogeographical regions for the African woodlands and showed quantitative similarities and dissimilarities between the West and Central African woodlands. His paper and accompanying species list of savanna and woodland trees served as a basis to compare the Selous flora with the Zambezian and Sudanian phytogeographical domains. Selous species were checked against the distributions in White's list and tables of similarity drawn up.

3.32. Results.

To date (1 January 1977) using Vollesen's additions to the checklist of Rodgers and Ludanga (1973) 1250 species of vascular plants have been collected from the immediate study area. This compares with a present collection of 1800 species from the whole of the Selous Game Reserve, Vollesen (pers. comm.); and an estimated 10,000 species for the flora of Tanzania, Wingfield (pers. comm.). The study area flora is contained in 118 families and 541 genera.

Of these families; 53 contain 1 genus, 41 contain 2 to 5 genera and 24 contain more than 5 genera. The largest families are: Gramineae (135 species), Rubiaceae (75), Cyperaceae (48), Euphorbiaceae (57), and Papillionaceae (101).

Of the genera, 326 contain 1 species, 175 contain 2-5 species and 40 contain more than 5 species. The largest genera are: Indigofera (19 species), Crotalaria (16), *Combretum* (17), *Ipomoea* (18), *Vernonia* (13), *Acacia* (13) and *Cassia* (11). Note that *Indigofera* and *Crotalaria* are the two largest genera in East Africa.

A total of 135 grasses have been collected, including 42 annuals and 155 legumes. Note that herbs and sedges are under represented in this collection as compared with woody elements and grasses. It is probable that the riverine and thicket associations, with many species that flower irregularly, are under-collected as compared to the woodland and grassland associations.

The Eastern Selous flora as described in this thesis shows strong affinities to both the Kenyan (mainly coastal) flora and the Zambian flora. 323 woody species from this study area were used to assess the affinities quantitatively. Of the 323 species:

64 did not occur in Kenya or Zambia,
95 occurred in both Kenya and Zambia,
93 occurred in Kenya but not Zambia,
71 occurred in Zambia but not Kenya,
188 occurred in Kenya (total), and
166 occurred in Zambia (total).

Sneath's coefficient of similarity shows that this study area has comparable levels of similarity with both Kenya and Zambia, eg. E. Selous and Kenya: 58.2%
E. Selous and Zambia: 51.4%.

However, closer examination of separate vegetation types reveals a very different picture. The woodland elements of this area show a close affinity to Zambia (especially the legumes), and the thickets and riverine communities show a close affinity to Kenya.

eg. E. Selous woodland species (total 108);
E. Selous and Kenya 45%
E. Selous and Zambia 79%
E. Selous thicket, riverine and ground water forest species (total 251)
E. Selous and Kenya 63%
E. Selous and Zambia 37%

Note that some species in the eastern Selous are found in both vegetation types and so are included in both comparisons.

Comparison of the species restricted to Kenya or Zambia showed that:

Of the 93 species restricted to Kenya (50 to the Coast Province);
10% are miombo species

43% are riverine species

42% are thicket species

20% are ground water forest species

8% are legumes.

Of the 71 species restricted to Zambia;

64% are miombo species

18% are riverine species

20% are thicket species

1% is a ground water forest species

37% are legumes.

Analysis of vegetation checklists from smaller areas in Zambia reveals a close similarity with the woodland flora but little with the thicket or riverine floras. From the brief species lists of Lawton (1963), out of 47 species from Brachystegia woodland 62% occur here; out of 46 chipya species 67% occur here; whilst of 70 riverine and forest species only 13% occur here. Similar patterns emerge from the Zambian district species lists of Fanshawe (1960-69).

Comparison with a species list from the University campus of Dar es Salaam, Harris (1970), shows that out of

402 identified indigenous species, 48% also occur in this study area. A comparison of the Ruaha National Park's flora (Central Tanzania), with this study area's complete flora (as per 1973, 894 species) by Bjornstadt (1976), showed a 44% similarity.

White's (1965) list includes 136 tree species found within the Selous. Of these 2 were present in West Africa and not in Zambia, 86 were present in Zambia and not in West Africa and 48 were common to both. Of the 134 species common to Zambia, White notes that 38 are widespread, 35 are miombo species and 24 are <u>Acacia</u> - <u>Combretum</u> - <u>Terminalia</u> woodland/wooded grassland species. No Selous species are recorded in the Katangan or Barotse centres of endemism but 29 are common to the Kariban centre of endemism (species confined to low lying hot valleys). Ten Selous species have small restricted distributions in Zambia. Only 7 species are constituents of thickets in Zambia.

3.33. Discussion.

The ecological system in this study area is closely duplicated through central and southern Africa. Upland ridges of miombo and chipya woodland interspersed with areas of thicket and forest, descending to an alkaline river terrace of more open scattered tree grassland and shrubland and eventually to a riverine system of channels or floodplains are a common pattern. The Ruvuma valley in southern Tanzania has many resemblances (Rodgers aerial survey). The Luangwa valley of Zambia (Astle et al 1970), the Zambezi valley, (Jarman pers. comm.); the Saabi-Lund valley of Rhodesia (Farrell 1968 and Rattray and Wild 1964), and the areas surrounding the Kruger National Park in South Africa, (Hirst 1975)· all duplicate many of the land systems, vegetation communities, genera and very often the species of this study area.

I was able to see these similarities on a visit to South Luangwa National Park in Zambia in March 1970. In Luangwa a plateau woodland of *Brachystegia* species descends over a steep escarpment with patches of scarp forest and thicket, through a transitional *Combretum* - *Terminalia* zone to a flat highly alkaline wooded grassland with a short mixed annual perennial grass cover. *Terminalia spinosa* is replaced in Zambia and Rhodesia by *Colophospermum mopane* (Kirk ex Benth) Kirk, a tree of very similar habit and ecology. This association merges into the Luangwa river communities of floodplains and lagoons.

Farrell (1968) describes several vegetation communities in the Saabi - Lund system which closely resemble this study area, in particular the Pteleopsis - Millettia - Spirostachys woodland and thicket systems. The Brachystegia glaucescens (a southern ecotype of B. microphylla (White 1962), thicket is similar in distribution, ecology and species composition to B. microphylla thickets here. The Saabi - Lund area contains several coastal elements of the Mozambique flora and the riverine and Acacia scrub associations show strong affinities to this area.

Plant collections from this study area, and even more from the south Selous (Rees specimens, lodged in the MRC herbarium) illustrate the strong link between the Selous and Mozambique floras, with the Selous collections turning up several new E. African species which are common in Mozambique. These species tend to be restricted to riverine or thicket habitats.

Similarly, the coastal forests of Kenya as described by Dale (1939) and Moomaw (1960), show strong affinities to the Selous forests. In particular the Boni forest of Kenya, Dale's Evergreen Dry Forest and Moomaw's Manilkara - Diospyros Lowland Dry Forest, resembles the coastal thickets on alkaline clay sands described here. Moomaw's Manilkara -

Cynometra Lowland Dry Forest resembles the coastal evergreen forests of this area. The woodland forest system of Kenya's Shimba Hills Game Reserve has strong similarities with this area and many of the woodland trees and grasses are the same.

To conclude it seems probable that in historic times the Selous was covered by forest and thicket communities which are now more restricted to the coastal areas of East and Central Africa. The postulated climax and past forest cover for Central Africa of Khaya - Trichilia - Diospyros (see section 5 of this chapter) possibly did not reach the drier areas of the coast, but are now more common in the West Selous and South and Western Tanzania in areas of higher rainfall.

With the decrease in forest cover as a result of climate amelioration and human activities, the predominantly coastal forests have given way to woodland systems with origins in the Zambian flora. Thus the Selous has a bivalent flora with past links to Kenya and the coast in its thicket and riverine communities and more recent affinities to Zambia in the woodland communities.

In phytogeographical terms the Selous is an integral part of the Zambezian Domain with a low index of similarity with the Soudanian Domain. The affinities with the Zambezian flora are through the miombo and wooded grassland floras, not through the riverine or thicket floras. There is no contact with the western (Katanga and Barotse) centres of endemism. Superimposed on the dominance of the Zambezian Domain is the strong influence of the coastal flora (especially in the thicket/forest formations) with elements of both the Kenya and Mozambique floras.

3.4. VEGETATION AND THE ENVIRONMENT.

3.40. Introduction.

This section describes the distribution of the vegetation formations and associations with regard to the environmental factors of soil and topography. Such factors affect vegetation not only at the association level but also at community and individual species levels. Soil and topographic factors have been described in chapter two and are not discussed in detail here.

The section concludes with a discussion of the topics of the vegetation catena, the distribution patterns of the miombo and chipya woodlands, an ecological classification of grasses, the phenonona of spatial and temporal grassland mosaics and a brief analysis of factors affecting the annual or perennial nature of grassland composition.

3.41. Methods.

Formation and association distribution patterns were examined by drawing scaled profile diagrams across the whole or parts of the study area from published 1:50,000 contour maps. Vegetation boundaries were superimposed on these diagrams by reference to air photographs or composite air photograph mosaics.

The woodland thicket systems were further analysed for slope position by selecting random points on air photograph stereo pairs and allotting such points to three slope positions: upper, middle and valley; and three vegetation associations, thicket, miombo and chipya. Some 272 points were so chosen and data analysed by a 3 x 3 chi square contingency table. Points falling on other minor communities or community boundaries were ignored.

Finally, and as was mentioned in chapter 2, soil samples from 10cm depth from 56 woodland sites in the eastern Selous and from 110 transect mile posts in the study area were analysed for pH and clay content. Vegetation at these sites was assigned to the association types listed in chapter 3.1.

3.42. Results.

3.421. Profile Diagrams.

a) Distribution at the formation level.

Scaled East-West profile diagrams were drawn for every 15' of lattitude across the study area. One example, for 9°S., is shown as figure 3.18. These diagrams showed that grasslands are confined to low lying flats or flood plains.

The wooded and shrubbed grasslands are confined to the alkaline river terrace and the woodlands are confined to the upland areas of Karoo sandstones. The thicket and forest patches (excluding riverine or groundwater communities) were restricted to the karoo sandstones and usually to the upper slopes or ridge tops. Formation distribution is thus topographically (and edaphically) controlled.

(b) Distribution at the community level.

Profile diagrams across a steep valley ridge system (A-B), across the miombo catena system (C-D), and across the alkaline river terrace (E-F) are shown in figures 3.19, 3.20 and 3.21 respectively. Letters in brackets identify these profiles on figure 1.3.

Examination of these (and other) profiles shows the following features:

1) Within the Forest/Thicket formation
   - (a) Coastal dry forest is restricted to the western watershed on flat topped ridges.
   - (b) *Brachystegia microphylla* thicket is confined to steep scarp slopes on shallow stony soils.
   - (c) Costal dry thickets on sandy soils are absent from valley areas.

2) Within the Woodland formation.

There is virtually no difference between the various associations as to their topographic position. Valley communities are, of course restricted.

3) Within the Wooded Grassland formation.

   (a) Cassia - Combretum communities are restricted to the low ridges of sandy loam traversing the river terrace.

   (b) Terminalia - Spirostachys communities are restricted to the river terrace. These communities also contain small areas of wetter conditions with their characteristic species which are not mappable. The profile diagram of 3.20 illustrates these communities.

(c) Distribution at the species level.

All species can be defined in terms of their autecology and distribution, but only three grass species are given here as an example.

1) Sporobolus virginicus is confined to saline seepages
2) Oxytenanthera abyssinica (bamboo) is confined to steep rocky gorges.
3) Alloteropsis semialata is confined to rocky shallow soil hillocks.

(d) The effect of treeshade.

A transect of contiguous 25cm square quadrats across a patch of dense tree shade (Cassia abbreviata) from the wooded grassland is shown in figure 3.12. Broad-leaved grasses such as Panicum infestum and Urochloa trichopus tend to dominate in the moister area of tree shade.

3.422. Woodland associations and topography.

The 3x3 chi-square contingency table for 272 points analysed on stereo photo pairs is shown in table 3.10.

Comparing expected with observed values, the thickets show a significant association with the upper slopes, miombo woodland with middle and lower slopes, and chipya occurs with equal frequency in all positions.

3.423. Vegetation association and soil types.

Results for all 166 sites are shown in table 3.11. There is no significant difference between miombo and chipya distribution in terms of soil acidity and clay content. Wooded grassland and shrubbed grassland associations are dominant on sites of higher alkalinity and clay with the Terminalia - Spirostachys community areas showing especially high alkalinities.

3.43. Discussion.

3.431. The vegetation catena.

The concept of a soil catena was discussed in chapter 2.2.

Vegetation communities are associated with such soil and topographic sequences, especially on the karoo sandstones where the relief is greater than on the flat river terrace and floodplain. Burtt (1942) showed the existence of vegetation catenas both on a small scale within a woodland association and on a larger scale from formation to formation. The distribution of associations as shown in figures 3.18 to 3.21 may be described as catenary.

Howard (1970) discusses the miombo woodland - Combretum woodland - clay soil grassy mbuga sequence so typical of the western Tanzania miombo formation type. In this case the Combretum woodlands are transitional on the lower slopes of the toposequence. Combretum woodlands on the large scale appear to be transitional between the miombo and Acacia - Commiphora formation types in Central and Western Tanzania.

In this study area the Combretum woodlands act as an ecotone between the miombo - chipya associations and the valley associations ; their position on better soils of a high water table makes them a favoured dry season habitat for several grazing mammals.

The genus *Combretum* with some 18 species in this study area does show a distinct zonation in species distribution which follows a catenary pattern viz:-

Thickets on upper slopes:-	*Combretum padoides*.
Woodlands on upper slopes:-	*C. zeyheri*, *C. collinum taborense*, *C. psidiodes*
Woodlands on lower slopes:-	*C. molle*, *C. collinum suluense*, *C. fragrans*.
River valleys:-	*C. goetzei*. *C. pentagonum*.
Alkaline river terrace:-	*C. hereoense*
Flood plain edges:-	*C. imberbe*
Flood plain channels:-	*C. constrictum* *C. mossambicensis*

Similar patterns could be described for species of *Brachystegia* (6), *Acacia* (7) and some grasses.

3.432. The Miombo-Chipya distribution pattern.

Cole (1963), working in Zambia, believed geomorphology (and hence soils) to be the major factor affecting woodland association distribution and stated that fire and human agencies of succession are secondary factors. Briefly, she states that:-

"miombo woodland is restricted to undissected plateaux on old infertile sandy soils; chipya woodland is restricted to dissected undulating country on well-drained, mature chocolate loams; open woodland forms (scattered tree grassland and the Zambian 'mopane' and 'munga' associations) on alkaline clays and valley slopes and that grassland is restricted to poorly drained pediplains and valley bottoms."

These conclusions agree with the data presented here, with the exception that in this area one cannot distinguish between the miombo and chipya communities using broad topographic or edaphic factors. Tables 3.10 and 3.11 show no real difference between slope or soil acidity and clay factors. However it must be stressed that in Zambia the term 'chipya' is used in a broader sense than in this study area and Cole's remarks could apply to several different communities.

Lawton (1964) working in Northern Zambia gives data (shown in table 3.12) to show a soil clay factor determining chipya and miombo distribution. He writes, "It is suggested that the edaphic factors determine distribution, miombo being confined to clay soils and chipyas to sandy soils." The very high clay values (falling into the heavy sandy clay class of the Zambian soil survey, Savory, 1963) given by Lawton are not found in the woodland soils of S.E. Tanzania where clay content of horizons down to 1m depth average much less than 10%. Lawton's data appear to contradict that of Cole given above.

Anderson (1952) working in the Nachingwea district of S.E. Tanzania (160km S.E. from the Miombo Research Centre), reaches the opposite conclusion. His data are shown in table 3.13 and he writes , "It is seen that miombo woodland is predominant on the sandy soils with clay content up to about 12% and chipya occupies the heavier soils with clay content over 12%." This he qualifies as follows: "More often texture differences are due to the development of a catenary sequence with the miombo predominant on the sands of the lower slopes with the chipya on the sandy loams of the ridge tops."

Again soil clay contents in this area do not reach 12% although there is a tendency for miombo types to associate with middle and lower slopes. However, as chipya and miombo occur with equal frequency on similar soil types it is concluded that edaphic factors are not important in this area. The next section introduces considerable evidence to show the two associations are seral stages in a pyrosere leading to or from a climax thicket.

3.433. Grass Species Distribution and Ecological Classification.

Mention has been made of the large numbers of grass species in this study area and how only a few species dominate in each association. This grass cover can be classified according to ecological characters, as well as on taxonomic features. An ecological classification has more relevance to a study of the array of grazing mammals. These ecological characters may be listed as follows:

1) Distribution patterns.

(a) Species of restricted ecological tolerance. Mention has already been made of Sporobolus virginicus, Alloteropsis semialata etc.

(b) Species of broad ecological tolerance but never dominant, eg. Sporobolus ioclados, Digitaria milanjiana. Eragrostis superba, Panicum infestum.

(c) Dominant species but restricted to one habitat type, eg. Andropogon schirensis in chipyas, Setaria sphacelata in floodplain communities.

2) Growth type (excluding morphological habits of rhizomatous, stoloniferous or tussock growth).

   (a) Short grasses, (less than 60cm) including most annuals and creeping grasses. These can be dominant as on the alkaline soils or inconspicuous as in the woodlands.

   (b) Medium grasses, (from 60 to 100cm) including some annuals and many perennials. These are often edaphically caused stunted forms of taller grasses, eg. *Heteropogon contortus* and *Themeda triandra* on alkaline soils. They are also a common constituent of intermediate communities, eg. the *Combretum* - *Terminalia* woodlands and the *Combretum* - *Cassia* ridges.

   (c) Tall grasses (100-300cm) which are nearly all perennials, but include some rare annuals, eg. *Cleistachne sorghoides* which grows to 250cm. These dominate the woodland and floodplain communities.

3) Nutritional and Grazing Values

   (a) 'Sourveld', usually tall or medium grasses with a coarse tussock growth form, often perennial in habit with a high stem to leaf ratio. These are basically not palatable in the mature growth stages.

(b) 'Sweetveld', usually short or medium grasses, with soft stems and broad leaves, either annual or perennial in habit and have a low stem to leaf ratio. These are basically palatable in all growth stages, but tend to breakdown and fragment in the dry season.

4) Regenerative type:

(a) Annual species which regenerate from seed only, with a life span of one year or less.

(b) Perennial species which regenerate from seed and rootstocks and have a life span of several years.

(c) Occasionally species can exhibit either habit depending on habitat type eg. *Perotis* and *Enteropogon* spp.

Many of these characters are linked and characteristic of major habitat types, eg. tall sourveld perennials dominate the woodlands (some 42 common grass species including only 3 annuals). Short sweetveld annuals and perennials dominate the alkaline outwash plain, (42 species with 20 annuals). Tall coarse perennials dominate the flood plain with no annual species. These terms of short, tall, sweet and sourveld are of importance to grazing mammals and are used extensively in following chapters.

3.434. Spatial and Temporal Mosaics in Grass Distribution Patterns.

Superimposed on the broad edaphically controlled distribution pattern outlined above is a smaller pattern consisting of a mosaic of areas or synusia of single species or small group of species dominance. Such mosaics may vary from a pattern scale of 1 or 2m up to several hundred metres in size. Sometimes these may be immediately relatable to soil or micro relief patterns such as old termite mounds, animal wallows, depressions or deep shade, but often they are due to the species clumped growth and spread where a species competitive ability may be favoured by fire or grazing pressure.

Such single species mosaics are more typical of the non-wooded areas such as the scattered tree grasslands and the floodplains. A prominent example is Bothriochloa pertusa in the more open areas of the scattered tree grassland, which exists as a pure monotype over areas of up to 100m^2. In this case B. pertusa is non-palatable and fire resistant and spreads at the expense of more palatable heavily grazed grasses. This species growth and spread is further discussed in chapter 4. To the south of the alkaline terrace mosaics of Themeda and Heteropogon are common, forming pure species monotypes over large areas. Areas of the central floodplain are often monotypes, although in this case species diversity has decreased with an increase in clay percentage and duration of flooding.

Woodland grass layer mosaics are not so noticeable. Grass clumps are more discrete and further apart, allowing a second shorter grass and forb layer to exist under the tall perennials. The density of trees and shrubs with their attendant shade breaks up areas of species dominance.

Walker (1974) discusses the impact of canopy cover on grass species composition and describes a case similar to that of figure 3.22 where tree shade provides a habitat for broad leafed grasses, usually Panicum maximum, P. infestum and Urochloa species in Walker's Rhodesian lowveld study area. Walker ascribes this shade effect to lowered temperatures, increased nutrient status and better soil texture and moisture conditions under tree canopies.

In addition to such spatial mosaics, there exists a temporal or seasonal mosaic or pattern with different species germinating and flowering at different times. As the flowering grasses tend to dominate the sward, a gap of 2 months can give very different visual impressions of species composition and dominace

This effect is most pronounced in the scattered tree grasslands where at the onset of the November rains the sward is dominated by *Mariscus* species, a small sedge, and later *Dactyloctenium*. By mid rains in March the sward is covered by flowering *Digitaria* and *Sporobolus* and in April *Chloris virgata* starts flowering. Finally during the dry season, a short woody suffrutex, *Maerua edulis*, appears, flowers, fruits and dies back in less than 6 months. After an early fire this is virtually the only green plant in the entire ground layer.

3.435. Perennial or Annual Grasslands.

Several authors dealing with tropical grasslands state that misuse or overuse in terms of fire and grazing pressure causes a successional change from a perennial grass cover to a more annual grassland, eg. Humphrey (1962), Rattray (1960 a&b) Riney (1963), Savory (1966), Bayer (1955) and Walker (1974). There is however considerable evidence to show that for this area and other similar systems, the high annual grass content of the alkaline terrace is due to edaphic factors and only secondarily due to grazing pressure.

Studies in Central Africa indicate that heavy grazing pressure in the growing season (the rains) coupled with early dry season burning considerably reduces plant "vigour and competitive ability" (Bayer 1955). In this study area the scattered tree grasslands carry a very high rainy season density (of up to 100 animals per km^2, see chapter 5) of predominantly grazing mammals. Several areas do show signs of heavy utilisation, forage being removed almost to ground level and large bare areas, dominant unpalatable herbs and sheet erosion becoming common. This phenonomen can be accentuated by the brief drying up period in January or February when high radiant ground temperatures scorch and wilt young growing grasses. Areas relatively inaccessible to grazing animals such as around low thorn bushes and between branches of fallen trees show a medium height good grass cover including many perennial species.

Species such as Mariscus mollipes, a sedge, and annual grasses such as Aristida barbicollis, Brachiaria deflexa and Eragrostis ciliaris as well as unpalatable herbs such as Cyathula lanceolata dominate these heavily grazed areas. Better rangeland has a denser cover of Digitaria milanjiana, Urochloa spp, Sporobolus ioclados and Panicum infestum.

However, this does not necessarily mean that the high percentage of annual grasses in this zone is primarily due to overuse and a resulting succession from a perennial grass sward. There exists considerable evidence from Central and Southern Africa to show that edaphic conditions cause a high percentage of annuals. The Luangwa, Zambezi and Saabi-Lund **Valleys** and areas adjacent to the Kruger National Park, all have extensive areas of heavy alkaline sodic clay sands, with poor drainage. Plant species composition is very similar to that of this study area. Rattray (1966) for example, discussing the Saabi valley grass cover, states that Urochloa, Chloris virgata, Dactyloclenium Brachiaria spp, Aristida spp and Eragrostis spp are common, a list closely resembling this area. Anderson (1963) discusses Tanzanian saline, alkaline and hard pan soils at some length. Such soils characteristically bear a sparse ground cover including many ephemeral and annual grasses. The high sodium content restricts water uptake, and affects plant nutrient absorption, especially phosphorus. These soil properties cause the vegetation to exhibit a drier form than would be expected on the basis of the actual rainfall.

Bogdan (1958) discusses grass species distribution on halomorphic soils from the Kiboko area in Eastern Kenya. His suggested plant-soil relationships are shown in figure 3.23 which is modified and enlarged for this study area.

I conclude therefore that the grass cover of the alkaline terrace is edaphically controlled and the best quality forage contains a high percentage of short sweet perennial grasses such as <u>Panicum</u>, <u>Digitaria</u> and <u>Sporobolus</u>, with some annual species and herbs. The community is relatively delicate and susceptible to heavy grazing and trampling which will cause a rapid deterioration in range quality with perennials decreasiing and annuals, forbs, and bare ground increasing.

3.5. VEGETATION SUCCESSION AND DYNAMICS

3.51. Introduction:

Mention was made in Chapter 2 of the historical background to "miombo" and the effects of Pleistocene climatic change. Evidence was discussed showing that the open woodland forms have developed at the expense of mesic and xeric forest or thicket types by the effect of fire and human activities. Within the more rigid limitations of climate, geomorphology and soils, it is the effects of fire and cultivation that have the greatest effect on plant communities, both their physiognomy and species composition.

Unlike the physical limitations, fire and human factors are not permanent, and vegetation change may be modified or reversed by altering or removing the causative factor. Such factors change the seral stages in community succession. Without such factors succession would proceed to the climax type for the particular soil and climatic regime.

Boaler (1966b), in a monograph on the ecology of Pterocarpus angolensis, quotes evidence as to the age of the miombo formation type as being at least 38,000 years. He notes the miombo species as possessing certain non-forest characteristics such as fire resistance and annual seedling dieback. Boaler estimates that at any one stage, over 90% of the woody plants in a miombo community are growing as suffrutices. This is called a Cryptodrymion type by Glover (in Boaler, 1966).

Considerable evidence from tree growth plots and ring counts show the lifespan of many miombo dominants to be in the order of 100 to 150 years, and that woodland can reach maturity within 100 years of clear felling. (Glover 1946; Boaler and Soiwale 1966). This rapid turnover in a vegetation type marked by unequal fires and scattered settlement results in a mosaic of vegetation communities, in several different seral stages.

Botanical evidence points to the centre of evolution of this leguminous woodland as Zambia and the Eastern Congo, which have 17 full species of *Brachystegia*, the dominant genus. The number of species decreases away from this centre, e.g. 11 in western and central Tanzania, 6 in eastern Tanzania, 1 in Kenya and none in Uganda (Wild 1964). The large number of hybrids between species in this genus would indicate considerable recent extension and or contraction of range. The Zambian flora also shows a high degree of endemism in other tropical genera, e.g. *Crotalaria* (another legume) with 70 endemic species (White, 1966). Other taxonomic groups such as the Lepidoptera and birds show similar effects. (Carcasson 1962 and Moreau 1966). This evidence fits well with a history of recent climatic change.

3.52. Methods.

Detailed investigation of vegetation successionary trends requires the establishment and analysis of longterm experimental plots. Experimental fire plots were established in 1968 and have been used to investigate the effects of fire and grazing on the ground layer; these effects are discussed in chapter.4.

As a 7 year period is insufficient for obtaining data on woody species successionary trends, the bulk of the evidence presented in this chapter is taken from the literature and from a visit I paid to the Zambian Forest Research Division fire plots in 1970.

Within this study area the existence of documented settlement enabled me to investigate clearing and fire effects by the questioning of previous residents, by examining air photographs and by visiting sites of past settlement.

In 1971 an aerial survey of the eastern Selous was undertaken along 5 East-West flight lines some 30km apart. Flights were made twice, in the early dry season in late July and the late dry season in mid October. Data on the extent of burning was collected by using a stop watch to indicate the time of flight over burnt areas and expressing this as a percentage of the total flight time for each transect. Areas of thicket and forest were excluded.

Finally data from the woodland computer analysis records (as presented in chapter 3.2) were used to show community relationshipsin the woodland formation.

3.53. Results.

3.531. The Zambian Fire Plots.

The Forest Research Division of Zambia in 1933 set up 3 experimental fire exclusion plots of some 5 ha each at Ndola in homogenous *Brachystegia* woodland. The area receives some 1100 mm rain per annum and soils are moderately high in nutrients. The woodland is taller and denser than that found in the Selous. Each plot is surrounded by a graded fire break, one plot is completely fire protected, one burnt early in the dry season and one burnt late in the dry season. I visited the plots at the end of the rains in May 1970 when the experiment was some 37 years old. The experiments are discussed by Trapnell (1957) and White (1966).

The early burn plot showed no structural change from the surrounding woodland (which is also burned early in the dry season). Species diversity was maintained, Brachystegia spp remained dominant with some 100 to 120 trees per ha. Annual and short perennial grasses and many herb species were encountered in the ground layer and small thicket patches occurred around termitaria and in deep shade.

The late burn plot showed a drastic change with virtually all trees except Pterocarpus angolensis having been killed. Tree stem density was 5-6 per ha. Grass growth was tall and tussocky and predominantly Hyparrhenia spp. Occasional patches of fire tolerant suffrutices remained. Herbs were scarce in the ground layer. Lack of vegetation cover at the start of the heavy rains had creted a hydrophobic impermeable crust (pavement erosion) which severely decreases water infiltration. Soil height under grass tussocks was some 4-5 cm higher than the surrounding pavement.

Fire effects in the no burn plot were equally drastic.

All grass cover had disappeared, being replaced by evergreen shrubs, forbs and climbers amongst which Rubiaceae and Euphorbiaceae dominated. Miombo woodland elements remained dominant in the tree layer but were scarce or absent in the underwood, shrub and ground layers. Several forest species seedlings were encountered in the ground layer, notably Marquesia spp.

3.532. Extent of Burning in the Selous Woodlands.

The 1971 coverage of the Selous showed that in July 36% (± 19% as 95% confidence limits) had been burnt whilst in October 58% (± 27%) had been burnt (n was 10, each half transect counting as one sample). High confidence limits are partly due to the distribution of game scout patrols and legal trophy hunters who burn as a matter of policy. The September aerial survey gave further information on burning status for the east Selous, each 18 x 18 km sq. being assessed in five classes as: no burn, 1-25%, 26-50%, 51-75% and 76-100% burnt. Results were 12, 12, 18, 17 and 5% respectively. No hunters and reduced level of field patrols have caused the decrease in fire prevalence early in the season.

3.533. The effects of past human settlement.

Appendix 2 gives a detailed account of the history of human settlement in the eastern Selous Game Reserve and the effect of such settlement and its attendant agricultural clearing on the vegetation. A summary of these effects is given here.

Prior to 1920 much of the settlement was confined to the upland thicket areas as a means of defence against neighbouring tribes, slaving expeditions and German rule. Clearings lasted some 3-5 years and then were left to regenerate. Where clearings were enclosed by thicket communities, the clearings rapidly reverted to a thicket cover. Where clearings were open to woodland communities and fire a typical chipya woodland resulted.

Plate 11 is an air photograph of an area of past settlement known as 'Nunga' which is marked on figure 1.3. Within a few km^2 it is possible to find climax thicket, open chipya woodland and several intermediate stages of thicket reinvasion. One area shows an invasion of mature chipya woodland by thicket species. A tree canopy of chipya species covers a dense shrub canopy of Landolphia and Vernonia zanzibarica which has suppressed all grass growth. Within this shrub canopy can be found faithful thicket species such as Fagara, Gardenia, Grewia conocarpa, Suregada and Uvaria spp. Comparative species lists for adjacent plots of climax thicket, open chipya and chipya thicket are shown in table 3.14.

3.534. Air photograph analysis of thicket/ woodland systems.

Plate 10 shows an air photograph of a thicket woodland system. The large dense blocks of thicket are edged with white, (a Markhamia obtusifolia - Millettia micans edge community) which merges into an evenly spaced chipya woodland turning more abruptly into denser Brachystegia woodland.

The successionary sequence from thicket could be observed around a large thicket to the north of the study area where one can see tree density increasing with distance away from a fire produced thicket edge. The vegetation passes through Markhamia to Combretum then chipya communities, culminating in a Brachystegia woodland.

Investigation of a xerophytic sandy soil thicket in Biharamulo Game Reserve, West Lake Region of Tanzania in October 1973, showed a steady increase in woodland tree height and girth away from a thicket edge. Trees were species of Combretum, Ozoroa and Pericopsis not found in the thicket. In this case a soil change had taken place, the woodland occurring on truncated shallow soils having lost up to 50cms soil depth since thicket clearing. Fire was the destructive factor (Rodgers, Ludanga & DeSuzo 1978).

3.535. The Woodland Formation Computer Analysis.

Chapter 3.2 detailed the results of a computerised association analysis of the tree and ground layer elements of a woodland complex. Results are displayed as a constellation diagram in figure 3.10. It is immediately obvious that all the woodland species are associated within one grouping whilst the valley community is separate. This can be used as further evidence for the fact that the woodland and valley associations are edaphically controlled distinct entities. In contrast within the woodlands the different communities are associated seral stages within one successionary series or a very close continuum of communities. Within the constellation diagram there are definite sub groups of stronger associations. These may be taken as the chipya community at the top of the diagram which includes the dominant chipya grasses, (Tristachya, Andropogon and Schizachyrium) and a central grouping of Brachystegia woodland species. This latter category gives rise to a thicket precursor group of species centred on Landolphia kirkii, and another smaller group centred on Markhamia obtusifolia.

3.54. Discussion.

3.541. Successional series and climax vegetation.

Three major successional series are put forward for this study area and the whole of the Selous Game Reserve. These series which may occur singly or together are as follows. Firstly a climatic succession which changed from mesic to more xeric conditions within the last millenium (Moreau 1966). This succession, which is very slow acting, could conceivably alter the species composition and structure of the climax communities. Secondly, and much more importantly, is a pyrosere or fire successionary series, and finally a succession following human cultivation and clearing.

Two major climax vegetation types are postulated for the woodlands of the study area, and the bulk of S.E. Tanzania. These are a xeroseric climax of dry thicket forest communities and a hydroseric climax of riverine thicket and forest communities.

All three successional factors, climate, fire and man, affect the development of both climax types. But the nature of their effects and the concept of a closed canopy climax in the miombo woodland formation type is a matter of much controversy in the literature. Most authors envisage the climax for the miombo woodlands as a forest or thicket type with variable degrees of evergreen or deciduous components depending on climate and soil conditions (Wild 1964; White 1965, Lawton 1963, Boughey 1959, Glover 1949, Anderson 1963; Fanshawe 1960; and Freson et al, 1974).

Ramsay and Rose-Innes (1963) in a detailed paper on fire effects in the Guinea savanna state that, "Complete fire protection ensures a rapid development towards a closed woodland or forest climax which would ultimately reduce or eliminate the present herbaceous cover. Protection encourages the spread and diversification of shrubs and trees whilst reducing the number of and percentage basal cover of grass species. Fire produces the opposite result. Given protection from all forms of disturbance over a long period it seems possible that this type of modified woodland subclimax would develop to a closed forest climax of deciduous trees with an evergreen shrubby ground cover. If such is the case, changes in composition would be extremely slow, owing to the lack of mobility and or scarcity of seed of suitable climax species in the surrounding country."

Keay (1959), working in West Africa suggests three distinct climaxes for the three major climatic/vegetation belts. Firstly, in the southernmost more mesic areas, the present derived savanna with large open woodland tracts with some forest remnants would, with complete fire protection, proceed to an evergreen forest. Secondly the submesic areas of the southern Guinea savanna which have a present open woodland of mixed composition, riverine forest and thicket remnants would move to a transitional climax with evergreen forest on the moister sites and a closed deciduous canopy of Afzelia, Vitex, Albizia and Khaya over an evergreen Guinea savanna (miombo) with an open deciduous canopy of Isoberlinia and Pterocarpus with no forest remnants. Fire protection would lead to a dense deciduous woodland of an open or closed canopy of present savanna elements over a partly herbaceous, partly evergreen shrub ground layer.

Lawton (1963), Fanshawe (1960) and White (1965) working in Zambia describe several dry evergreen forest types which they believe to have covered much of the Zambian plateau during a wetter period of the Pleistocene, and are probably the present day climax vegetation types. Several components of these forests have montane or rainforest affinities, but the forests can maintain themselves under present day conditions in the absence of fire. Under fire conditions they are rapidly degraded to a chipya or Brachystegia woodland type.

Analysing the Ndola experimental fire plots, Trapnell (1957) hesitated to state fire protection would lead to a closed forest. This was following some 23 years of protection. The observations of White (1966) and my own in 1971 however, show that following some 37 years of protection, the protected plot is slowly turning into a forest community but the complete cycle may take over 100 years to complete.

Freson et al (1974) working in Katanga compared many parameters of a thicket, Brachystegia woodland and a fire degraded woody savanna (a poor chipya community) successionary series. They state that, "Late fires occur during the austral spring's vegetation flush and have a strong depressive effect. Early fires have a lesser impact as they take place at the end of the vegetative period. Spatial and temporal variability of fires induces a large heterogeneity of miombo communities which are in constant change." Their ecological measurements are summarised in table 3.15 which shows the intermediate position of the Brachystegia woodlands in most ecological parameters, leading to the greatest species diversity.

Glover (1949) suggested two climax communities for the Nachingwea area of S.E. Tanzania. These are a xerosere leading to a Brachystegia microphylla thicket and a hydrosere leading to a riverine forest community. This latter type (postulated for this study area as well) would equate to the Diospyros - Trichilia - Khaya lowland forests supposed to have covered much of Central and Eastern Africa during the Pleistocene pluvial periods (Wild 1964). Similar forest patches occur in this study area, (see association type A2 in chapter 3.1) but Khaya spp are more common to the west in wetter areas of the Selous reserve.

3.542. Fire and Thicket Destruction.

The thicket vegetation communities are extremely vulnerable to fire. Tree and shrub bark is thin and papery, and leaf loss to evergreen species can be fatal. The protective suffruticose habit is rare in forest or thicket communities. Fires attack thicket edges, and a fierce late season fire before the wind can cause considerable destruction. Human clearing, elephant paths and tree destruction can allow fire to enter. Grass species quickly invade and fires become annual events. Within this study area comparison of aerial photographs of thickets show their areas and shapes have remained relatively constant from 1949 to 1965. No significant decrease in size could be detected. Riverine forest has however been severely depleted.

In open areas adjacent to thickets, grass growth becomes vigorous and a dense sward of up to 1.5m height is normal. This sward can produce fires of 400°C and above (West, 1965). Such fires will prevent seedling germination of all but the most tolerant species. Two dominant thicket trees, *Pteleopsis myrtifolia* and *Millettia stuhlmannii* are also common in the chipya and miombo communities of coastal Tanzania. These species are often left unscathed after fire destroys the thicket and are frequently left standing by native cultivators. Such trees provide shade islands where grass growth is suppressed. Tangles of *Landolphia* spp are common and tree seedling growth often starts in these patches.

Mention has been made of a *Pteleopsis* woodland community (type C.3 in chapter 3.1) found in 3 areas adjacent to thickets in the study block. These communities reflect an early stage after thicket destruction and occur with shrubs of *Millettia micans* and *Markhamia obtusifolia*, two thicket edge species. Anderson (1963) quoting Glover's work in S.E. Tanzania, mentions a *Millettia* - *Markhamia* community which he ascribes to recent clearing and regeneration of upland thickets.

In the course of time the fired thicket will develop into a woodland community with fire tolerant species, i.e. a chipya community. Trees here are fire resistant with thick corky barks and have seedlings which can resist frequent burning. Fire destroys the above ground tissue but the woody root-stock continues growing. *Pterocarpus angolensis*, a common constituent of chipya, requires fire to crack the hard seed coat before germination can take place (Boaler 1966b). All thicket edges, except those on steep slopes, show an ecotone of some 20-40m width characterised by thicket relicts such as *Vitex sp c.f. altissima* (a tree resistant to fire when mature but with fire sensitive seedlings and saplings), *Pteleopsis*, *Millettia*, *Grewia conocarpa* and *Markhamia*. Outside this is a chipya woodland characterised by trees of *Pterocarpus*, *Pseudolachnostylis*, *Combretum zeyheri*, *Strychnos*, *Vitex mombassana* and *Millettia* and *Pteleopsis*.

The place of the *Brachystegia* woodlands in this scheme is not clear. Trapnell (1957), has pointed out that *Brachystegia* spp. are sensitive to fierce late season fires, and *Brachystegia* communities are never found adjacent to thickets. Previous sections of this chapter have shown no topographic or edaphic criteria separating the chipya or *Brachystegia* woodlands. Where chipya wooodlands are burnt infrequently or early in the dry season, conditions may exist for *Brachystegia* components to develop. The shade islands under chipya trees would provide relatively fire-free starting points and developing *Brachystegia* saplings and seedlings have been seen in such situations. In support of this theory it is rare to find mature *Brachystegia* trees in a chipya community although many chipya species are frequent elements in *Brachystegia* woodland.

3.545. Succession Following Cultivation.

Boaler and Sciwale (1966) described the successional series following cultivation and clearing of Brachystegia woodland at Lupa in south west Tanzania. Mention has been made of the large number of suffruticose seedlings of miombo species, Boaler gives a figure of 10,000 per ha at Lupa which is similar to 7,200 per ha here (see chapter 4). Many suffrutices are left (up to 40%) following a 4-5 year cultivation period, and it is this seedling source which supplies the woody regeneration, much more so than seed. There is evidence to support a return to miombo conditions, within 100 years of cessation of cultivation (Boaler and Sciwale 1966).

Four periods of woodland growth are discussed by Boaler, these are as follows. Immediately after cultivation, a dense grass cover with suffrutices and fierce fires lasts some 4-7 years. This is followed by a period of sapling growth which may suppress much of the grass cover and hence fire effects. A part canopy may form at 20-25 years. In this case it is thought that where suffrutex densities are high enough they can eliminate grass and/or it is possible that a suffrutex with a big enough root stock may produce sufficient above ground growth for its apical meristems to escape a cool early season fire. Thirdly, a period of sapling competition opens out stands of woody plants, and grasses reinvade. Lastly a balance is achieved between woody and herbaceous growth and a mature woodland results.

At Lupa and this study area, there exist three stages of species composition. Following cultivation initial species such as Terminalia sericea and Combretum zeyheri dominate and then lose prominence. Secondly, the broad spectrum species which are relatively fire tolerant such as Pterocarpus and Pseudolachnostylis regenerate; and thirdly, the more fire sensitive species such as Brachystegia and Julbernardia regenerate under the initial canopy and then dominate the community. These growth stages are illustrated diagrammatically in figure 3.24.

Several of these stages may be seen in this study area. The Combretum - Terminalia woodlands south of the Lihangwa river illustrate stage 3 with many Brachystegia and Julbernardia saplings under a Combretum - Terminalia - Pseudolachnostylis canopy. Small patches of mature Brachystegia are found which may have regenerated in fire free areas or be relicts from cultivation in the 1930s.

3.544. A Successionary Model.

From the evidence discussed above a dynamic relationship between the thicket, chipya and Brachystegia communities can be suggested. The relationships as suggested by Anderson (1963) and Lawton (1972) are also shown in figure 3.25. Anderson's ideas presuppose an edaphic difference between chipya and miombo associations. This possibility was discussed earlier in this chapter and in my opinion the two woodlands are different stages of a successionary series and edaphic differences are negligible in this and similar areas.

3.545. Other Vegetation Formations.

Previous discussion has centred on the thicket and woodland formations. To conclude this section mention must be made of the grassland and scattered tree grasslands.

The grasslands of this study area are edaphically controlled and fire and cultivation will have no effect on their structure or physiognomy although they may very well affect species composition. All floodplains in the study area burn, at least in part, every year.

The scattered tree grasslands and shrubbed grasslands are affected by fire. Mention has been made of a shift to more annual grasses and forbs with an increase in fire and grazing pressure. Quantitative effects on grass structure are discussed in chapter 4.

Further, fire plays a role in preventing the wooded grassland from reverting to its probable climax, the coastal thickets of clay sand alkaline soils. These thickets described as type B3 in chapter 3.1 are xeric in character and include many of the tree species common to the open scattered tree grasslands. Terminalia spinosa is affected by fire. With no burning its seedlings tend to form dense thickets and sapling clumps although these are frequently opened up by elephant. (Rodgers, unpublished data).

3.546 Comparison with Northern Zambia

In late 1976, the Land Resources Division of the British Ministry of Overseas Development published their assessment of the land resources of Northern Zambia. This resource assessment contains an analysis of the soils and vegetation of the region (M.O.D. 1976).

The very detailed soil survey has shown no significant difference between miombo and chipya soils, viz: "Chipya-carrying soils differ only marginally from miombo soils, contrary to frequently expressed opinion", (M.O.D. 1976; conclusion 67).

"Differences between soils under miombo and chipya vegetation types were generally insignificant and showed no underlying trend" (M.O.D. 1976; page 93).

R.M. Lawton, who undertook the vegetation survey, used P.C.A. analysis to investigate site and species relationships within 206 sites using woody species only. He concluded: "The continuous spread of the samples on the graph indicates that the vegetation is a continuum. This is so, there is an overlap of species and groups of species, and the relationship between dry evergreen forest, chipya and miombo woodland is complex and dynamic." (M.O.D. 1976; page 119.)

These conclusions agree very closely with the ideas and conclusions presented in this thesis. Lawton's discussion of fire ecology and vegetation successionary trends under different fire treatments agrees well with observations I have reported here. With these new conclusions from Zambia the controversy reported for miombo-chipya soil types is now closed. Both vegetation types occur on a variety of soils within the acidic sandy loam series. Differences between them are successionary and fire induced and not edaphic.

3.6. THE CONCEPTS OF DIVERSITY, EQUITABILITY AND MATURITY IN THE VEGETATION COMMUNITIES.

3.61. Introduction.

The past decade has seen a growing interest by ecologists in the concepts of diversity, stability and maturity, eg. Krebs (1972), Margalef (1963) and a series of papers in the First Int. Congr. Ecol. (1974). These concepts aid the understanding of succession and have been used in studies on productivity, distribution and genecology. Given the variety of communities in many different stages of successional development and the frequent perturbations in terms of fire, it was thought to be of value and interest to determine values for these parameters for the ground layer communities of this study.area.

Diversity may be defined as a measure of species richness weighted by species abundance. Numerically the Shannon-Weiner function of information theory , 'H', is used.

Where $H = \sum_{i=1}^{s} - (Pi)(\log Pi)$ for all species

'Pi' is the proportion of the sample belonging to the 'ith' species, Krebs (1972).

Equitability is a measure of eveness of distribution patterns and numerically is the ratio of H : H (max) for each species in a community. In this case the Lloyd and Ghelardi function, 'E' is used where E is H/log S, H is the community diversity and S the number of species in the sample (Krebs 1972).

Stability and maturity are controversial terms and difficult to define and measure. Stability is the ability of a system or community to recover after disturbance or perturbation. Maturity is an attribute of climax vegetation and therefore should increase with time along a successional series.

Community Dominance Index (CDI) is the degree by which the community is controlled by the abundance of one or a few species and numerically is given as

$$CDI = \frac{y_1 + y_2}{\sum_{1-n} y} \times 100$$

where y, and y_2 are the abundances of the first and second most abundant species (Walker 1974).

3.62. Methods.

Data have been drawn from the computerised ground layer vegetation survey described in chapter 3.2. Calculations have been made as follows.

The index of diversity 'H' was determined from normal association analysis outputs which produces list of frequencies within associations. Data were used from the total data set for all positive associations as determined by the association dendrogram.

The index of equitability was also determined from these data. Values for the thicket community were estimated for woody species by a subjective evaluation of abundance on a 1-5 scale for all woody species recorded within the thicket on sand associations.

The CDI was calculated for each of 4 vegetation types by selecting 5 representative sites for each type from the survey data and using % frequency data as a measure of abundance. CDI and the number of species per community appear to be inversely proportional and a regression for these 2 parameters was calculated.

3.63. Results and Conclusion.

Values for diversity, equitability and CDI are shown in table 3.16 for up to 11 computer produced associations in 5 distinct vegetation types. The graph and regression line for CD1 and species number is shown in figure 3.26.

Four main conclusions may be drawn from table 3.16. Firstly the climax communities of swamp and thicket have the highest equitability ($E > 0.96$) although all values are high ($E > 0.83$). Secondly, the two climax communities have opposite diversities, very low for the swamp ($H = 2.97$) and high for the thicket($H = 4.62$). Thirdly, the woodland associations generally have low diversity and equitability values. Lastly, the swamp and woodland associations with a low mean number of species per sample site have high dominance (CD I) values.

These results may be interpreted as follows. The floodplain and woodland associations are tall grass areas with little or no small scale spatial species mosaic in the major species. Within the floodplain formation <u>Ischaemum</u> and <u>Setaria</u> dominate over large areas and in the woodlands <u>Andropogon</u> is dominant. Smaller grasses and forbs appear to be at low levels of occurrence and hence the associations show high CD1 values.

Conversely the wooded grasslands with short grasses, many small scale mosaics and many forbs have low CDI values.

As equitability is an attribute of community maturity (Margalef, 1963), one would expect climax communities to have high equitability values. What is interesting is the disparity in H values. The swamp community is an edaphic climax with a demanding environment involving seasonal flooding and heavy clay soils. Maximum diversity and equitability involves the resource, base being taken up by many genotypes as evenly as possible. For a harsh environment, fewer genotypes would be as adapted as for a more equable environment. This appears to be the case here, the swamp having few species (22) but with an even distribution pattern and the thicket with many species (118) with again a near equal resource sharing or distribution pattern. As a comparison values for diversity for a number of eastern USA deciduous forest communities vary from 1.69 to 3.09 (Krebs, 1972).

The woodland habitat has low E & H values. In the grass layer one species is dominating, leading to an uneven resource distribution and the species total is not high.

What do these values mean? The results agree with the previous choice of climax communities, in that climaxes have high equitability values. The two communities exhibit different levels of maturity as defined by Margalef (1963) in that maturity leads to an increase in biomass, diversity, stratification and individual life span, but a decrease in productivity per unit biomass. These would hold for the thicket but not the swamp, which as an edaphic climax is perhaps an anomaly.

3.64. The Effects of Fire and Grazing on Diversity Values.

Data from experimental fire and grazing plots as described in chapter 4 were used to show the effects of fire and grazing on diversity. Data are drawn from tables 4.1, 4.2 and 4.5 and 4.6. Results for 'H' are shown in table 3.17. Results are not conclusive because experiments lasted only a few years, but they do illustrate trends.

Late fires tend to reduce diversity both in the shrub and ground layers. No burning has increased diversity in the ground layer due to an influx of herbs and woody seedlings. The Woody layer shows a small but probably non significant decrease in diversity.

Diversity values from the grazing exclosures show no pattern of change. Grazing will tend to affect species composition balance in that perennials will replace annuals with a decrease in grazing pressure, but numbers of species may not be affected. The sharp rise in diversity in the Terminalia plot for 1975 is conspicuous and caused by an influx of herbs.

Kelly in Rhodesia (quoted in Walker 1974) has shown a decrease in productivity with an increase in community dominance index. Data from this study (table 4.6 and 4.7) agree with this finding.

CHAPTER FOUR: FORAGE PRODUCTION AND NUTRIENT CONTENT

4.1. Introduction

The rangeland parameters of forage production and nutrient content are important in determining animal distribution and densities within the more rigid strictures of vegetation type and water availability. Production and nutrient content are correlated and both seasonally and annually variable, they are therefore to some extent predictable. Through the use of fire levels of both production and nutrient content are controllable. Published information on these parameters for the woodland areas of Africa is scarce and often controversial. Soils, gross and microclimates; incidence, frequency and timing of fires; and different plant species will all affect production and nutrient content.

The woodland grasses are typically Andropogonae, tall, sour and generally considered as of low palatibility. Lind and Morrison (1974) quote evidence showing the Andropogonae as being inferior to other grass tribes, eg. Paniceae, in nutrient turn over. But judicious fire management of this coarse grass cover can provide good quality forage for a large part of the year.

West (1965) and Daubenmire (1968) provide a detailed review of fire effects on tropical grasslands. Bourliere and Hadley (1970) review the factors affecting savanna production.

The investigations detailed in this chapter were designed with the following objectives:

(a) to determine the effect of annual fires on the structure and floristic composition of the grass layer,
(b) to determine gross production and seasonal rates of production of forage grasses,
(c) to describe the nutrient content of such forage and its seasonal changes,
(d) to examine the role of grazing in range floristic composition and production,
(e) to examine the role of fire in controlling production and nutrient content.

As in previous chapters the overall aim was to describe these parameters and effects to allow an understanding of animal distribution and habitat utilisation and to allow the implementation of a fire management policy for the immediate study area and the Selous Game Reserve.

Investigations detailed in this chapter are presented in two sections: the field studies and analyses separated into the woodland formation and scattered tree grassland formation, and the laboratory analyses.

4.2. Limitations

Six years (1970-1975) are not sufficient to investigate floristic successional changes due to fire and grazing effects on complex communities. At best, trends in succession may only be suggested.

Difficulty was experienced in burning the short grass habitats due to the lack of fuel resulting from heavy grazing pressure and fragmentation of the annual grasses. Conversely, grazing was only detectable in the tall grass habitats, the woodlands, following burning. For this reason the effects of fire and grazing were not separated for this zone.

Production and nutrient content sampling was restricted to forage grasses and did not include browse herbs or shrubs. Above ground tissues only were sampled, no estimate was made of root production. Sampling intensity for production studies was low as grazing exclosures were required for investigation of floristic change. No attempt was made at determining optimum quadrat size or shape, a standard square 25x25cm quadrat was used throughout for floristic sampling. Two 1m square quadrats were used per area and time period for production sampling. This small sample size precluded estimating variances for production data.

4.3. Field Investigations

These included the setting up of fire experimental plots and grazing exclosures. These are located in figure 1.2.

4.31. Experimental Fire Plots.

Two sets of plots were set up in late 1968, one set in the *Combretum* - *Terminalia* tall grass woodland (chipya), and one set in the *Terminalia* scattered tree grasslands. Studies in the latter set were abandoned due to the impossibility of setting fires.

Plots consisted of early season fire, late season fire and unburnt areas, early fires being set in July and late fires in October. Each treatment area was 100m square and all 3 treatment areas were adjacent. Plot sites were chosen subjectively close to permanent tracks and in homogenous areas representative of the vegetation type. It was apparent that the unburnt plot had not burnt in the 1968 dry season, the other two plots had burnt. The unburnt area in the woodland plot was partially burnt by accident in 1970 (about 40%), this burnt portion was not sampled in later analyses. All plots were burnt in late 1974 during my absence from the study area. No further analyses were undertaken.

4.32. Grazing Exclosures.

Three exclosures were built, one adjacent to each fire plot and one in a heavily grazed area of short grassland to the north of the study area. Exclosures were built for the dual purpose of measuring above ground biomass in year one (1969) and studying vegetation floristic change in subsequent years.

The exclosures are 15m square and constructed with heavy gauge angle iron embedded in concrete and 2 inch heavy duty weld mesh. Exclosures were surrounded by an "anti-elephant ditch", one metre from the exclosure, one metre wide and one metre deep with the soil piled outside. Ditch efficiency can be judged by the fact that these have lasted seven years while two earlier less robust exclosures were destroyed by elephant within one month of er ection. In some situations ditching can lead to an alteration of soil drainage and consequent changing moisture availability for the plants under study. In this case the very hard poorly drained soils of the area would minimize such changes, but no clippings or measurements were made within one metre of the exclosure fence to reduce possible drainage effect.

4.33. Clipping and Measurement Techniques.

All plant material clippings were taken from a $1m^2$ quadrat, plant material being clipped to 1cm above ground by hand held scissors. Obvious ground litter was discarded, dead material being acceptable if joined to the plant base or root system. All clippings were packed in polythene bags and transported to the laboratory within an hour of clipping. Material was weighed, separated into grass green leaf, dry leaf, stem, sedge and forb components, reweighed, oven or sun dried to constant weight and then repacked for later analysis.

Quadrat positions within plots were chosen by random numbers from a numbered grid of squares of 1.25m square. Quadrats were placed centrally in the selected square. Quadrats outside exclosures were placed at random within subjectively chosen localities. Such quadrat sites were marked to prevent reuse.

Techniques of plant measurement, such as % frequency, density and cover were standardised and followed those described by Brown (1954) and Milner and Hughes (1968).

4.34. Investigation of Fire Effects.

4.341. Tall grass woodlands.

Ground layer species frequency values were determined by the use of randomly placed 25cm square quadrats. Species presence was noted for each of 100 quadrats within each of the treatment fire plots. Note that the early burning plot acts as a control in that the surrounding area is early burnt as a matter of management policy. Field data wee entered in tables and % frequency of occurrence totalled for each species. The first analysis was carried out in April 1969 (peak flowering period) and the plots were reanalysed in April 1973. Results for each plot and each period are shown in table 4.1.

Woody seedling, suffrutex and shrub species frequency and density were determined by the total counting of individuals within ten 10m square plots per fire treatment plot. Small plots were located randomly on each sampling occasion. Results are shown in table 4.2 for the first analysis in late December 1969 and the second analysis in late December 1973. December was chosen as small woody plants were easily seen amongst the short green grass. Note that the unburnt plot had not been burnt for 2 seasons at the time of first analysis and so initial densities are considerably higher than those of the burnt plots.

Seedlings, suffrutices and shrubs above 25cm in height were measured as to height class in 25cm classes up to 2m. Results are shown in table 4.3.

Ground cover values were determined by an aerial pin projection technique as described by Brown (1954). 10 frames of 20 points were used per analysis time and site. Results are shown in table 4.4.

4.35. Investigation of Grazing Effects.

4.3511. Scattered tree short grasslands.

Both short grass habitat exclosures were used and as their initial and final species composition differs, results are shown separately. Plant species composition as indicated by % frequency was determined by recording species presence in each of 100 $25cm^2$ quadrats inside and outside the exclosure in April 1970, 1971, 1973 and 1975. Results for both exclosures are shown in table 4.5.

4.36. Investigation of Plant Production.

Clipping of different quadrats took place at monthly intervals in the grazing exclosure in the Terminalia scattered tree grassland habitat from November 1969 to October 1970, and at less frequent intervals in other grazing exclosures, fire plots, and other grassland habitats throughout the study area. Only one year's intensive measurements were taken as the exclosure plots were required to be free from both human and animal grazing to show species composition change. All woody growth was removed from the grazing exclosures before clipping commenced. Two quadrats per month were clipped in the main exclosure and two or more for other sample areas. Results for each quadrat were combined after drying and separation and weighing. Mean values only are given in the results in this thesis. Monthly growth increment quadrats were also used in the Terminalia exclosure. The same two quadrats were clipped to a uniform height of 5cm above ground every month from November 1969 to October 1970 to show the monthly growth increment or yield under an intensive clipping (simulated grazing) regime.

Data for the Terminalia grazing exclosure are given in table 4.6. Biomass or standing crop production is expressed as grammes dry matter per metre square (gm dm/m^2). Rainfall as measured at the research centre, a distance of 3km, is given in mm for the 30 day period prior to clipping. The linear relationship between plant growth and rainfall is shown in figure 4.1. Production and monthly increment results for each component of the grass layer is shown graphically in figure 4.2.

Data for the long grass woodlands exclosure are given in table 4.7 and figure 4.2. These results cover a 12 month period following burning in August 1970. Data for other sites in the study area are shown in table 4.8 where single values only are given, this is at the time of estimated peak production.

4.4 Laboratory Analyses

4.41. Investigation of Plant Nutrient Content.

Grass samples from many different growth stages, species and habitats have been analysed for nutrient content. All samples have been analysed by the Chemistry Section of the Central Veterinary Laboratories, Dar es Salaam, using standard analytical techniques. Samples for analysis were taken from the productivity clippings or collected especially in the field. All samples were sun or oven dried before despatch for analysis.

All samples were analysed for crude protein and crude fibre content. Many of these were further analysed for mineral (calcium, phosphorus, magnesium and copper) content. A few samples received full proximate analysis for crude protein, crude fibre, minerals, ash, fat and nitrogen free extract. Emphasis was placed on crude protein and crude fibre analyses as these are the two most seasonally variable nutrients in total content. Protein content alone is a commonly used indicator of nutritive value, (French, 1959, Long, Thornton and Marshall, 1969).

Table 4.9 gives data showing the seasonal variation in protein content for the monthly clippings from the Terminalia grazing exclosure. Total available protein as gms/m^2 is also shown for each month. These data are shown diagrammatically in figure 4.3. Similar results are shown in table 4.10 and figure 4.4 for the tall grass exclosure.

Table 4.11 shows full proximate chemical analysis for different grass species at different growth stages. Table 4.12 shows details of mineral analysis. Appendix 5 to this thesis

discusses the relationship between soil, forage and animal tissue mineral content for this study area.

4.42. Investigation of fire effects on plant nutrient content.

Forage samples have been collected from the fire treatment plots in the tall grass woodlands. Samples were separated into grass leaf and stem and analysed for crude protein. Figure 4.5 shows the change in protein content of grass leaf following burning over 120 day period.Calendar dates of burning are not considered but they vary from late July to early December from 1969 to 1971 and include several different grass species.

As there is virtually no regeneration following burning in the short grass areas until after the first rains, the question of fire effects on nutrient content has not been considered.

4.5. Discussion

4.51. Effects of fire on plant species composition, structure and ground cover, in the tall grass woodlands.

The time period since establishment of the fire treatment plots was not sufficient to show major changes in grass species composition, table 4.1. The late burning plot could be considered as tending towards species reduction, a trend also described from Zambia, in the Ndola fire plot (Trapnell, 1957). Chapter 3.6 showed a small decrease in plant species diversity in the late burning plot.

The unburnt plot has shown no real change in grass species composition, but an apparent increase in herbaceous and seedling material. Macrotyloma maranguense, a spreading herb which scrambles over the grass layer, accounts for much of the increase in forb content.

Shrub and seedling composition and density show marked changes between the three treatments, table 4.2. The early burn plot maintained the statusquo with the shrub layer being partially dominated by *Combretum*, *Terminalia* and *Lonchocarpus* species, but a wide range of species is present in the plot. Shrub density remained the same. The late burn plot shows a marked decrease in shrub and seedling density and a decrease in species diversity. *Terminalia sericea* increased in dominance. *Terminalia* here grows in clumps averaging some 80cm in height, which regenerate after burning each year. The 80cm height is reached some 2 months after burning and there is little vertical growth for the rest of the year. Difficulty was found in determining which were seperate plants and which were multiple shoots of one plant. The unburnt plot showed an increase in shrub density especially of *Combretum zeyheri* but also an influx of thicket pioneer species, eg. *Dichrostachys*, *Markhamia* and *Commiphora*.

Table 4.13 shows density data for similar fire treatment plots from other published studies on the African woodlands.

Height distribution classes of seedlings and shrubs, table 4.3, illustrate the development and growth of woody material in the unburnt plot. The dominance of the 50-100cm class in the late burn class in due to the uniform growth of regenerating

Terminalia seedlings described above. The decrease in bare ground due to leaf litter and falling grass stems in the unburnt plot is clearly shown in the ground cover data, table 4.4.

As was discussed in chapter 3, it is clear that in the absence of fire, miombo type vegetation becomes more and more dominated by woody growth until eventually the grass layer is excluded and a thicket type is formed. The results given here, albeit over a short period of time, support this conclusion.

Several grass species show different degrees of tolerance to fires. There is evidence that *Themeda* and *Hyparrhenia* spp. pastures are maintained by frequent burning, (Brockington, 1961). *Bothriochloa* sp. are aromatic and rarely utilised by wildlife in any but the youngest growth stage. Where grazing pressure on other species is high and fires are common, *Bothriochloa* spreads rapidly. In the Kruger National Park,a fire prevention policy has been introduced in selected areas to eradicate this unpalatable species, (Brynard, 1965).

Chapter 3.4 made mention of the loss of valuable grazing species such as *Panicum* *infestum* and *Urochloa* by the removal of shade trees by late season fires. This removal can be accelerated by elephant activity, (Rodgers, unpublished data).

4.52. Effects of grazing on plant species composition.

Table 4.5 gives data from two seperate sties of different initial species composition. The two sites show similarities in their response to grazing exclusion but also some apparent contradictions. Basically there is a decrease in grass species variety (especially annuals) and a tendency to domination by one or two perennial species, Digitaria milanjiana and Panicum infestum on one site and Eriochloa and P. massaiense on the other. The apparent reduction of Dactyloctenium and tremendous increase of Sporobolus outside the second exclosure is difficult to explain. Also difficult to explain is the increase in herb and sedge frequencies from one site or enclosure and not the other. Part of this due to an influx of Commelina species in one plot. Blepharis, a tough spiny herb not selected by grazing animals, seems to disappear with exclusion from grazing.

Although not directly measured, grass cover value appears to increase with exclusion from grazing.

The results give the impression of great variability and apparent trends of species, diversity value and annual grass content are certainly not significant. It would appear that a longer time period than 5 years is necessary to show real changes in species composition.

4.53. Plant production and biomass.

Data on primary production for the woodlands of Central Africa is extremely limited. There is some data from West African woodlands and Malaisse and co-workers at Lubumbashi, (Zaire) have accumulated much data on tree/shrub production but little on the grass layer (Malaisse, 1975; Freson, 1973). Table 4.14 lists comparable data from other published studies. Values of 360gms/m^2 for the tall grass sward of this study, table 4.7, are low for tropical grasslands but compare well with similar woodland areas of similar rainfall patterns.

The linear relationship between plant production and accumulative rainfall has been described by Khan (1970), Walker (1974) and is discussed briefly by Phillipson (1975) and Bourliere and Hadley (1970). Such linear correlations allow the prediction of primary production when rainfall is known.

The yield pattern of the short grass exclosures is as expected for a mixed annual/perennial sward. There is no growth until the first rain which stimulates a burst of leaf production followed later by stem and inflorescence production. Leaf production decreases as stem growth increases. Immediately after the rains there is a decrease in standing crop due to nutrient translocation of nutrients in perennials and the breakdown and withering of annual grasses. No new growth is recorded until the following rainy season.

Data for the tall perennial grass plot reveal the influence of fire. Following a clean burn, there is a rapid burst or flush of fresh leaf production up to some 10-15cms height or 20gm/m^2 dry matter. This growth occurs on slopes with some soil moisture in the complete absence of rain. Deep excessively sandy ridge top soils and hard clay soils of valley bottoms do not exhibit the flush. Following there is a period of wilting and no production until the next rains when normal growth occurs. Leaf production decreases with the onset of flowering, and there is a decrease in standing crop after the rains due to nutrient translocation and some leaf fall.

The role of grazing in increasing yield has not been closely investigated in this study, although the experimental clipping of miombo grasses at different intensities and frequencies can significantly increase annual production (e.g. Van Voorthuizen 1972). In this study the monthly clipping of the short grass sward resulted in a total yield almost equal to the unclipped plots maximum standing crop. However yield of green leaf (the portion of greatest value to grazing mammals) is considerably in excess of the maximum green and dry leaf standing crop of the unclipped plot, 173gms compared to 122gms/m^2 dry matter, table 4.6. In terms of protein yield the green grass leaf of the clipped plots average 9.1% crude protein giving an annual total of 25gms crude protein per m^2, compared with an annual average of 8.1% and a peak of 13.0 gms/m^2 for all growth in the unclipped plots, table 4.9. It is probable that a less vigorous clipping regime would have resulted in even greater yield.

Some investigators have shown a decrease in yield from burnt as compared with unburnt pastures (West 1965) although Dauhenmire (1968) presents much conflicting evidence. A common case is fire reducing individual plant size (eg. height and leaf area) but an increase in tillering resulting in normal rates of production. Weigert and Evans (1970) consider that the measurement of peak standing crop gives an artificially low value for total production due to the continual break down and loss of matter in annual swards. This fact and the unknown amount of grazing by small rodents and insects will have depressed estimates of plant biomass given in this chapter. Bourliere and Hadley (1970) present evidence suggesting a +25% correction factor may compensate for these losses.

4.54. Plant Nutrient Content.

There are a great many papers published on the nutrient content of East and Central African forage grasses but very few have readily comparable data for growth stage, season, plant components or species or ecological types, (eg. Stent 1933;

Bredon and Horrell 1962; Bredon and Wilson, 1963; Dougall, 1963; Dougall et al 1964; Naik 1967; Lawton 1967; Field 1968; Long, Thornton and Marshall 1969; and Taerum 1970).

It is readily agreed that plant species is of little importance in determining plant nutrient content; plant component and growth stage of much more importance, (French 1959; Worden, Sellers and Tribe, 1963). In the African context an ecological division into annual and perennial classes or tall and short grasses or sour or sweet veld can be useful in assigning grazing values. However, while the same plant part of two species may have identical nutrient contents the physical properties of the grass, such as needle or broad leaf, leaf stem ratio, spiky awns etc. may affect palatability. Chemical properties such as aromatic leaves and other secondary plant compounds may also affect palatability.

Tables 4.9 and 4.10 illustrate the differences between stem and leaf fractions in protein content and table 4.9 shows the effect of clipping in maintaining higher protein values. These tables also serve to show the very low levels of protein available in dry season forage in African range land. Table 4.11 shows the similarity in nutrient content between the same growth stages of different grass species of the same ecological type.

The mineral content of several grass samples is given in table 4.12. Levels of calcium, magnesium and copper fall within recommended feeding levels for domestic ruminants as detailed by Maynard and Loosli (1971) and Davis and Skidmore (1966). Phosphorus values are low in comparison with reccomended levels (Naik, 1965; Davis and Skidmore, 1966). Appendix 5 discusses the question of mineral content of forage and animal tissue and points out that forage phosphorus values are low enough to cause deficiency diseases in cattle and that wildebeest blood phosphorus levels would be fatal in cattle. Russell (1961) mentions that in soils of high sodium content, plant phosphorus uptake is reduced, this could well be the case here, see chapter 2.2.

4.55. Fire Effects on Forage Nutritive Values.

Like most aspects of tropical fire ecology (Phillips 1965), the question of the value of the fire induced flush is a source of controversy (West 1965; Daubenmire 1968). The miombo woodland perennial grasses show this characteristic property of dry season post burn flush. The cause of the flush has been variously attributed to increased temperatures, high ash mineral input, increased microbial activity and dew reaching the growing points. One more plausible theory is that the flush is due to the removal of dead litter and senescent stems and leaves which otherwise have an inhibitory effect on the apical meristem, (Mes 1958; Daubenmire 1968).

A slightly similar but more recent theory is that removal of senescent tissue releases the plant from hydrostatic tension allowing scarce nutrients and water to be used for new growth, (Agnew. 1974, pers. comm.). This theory fits with evidence from grass cutting (e.g. the mowing of road side verges in the dry season) which also stimulates fresh growth in the dry season, but without removing dead litter or stem bases.

As is shown in figure 4.5 the protein content of the post burn flush is extremely high, occasionally reaching over 20%. Such growth has a higher protein content than the green growth of unburnt leaf at the start of the rains, (this study, and Mes 1958). Using a policy of small patch work burns in the early and middle dry season it is possible to provide a continuous supply of high protein forage for grazing animals. Despite a low yield at this season the low grazing intensities in the woodlands prevent excessive damage on these burnt areas. As the dry season progresses the new growth on upper slopes begins to wilt and only those grasses with access to shallow water tables continue growth.

West (1965) and others, eg. Staples (1945) consider the practice of early burning to be detrimental to the grass cover, and that individual grass plants suffer from loss of "physiological vigour". I suppose that their term "physiological vigour" is analagous to "competitive ability". Such authors advocate a late burn, just after the first rain. Figure 4.6 gives a diagrammatic picture of the effects of early and late burns on the grass and its nutrient cycle. It is apparent that too late a burn will destroy new growth formed with the root stock nutrient reserves. An early burnt plant is subject to wilting which if prolonged can also harm to the plant. Daubenmire (1968) and Phillips (1965) consider that the prolonged dry season, low annual rainfall, and chance of dry cold season post burn frost are important damaging factors for early burning in Rhodesia, the area of West's and Staples' work. They consider, however, that in the higher rainfall areas of Zambia and Tanzania an early burn can be preferable to a late burn.

An overall discussion of fire effects, including vegetation change, effects on grass production and animal feeding and distribution patterns is left until chapter 9 when a burning policy is put forward.

PART TWO

Chapter 5 Animal Population Census

Chapter 6 Animal Species Distribution Patterns

Chapter 7 Feeding Ecology and Nutrition

Chapter 8 Population Parameters

CHAPTER 5. ANIMAL POPULATION CENSUS

5.0. Introduction.

The estimation of animal population abundance was one of Game Division's major requirements for this study. Such estimates were needed for consideration of possible population exploitation trophy hunting and cropping. As the study was designed to be a long term project then repetitive abundance estimates could determine population growth and performance patterns. Further, if the census technique could estimate the distribution of abundance spatially and temporally then questions of seasonal habitat occupance and movement could be answered. It was for these reasons that the census operations became one of the most important aspects of the study, both in terms of time and energy expended and in the quantity of data collected.

There are few, if any, really satisfactory methods of assessing the abundance of wild animals. "Difficulties and limitations with current methods include biases, substantial variability in time and space, their suitability for different habitats and animal species, and cost", (Eberbardt, 1968). Within East Africa over the last decade there has been a major dichotomy in census methodology into aerial census and ground census techniques. Despite the increasing use of aerial techniques in the open savanna areas of Kenya and northern

Tanzania, I chose ground census techniques for the Selous, due to the difficulties of obtaining an aircraft in 1967/68 and to earlier ideas that aerial census was not practical for woodland communities. In addition, ground census techniques enable one to correlate animal presence to environmental variables on a much finer scale than from the air. Later in the study I used aircraft for reconnaissance, counting the floodplain and, in 1976, a 3% sample census of the whole Selous Game Reserve (see below).

Ground census techniques can include index counts, total or sample counts, line transect or quadrat counts, foot or vehicle counts, and random or systematic counts. In the mid 1960s there were few published census studies involving ground techniques for African mammals. Most such studies were total counts of small areas such as Nairobi National Park or Ngorongoro Crater, (Turner & Watson, 1964; Foster & Kearney, 1967).

The College of African Wildlife Management at Moshi, Tanzania was advocating the use of line transects systematically placed, based on the original King census methodology, (Robinette & Hemingway, pers. comm.). I chose the same technique but preferred the use of right angled sighting distances (Webb, 1942) which are more suitable for vehicle counts. Over the last 10 years the basic mechanics of collecting ground census data have scarcely been altered, but a large and controversial, literature has built up dealing with the analysis of such data. Major papers are Eberhardt, 1968; Gates, et al, 1968; Gates, 1969; Robinette et al, 1974; Hemingway, 1975; Hirst, 1969; Seber, 1974; Burnham & Anderson, 1976; and Kovner et al, 1977. This controversy is discussed at length in appendix 9.

Two distinct phases of census operations existed in this project. The first, from early 1968 to mid 1972 when transects crossed the whole of the study area for each month of the year. Objectives here were to estimate densities in each of the habitats for each season for all major ungulates as well as to determine overall population abundance. No formal censuses were run in 1973, and the second phase, from 1974 to the present time, consisted of census operations restricted to the middle rains (March, April) in the scattered tree grassland habitat only. At this time over 95% of the study block's wildebeest, zebra and impala population are found in this one habitat (Rodgers, 1970). These census operations were designed to estimate population abundance. This chapter considers only the total abundance estimate; details of habitat occupance are discussed in the next chapter.

Systematic transects were chosen so as to ensure an adequate coverage of the study block with few transects and to allow counting along a permanent grid (1 mile sections) of known vegetation and habitat variables. Formal assumptions underlying census theory state that sampling units must be randomly placed to allow the use of statistical analysis of census data. However, provided the sampling units are randomly placed in respect to animal distribution patterns instead of randomly placed across the study surface, then the sample units can be considered a special case of the random situation and statistical analysis can be carried out accordingly (Jolly pers. comm., Seber, 1974 and Caughley, 1977).

At the start of this study, two straightline bush tracks were available as line transects, one running north-south through the scattered tree grassland (Mwende road) and the other running south west across the major habitats (Kizunda road). Mwende road was used as a baseline transect and at first three and eventually five transects were marked out running from Mwende and parallel to the Kilunda road.

These transects are marked on figure 1.2 and are named (from north to south) as follows:

NAME	TOTAL LENGTH		SHORT GRASS AREA LENGTH		
Lihangwa transect	49.6km	(31 miles)	20.0km	(12½ miles)	
Kariokoo transect	14.4	(9)	14.4	(9)	Opened in 1971
Kilunda transect	40.0	(25)	14.4	(9)	
McLaughlin transect	9.6	(6)	9.6	(6)	Opened in 1971
Chimbiriri transect	28.8	(18)	0	(0)	all woodland

Malemba transect	20.8km	(13miles)	0km	(0miles)	all woodland
Mwende transect	40.0	(25)	40.0	(25)	baseline transect.
Totals	203.2km	127miles	98.4km	61½ miles	

The first pair of figures are total lengths and the second pair are lengths in the scattered tree grassland habitat.

5.1. Field Methods.

During the study the transect system was covered by vehicle except for some rainy season months in 1968 and 1969 when a foot coverage was made in the woodland habitats. Only vehicle counts are considered here. Vehicle censuses were run in the early to mid morning, using a team of four: driver, front seat observer/recorder and 2 stand up rear observers in an open Land Rover pick up. At least one complete coverage of the transect system was made per month and usually two or three in the 1968 to 1972 period. In later years three or four complete coverages were made in the census period of March-April each year.

Counts were run at a speed of 20 to 30 km/hour, slower in areas of game concentrations. Observers, equipped with binoculars scanned a forward arc of 90° each side of the track.

The vehicle stopped on sighting an animal group, individuals were counted and their position noted. The vehicle then moved forwards to a point where the animal group position was judged to be perpendicular to the track, and the right angle sighting distance estimated or measured. Details of the observation would be entered on specially prepared forms, (an actual field example is shown in table 5.1). The forms required observations of the following data:

1) Transect data:
   - a) transect name, eg. Kilunda,
   - b) date,
   - c) observer crew names,
   - d) time start and finish,
   - e) weather.

2) Observation data:
   - a) observation number (1,2,3,4 etc),
   - b) mile segment of transect (eg. 0-1 or 5-6 or 17-18),
   - c) side of track, left or right,
   - d) perpendicular distance from animal to to track,
   - e) species of animal observed,
   - f) number of animals in group observed,
   - g) notes on group, eg. number of calves or sex age composition for rare species,

h) habitat notes relating to the point of observation, eg. fire conditions: burnt, burnt and regenerating, unburnt; grass height; colour, water proximity etc.

At the end of the day, the number of groups and number of individuals of each species observed were totalled and entered on each form.

Figure 5.1 (a & b) illustrates the method of measurement of perpendicular sighting distance, labelled 'y' in the diagram For animal groups, distances were measured to the group centre. Measurements were estimated into 50m classes and estimates frequently checked by using a "Wild 0-1500 feet rangefinder" or by pacing. The 1500 feet rangefinder was adequate, very few observations being made at distances greater than 350 metres. All species encountered except small mammals, lesser carnivores, primates and species which flushed rather than being freely sighted such as suni and duiker were observed. Observations at all distances were recorded; there was no cut off distance point.

All transects were split unto mile long segments which were marked by painted tin markers on prominent trees. Their use is fully described in the next chapter. Observations were assigned to left or right side of the transect, so as to maintain a check on burning conditions (the track often acting as a fire break) and to provide two replicate counts per transect if needed for later analysis.

Transect lines were cut as straight as possible, obstacles being removed so as to ensure that travel distance provided an accurate measure of actual transect length. Transect counts were made from both directions (but not on the same day), so as to obviate observer preference for viewing any particular side or direction. On sighting large groups of animals, all observers assisted in the counting, and the most frequent count total taken as correct. Very large groups were counted in fives or tens as animals were not "overly tame" and prolonged observation was not always possible. Groups were not followed off the track to get better estimates as it was thought that this may disturb animals further along the transect.

On occasions difficulty was experienced as to what constituted a group, especially zebra in the rains, as some groups could be spread over a large area, or loose aggregations of groups could occur, (Rodgers, 1977b). The standard criterion applied was that if animals bunched together on disturbance, they were a single group. Mixed species assemblages were recorded seperately.

5.2. Analytical Methods.

Data analysis was undertaken separately for each species and each month for the period 1969 - 1972. Later, 1974 - 1977, counts were analysed on a yearly basis. As this chapter deals with total population abundance, only rainy season results for the scattered tree grassland habitat are given, as this includes over 95% of the impala, wildebeest, zebra and warthog populations. Less frequent results for other species are also shown.

Use of ground transect sampling techniques and the statistical analysis of data obtained from such techniques depends on a number of assumptions being met or approximated. Assumptions used in this case (Gates et al, 1968) are:-

1) The animals are distributed uniformly and independently (randomly) over the study area,
2) The sighting of one animal is independent of the sighting of another,
3) No animal is counted more than once,
4) An animal is virtually at rest and its position at first sighting is the true location of that animal, i.e. it has not been startled into flight, and its flight alerts the observer to the animals presence,

5) The response behaviour of the system of the whole does not change during the course of running a transect.

Of these assumptions the latter three may be taken as being met but the first two obviously are not met in the case of gregarious animals. In these cases animals are aggregated or clumped into large herds (up to 1000 for buffalo) and the sighting of one animal is very much dependent on the sighting of another. If however the herd or group is used as the sighting unit then these groups may approach a random distribution. An extreme example of this would be where a biologist wishes to census colonial ants in a field. One would census anthills first and then from a knowledge of ant number per hill one could estimate total ant numbers. For this study the sampling attribute is taken as the group or herd of individuals, a practice which Yapp (1956) described for bird populations, I have used since 1970, and for which Kovner, Hemingway and Patil (1977) discuss the mathematics in detail. Rodgers (1977b) describes the parameters regulating group size in gregarious ungulates; this paper is included as appendix. 7

Analysis uses four parameters; distance sampled (total transect length L), number of animal groups seen (n), mean group size ($\bar{g}$) and mean perpendicular sighting distance ($\bar{y}$). The parameters of mean sighting distance and transect length can give the area censused (a) which is related to study area size (A) by the sampling proportion (P) where $P = a/A$

These parameters were calculated as follows:

Mean perpendicular sighting distance $\bar{y} = \frac{\Sigma y}{n}$

Mean group size $\bar{g} = \frac{\Sigma g}{n}$

(single animals, i.e. $g = 1$, were included in the calculation of mean group size).

There is considerable evidence to show that mean strip width (or strip visibility) is a function of sighting distance. In this case, for animals which are sighted, not flushed, in wooded habitats and using a perpendicular sighting model, it can be taken that

Strip width (SW) $= 2\bar{y}$ per side of transect

or SW $= 4\bar{y}$ for the complete transect

The rationale behind this statement is explained in appendix nine.

From this expression the following can be determined:

$$a = 4\bar{y}L$$

$$P = \frac{4\bar{y}L}{A}.$$

Density of groups $d = \frac{n}{a} = \frac{n}{4yL}$

Density of animals $D = d\bar{g}$

Number of animals per study area $N = DA$

Eberhardt (1968) stresses that the estimation of sample variance depends on a random distribution of the sampling unit in space (the horizontal plane of the study area). Such a distribution can be ascertained by testing the observed distribution against a Poisson distribution. Sets of data were so checked for several months in the census period using wildebeest and warthog figures. For this test the sampling space is taken as the mile segments along transects over all transects for the period in question. Such segments were tallied as per their occupance by 0, 1, 2, 3 etc groups of wildebeest and warthog. This occupance distribution was then tested against the theoretical Poisson distribution for that number of sightings. Comparisons were made by means of a 't' test. Two example results are shown in table 5.2, and it is seen that distributions do approach the random, there being no significant difference from the Poisson distribution. Such differences as do occur, tend towards a clumped distribution pattern, probably due to local concentrations around favoured resources.

As animal group spatial distributions can be considered random, estimates of variance can be determined. The estimator for the coefficient of variation (C) as described by Hemingway (1975) has been used, where:

$$C = \frac{\sqrt{\frac{dA}{P} \times g^2(1-P) + n\left(\frac{3Z + g^2}{n} + Z\right)}}{dAg}$$

where Z is an expression $\frac{3v(1-P)}{n}$ and v is group size variance

Eberhardt (1968) states that with a random distribution, the variance of the density estimate is proportional to the square root of the number of objects counted in the survey (n). Hemingway's variance estimator contains n in the denominator and it is clear that the efficiency of the method (as regards precision) depends on the number of sightings made. This fact is important in the discussion later in this chapter and in appendix nine.

Census data have been analysed by computer (using the computer facilities of the University of Dar es Salaam). An example of a computer input and output is shown in table 5.3. This example is for warthog for 1972. The area of the scattered tree grassland habitat is 432km^2 and 1102km of transect were run that season and 596 observations were made. Output parameter 'E' is the ratio of $\bar{y}^2$/var y used by Hemingway as a determinant parameter for choosing strip width model. Its use is described in appendix nine.

Data have been analysed in detail for four species (wildebeest, impala, zebra, warthog) for each year, for each month (1969 - 1972 only) and for each transect within each sample period.

Sable, hartebeest and elephant data have been analysed by hand for the period 1969 - 1972 only. Estimated densities for other species are mentioned briefly.

5:3 Results

5.31 Major species

Estimates of density are shown for four species for the years 1969 to 1976 in table 5.4. These estimates are also shown graphically in figure 5.2, and 1970 - 1976 values shown here:

Species	1970	1976
Wildebeest	22.1/km^2	27.2/km^2
Zebra	7.9	16.2
Impala	27.5	28.7
Warthog	4.7	9.4

The estimates indicate growing populations of zebra and warthog and, since 1971, a fluctuating but relatively constant population of wildebeest and impala. These figures agree well with subjective impressions of animal population size made by persons familiar with the eastern Selous Game Reserve. As this area of the Selous was gazetted as full reserve in 1961 (albeit a Game Controlled Area since 1955) and anti-poaching measures were strengthened in the early 1960s it is understandable that populations would rise. Wildebeest, (and, to a lesser extent, impala) suffer considerable mortality due to anthrax (a fatal bacilliary disease) and it is possible this has checked further population growth. This topic is discussed in later chapters in more detail, see chapter 8 and 9.

Detailed census data are shown for individual species: wildebeest, zebra, impala and warthog, in tables 5.5 to 5.8 respectively. These tables give data on number of observations made, transect length traversed, mean group size, mean sighting distance, density, population size and 95% confidence limits for each year. Figures show an increase in transect coverage from 1969 to 1972 and a relatively constant coverage from 1974 to 1976. Confidence limits reflect the intensity of sampling, limits of less than 10.0% being achieved for coverages of 1000km and over. Mean sighting distances fluctuate slightly from year to year, although in no case significantly (using a 't' test to investigate differences between means). Sighting distances have a tendency to increase in later years.

It is not known if this is a function of observer estimation, a decrease in vegetation cover due to increased burning or to greater animal flight distances due to increased shooting and hunting programmes. Population size estimates are computed for the 432km^2 scattered tree grassland habitat of the study block, which is assumed to contain the total study block populations in the rains.

Densities for individual months are of interest as they show the pattern of habitat use; eg. zebra numbers building up from January to a peak in March/April followed by a decline in May as animals leave the open habitats for the woodland. This pattern is described in detail in the next chapter. Data for monthly densities are shown in table 5.9.

As is to be expected different transects show different density patterns for different species as the habitats are not identical. Mwende transect for example, which is relatively open with low levels of woody cover favours wildebeest and warthog, whilst impala densities are consistently higher along the more wooded Kilunda transect. Individual transect densities are shown in table 5.10 for two representative months. Average density figures for each mile segment of the Kilunda transect are given in chapter 6.

5.32 Other species

Less detailed information is available for elephant, hartebeest and eland from the transect census data (table 5.11). Estimates of population size are available for some other species by a variety of techniques. These may be listed as:-

(a) Sable antelope. Assuming sable antelope to have the same sighting characteristics as Lichtensteins hartebeest, (i.e. body size, group size, habitat preference, flight behaviour), then as the hartebeest population can be estimated by transect data, an estimate of sable population size can be made by use of a ratio of hartebeest to sable sightings from transects, vegetation transects and other studies in the woodland habitat (Caughley, 1977).

(b) Buffalo. Large herds of buffalo were plotted on maps and by watching movement patterns, information on the number of buffalo herds could be obtained. Estimating herd size could give a measure of population size. Small groups of males form a very insignificant part of the buffalo population in this area.

(c) Lion. Details of a lion census are described in Rodgers (1975) and this paper is included in this thesis as appendix number 6.

(d) Common duiker. Density estimates were obtained by a series of foot transects by C.A.W.M. students in 1970, (Hemingway, pers. comm.).

(e) Waterbuck. Waterbuck are restricted to a small area in the vicinity of Kingupira forest. Total counts have been made from 1968 to 1976, (Rodgers, 1970, Callendar, 1974).

(f) Hippopotamus. An estimate of population size was obtained by counting animals at dry season water holes.

Population details for these species are shown in table 5.12.

5.4. Discussion.

5.41. Census Methodology.

5.411. Choice of methods.

The reasons for choosing ground census techniques instead of aerial techniques have been stated briefly: the non availability of aircraft prior to 1970, my non familiarity with aerial census, the need for a fine scale of census unit to correlate with environmental parameters and preferably such coverage repeated continually over a known route, and the past belief that aerial census is not practical for low density game populations in woodland habitats. Added to this there was a need to develop a census methodology that could be used by Game Division personnel in other woodland reserves and game areas. The College of African Wildlife Management was teaching students the basis of King census methodology and it seemed advisable to use similar methods for this purpose.

Within the spectra of ground census techniques, total counts were impractical due to the large areas involved; quadrat counts were excluded due to the difficulty of accurate counting of blocks in woodland and to the difficulties of marking quadrat boundaries in rough and wooded terrain. Transect techniques, those chosen, may be divided into three classes as follows:-

(1) Prior mapping of visibility profiles along transect routes.
(2) Fixed boundary transects.
(3) Open boundary transects.

Visibility profile mapping was used by Lamprey in Tarangire Game Reserve, (Lamprey, 1964). This method has advantages in use with short transects of relatively homogenous vegetation cover, and animals of similar size. Where vegetation cover changes drastically (as in a seasonally burnt environment) and animal sizes vary from warthog to elephant, the method would appear to have serious draw backs.

2) Fixed boundary transects are easier to use than those of open or idefinite boundaries, but they depend on habitats with little or no obstruction to visibility, i.e. open plains, or transect widths will become very narrow and hence inefficient. With alternating patches of dense woodland and wooded grassland and with grass height up to 2 metres then a fixed transect width would of necessity be of the order of 50 metres or less to avoid missing animals. As some animal species are very rare, the exclusion of sightings by the adoption of a fixed boundary system 'wastes' considerable amounts of data. Caughley (1977) discusses this and the open boundary methods and states:

> "Data from transects of indefinite width are analysed differently from counts on transects of fixed width, and require additional information, of which estimates are subject to error. As such the decision to use transects of fixed or indefinite width must balance the simplicity and reduced experimental error of the first against the added precision accruing from the

greater number of animals counted by use of the second. In general the second design is more apprppriate at lower densities."

For this study transects of open boundaries (or indefinite width) were used.

c 5.412. The parameters of the open boundary transect method.

The use of this depends on several factors:-

(1) Sampling design
(2) Sampling intensity
(3) Animal sighting and enumeration
(4) Transect area, a combination of transect length and width.

Sampling design in this study was based on systematically placed transects. Justification for such a system rather than random transects has been given above. Caughley (1977) discusses this problem at length and concludes, "A confidence limit calculated from non-random samples may be invalid but it is seldom much different from limits calculated from random samples. So long as the siting of systematic transects is not biased with respect to what lies on the ground, the axioms of the statistical model are not grossly violated."

With the exception of the Mwende transect which runs through the centre of the longest (North South) axis of the scattered tree grassland habitat, all other transects run at right angles to the major topographical and vegetation variation. Transects were spaced 5 miles (8km) apart and did not follow repetitive pattern in the environment.

Sampling intensity within the scattered tree grassland habitat of 432km^2 was based on a transect total length of 98.4km. For wildebeest with an approximate average strip width of 0.50km this gives a sampling area of 49.2km^2 and a sample fraction of 11.4% per single transect system coverage. I have taken the view that repeated transect coverage per sampling period (month, season or year) directly increases the sampling fraction. Justification for this comes from the fact that although the same area of ground is covered (and space is the sampling unit), the sampling attribute - animal presence within this space, is not the same, and within a small time period this attribute varies, perhaps randomly, for a single transect. In other words, for repeated counts along one transect I am not counting the same animals. For example in February 1972 repeated counts of wildbeest along Kilunda transect showed

78, 4006, 91, 373, 271 and 159 animals, (mean = 230 animals). For warthog, a more sedentary species, equivalent totals were 67, 32, 26, 24, 32, and 43 (mean = 37 animals). Repeated transect coverage gives a higher sampling fraction. When monthly data are combined into seasonal figures, the sampled area can in fact exceed the study area. During confidence limit calculation, the computer was programmed to use a maximum of a 90% sampling fraction.

Animal sighting and enumeration is a function of observer efficiency, provided the animal is in a position to be observed (i.e. distance and non interference by vegetation obstructions to vision). The usual precautions were taken to increase efficiency: silence, slow vehicle speeds, trained observers, front seat and rear observers, early and mid morning counts when observers are not over tired etc. It is noteworthy that 2-tier observers, front seat sitting and rear standing are more efficient than just one tier. On many occasions the front seat observers saw animals missed by the rear observers and vice versa.

Sample area or transect area is computed from the parameters of transect length and transect (strip) width. Transect length can be determined by pacing, vehicle mileometer or from 1:50,000 maps. Transects should run as straight as possible to avoid over estimation of length and inaccuracies due to wrong perpendicular distance estimation. Transect width is more difficult to estimate in the open transect model. Methods are controversial and are discussed in detail in appendix nine. Variance estimators are also discussed.

5.42 The results.

5.421 Other census methods

During the course of this study I had the opportunity to use helicopters for wildlife research and management exercises (Tanzania Police Air Wing, Bell 47 helicopter). One such exercise was a wildebeest census for which I was assisted by Gordon Matzke, (Matzke, 1976). The exercise took one morning in March, 1974 and covered 10 equi-distant transects of width 0.3km across the study area. Results showed a mean density of 22.9 wildebeest/km^2, a figure within the 95% confidence interval of the 1974 ground census estimated density of 27.6 ± 17.7%. The helicopter survey appeared to undercount large groups and miss single males.

In August 1976, Douglas Hamilton, Rodgers and Mbano (unpublished) undertook an aerial census of 76,000km^2 in S.E. Tanzania. The whole survey was based on a 3% sample count so the coverage of the research study area was minimal, with only three transects passing north south over the wooded grassland habitat and five passing over the adjacent woodlands. Population totals for several species extracted for this study area are as follows:

SPECIES	1976 AIR CENSUS	1976 GROUND CENSUS OR ESTIMATE
Wildebeest	8,938	11,730
Zebra	4,536	6,974
Impala	5,256	12,397
Warthog	1,709	4,071
Buffalo	2,848	3,500
Eland	813	1,226
Hartebeest	2,308	4,978

The aerial count figures are in all cases less than those of the ground count, but this is to be expected as the aerial figures are not corrected (Norton-Griffiths, 1974). However, the general order of magnitude is the same, especially for larger animals such as buffalo, wildebeest, and zebra.

These two census operations show similarity of results with the ground census techniques described in this chapter and help to justify density estimates for the study area.

5.422 Which result to accept.

Appendix nine discusses the use of two potentially valid strip width estimators. One such estimator (published recently) gives results some 33% higher than my estimator of $4\bar{y}$ used throughout this study. Both estimators show confidence limits of similar magnitude so neither can be preferred for investigating trends. Bearing in mind that:-

(a) My estimator of $4\bar{y}$ is easier to compute than Hemingways $(2 \pi \mathrm{MSy})^{\frac{1}{2}}$

(b) The $4\bar{y}$ estimator agrees closely with King's estimator and with empirical, or non parametric results

(c) Aerial census results show closer similarity to ground results using $4\bar{y}$ and,

(d) It is perhaps preferable to underestimate population size rather than overestimate.

I accept the $4\bar{y}$ estimator and its results as being valid.

5.423 The animal populations

The ungulate populations of the study area have been treated as if they were a finite unit. This is basically true as seasonal movements take place east to west across the drainage slope, and not from north to south in and out of the study area. Population sizes put forward in this chapter appear correct on subjective grounds and their population growth rates also appear realistic according to local knowledge and experience. Questions of biomass, population growth and population limitation are discussed in chapters eight and nine.

CHAPTER 6. ANIMAL SPECIES DISTRIBUTION PATTERNS

6.0. Introduction.

Earlier in this thesis I discussed the distribution of the four major vegetation formations: floodplain, scattered tree grassland, woodland and thicket. The introduction to chapter four stated that within the confines of these fixed vegetation types, the changes in forage nutrient content, availability and production as affected by season and fire play a major role in determing animal movements and their use of different habitats. This chapter examines and analyses these movements.

Animal movements can be investigated in different ways. The following of, or continued relocation of known individuals (on the basis of radio telemetry or distinctive colouration or markings), can give very detailed data on daily and seasonal movements and habitat use, (Leuthold, Pellew, Frame, pers. comm. 1972-1975). On a much broader scale ecological monitoring flights over large areas can assess species densities and distribution patterns and correlate these with environmental variables such as vegetation, fire and water.

Individual tracking is valuable in single species studies, but of limited application for multi-species studies involving large populations in large diverse habitats. For this reason no attempt was made to recognize individual animals in this study although estimates of lion populations in the eastern Selous were in part based on known individuals, (Rodgers, 1975), see appendix six.

Aircraft were available from 1971 and were used for extensive reconnaissance, especially in the more inaccessible areas of the Selous. No attempt was made at systematic data collection until 1976, partly due to my inexperience with the techniques and partly due to the problems of visibility in the woodland areas. In 1976 an aerial survey was made for 76,000 km^2 of south east Tanzania during the rains and again in the dry season. Detailed analysis of these surveys is not complete but broad results are partially used in this chapter.

The majority of the results shown here have been taken from the road transect counts with additional data from broad scale surveys and from much finer scale investigations. Studies were aimed at analysing population shifts and habitat selection and not at movements of separate groups or individuals. Habitats were assessed at broad levels and only rarely at small community levels. As chapter two pointed out, water is not a major limiting factor in the study area and it was considered that as water was always within easy access of animal populations, water and animal distribution correlations were of only minor importance. All animal species in the study area are surface water dependent, (unlike the Amboseli Game Reserve in Kenya, for example, where both water dependent and independent species occur, (Western, 1973, 1975)). It was unlikely therefore that different species would be affected by water in different ways. Vegetation association differences, seasonal differences and fire distribution were considered to be of major importance and investigation and subsequent analysis was directed towards these factors.

Whilst there are many studies dealing with single species distribution and habitat use patterns, viz: buffalo (Sinclair, 1974, 1975), wildebeest (Watson, 1967), topi (Duncan, 1975) cokes hartebeest (Price, 1975) and lechwe (Bell & Grimsdell, 1975); there are much fewer dealing with the total species array in diverse habitats. Studies of Mkomazi (Harris, 1970), Serengeti corridor (Bell, 1969, 1971), Amboseli (Western, 1973) and Tsavo (Cobb, pers. comm.) attempt this for the savanna areas of E. Africa and studies of Hirst (1975) and Ferrar and Walker (1974) do the same for the long grass woodland formations of southern Africa.

Such habitat - population integrated studies form a major stage in data collection for a comprehensive management policy for conservation areas. When this data is coupled with a knowledge of the means and effects of habitat manipulation then actual management of the resource can be attempted.

6.1. Methods.

Distribution and habitat selection were investigated at several different scales: A) a distribution plot for the whole of mainland Tanzania B) an aerial survey of the Selous Game Reserve and environs; C) the comparison of 4 different areas within the Selous Game Reserve; D) the transect system of the study area; and E) a detailed investigation of the miombo ridge and valley catenary system described in chapter three . Finally, animal use of the floodplains and data for the rare species distribution were briefly analysed.

6.11. Species Distribution within Tanzania.

During 1973 and 1974 I undertook a survey of the distribution of 51 major game species in Tanzania, (Rodgers, unpublished data). The survey was carried out by map questionnaires presented to Game Division and National Parks personnel, biologists and hunters, by examination of Game Division and other records and by personal reconnaissance. The survey covered the period from

1955 onwards. Distribution data were put on a 1: 3 million map overlaid with a ¼ degree, (15n.m.) grid. An example of a completed map sheet for sable is shown as figure 6.1. Preliminary results of the survey have been published by the East African Wildlife Society (E.A.W. Soc., 1977).

From the Atlas of Tanzania (Tanzania Survey Dept., 1969), vegetation types were assigned to each map square. The following broad categories were used: tall grass woodlands, short grass savanna and scattered tree grasslands, tall grassland including swamp and floodplain, short grassland, thicket and bushland, forest and finally human settlement and cultivation. In all cases the squares were described by the dominant type when two or more types overlapped on one square.

The total number of squares under each vegetation type and the number of squares of each type with and without each animal species were counted. Animal occupance for each type was expressed as a percentage of the total number of squares for the type. Forest and cultivation squares were later ignored. Distribution data for the following 16 species were analysed: sable, Lichtenstein's hartebeest, wildebeest, impala, zebra, warthog, buffalo, common duiker, and greater kudu (all found in the Selous) and roan, lesser kudu, Thompson's and Grant's gazelle, Coke's hartebeest, gerenuk and oryx (from outside the Selous).

Statistical analysis of the data was complicated by the fact that figures were not estimates from sample observations, but actual parameters for the whole population, as all squares in the population of squares were examined. However, accepting the use of sample statistics on whole population data I attempted to show any significant departure from an equal distribution amongst vegetation types for each species. Secondly I divided species into three ecological groupings based on their distribution patterns; miombo species, savanna and bushland species and widespread species. For these groupings I attempted to test for homogeneity within the species.distribution patterns.

Chi square analysis was used to test for distribution differences for each species by using a 5 x 2 contingency table for 5 vegetation types and the 2 characters of number of squares occupied and number unoccupied in each type. Tests were done on the raw number data, not percentages. But as numbers of squares in many types are large, eg. Miombo with 460 squares (see table 6.1) the figures are extremely precise and even small differences between types become highly significant. For example zebra data in table 6.1 appear to show a roughly equal distribution between vegetation types. Chi squares analysis however shows a highly significant departure from the expected values, (Chi square = 20.49, 4 d. of f, significant at $< 0.1\%$), consequently analysis was abandoned.

Visual checking of the data in table 6.1 indicated species could be arranged into the three groups mentioned above, (two species, impala and wildebeest, formed a fourth group of transitional species).

A two-way analysis of variance test was run on each of the three groups, using arc-sine transformed data. Use of anovar can be criticised on the grounds that it examines the difference between means of each row and if, for example, the same figures for sable were re-arranged and put in the roan and hartebeest rows then the mean for each species would be equal and anovar would show no difference in distribution, although the column data would show major differences. However it was thought that anovar testing could be of value in conjunction with a visual examination of the data sets.

6.12. Species Distribution within the Selous Game Reserve.

In 1976 an aerial survey of 76,000 km^2 of S.E. Tanzania was undertaken in cooperation with Dr. I. Douglas-Hamilton. The survey area comprised the Selous Game Reserve, Mikumi National Park, the Kilombero Game Controlled Area and their immediate environs. The survey data have not been completely analysed (Douglas-Hamilton, Mbano and Rodgers, unpublished data) but the following summary of techniques used to determine preliminary species distribution will suffice to understand the data presented here.

The area was split into a network of 5 n.m. by 5 n.m. squares, based on the longitude and lattitude grid. North South transects were flown along the centre of each grid square with wing strut markers delimiting a strip width of some 150m either side of the aircraft. This sample strip gave an approximate 3% sample coverage of the whole area. Rear seat observers counted animal groups seen and the front seat observer (myself) navigated, monitored flying height and environmental variables including vegetation type, vegetation cover, fire, water and topography.

Species sightings were totalled for each grid square and plotted onto maps of the survey area. Grid square totals were calculated into approximate densities by converting the 3% sample to complete coverage and dividing by the area of each grid square in km^2. Data was amalgamated into 4 square blocks and the blocks shaded for easy visual assessment of changing density and distribution patterns. The survey was run twice; once in the rains, February to April; and once in the dry season, August to September; only the rainy season data are shown here.

6.13. Species Distribution and Densities in Five Areas of the Selous Game Reserve.

Using vehicle transect counts as described in the last chapter, estimates of species density were obtained for five areas in the Selous: the east (this study area) the west (north and south of the Kilombero river), the north west (near Mlahi), the centre (Madaba-Mswega) area and the far south east (the Njenje river). These areas are shown in figure 6.2 (a). Data was obtained for the study area from the 1967 - 1973 transects, for the centre in 1971 and 1972 dry seasons and data for the west and south east obtained from counts undertaken by Allen Rees, past Principal Warden, West Selous Game Reserve. Data for the north west was obtained by the author in collaboration with 30 students from C.A.W.M. Mweka who carried out a series of foot transects in October 1974. The area was recently burnt and we believed animal densities were higher than normal due to immigration from surrounding unburnt areas. Estimates of densities were determined for wildebeest, zebra, buffalo, sable and hartebeest. Data for the study area was split into rainy and dry seasons and into the woodland and scattered tree grassland habitats. Data are self explanatory and no analysis was undertaken.

6.14. Species Distribution and Habitat Selection in the Study Area.

The previous chapter described the road transect system and census technique. In addition to determining estimates of species numbers, the transect data was analysed to show mean densities for each major species for each one mile segment of the transects for each calender month. Data were amalgamated for the 1969 - 1973 counts.

These species - segment - transect - month data sets were later analysed to show seasonal change in density from area to area, to show occupance of different vegetation types from month to month, and, for three species, to show the effects of dry season fires on distribution within the scattered tree grasslands.

6.141. Large scale movements.

Histograms for each transect for each species for representative months were drawn to illustrate changes in density along the transects. Histograms were annotated with transect topographic profiles (from 1:50,000 contour maps), with broad vegetation categories, with water availability and, where fire had a significant impact on distribution, by drawing attention to burning regimes. As histograms for all species, transects and months number over 100, only data for 5 species, wildebeest, impala, zebra, hartebeest and warthog, are shown here for Kilunda transect for the months of January, May, July, August and November.

6.142. Distribution between different vegetation types.

The transect segments were split into 5 different vegetation categories: Terminalia grassland, Combretum -Cassia grassland, miombo woodland, chipya woodland and valley woodlands. Mean animal densities were determined for the total number of segments in each vegetation type for each month. Data for 5 months, January, May, July, August and November were used to represent the different seasons of the year. Analysis was undertaken to look for significant patterns in distribution between vegetation types and different distribution patterns between months.

Analysis of variance tests were run on the complete 5 x 5 data set for each species to examine overall differences between months and between vegetation types. Full details of the analysis are shown in **table** 6.3 (a) for wildebeest. Analyses for all species indicated no overall pattern between months (looking at monthly means) but significant differences between vegetation types.

To examine which pairs of vegetation types differed in species occupance, a set of one-way anovars was run for selected vegetation pairs, e.g. chipya and miombo or, miombo and valley, etc. These vegetation pairs produced a 2 x 5 data set.

Thirdly, analysis was needed to examine differences between pairs of individual months within each vegetation type. Anovar was invalidated as monthly means were very similar and 't' tests were possibly invalidated as data sets varied in size and possibly in population variance. Accordingly a 'd' test, to examine differences between means of large samples was used (Bailey, 1969):

Where $$d = \frac{\bar{x}_1 - \bar{x}_2}{\sqrt{\frac{s_1^2}{n_1} + \frac{s_2^2}{n_2}}}$$

where $\bar{x}$, s and n are the mean, variance and sample size of each sample. Only the valley type has less than 30 segments which invalidates the use of the 'd' test.

6.143. Distribution between different burning conditions in the wooded grasslands.

Census transect data for the months of July-October in 1971 were used, as that year a very patchy burn offered considerable choice of burnt or unburnt habitat in the wooded grasslands. Each mile segment for each month was classified as burnt or unburnt and mean animal densities calculated for each category. Only three species were used, warthog, impala and wildebeest. As reference to figure 6.3 shows, very few hartebeest or zebra were present in the wooded grasslands during the dry season.

The data set is shown in table 6.4 and two-way analysis of variance tests were run on the burnt and then the unburnt data sets examining differences between months and species. As these tests showed no significant differences or irrelevant differences (e.g. there is a significant difference in species density, but this is irrelevant to burning conditions), separate one way anovars were run for each species testing differences between burning conditions.

6.15. Distribution patterns within the miombo ridge catena system.

The four transects across a miombo valley ridge catenary system which were discussed in chapter 3 were used to show species distribution patterns on a detailed scale in the woodland formation. During the dry season (July-December) of 1971 and 1972 the four transects of 6.0, 5.4, 5.4 and 3.6km length were walked four times a month, recording animal sightings, grass height, and burning state for each 300m long segment along the transects.

Each segment was assigned to a slope category of ridge tops, middle slopes or valley bottoms and lower slopes, from transect profiles and field obervations. Slope as an ecological character combines proximity to water, change in woody density from high on the ridges to lower in the valleys, water table depths giving a greater flush in the valleys and differences in grass and woody vegetation species composition.

For 1971, for the period of the first burn to the whole area being burnt (seven weeks in July, August, September) each segment was classified as to its burning condition; unburnt, burnt with no regeneration and burnt with green grass regeneration. In 1972 the whole area was burnt at one time so data could not be included.

Analyses were also attempted using a segment classification of grass height, of vegetation types drawn from the computerised association analysis of chapter 3.2 and of tree density using woody data from chapter 3.2. These analyses showed no significant pattern and are not discussed further.

Data were produced in tabular form for each of 7 species for 4 transects for the 3 slope and for the 3 burning classes. A full example is shown in table 6.5. Each table was subjected to a two way analysis of variance looking at differences between transects and ecological classes for each species for each factor.

Data in the tables are transformed mean numbers of animals seen per segment in the slope or fire class in each transect. Animal sightings were not re-calculated as densities as in many cases insufficient sightings were made and as visibility was relatively uniform throughout all segments it was thought advisable to use basic numbers seen.

Transformation was necessary as there were different numbers of segments of each class in each transect. Transformation was affected by the formula.

$$x = \frac{a_1 \times \sum_{1}^{n} b}{b_1 \times \sum_{1}^{n} a}$$

where a_i is the total number of animals seen in any slope (or fire) category in any one transect and b_i is the number of segments of that category in that transect. 'a' and 'b' are then summed for all sightings and all numbers of segments for all transects.

eg.		TRANSECT 1			TR 2			TR 3			TR 4			TOTALS
		R	M	V	R	M	V	R	M	V	R	M	V	
	A	a_1	a_2	a_3	– – – – – – – – – – – – – –								a_{12}	a
		b_1	b_2	b_3	– – – – – – – – – – – – – –								b_{12}	b

Where analysis of variance showed significant differences between classes then class data pairs were tested for differences by a two-tailed 't' test (Bailey, 1966) where

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s\sqrt{\frac{1}{n_1} + \frac{1}{n_2}}} \qquad \text{and } s = \frac{\sum(x_1 - \bar{x}_1)^2 + \sum(x_2 - \bar{x}_2)^2}{n_1 + n_2 - 2}$$

6.16. Seasonal patterns in the use of the floodplain.

It was not possible to include the Lungonyo floodplain (137km^2) in the vehicle or foot transect system. All data concerning animal use on this plain is based on 17 aerial census total counts and a number of reconnaissance flights and foot traverses. Counts were carried out from 1969 to 1974 at all times of year, but concentrating on the dry season. Flights were flown east west at 300' asl (97m) in a Cessna 182 or a Piper Super Cub and one, two or three observers were used. All species and animals seen were counted. The small area surrounding Kingupira forest was later excluded as the vegetation type was not homogenous with the remaining area. Data are given in table 6.7 and are not analysed except to show simple seasonal average densities.

6.17. Other species distribution patterns.

Because of their rarity or distribution pattern, some species were not covered by the detailed analysis outlined above. However, some data is available for all species from the transect systems and from general observations during the 10 years of the study.

For elephant, buffalo, eland, sable and greater kudu, it was possible to analyse for species association with the woodland and grassland formations for both the dry and rainy seasons. Data from all transects and for all years were pooled for each month and transects divided into short and long grass areas, with a preponderance of long grass area due to the nature of the transect system. To adjust this the short grass sightings were raised by the proportion of long grass/short grass transect lengths. As sightings for these species were infrequent it was thought not worthwhile to adjust different transect coverages for the rains and dry seasons. This means that while valid deductions can be drawn from the differences between numbers in the two habitats within each season, no deductions can be made from rainy season to dry season. This precludes statistical analysis and data have to be studied subjectively.

6.2. Results.

6.21. Tanzania Distribution Patterns.

Figure 6.1 shows the distribution of sable within Tanzania and table 6.1 gives the distribution pattern for each of 16 species within 5 broad vegetation types. Visual analysis of this data set allowed the seperation of three groups of species. A "miombo" group comprising sable, roan and Lichtensteins hartebeest was characterised by high occupance of the tall grass habitats and lower occupance in the shorter grass habitats. A "savanna/bushland" group comprising both gazelle, Cokes hartebeest, lesser kudu, gerenuk and oryx was characterised by total absence from the tall grass areas and high occupance of the short grass areas. This group can be subdivided with the latter three species showing little occupance of the short grassland and savanna and higher occupance of the bushland. A widespread species group of common duiker, greater kudu, zebra, buffalo and warthog was characterised by high occupance of all five habitats. Two species, wildebeest and impala, did not fit into this pattern and were separated as "transitional" species.

Analysis of variance tests on these data sets showed that distribution patterns for species in each group are similar and thus the groups are homogenous units. For the miombo and savanna groups vegetation types had significant differences in animal occupance, but there was no such difference between vegetation types for the widespread species.

6.22. Distribution Patterns within the Selous Game Reserve.

Figure 6.2 (b) shows a schematic vegetation types map for the Selous and environs. These categories are self explanatory except for the Combretum communities. This is a mixture of habitat types, varying from short grass Acacia - Combretum scrub to degraded woodlands to early successional stages in the woodland formation to the highly dissected and eroded habitats to the south of the reserve. It should be noted that the map portrays the dominant vegetation type for the square as assessed along the central aircraft flight line and that several habitats, not only one, may occur in each square. An important feature of the map is the dominance of short grassland habitat in the north and East of the reserve.

Figures 6.2 (c), (d), (e), (f) and (g) show distribution patterns for wildebeest, impala, zebra, hartebeest/sable combined and buffalo respectively. Note the strong association of wildebeest and impala with short grass areas both in terms of presence and of density. Zebra have a much wider distribution but densities are higher on the short grass areas. Hartebeest have a more equable density distribution. Sable are much less frequently encountered but are definitely associated with the miombo and Combretum habitats. Note that sable replaces hartebeest in the highly dissected country to the south of the reserve.

Figure 6.2 (a) shows the distribution of short grass habitats and the five study areas described in section 6.13.

6.23. Species densities in five areas of the Selous.

Data on species density are shown in table 6.2 with brief descriptions of the habitats within each study area. The table clearly shows the absence or low densities of wildebeest and impala away from the short grass areas. Hartebeest, sable, buffalo, and to some degree zebra have more equable density distributions. Within the Eastern Selous study area the change in habitat occupance with changing season is very evident, with wildebeest,impala and zebra cooentrating on the short grass areas in the rains.

The same pattern exists on a much smaller scale in other parts of the Selous with isolated groups of wildebeest and impala associating with small areas along river valleys where edaphic factors or heavy grazing pressure maintain a short grass sward.

6.24. Species Distribution, Habitat Selection and Movements within the Eastern Selous Study Area.

Data tables were composed of mile segment densities for each of 5 species for each of 5 transects for each of 12 months averaged over the 1968-1973 period. It is from these basic tables that the analyses of section 6.14 were taken. Upto 6 months are used to represent different seasons in the analyses that follow. These are:

January	early rains, annual grasses in rapid growth.
May	end of the rains, all grasses flowering.
July	early dry season before burning.
August	dry season and most early burning accomplished.
October	late dry season, water becoming more scarce.
November	end of dry season and commencement of rains.

6.241. Large scale movements.

Density histograms annotated for environmental factors are shown in figure 6.3. The division into short grass and tall grass areas is clearly shown. Hartebeest are restricted to the long grass areas on all transects except the Mwende, where low densities are encountered in shade along the edge of the Lungonyo floodplain and on a raised Combretum-Cassia medium grass ridge between miles 6-8. Data for sable and duiker are insufficient for inclusion, but these species are totally confined to the long grass areas.

During the calendar year zebra are the first species to make a distinct habitat change. Zebra leave the short grass areas as the rains cease and the annual forage dries up and begins to disintegrate. Zebra move to the edges of the floodplain and into the woodland areas. This move correlates with a rapid decrease in mean group size, (Rodgers, 1977).

Wildebeest start to leave the short grass areas only at the commencement of woodland burning. The exodus is not as complete as that of zebra and depends on the degree of burning in the short grass areas, less burning involving less movement (see table 6.4.).

Impala move less than wildebeest and do not penetrate as far into woodland system. The increase in warthog in the woodland areas in the dry season is probably due as much to increased visibility as to immigration.

Within the woodlands movement and distribution patterns are determined largely by areas of post burn grassflush and available water. The Kilunda transect is not well watered and the decrease in overall densities of zebra and wildebeest in October is conspicuous.

At the commencement of the rains, zebra, wildebeest and impala move back to the short grass areas, concentrating in the medium grass areas (eg. Kilunda miles 7-9) which flush more rapidly at the start of the rains. By January almost all of these three species have left the woodland system.

6.242. Habitat selection.

Tables 6.3 a-e analyse the distribution of 5 species within 5 habitat types at different seasons. Analysis of variance results show for all 5 species that there is no significant difference between months in mean densities across the 5 habitats, providing an indication that the populations do not leave the area encompassed by the transect system to any great degree. As the different habitats are of different size the mean densities will not agree exactly.

All species except zebra show a significant difference in density between different vegetation types averaged over the year. Wildebeest, impala and warthog show selection for the short and medium grass habitats (the Terminalia and Combretum wooded grasslands), whilst hartebeest select the woodland types.

The tables illustrate numerically the pattern shown in the histograms of figure 6.3. Wildebeest concentrating in the Terminalia zone in the rains and moving up the drainage slope through the Combretum, chipya and Miombo communities to the valleys of the woodland. The importance of the valleys is brought out in a later section. The higher densities in the chipya communities compared with the miombo is due to the inclusion of the Terminalia sericea-Combretum - Pseudolachnostylis woodland in the former. These woodlands are closer spatially to the Terminalia and are lower down the drainage slope.

Impala densities in the Terminalia and Combretum communities are not significantly different. This trend is masked by the coarse scale of 1 mile grids, where the Terminalia areas contain narrow ridges of Combretum - Cassia with high densities of impala. This was apparent for the Mwenda transect, miles 1-2 and 5- 6. Impala numbers are relatively constant in the woodlands through out the year with only a slight increase in the dry season.

Zebra are more equally distributed with little selection for habitat. Valleys carry higher numbers in the rains, but see section 6.25 below.

Hartebeest show little selection for habitat except an avoidance for the short grass Terminalia communities. Large discrepancies in monthly mean densities are not readily explainable, especially the low values for May.

Warthog show strong selection for the short grass areas but little seasonal shift in densities from month to month within any community.

6.243. Selection for burning conditions in the wooded grassland habitats.

The grasses of the wooded grasslands show no green flush following burning except for the more deeply rooting perennial Panicum infestum and to a lesser degree some of the grasses of the Combretum ridges.

Table 6.4 shows species occupance of burnt and unburnt areas through the dry season. Results show no difference between months in terms of species densities. A difference between species density was significant but is irrelevant to the topic under discussion. One-way anovar testing for differences between burning conditions showed a significant selection for unburnt conditions for all three species, wildebeest, impala and warthog.

6.25. Species distribution patterns within the woodland catenary system.

Tables 6.5 and 6.6 present data for species selection for slope and burning conditions respectively. Analyses for vegetation type, grass height (related to fire) and tree density showed no significant pattern and are not shown.

Anovars for both slope and burning conditions showed no significant differences between transects for any species. There is a trend for higher numbers of animals from transect 1 to 4 which is down slope. This trend is reversed for duiker.

Wildeest, impala and southern reedbuck show a highly significant avoidance of ridge areas and a selection for valleys. Zebra and hartebeest show a selection for valleys but a less significant avoidance of ridges and slopes. Duiker show a significant selection for ridges but are present in reasonable numbers throughout the catena. This selection for ridges is probably associated with greater amounts of shrub cover and thicket clumps. Sable show no real trend in distribution. Warthog with a small and variable data set, show no significant selection but a strong trend towards valley conditions.

Fire analysis was of necessity a much smaller data set with lower significance levels. Results show a significant selection for burnt and regenerating conditions for wildebeest and impala and no significant selection for burning conditions for hartebeest and zebra. Data for sable and warthog were inadequate for analysis. All these 4 latter species showed a trend to avoid burnt with no regeneration conditions and no selection between unburnt or regenerating conditions.

6.26. Seasonal use of the Lungonyo floodplain.

Data on buffalo and elephant were excluded from this analysis. Both species utilise the floodplain at all seasons, especially in the vicinity of Kingupira groundwater forest. Burning conditions and waterlogging seem to have little effect on their pattern of use.

Eland are infrequent visitors to the floodplain in the dry season. Following their tracks shows feeding on flushing grass shoots and the many herb species of the plain. Hartebeest are present on the plain in the dry season and around the edges for all seasons. Bohor reedbuck are restricted to the Lungonyo floodplain in this study area. They are found on the plain at all seasons (leaving it to 'raid' rice fields in neighbouring settlements) but they have never been seen on the short grass areas.

They are easily seen whilst concentrated on fresh post burn flushes and their forms or resting places are frequently encountered. Aerial reconnaissance indicate a population of some 300-500 animals.

Results in table 6.7 are mainly concerned with zebra and wildebeest which congregate on the plain in the dry season. Floodplain use appears to be governed by two factors, the degree of burning and the presence of water at Mtawatawa and Kingupira. Zebra have been seen in unburnt areas but wildebeest very infrequently and then usually near water.

Zebra congregate on the floodplain edge in the early dry season of May and June before annual burning. The intermediate zone of Echinochloa - Digitaria grasslands is used at this time as the central plain is still water logged.

6.27. Distribution Patterns of Other Species.

6.271. Selection for long and short grass conditions.

From table 6.8 sable show a complete avoidance of short grass conditions and greater kudu show a tendency to select longer grass conditions. Eland show no apparent selection in the dry season but a possible tendency to select short grass in the rains. Elephant show no selection in the rains but a possible avoidance of the short grass areas in the dry season. Buffalo results are problematical as is to be expected with a species varying in group size from 1 to 1100 animals. It appears impossible to draw conclusions from the data shown in the table.

6.272. General Comments on the rarer species.

(a) Reedbuck. Southern reedbuck are virtually restricted to the woodland valleys (see table 6.5) and to areas of permanent water in the broader river valleys eg. Mpapule and Namahema. Bohor reedbuck are totally restricted to the Lungonyo floodplain (and similar habitats along the Matandu river system south of the study area).

(b) Red duiker. This species is occassionally seen in thickets and denser woodland areas.

(c) Blue duiker. Although not recorded for the study area they are probably present in the dense forest/thicket areas of the western watershed. They have been seen in similar habitat near the upper Matandu river.

(d) Suni. Seen on only 3 occas ions during 1967 to 1976; suni are restricted to thicket areas.

(e) Oribi. Peters oribi are restricted to S.E. Tanzania, (Rodgers, unpublished data) and just reach the southern part of the study area. They have been recorded in valley woodland and Combretum scrub 11 times since 1966.

(f) Bushbuck. Bushbuck are scarce in the Eastern Selous but can be seen in the watered valleys of the western half of the study area.

(g) Waterbuck. A small population exists in the vicinity of Kingupira forest. This population has grown in size from 25 in 1967 to some 140 in 1976, (Callendar, 1974 and Rodgers, unpublished data).

(h) Bushpig. Bushpig are found throughout the study area.

(i) Hippopotamus. There is an estimated population of 200 hippopotamus in the study area which disperse to small water holes and wet valleys in the rains and concentrate in Kingupira forest in the dry season.

(j) Rhinoceros. Seen on 26 occasions since 1966, rhinoceros apparently have a wide distribution but are more commonly seen in the woodland close to thickets.

(k) Predators

1) Lion (Rodgers, 1975), hyaena and leopard are widely distributed. Wild dog are seen frequently in the short grass habitats and less often and in smaller size packs in the woodlands.
2) Cheetah. Cheetah have been seen on 13 occasions since 1966; several of these sightings being within short time periods which perhaps suggest that cheetah cover large distances in this area.
3) Jackal have been seen twice in the study area but several times in the neighbourhood of settlement close to the reserve boundary. This unusual distribution with jackal associating with human settlement and absent from the game reserve is found along the complete periphery of the Selous, see Chapter 9.

6.3. Discussion.

6.31. Ecotones.

The habitats mentioned in this chapter are not completely discrete units but merge slowly or have inclusions of other types. Such edges or vegetation differences are of importance to some species, especially impala, warthog and, to a lesser extent, greater kudu. This is the ecotone or edge effect (Lamprey, 1963).

Impala associate strongly with anthill thickets and the narrow, low *Combretum* ridges in the more open *Terminalia* scattered tree grassland. These minor habitats offer important food sources, e.g. *Salvadora* and *Jasminum* from anthills and *Combretum*, *Turraea* and *Cassia* from the ridges, as well as shade and cover.

Warthog densities reach their peak along the border of the Lungonyo floodplain and the *Terminalia* habitat, especially in the dry season (e.g Mwende transect miles 0 to 5). In this case the warthog feed on the perennial root bases of the floodplain grasses and use the shade and sleeping or retreat holes present in the *Terminalia* woodlands. Densities decrease away from this edge (Rodgers, unpublished data).

Greater kudu are often found alongside water courses with patches of riverine thicket or forest. When alarmed the animals retreat into the denser cover.

The maintenance of such variety within habitats is of major importance for optimum wildlife management.

6.32. The role of thickets.

It has been difficult to assess the importance of thickets to the game species of the area. Visibility is almost nil either by vehicle, aircraft or foot. Several foot traverses of the sand soil thicket blocks have shown a large number of elephant trails both around and through the thickets. Casual observations show little feeding use or damage by elephant on the vegetation and local opinion has it that the thickets are mainly resting places. Apart from suni and duiker the only other species encountered in the sandy soil thickets are eland and, from spoor only, buffalo. Kudu have never been seen in or near the sand thickets but are common in the clay variant. Sable, when alarmed, will occasionally retreat into the thickets.

With the exception of two minor species, thickets do not play a large productive role for the animal population. Their major importance is in watershed conservation.

6.33. The role of the floodplains.

The floodplain community provides the habitat for Bohor reedbuck, as do similar plains along the Matandu and Kilombero Rivers in other parts of the Selous Reserve.

In the rains the only other animals using the plain are elephant and buffalo, and to some extent zebra and hartebeest before water logging and rapid grass growth occurs. The edge of the floodplain, an Echinochloa - Digitaria community, provides valuable grazing at the end of the rains (May and June) for zebra.

Following burning, usually from August to October, the floodplain offers fresh grass growth and abundant water. As the dry season progresses numbers of zebra and wildebeest build up until the first rains fall in late November.

Fire is necessary to create short grass grazing conditions over most of the plain, but concentrations of buffalo and other game at permanent water at Mtawatawa, Kibuli and more recently near the Research Centre (as a result of a concrete dam across the river) create local areas of short grass grazing without fire.

6.34. Species Distribution Patterns.

Each species in the study area, even those of similar ecological requirements, shows differences, in total or seasonal distribution patterns. These differences may be due to the need to maximise food quality input in a diverse environment. From the data presented earlier in this chapter it is possible to summarise each species distribution and movement pattern and to draw conclusions regarding its habitat needs and preferences.

(a) Sable antelope. Within Tanzania the sable is completely restricted to the miombo woodlands. Table 6.1 shows an approximate 65% occupance of tall grass areas and the lesser figures for other habitats are due to woodland presence in squares dominated by shorter grass types. The gap in sable distribution as shown by figure 6.1 is real, and has resulted in subspecific variation in horn length, facial pattern and sexual dimorphism in colour between H. niger roosevelti to the east of the Iringa Highlands and H. n. niger to the west. The forest grassland mosaic of the highlands having acted as a complete barrier.

At the northern limits of its range in Africa the sable mirrors the distribution of miombo woodland, ie. in the Shimba Hills of S.E. Kenya and Biharamulo of N.W. Tanzania (Rodgers, Ludanga and De Suzo, 1978). At the southern limits, Sable extends into the northern part of the Kruger National Park, a short distance south of the southern limit of Brachystegia. Fossil evidence for previous distribution limits of Hippotragines is scanty but no remains assigned to H. niger have been found outside the historic area of distribution, (Wells, 1967 and A.W. Gentry, pers. comm.).

Sable are never very dense in number and can apparently move large distances (Child & Wilson, 1964, Estes & Estes, 1969) but out of several hundred personal sightings, only one instance has been recorded from the short grass habitats and that was from Balani waterhole some 2km from the woodland. Within the Selous woodlands, sable are not restricted by steep terrain (as are hartebeest) and they have been seen on very steep hill slopes. Sightings in the study area during the rains are scarce but this is attributed to poor visibility rather than emigration or dispersion.

In conclusion, sable is the species most closely associated with the miombo formation, more so than roan, which has a broader distribution in Africa and within Tanzania (see table 6.1). Sable do not appear to select for post burn flush or valley conditions but do avoid newly burnt areas. Densities within the Selous and other areas in Tanzania appear similar and usually less than 1 per km^2.

(b) Lichtenstein Hartebeest. This is the miombo woodland species of a widely adapted genus, (Ansell, 1974). Its fossil history is unknown. The northern limits approximate those of sable in the north west but it is replaced by Cokes hartebeest well south of the Shimba Hills and by other members of the genus in the south of the Central African woodlands.

Within the Selous, this species is absent from short grass areas and restricted to woodlands and less wet floodplain areas, eg. Lungonyo and Mkigura (N.E. Selous) but absent from wetter plains such as the upper Kilombero. In western Tanzania it is excluded from floodplains by the topi, (Rodgers, unpublished distribution data). Unlike sable, it is not found on steep terrain. I have no evidence of seasonal movements, and it is likely that family groups occupy semi permanent home ranges (Dowsett, 1966). Within the woodlands hartebeest show no selection for burning conditions but do appear to select for valleys and lower slopes.

(c) Zebra. As table 6.1 shows, the zebra is a widespread species with no apparent predilection for habitat in terms of gross distribution. This habit is reflected within the Selous and the study area, zebra showing no significant difference in overall density between habitat types (table 6.3) or between burning conditions in the woodlands.

Seasonally, however, there is considerable difference in density and corresponding movement. Within the Selous (and within Tanzania) zebra densities are highest in areas with available short grass in the growing season, (Serengeti, Moyowosi, Rukwa, N.E. Selous and E. Selous) and considerably lower where such forage is not available, (Biharamulo, Ugalla, Rungwa, South Selous). Mean group size varies with habitat type in the same way, (Rodgers, 1977).

Table 6.3 was compiled with 1969-1972 data and since then zebra densities have risen to approach some 13/km^2 on the short grass habitats during the rains. At the end of the rains in May zebra move away either onto the edge of the floodplain or into the woodlands. By August very few zebra remain on the short grass areas. Within the woodlands zebra show some selection for valley conditions. At the end of the dry season zebra return to the short grass areas. A considerable number (up to 30% of the population) use the burnt areas of the floodplain during the dry season.

In conclusion, zebra have a broad distribution and are able to exist in most habitat types, but densities reach their peak where short sweetveld forage exists in the growing season.

(d) **Wildebeest.** Wildebeest do not fit into table 6.1's categories of miombo, widespread and savanna species, as such they (and impala) are seperated as transitional species. It is noteworthy that if the Nyassa wildebeest are removed from table 6.1 data then the remaining wildebeest do approximate the savanna species pattern. Chapter 2.5 describes wildebeest distribution in Africa. Wildebeest are found in low numbers throughout the Selous except the far south and west. Reference to figure 6.2 shows how their distribution in the central Selous follows the outline of the major rivers, Luwegu, Kilombero and Ulanga. Along these rivers wildebeest are virtually restricted to localised areas of short annual/perennial grasses on shallow soil ridges and interfluves. Nkoma N'gasha on the Luwegu is a typical example. Figure 6.2 shows 4 main centres of distribution, Mikumi plains, Beho Beho, Utunge and the study area. These are all areas of extensive scattered tree short grassland.

Data in this chapter show wildebeest have very highly significant associations with short grass habitats (table 6.3) and only utilise the woodlands in the dry season following burning. Within the woodlands wildebeest select valleys and lower slopes avoiding ridge tops and select post burn flush and avoid unburnt and burnt non flushing areas. A sizeable proportion of the wildebeest population remain on the short grass habitats throughout the dry season and here they select against burnt areas. The extent of burning in this habitat appears to determine the proportion remaining (Rodgers, 1969). Wildebeest use the floodplain less than zebra and only on burnt flushing areas in the late dry season. At the onset of the rains virtually all the wildebeest return to the scattered tree grasslands.

There is some evidence that a few small groups of wildebeest do remain in the western woodlands of the study area throughout the year. Groups at Nahomba valley and Kinjekejeke valley seem to follow this pattern. This is discussed further under seasonality of calving in chapter 8.

(e) Impala. Impala have a similar distribution pattern to wildebeest but are able to penetrate the woodland system in Tanzania along river valleys, eg. Ruaha, Ugalla, Rungwa and Nzombe. Impala appear to reach their greatest densities away from competition with gazelle (and spring bok) as in the Kruger, Wankie, Luangwa and Manyara National Parks and the eastern Selous Game Reserve. Ecologically, impala seem to replace the gazelle as the dominant short grass small throughout central Africa.

Within the study area impala are totally absent from the floodplain and thicket formations (low densities may be found around the coastal thickets on alkaline soils to the north of the study area). Greatest densities and occupance values are found in the short grass habitats but the shrubby Combretum - Cassia ridges are preferred over the pure Terminalia stands. A few impala do remain in the woodlands throughout the year but the high densities for chipya in table 6.3 reflect the ecotonal communities adjacent to the short grass habitats.

A greater proportion of impala remain in the short grass habitats during the dry season (avoiding the burnt areas) and this is due to their switching to a high browse diet (Rodgers, 1976). This is discussed in detail in chapter 7. The impala in the woodland show a significant association for valley and slope conditions and an avoidance of ridges. Impala select for post burn flushes and avoid non-flush and unburnt areas.

Like wildebeest and zebra impala exist at much lower densities away from short grass conditions (table 6.2).

(f) Warthog. Warthog are classified in table 6.2 as a widespread species and they can be found in all habitats in the Selous Game Reserve. Table 6.3 shows a significant difference in density between the *Terminalia* and all other communities but no difference between the woodlands. There is no change in seasonal densities beyond a slight increase in dry season woodland data which may partly be due to increased visibility. As section 6.31 points out, there is a seasonal change in warthog density within the *Terminalia* community, densities increasing along the floodplain edge as the dry season progresses. Warthog densities seem highest where adjacent short grass rainy season habitats are adjacent to perennial floodplain grasses as in the Moyowosi, Ugalla and Luangwa valley game areas.

(g) Buffalo. Buffalo are an extremely widespread species and table 6.2 shows they have densities of the same order of magnitude in all areas and habitats of the Selous. Little data has been presented for buffalo in this chapter as they are a species extremely difficult to census or on which to collect accurate quantitative data (see table 6.8). Subjective impressions and attempts to plot positions of the large (1000 +) herd in the vicinity of the research centre show the bigger buffalo groups to be mobile within extensive home ranges.

Movements do not appear to be seasonal or related to distinct changes in the habitat. There is a tendency towards heavier use of the floodplain in the dry season but this may be related to water use.

Group sizes are larger in the more open habitats and road counts show densities to be higher. The research centre herd seems to make no use of the woodlands but to rotate between the short grasslands, forest and floodplain throughout the year. Two further large groups also frequent the floodplain and southern short grass areas. Four large herds (200-400) are known within the woodland where they appear to be resident.

6.35. Grazing Successions.

There is no evidence for a grazing succession in the sense of Bell (1969, 1971) or Vesey-Fitzgerald (1965). Fire, by reducing taller grasses to short green growth, plays the part of the large primary members of the typical succession in making short grass available for the smaller, later members of the succession. Interestingly however, the timing of movement from the short grass habitats at the end of the rains is similar to that of the Serengeti in that the order is zebra, wildebeest, impala.

Buffalo perhaps play a role in creating localised short grass conditions by their dense herding activities of trampling and low level grazing. These activities are conceivably of value to smaller species in the floodplains and woodland habitats.

6.36. Species Spatial Separation.

Lamprey (1963) used the term ecological separation to describe the stratification of ungulate distribution and feeding patterns in savanna woodland of Northern Tanzania. He showed that species separation could be achieved by combinations of spatial and temporal distribution patterns and by different feeding levels, habitats and selectivity. Such concepts of separation fit the theoretical basis of niche structure as described by Hutchinson (1957) and Levins (1968). Hutchinson described the niche as a multidimensional hypervolume whose location and size is determined by the nature, number and size of its dimensions which are the environmental factors or pressures relevant to the species existence.

Physical separation in space or time is accomplished by species reactions to many of these dimensions. Other dimensions restrict species feeding level and selection of floristic components. Fire and seasonal variation in factors such as rainfall can alter the size and nature of these dimensions, (Blankenship and Field, 1972). This chapter has dealt with patterns of distribution which affect spatial and temperal separation. Feeding patterns are discussed in chapter 7.

Recent studies in southern Africa (Ferrar and Walker, 1974; Hirst, 1975) have used multivariate statistics to attempt to quantify environmental variables and species reaction to them. Results of these studies and earlier studies from E. Africa (Bell, 1969; Western, 1973; Harris 1970 & 1975) agree well with the distribution patterns described in this thesis.

Bell (1969), working in the Serengeti corridor, showed wildebeest to be associated with short grass at all seasons and only using longer grass communities after initial grazing by zebra (and buffalo). Zebra showed an association with short grass in the rains but no selection as to grass height in the dry season. Western (1973) gave quantitave evidence for wildebeest selecting green forage, short grass and previously grazed components. Impala showed similar associations but greater association with wooded communities.

Zebra showed no selection for grass height, less selection for green forage and preferred less grazed components. Hartebeest selected for longer grass green forage and previously ungrazed components.

Hirst (1975) in a major publication dealing with ungulate habitat preferences in a small hunting area adjoining Kruger National Park, used computer techniques to determine environmental factors and their effects on species distribution. His results may be summarized as follows:

Wildebeest selected for savanna vegetation, short grass, high grass and low forb cover and for open woody vegetation. Other habitats, notably the large areas of deciduous woodland, are mainly utilised during the dry season. Zebra showed a similar pattern to wildebeest but a more equable distribution in the dry season. Impala were found in all habitat types but showed selection for areas of short grass, areas with a distinct shrub layer and areas with a prominent forb element in the ground layer.

Ferrar and Walker (1974) showed a multidimensional niche occupance diagram for 14 species. The three major dimensions were increasing ground layer height, increasing woody density and icreasing dissection and rockiness in terrain. Results were interesting in the considerable overlap of spatial distribution with only 4 species of specialist feeders, klipspringer, bushbuck, steinbok and reedbuck, being well separated. Wildebeest and impala favoured short grass areas whilst zebra and sable were similar in having a broad central niche occupance. Wildebeest (and Tsessebe) were shown to have a high selectivity for burnt and flushing areas, zebra less so and impala only slightly. Duiker appeared to avoid such areas. Wildebeest selected for homogeneity in the environment (grasslands), whilst zebra and impala selected for heterogeneity.

All studies show a differentiation in niche occupance or habitat selection between wildebeest, zebra and impala. Within an environment of considerable small scale heterogeneity of habitat both spatially and temporally, there is bound to be considerable overlap. Such overlap is further reduced by feeding selectivity within habitats and this forms the basis of the following chapter.

As a summary for this section table 6.9 lists a number of habitat or environmental variables and gives a subjective rating of their effects on species distribution within the eastern Selous. Variables are rated as positive (++, +) or negative (- -, -) or no effect (0). A possible index of habitat selectivity is $\Sigma(+)/\Sigma(-)$ and this is shown at the base of table 6.9 and shown as a histogram in figure 6.4 (a). Figure 6.4 (b) is a bar chart showing species occupance of differing habitats on a grassland to thicket woody vegetation. scale.

Figure 6.4(a) shows three major groups of species based on habitat selectivity. These are the widespread species: elephant, kudu, buffalo and eland; 3 intermediate species: common duiker, impala and zebra; and 4 species of restricted distribution: wildebeest, hartebeest, sable and reedbuck.

CHAPTER SEVEN

FEEDING ECOLOGY AND NUTRITION

7.0 INTRODUCTION

This chapter documents details of animals' use of the different habitats they occupy in terms of their feeding ecology. As later sections describe, field observation of detailed feeding activities was difficult to undertake and this study relied heavily on examination of post-mortem material. Animals were collected from habitats close to the research base, principally the short grass wooded grasslands. This chapter concentrates on this habitat therefore and the main species found there, wildebeest and impala. Less data are presented for other species and other habitats in the study area.

Once broad feeding patterns have been described it is pertinent to ask the questions; "how much food do the animals eat and of what quality is it?" And secondly "Is this adequate for their needs at all seasons and in all habitats?" A large part of this chapter attempts to answer these questions. It is apparent from the data in chapter 4 that the quantity and quality of available forage changes from season to season and from habitat to habitat. Fire is of great importance in determining these parameters. Levels of nutrients in the ecosystem, protein, energy and water, are ultimately limiting to animal populations, (Wiener 1975).

Nutrient levels can also influence proximate limiting factors such as predation and pathogens by altering the animals' susceptibility to these factors (Sinclair 1977). Do nutrient levels limit species numbers or production in this area, either totally or seasonally and spatially? is another question this study asks. If there are such limitations then can different species alter their feeding strategies in order to overcome the limitations? This chapter describes these factors and lays the nutritional groundwork for later discussion on animal performance and factors limiting species production.

A great deal has been published on the feeding and diet of African ungulates but little, unfortunately, on those inhabiting the woodlands. In recent years quantitative studies of feeding behaviour have concentrated on aspects of niche separation amongst sympatric bovids, e.g. the studies of Field (1968, 1970) in Uganda, Bell (1969, 1971) in the Serengeti and Owaga (1975) and Casebeer and Koss (1970) on the plains of Southern Kenya. Much of this effort has gone into investigating the possibility of diet selection in terms of plant species and plant part ingested. Stewart and Gwynne have been instrumental in perfecting such techniques (Stewart and Stewart 1970, Gwynne and Bell 1968). Adaptations to different habitat and forage types in the various ungulate species have been examined within the rumino-intestinal tract (Hoffman 1973) but little has been published on adaptations within the food gathering organs of the head.

Recently two studies have examined ungulate feeding behaviour and nutrition in detail, Stanley-Price (1974) on Cokes hartebeest in Kenya and Duncan (1975) on topi in Serengeti. Both studies have discussed the question of food adequacy and selection during the year, S-Price by comparing estimated intake with theoretical needs. Determination of theoretical nutrient requirements demands knowledge of species metabolic rates, information which is still almost totally . unknown for most African ungulates. Rogerson (1970) produced data for wildebeest and eland, but there is a need for much more. As such data is unavailable, considerable extrapolation from livestock, cattle and sheep, is necessary. Where such data comes from temperate areas and deals with livestock bred for maximum production, there may be considerable error in applying such data to indigenous African wildlife.

Such problems are discussed in the following sections and it is realized the assumptions and extrapolations that are used may contain inaccuracies. As these assumptions and the study itself are not used to determine absolute levels of intake or requirement but used to compare relative intakes from season to season or species to species then the assumptions become less critical and the comparisons and conclusions more robust.

7.1 METHODS

7.11 General

Initially the chapter sets out to accomplish three tasks.

a) To determine the gross dietary characteristics of the commoner large ungulates in the study area, in terms of the broad feeding categories of browsers, grazers and grazer-browsers. Within these categories I hope to show differences in species feeding behaviour and their ability to select specific food items (Hoffman and Stewart 1972).

b) To determine the quality of food intake in terms of nutrient values, using protein content as the main determinant of quality. I intend to present evidence for selection of protein content within this section.

c) To determine the rate of food intake per day.

Secondly by combining these separate sets of data, it is possible to estimate intakes for protein and energy per day for different seasons of the year.

Finally, by extrapolation from requirements for nutrients from domestic livestock, it is possible to estimate nutrient requirements for species in this study and compare these values with actual intakes for different seasons and habitats.

Information comes from three main sources.

a) Qualitative observation of animal feeding behaviour.

b) Analysis of dietary components from post mortem examination of shot animals.

c) Extrapolation of results from feeding studies on other ungulates, both domestic and wild.

7.111 Field observations

Individuals and groups of different species have been observed at intervals throughout the study in an attempt to obtain information of feeding behaviour. Observations can be categorised as:

a) Information on habitat occupance.

b) Information on gross diet selection - browse or graze.

c) Information on feeding level for grazing species, including grass height and grazing height.

d) Information on plant species selection.

Information on habitat occupance was presented in chapter 6 and methods and results are not considered further here. Information on the other aspects was difficult to obtain. Duncan (1975) has detailed the difficulties of observing feeding behaviour in wild ungulates, and animals in the Selous are considerably "wilder" or more observer shy than in the Serengeti. Opportunities for prolonged observations of undisturbed feeding from distances of less than 100m were rare. Quantitative or precise information on feeding in terms of species selection, level and intensity was not obtained for grazing ungulates. Browsing was easier to observe and species and plant part fed on could frequently be identified. A compilation of species fed on was made for impala and less detailed notes and lists prepared for other species, both grazers and browsers.

7.112 Post mortem examinations

Large samples of wildebeest, impala and wart hog, and smaller samples of hartebeest, zebra, buffalo and sable were examined by routine post mortem procedure. Gross details of these procedures are given in chapter 8. During examination, the weights of rumen (or stomach) contents, rumen empty weights and hence rumen or stomach contents weights were determined. From the rumen contents several grab samples were removed, thoroughly mixed and divided into two parts.

One part was air dried to constant weight , allowing the calculation of rumen contents dry matter weight. Following drying this portion was analysed for nitrogen content by the Central Veterinary Laboratories (CVL) in Dar es Salaam. The other part was preserved in formalin or air dried for eventual determination of plant type and plant part ingested: monocot or dicot: leaf, fruit, or flower, or grass leaf or grass stem. In all cases rumen contents were sifted through for large easily identified plant particles or other objects, e.g. feathers, bones etc. Faeces samples from the posterior portion of the rectum were collected, air dried, and sent to the CVL for nitrogen analysis.

7.113 Source data

This study has benefited from the work of Price (1974) on the feeding ecology of Cokes hartebeest, and Duncan's (1975) study of topi. As these authors point out the great similarities in the gross mechanics and physiology of feeding and digestion amongst ruminants means that results for one species or habitat or forage type may be extrapolated and applied to similar species, habitats and forages. Frequently where a range of values is given in the literature, the most appropriate figures have been extracted for this study. As is to be expected there is a great deal of literature on the nutrition and feeding of domestic stock, much of this work, including methods, results and conclusions are appropriate to wild stock of similar feeding habits. Similarly the work of pasture ecologists and agronomists on tropical forage can be utilised in studies such as this. Frequent reference will be made to such studies throughout this chapter and in appendix 10, which discusses choice of methods.

7.12 Gross dietary characteristics

Information was obtained from field observation and examination of rumen contents for identifiable fragments of food items. Two aspects of morphological adaptation to feeding behaviour, jaw shape and animal posture have been examined.

7.121 Field observations

As was mentioned above no quantitative data were collected on feeding behaviour, either as to species selection or to feeding level. Qualitative results were obtained and these are discussed below.

7.122 Rumen/stomach contents analysis

As detailed above, grap samples of rumen/stomach contents were obtained, mixed and stored in formalin for later analysis. Analysis thereafter followed the methods of Stewart (1971) which are described in appendix 8 for impala. For other browsing or partially browsing species (for which I had much smaller samples), rumen content grab samples were separated into dicot/monocot categories, air dried and weighed to give % dicot material by weight in the rumen contents. Rumen samples for grazing animals were to be analysed for plant part by Dr M. Gwynne in Nairobi. Methods and results are described below:

7.123 Morphological adaptations to feeding

The muzzle is the main tool of gathering, selecting and ingesting food items for all ungulates, (Leuthold 1977), as such it can be expected to show functional adaptations to differing dietary types and modes of feeding, both in its basic shape and in the form of the associated structures of teeth, lips, tongue and organs of olfaction and taste. Only permanent bony structures, the lower jaw and incisiform teeth, have been examined in this study.

Intact lower jaws from ten ungulate species were examined to show possible adaptation. One obvious factor was jaw width, animals which graze being expected to have a broad flattened jaw to facilitate close cropping near ground level and animals which browse being expected to have a narrower more rounded jaw suitable for more delicate feeding involving selection and ingestion of small discrete food items. To demonstrate this quantitatively, intact jaws were measured across the broadest section of the jaw immediately posterior to the site of incisor teeth insertion. Jaw width was expressed as a function of jaw length, JW/JL, to discount differences due to body size. Jaw length was measured along the longest anterior-posterior axis excluding incisor teeth. Measurements used are shown in fig 7.1. Note was also made of the mode of incisor teeth insertion, vertical or angular.

Animal posture or stance should be related to feeding style (artiodactyl extremes being the giraffe and the hippopotamus) where animals grazing at low level would be expected to have a head low posture; and animals feeding at higher levels, the tall grass selective grazers and browsers, would be expected to have a head high posture. Photographs of adult males in head up "alert" postures were used to quantify these ideas for ten different species. Two measurements were made, one from shoulder height to the ground (SH) and one from the horn base to the line of shoulder height - referred to as head height (HH). Results were expressed as a ratio HH/SH, and measurements are shown in fig 7.1.

Mean jaw ratios were calculated for each species and plotted graphically against the single measurement of posture ratio for each species.

7.13 Diet Nutritive Values

As has been discussed in chapter 4, crude protein is taken to be an accurate indicator of diet quality in terms of nutritive values, although other diet constituents such as soluble carbohydrate or gross energy content could be used. Without recourse to feeding experiments or fistulation experiments with tame animals, there are three basic methods to derive the crude protein content of the diet (CPL). These are:

a) Estimation of plant part (leaf, stem, dicot etc.) proportions in the rumen and determining the protein content of these items in the forage.

b) Direct analysis of the crude protein content of the ingested material in the stomach of non ruminants (zebra, warthog). Rumen contents contain much non dietary nitrogen so values of rumen N cannot be taken as direct indication of dietary N. (Note: crude protein is estimated as N x 6.25).

c) Estimating dietary nitrogen from analysis of faecal nitrogen content by using published regression values from feeding trials with the same or similar ungulate species on similar diets.

7.131 Analysis of plant part from rumen contents

Air dried mixed samples of rumen contents were available from post mortem analysis (see section 7.112 above). Thirty such samples for wildebeest from different seasons from the short grass wooded grasslands were sent to Nairobi for analysis by Dr M. Gwynne. Dr Gwynne is an acknowledged expert on dietary analysis for plant part and has undertaken such analysis for many ecologists in East Africa (e.g. Gwyne & Bell 1968). Lesser numbers of samples for other species were also sent for analysis.

Results from such analysis indicate the proportion of grass leaf, leaf sheath, stem and non graminaceous elements in the rumen contents. This can be assumed to equal the proportions ingested by the animal. Knowing the crude protein content of these plant parts in the forage it is possible to calculate a figure equivalent to total crude protein dietary input for the animal at the time of sample collection. Correction factors for differential throughput may be necessary however (Duncan 1975).

7.132 Analysis of rumen/stomach samples for nitrogen/crude protein content.

The oesophageal or anterior part of the stomach of non ruminants functions as a storage chamber for ingested food items with little or no digestion or absorption functions. As such, analysis of these stomach contents can give a direct indication of the diet both in terms of plant parts ingested and of chemical content. Values from nitrogen analysis of stomach contents (converted to crude protein by Nx 6.25) can be used as direct measurements of dietary crude protein content, "CPd", (McCullagh, 1969a&b).

The rumen on the other hand is a major digestive and fermentation chamber (Hungate 1966). Rumen contents contain nitrogen from several different sources, ingested food items, microbial nitrogen, free amino acids, saliva and inorganic nitrogen in the form of urea. Analysis of rumen nitrogen content therefore does not give a direct measure of CPd (Price 1974, Duncan 1975) but could give a relative index of CPd which can be used to compare different populations or different seasons or different habitats.

Rumen and stomach contents were collected from shot animals as described in section 7.112 and samples sent to the CVL for analysis. Results of % N content have been converted to CP% by N x 6.25, even for rumen samples as although rumen N does not all come from plant protein it is easier to visualise differences if all analyses are in the same units.

7.133 Estimation of dietary crude protein from faecal nitrogen values.

Determination of dietary protein content by faecal nitrogen regression equations has been an accepted technique in livestock nutritional studies for some considerable time, Stanley-Price (1974) and Duncan (1975) discuss the practical implications of this for wildlife research and point out that the method is more accurate than that of analysis of rumen contents for plant part composition.

A number of regression equations are available in the literature, some of these are discussed and compared in appendix 10. Two equations are considered suitable for use in this study, they are:

i) $CPd = 1.667\ CPf - 6.93\ (r = 0.958)$ of Bredon et al (1963)
ii) $CPd = 1.06\ CPf$ (dry season forage)
and $CPd = 1.15\ CPf$ (wet season forage) of Arman (pers. comm. Western)

Where CPd is crude protein content of diet and CPf is that of faecal matter.

Appendix 10 points out that both equations have their advantages although they do lead to different results. Where it is necessary to use a single value of CPd, I use a mean of values from both equations.

7.134 Estimation of drude protein digestibility coefficients

A number of regression equations to predict digestible protein (DP) values from crude protein (CP) values are available in the literature. These are discussed in Appendix 10. For this study I use the relationship of Bredon et al (1963) where DP = (100.89 log CP - 44.45) CP/100.

A graph plot of digestible protein against crude protein is shown in figure 7.6b.

7.14 Food intake rate.

Estimation of dry matter food intake (DMI) has been discussed in detail by S-Price (1974, 1977). Rate of food intake is governed by rumen capacity and rumen throughput times. Whilst rumen capacity can be considered a constant value for each species sex and age class, rumen throughput times are affected by the condition of the forage. Briefly, young growing green leaf with a high protein and moisture content will have a much faster throughput time than mature dry leaf or stem with a low protein and moisture content. Differences can be directly related to the specific gravity of the food item. Items of low sp. gr. will tend to float in the dorsal chamber of the rumen where little digestive or fermentative activity takes place, heavier particles will sink to the ventral chamber with a greater rate of digestive activity, break down and passage into the reticulum, (Hungate 1966).

Without recourse to detailed experimentation with tame animals, estimates of DMI must be based on assumptions extrapolated from other habitats and other species. For this

I use the results of S-Price (1974 & 1977) for Cokes hartebeest in southern Kenya. As he gives a detailed treatment of his methods and shows results for a wide range of forage nutritive values, it is possible to select the most appropriate results for the habitat and forage values of this study.

Earlier estimates of DMI have come from Anison & Lewis (1959) who assumed that DMI per day approximately equals half the dry matter weight of rumen contents. This relationship (determined for cattle) was used by Swank & Petrides (1965) in Uganda for a range of ungulates.

Hopcraft and Arman (1970) put forward a regression equation for estimating DMI from animal live weight. They stated the method was tested for a variety of wild and domestic ruminants, but few details and results were given. Their equation is:-

$$\text{Log DMI (Kg per day)} = 0.849 \log \text{live weight (Kg)} - 1.487.$$

Estimates of food intake rate can be made from grazing experiments where grazing offtake is measured. However in a natural environment with a mixture of grazing species the determination of mean rate of intake for any one species becomes virtually impossible. This is discussed further below.

7.141 Rumen fill.

Data from the post mortem studies outlined above gave information on rumen contents weights for several species. These data were tabulated into species, season and sex classes for closer analysis. Using known live weight for each species (chapter 8), rumen fill mean values could be expressed as a percentage of body weight. All results are shown as rumen contents dry matter weights to avoid the greater variability due to free and plant water in the rumen. Total moisture content of the rumen contents varied from 61 to 89% of the total weight for wildebeest.

7.142 Grazing offtake.

The grazing exclosures in the typical Terminalia habitat and the heavily grazed area of Lihangwa (both short grass wooded grassland areas) described in chapter 4 were used to determine grazing offtake. Methods followed those outlined by Milner & Hughes (1968), whereby sample plots were clipped outside the exclosure (open to grazing) and within the exclosure (closed to ungulate and African hare, grazing). Details of this method and its results are described in appendix 10.

7.143. Dry matter intake rate as a function of food quality.

Stanley-Price (1974) examined correlations between several variables considered relevant to the rate of food intake. These included: particle retention time in the rumen, rumen dry matter weight, rumen nitrogen, faecal nitrogen and forage moisture content. From these correlations Stanley-Price concluded that dry matter intake could be predicted from faecal nitrogen, grass moisture and particle retention time, knowing rumen dry matter content. He established regression equations for these predictions, which are discussed in appendix 10.

Stanley-Price (1974) also suggested correlation between forage crude protein content and forage specific gravity, and between specific gravity and grass moisture. By combining the relationships between these variables one can construct a predictive relationship for retention time from forage crude protein content and hence estimate dry matter intake (DMI).

Data from Stanley-Price's correlations have been combined into a graph plot of CP against Retention Time (RT). This is shown in figure 7.6a, Note that a retention time of 15 hours is taken as the maximum rate of throughput, this rate is achieved with a diet of 11% CP content.

This method gives results different from those using Stanley-Price's faecal nitrogen regression and from

Annison and Lewis's and Arman & Hopcraft's techniques, see appendix 10. As rumen contents weight and forage throughput times differ from season to season the predictive equations of Annison & Lewis, & Hopcraft & Arman are of little value. The choice lies between Stanley-Price's predictions based on faecal nitrogen content & dietary crude protein. I presume the structural relationship of crude protein to specific gravity to rumen retention time may be a more realistic interspecies relationship than extrapolating from the physiological basis of relating faecal nitrogen to intake for hartebeest on Themeda range in Kenya. For this study therefore I use crude protein to estimate dry matter intake rate.

7.15 Estimation of Nutrient Intake.

This thesis uses protein as an indicator of nutrient content but nutrients can also be expressed as total nutrients (protein, fibre carbohydrate & fat) or as gross energy. Estimates of nutrient intake rate depends on a knowledge of total food intake and the nutrient content of that food, viz:

Daily protein intake = Daily food intake x food protein content.

Nutrient intake is normally expressed in terms of digestible nutrients, e.g. Digestible Protein, Dp; Total Digestible Nutrients, TDN; and Metabolizable Energy, ME. Intakes may also be expressed as a function of the animals metabolic weight which allows interspecies comparisons to be made, e.g. gms or Mcal per $kg^{0.73}$ per day where $W^{0.73}$ indicates the animals metabolic weight (see below).

Values of TDN and ME can be obtained from feeding trials which are beyond the scope of this study, or from published regression values.

Butherworth & Diaz (1970) suggested that for tropical grasses:

$$TDN = 51.2 + 4.26 \log CP - 0.25 CF + 5.12 \log EE$$

where CF is forage crude fibre & EE is forage ether extract or fat. These values are discussed in appendix 10 and a graph plot of TDN against CP shown in Fig. 7.6c.

Rogerson (1970) working in Kenya showed that for tropical grasses:

$$ME = 0.0356\ TDN \text{ in Mcal/kg dry matter}$$

which closely agrees with Crampton (1969) who showed that

$$1 \text{ kg TDN} = 3600 \text{ kcal M.E.}$$

7.16. Estimation of theoretical nutritional requirements.

Nutritional requirements (DP, TDN, ME) are a resultant of the animals metabolic activities which are a function of the animal live weight. Brody (1945) proposed the following relationship between metabolic rate and live weight.

$$BM = 70W^{0.73}$$

where BM is the rate of basal metabolism in Kcal/Kg/day, 70 is a constant and $W^{0.73}$ is the inter species mean metabolic weight index for a wide range of mammals. Basal metabolism is the level of metabolic activity required for the maintenance of physiological homeostasis, it does not allow for work, growth or reproductive activity. More recent studies have shown some species to have metabolic rates very different to Brody's mean. This range of variation, the reasons for such variation and the choice of relationship used in this study are discussed in appendix 10.

Energy requirements for basal metabolism (MER) are identical to rates of basal metabolism. Requirements for maintenance, i.e. all activities except growth & reproduction, have been estimated at 1.36 MER (Stanley-Price 1974) and 1.33 MER (Moen 1973).

Digestible protein requirments (DPR) for basal metabolism have been estimated at $0.88 \times W^{0.73}$ gms DP per day, (Moen 1973). Estimates for DPR and for total digestible nutrient requirements (TDNR) for maintenance activities are very much higher.

Appendix 10 discusses my choice of three predictive expressions for each nutritional requirement (MER, DPR, TDNR). These expressions are used to show the likely range of requirements for animals in this study.

Expressions chosen are shown below with the calculated value of requirement for a 273 kg wildebeest (average adult male weight, see chapter 8). All requirements are for maintenance metabolism.

A) Metabolic energy requirement (Kcal/day)

Source	Expression	Wildebeest Requirement
Brody (1945)	$70W^{0.73}$	5463
Hopcraft & Arman (1970)	$70W^{0.85}$	10709
Rogerson (1970)	$104W^{0.73}$	8116

B) Digestible protein requirement (gm/day)

Source	Expression	Wildebeest Requirement
Brody (1945)	$3.65 \times W^{0.73}$	219.1
Elliot & Topps (in Stanley-Price 1974)	$1.30 \times W^{0.73}$	78.0
Maynard & Loosli (1962)	$2.78 \times W^{0.75}$	186.7

C) Total digestible nutrient requirement (gm/day)

Source	Expression	Wildebeest Requirement
Brody (1945)	$35.2 \times W^{0.73}$	2113
Elliot & Tops (in Stanley-Price 1974)	$22.0 \times W^{0.73}$	1321
Crampton & Harris (1969)	$31.8 \times W^{0.73}$	2136

Moen (1973) discusses estimates for nutritional requirements for growth and reproduction for North American wild ungulates and domestic stock. His findings (for DPR only) are summarised as follows:

Growth requirement (GR) = $0.16 \times dW$

where GR is in gm DP per day

0.16 is a constant

dW is netgain in growth per day in gm. (Note that Moen gives this in kg, which is obviously incorrect)

Gestation Requirement (PR) = $(e^{-3.121} + \frac{0.0298td)}{0.9}/45$

where PR is in gm DP per day per kg foetal birthweight.

td is length of gestation to date, in days.

-3.121, 0.0298, 0.9 and 45 are constants.

Lactation Requirment (LR) is not possible to estimate for this study due to the large number of unknown variables, but it is likely to be in the region of 120 gms DP/day for a wildebeest in peak lactation, i.e. some 1-2 months following parturition, (assumed from data in Moen 1973).

With no other published estimates that I know of, I assume these estimators hold for East African bovids for the purposes of this study.

7.2. Results

7.21 Gross dietary characteristics & species selection

7.211 Browsing species.

Observations of plant species, and where relevant plant part, ingested by five browsing or partly browsing ungulates - greater kudu, eland, impala, sable and waterbuck, are summarised in table 7.1A. Data include species identified from field observations and from rumen analysis, observations being combined into a subjective scale of abundance in the diet. A mean value of browse content in the rumen material (by % dry weight) is given for four species in table 7.1B. The value for impala is based on % frequency analysis and is described in detail in appendix 8. With the exception of the smaller antelope (common, red and blue duiker, suni, bushbuck, grysbok and klipspringer) no bovid species apart from those of table 7.1 has been observed to browse. In this study area, only greater kudu and eland of the larger bovids can be categorised as pure browsers; impala, sable and water buck being basically grazers with a tendency to increased use of browse as the dry season progresses, (appendix 8). Buffalo have been observed to take browse in many areas of Africa (Sinclair 1977, Hoffman & Stewart 1972) but from examination of a small sample of shot buffalo (n = 6) and from field observations, I have no evidence for their taking browse in this study area. Waterbuck browse input of 1.4% categorises this species as a grazer, but they do take browse in other areas.

7.211. 7.212. Grazing species.

Wildebeest, hartebeest, zebra, buffalo and warthog are grazing animals. On no occasion have I seen the first four species taking browse, and rumen/stomach content examination revealed only small quantities of dicotyledon material (forbs) of less than 1.0% of the total. These small quantities can be accounted for by accidental ingestion when cropping a forb rich sward. Warthog during the rains feed on the aerial shoots of grass material, but during the dry season they take increasing quantities of roots, tubers, rhizomes and bulbs of perennial grasses, sedges and fleshy monocot herbs such as the Iridaceae.

Results of an examination of 50 warthog stomach samples (obtained in 1974 - 1976) are given in table 7.2. The inclusion of fruits in the diet is of interest, the numbers of these items in the stomach would suggest they were selected for and not ingested by accident.

The three bovid species and zebra are complete grazers but observations on their habitat occupance, feeding behaviour and morphological adaptations indicate differences in mode of feeding. Lichtenstein's hartebeest and sable, apparently a pure grazer in the rains, are restricted to the tall grass woodland habitats, with a small number of hartebeest frequenting the medium grass wooded ridges and the flood plain edges throughout the year, (chapter six). Jarman (1974) has stated that the size of a food plant and the size of the feeding animal determine the homogeneity or heterogeneity of food item to the animal. For example a small grass plant may be heterogenous, i.e. composed of different parts of different food values, to a small grazer such as the oribi but is homogenous to a large grazer such as buffalo. The large grazer by virtue of its large feeding apparatus - the mouth, lips and teeth, is unable to select from the plant and can only accept all of it or ignore all of it. The very size of the woodland grasses, up to 1.5m tall means the plant is heterogenous to all sizes of grazing ungulates, and hence all are able to exercise some degree of selection of plant parts. Observations of sable and hartebeest show this selective style of feeding. As grazing pressure and animal density are low in the woodlands it is a relatively easy matter to watch a hartebeest or sable feeding from a distance of up to 100m and then to walk to the feeding site and find the plant fed on. Casual observations of such feeding show that from mature grasses, leaves and especially the distal portion of leaves are taken, and are taken from all heights within the leaf table from basal leaves to the upper leaves of the vegetative stems.

During the dry season after burning the pattern changes and the available forage consists of young fresh leaf growth of up to 10cm in length. This sized food item then becomes much more homogenous to the larger grazing animal and less selection can be made. But as this growth is uniform in size and dispersion and is high in nutrients, little selection is necessary to achieve an adequate dietary in take. (Immediately following burning, before regeneration occurs, I have observed hartebeest utilising parts of the basal tussocks of perennial grasses, the animal occasionally scraping the tussock with its forefeet to expose edible portions). This mode of feeding, which allows the ingestion of individual leaf blades at a range of heights I term selective grazing. Observations on sable were made less frequently but their feeding behaviour appears similar to that of hartebbest.

The wooded grassland habitat on the other hand has a high grazing pressure during the rains and grasses are short (leaf table $\nless$ 30cm) and so food plants will be homogenous to larger grazers throughout the year. Species diversity is high with often more than 6 grass and 6 forb species per m^2. Observation of the steady decrease in grass layer standing crop (in terms of leaf table height) throughout the year, would indicate that over the complete spectrum of grazing animals no obvious selection or avoidance of grass species is taking place. Exceptions to this include the single species patches of *Bothriochloa pertusa* which in its mature form is avoided due to its pungent smell. To the south of the habitat, monospecific patches of mature *Heteropogon* and *Themeda* are avoided and surrounding areas of *Sporobolus*, *Digitaria* etc heavily grazed. I do not discount individual grazing species exercising selection for different grass species, but as all grass species are similar in size, shape, growth stage and nutrient value, I do not expect such selection to be extreme or important. As this study is examining overall habitat use and nutrient input, and not investigating competition or separation between sympatric grazing animals no attempt has been made to study selection for plant species.

During the dry season the largely annual sward dries and begins to fragment rapidly (chapter 4). There would appear to be selection for greenness and growth stage by the animals remaining in this habitat. Microhabitats such as shaded areas, anthills, lowlying areas etc. receive heavy grazing pressure. The previous chapter discussed the intense grazing pressure on the flood plain margins at the onset of the dry season. Following burning, virtually the only grass to produce fresh growth before the rains is *Panicum infestum* and this is heavily grazed at this time, (chapter 3 & 4).

Large grazing animals appear to select for microhabitat involving grass growth stage (and hence nutritive value) rather than for plant species within the sward in this vegetation type. Observation of grazing by wildebeest, zebra and buffalo, shows a continuous low level cropping rate with no apparent sign of any examining, smelling or tasting of food items before ingestion. This mode of feeding which involves a minimum of selection within a chosen sward I term "coarse grazing". Comparison with impala grazing accentuates this definition of coarse grazing. Impala graze extensively in this habitat during the rains. Their feeding is less rapid and less continuous, more searching (testing?) is involved, with the animal moving from spot to spot taking few bites per time interval or per spot than the larger animals, (my subjective observations). Impala may thus be called a "selective grazer".

Chapter 6 has shown a major separation in habitat occupance between zebra and wildebeest in the dry season, although during the rains their selection of the same habitats and use of similar feeding styles makes separation difficult to vizualize at this season. During the dry season in the woodland habitats, wildebeest strongly select valley bottoms and lower slopes and areas of fresh green growth. Zebra show little selection for topography and none for burning condition (grass growth stage); I have no observations of zebra feeding behaviour in these long grass areas. Whether they can select plant part as do hartebeest or if they can maintain themselves on the coarse dry leaf and stem material, (c.f. Bell 1969, 1970, with Serengeti zebra occupying tall grass areas and ingesting a large proportion of stem and coarse leaf), I do not know.

Results of analysis for selection of plant part: grass leaf, sheath, stem are given under section 7.221.

7.213. Morphological adaptations to feeding.

Fig. 7.1 illustrates measurements used and also shows the generalised shapes of lower jaws for both browsing and grazing animals. Browsing animals have forward projecting incisor teeth in a rounded tooth row, grazing animals have more massive vertical teeth in a flattened incisiform tooth row. Table 7.3 gives details of the measurements and fig. 7.2 illustrates the linear relationship between the two ratios. It is apparent that the two pure browsers, duiker and greater kudu form a sub group, sable and impala which take graze and browse are close together, hartebeest and waterbuck which are selective grazers fall close to eland, a non-selective browser, and the three non-selective grazers, zebra, wildebeest and buffalo form another group. One can conclude that these physical measurements of the animals morphological adaptations do relate to feeding style and diet selectivity. Note that these groupings form a gradation, they are not distinct entities.

7.22 Quality of food intake

Results given here include an analysis of selection for plant part in the diet, which coupled with a knowledge of CP content for each part can lead to an estimate of protein value in the diet. Other results are for rumen/stomach contents CP analysis, estimation of CPd from FN, and estimation of digestibility coefficients for protein.

7.221 Selection for plant part.

Due to circumstances beyond my control it has not been possible to obtain results for plant part dietary composition from Dr. Gwynne in Nairobi (see section 7.131). However if such results are obtained before final compilation of this thesis they will be included as an addendum.

It is reasonable to suppose that results would show a pattern similar that to other large grazing mammals, i.e. a high grass leaf content in the rains and an increasing proportion of stem and leaf sheath as the dry season progresses e.g.

eg. Buffalo (Sinclair 1977) Cokes Hartebeest (Price 1974) Topi (Duncan 1975), Wildebeest and Zebra (Owaga 1975). Local differences due to the largely annual nature of the forage and the regeneration of Panicum infestum leaves in the dry season may become apparent.

Putting together rumen plant part composition and results of forage protein analysis to give data on dietary protein input assumes that the criteria used by the animal for selection and ingestion are the same as those of the ecologist when clipping and partitioning parts for analysis. This is very probably not so. Results for forage protein analysis usually come from a limited number of clipping samples of 1m square. The grazer however can select from micro habitats and within very small areas. As such the nutritive value of forage ingested is likely to be higher than that clipped by the ecologist. Results would therefore under estimate protein input. Both Duncan (1975) and Price (1974) discuss this shortcoming and suggest that results based on faecal nitrogen regression give more accurate results of protein intake. Accepting these conclusions indicates that the lack of data for rumen plant part composition is not crucial to the studies described in this chapter. Such results would, however, assist in the separation of niche occupance between sympatric species of similar grazing habits.

7.222. Stomach contents crude protein analysis.

Nitrogen analysis of stomach contents of non-rumninants, when converted to protein can give a direct measure of dietary crude protein values, CPd. Values for crude protein for 38 warthog stomachs and for 9 zebra stomachs are given in table 7.4. Values for both warthog and zebra show a significant decrease in protein value from high levels in the rains, to low levels in the dry season.

Warthog: rains $\bar{x} = 10.08\%$, n=16, dry $\bar{x} = 8.1\%$ n = 22,

$t = 2.12$. Sig, $p < 0.05$.

Zebra: rains $\bar{x} = 11.16\%$, n=5, dry $\bar{x} = 5.08\%$ n = 4,

$t = 12.39$, Sig, $p < 0.001$

Note that the significance level for warthog increases if the values for May, which vary from 5.4% to 14.5%, are removed from the totals for the rainy period, (see table 7.2).

Nitrogen analysis of rumen contents however can only give a relative measure of dietary protein, (see Price 1974, and Duncan 1975), and cannot be used as a direct measure in any season. Any relationship to dietary protein is likely to be nonlinear. Price showed no correlation between rumen nitrogen and diet protein in hartebeest in Kenya. Table 7.4

documents monthly mean values for rumen "protein" (N x 6.25) for wildebeest and impala and less frequent values for sable and hartebeest. Standard errors of the mean value are given when sample sizes are large enough. Figure 7.3 illustrates the seasonal change in rumen protein for wildebeest and impala and shows monthly rainfall and monthly forage crude protein levels as a basis for comparison. Figure 7.3 also shows values for seven wildebeest shot in the woodland habitat during the dry season. These woodland wildebeest show higher values than the wooded grassland animals, which is probably indicative of the higher protein values in the regenerating woodland grasses. Impala dry season rumen protein values are as high as the rainy season values and considerably higher than values for wildebeest. This can be explained by the increasing quantities of high nutrient content browse in the dry season diet of impala.

Significance levels for seasonal differences, using monthly means, are as follows:

Wildebeest: rains $\bar{x} = 17.93$, $n = 6$, dry $= 13.30$, $n = 6$,
$t = 3.54$ Sig. $p < 0.01$

Impala : rains $\bar{x} = 18.65$, $n = 6$, dry $= 16.90$, $n = 6$,
$t = 1.34$ NS.

7.223. Faecal nitrogen analysis.

Section 7.133 and A.10 detailed four regression equation for estimation of dietary crude protein from faecal nitrogen values. These equations give different results, especially for lower values of faecal nitrogen, and two were discarded. The expression of Bredon et al (1963) is an inter species mean value, and accepted for Serengeti topi by Duncan (1975). Arman's equations are specifically for wildebeest in the Amboseli Basin of Kenya, a habitat with some similarities with this (Western, 1973). Table 7. 5 shows faecal protein % (faecal nitrogen x 6.25) for four species and corresponding dietary protein values estimated by both methods. In the case of wildebeest, December to May are considered rainy season months for the purposes of using Armans' two equations. Values for impala (which take browse) and sable and hartebeest (which take fresh regenerating grass) ar considered as rainy season values throughout the year. Zebra stomach contents protein values are included as a comparison.

Using Bredon's estimator (CPd$_1$ in the table) it is clear that dietary protein values are higher in the rains than in the dry season for wildebeest, whilst there is little or no difference between seasons for impala. Sable and hartebeest mean dry season values show no significant difference (t = 1.96, d.f = 9) although means differ by some 3% protein content, eg. sable 9.73%, hartebeest 12.97%. Values for these two species are combined therefore and show a greater dietary protein value than wildebeest but no difference from impala in the dry season. Impala dry season values are considerably greater than those of wildebeest. It is possible that further data could show a difference between sable and hartebeest results. Wildebeest dry season data are from the short grass habitats, woodland data would show higher values.

Significance values are as follows:

Wildebeest rains: dry season $t = 2.76$ df 17 Sig, $p < 0.05$

Impala rains : dry season $t = 1.72$ df 10 N.S.

Dry season Sable: Hartebeest $t = 1.96$ df 9 N.S.

Dry season Sable Hartebeest Impala $t = 0.91$ df 16 N.S.

Dry season Sable Hartebeest: Wildebeest $t = 8.34$ df 19 Sig. $p < 0.001$

Dry season Impala: Wildebeest $t = 6.98$ df 17 Sig. $p < 0.001$

It is emphasised that sample sizes are small and variable, and so these results should be treated with caution.

Wildebeest dry season values (CPd_1) show no difference from zebra values (assuming zebra stomach CP to indicate dietary CP) although wildebeest values using Armans expression (CPd_2) do show a difference, ($t = 3.19$, df 12, Sig. $p < 0.01$).

Shot wildebeest and zebra were taken from roughly the same habitat, although it is possible zebra had been feeding on the flood plain. If they show no differences in selection of food items in the diet then one would expect dietary values to be similar, which would support the use of Bredon's estimator. But studies elsewhere (Bell 1969, Owaga 1975) have shown that zebra take greater quantities of stem and sheath than wildebeest which would indicate lower protein values in the zebra's diet, thus supporting Arman's estimator. The decision on which estimator to use cannot be made without further information. I therefore take the difference between the two estimates to be the range of possible estimates, and, where a single figure is required I take the average of the two.

Chapter 4 detailed the protein value of grass leaf, dry leaf and stem components for the Terminalia wooded grassland habitat (Terminalia exclosure, table 4.6 and 4.9). Combining these figures into a mean value for the habitat, it is possible to show whether selection for dietary protein by grazing animals is taking place. That this selection could be by selecting specific species (unlikely) or by selecting plant part or micro habitat is immaterial. The question here is if total selection for protein takes place. The possibility of selection can be seen from fig7.4. This figure indicates two major items:

(a) the proportion of each plant part, green leaf, dry leaf and stem, in the sward and the crude protein content of each part. These values are summed to give the weighted mean crude protein content of the total grass forage.

(b) for each of four species, wildebeest, zebra, impala and warthog, the estimated protein value of the diet as determined by faecal nitrogen regression or from stomach contents.

Where selection for protein takes place, the diet CP value should exceed the forage CP value, with no selection the values should be similar, and if avoidance of protein occurs then dietary CP should fall below the forage value.

The figure shows that during the early rains. December to February there is little evidence for selection. Note that the low values of dietary CP as compared to forage CP for zebra and wildebeest in December, can be explained by the fact that forage CP values come from clippings after burning, so there is *no* old leaf or stem component in the forage value given in the figure, but there will be in the total environment. Furthermore, new short grass growth may not be long enough to be available to the coarse grazers. Assuming half the habitat to have similar amounts of old forage to November, I have estimated a combined forage CP value for December; this value, of some 10%, is shown in fig. 7.4 and is close to the estimated values for zebra and wildebeest dietary protein.

From March to October dietary CP for all species is considerably higher than forage values, indicating selection for protein does take place. It is seen that impala have very high values, which can be explained by their taking browse items. Zebra and wildebeest dietary CP values are at a low period from August to November. Wildebeest values are for those animals shot from the wooded grassland habitat, whilst the bulk of the population have moved into the woodlands where the diet should resemble that of sable or hartebeest. This I have indicated in fig. 7.4, using an average of sable and hartebeest values for this period. Zebra, (according to Serengeti studies, Bell 1969) are able to exist on low protein/high cellulose diets due to the cellulytic fermentation activity in their caecum. Presumably warthog have a similar ability, although their protein intake will be increased by the selection of roots etc. This question of feeding strategies is discussed in more detail at the end of this chapter.

Unfortunately few of the rumen contents nitrogen analysis are for the same animal as the faecal matter nitrogen analysis. Only ten pairs of results are available for wildebeest, the species with most samples. A regression of rumen N values against faecal N values shows a weakly significant correlation, ($r = 0.691$, d.f = 8, Sig<0.05).

7.224. The digestibility of dietary crude protein.

Of the total crude protein ingested by an animal only a portion is available to the animal. Some proteins, bound in cell wall compounds, are not digestible. The proportion available increases as the total protein content in the food item increases. Available protein is termed Digestible Protein (DP), and this quantity has been estimated by the regression equation of Bredon et al (1963), for the range of CPd values encountered in this study. Results are shown in table 7.7 and figure 7.6b.

7.23 Quantity of Food Intake

7.231 Rumen fill.

Information on rumen contents weight is available for month, sex, and age class for wildebeest and impala, with lesser amounts of data for other species. Monthly change in mean rumen contents weight and an indication of range and sample size is shown in figure 7.5. Mean rumen weights for all species are shown in table 7.6. This table also shows rumen weight as a percentage of total body weight for adult animals, (body weight data is detailed in chapter 8).

A 't' test was used to test significant differences between rumen weights for different sexes and seasons. Results are as follows:

Wildebeest m:f $t = 11.02$ d.f. 22 Sig. ($p < 0.001$)

Impala m:f $t = 2.24$ d.f. 22 Sig. ($p < 0.05$)

Wildebeest male dry:rains $t = 1.27$ d.f. 38 N.S.

female dry:rains $t = 1.79$ d.f. 55 N.S.

An arcsine transformation test using simple % data was used to test differences between % body weights between the sexes, but results were not significant (Sokal and Rohlf, 1969).

Of interest is the trend towards reduced rumen fill in the rains for wildebeest males. This decline corresponds to the period of the rut and is thought to be due to increased reproductive activity reducing time available for feeding (Moen 1973). Females have significantly higher rumen fills than males, both as a direct weight comparison and as a % of body weight. This trend has been described for other species, elephant (Laws et al 1975). Thomson's Gazelle (Robinette & Archer 1971), hartebeest (Price 1974) and topi (Duncan, pers. comm.).

Percentage body weight taken up by rumen contents has a tendency to increase with increasing body weight. As data are scarce in the literature and are not standardised (e.g. wet and dry weights) little comparative data are available (see section 7.333).

7.232 Determination of Food Intake

a) Measurement of grazing offtake.

Results are shown in table 7.8 and discussed in appendix 10. Analysis of these data gives an estimate of wildebeest offtake (input) of 4.14 kg/day averaged over the year.

(b) From published studies

Arman and Hopcraft's regression equation based on live body weight and Annison & Lewis's simple formula have been discussed in section 7.14 above. As they do not take into account variation in rumen fill or forage quality they are not considered further. Results that follow are based on the correlation between forage crude protein and dry matter intake discussed by S-Price (1974) and the values for throughout time given in section 7.143 and figure 7.6c.

Table 7.9 shows estimates of voluntary food intake for male and female wildebeest for each month and table 7.10 does the same for impala. Figures show considerable variation in input from season to season. Values for wildebeest are summarised here.

	Wildebeest	
Month	Male	Female
February	5.6 kg/day	6.8 kg/day
June	2.8 kg/day	3.4 kg/day
September	1.7 kg/day	2.2 kg/day.

Results for male wildebeest of 4.14 kg, 3.81 kg and 2.10 kg per day determined by grazing offtake experiments, Arman and Hopcraft's regression and Annison & Lewis's formula respectively are of the same order of magnitude as the values in table 7.9, which show an annual average 2.9 kg dry matter ingested per day.

7.24. Total Nutrient Intake.

By combining details of monthly mean food intake per day, protein content of the diet and values for protein digestibility it is possible to determine daily digestible protein intake for male and female wildebeest and impala. Values for wildebeest are given in table 7.11 and those for impala in table 7.12. Similarly, values for TDN and ME can be determined. It can be seen from the table that intakes in the late dry season (October) drop considerably from the intakes in the early rains (January), for wildebeest protein drops 98%, TDN drops 74% and ME drops 74% (note ME is determined from TDN, hence intakes are proportional).

At the foot of the table nutrient intakes are expressed as quantity per unit of metabolic weight (gms or kcal per kg $W^{0.73}$) which enables inter species comparisons and comparisons with theoretical intakes to be made.

7.25. Estimation of Theoretical Nutritional Requirements and Comparison with Actual Intakes.

Section 7.16 and A.10 detailed the range of published estimators for theoretical nutritional requirements for maintenance metabolism. Three estimators for DP, TDN and ME were selected for use. Quoting requirements as quantity per unit metabolic weight, these can be summarized as:-

Digestible Protein (gms)

Source and Estimator		Species and Body Weight (kg)				
		Wm (273)	Wf (212)	Im (52)	If (38)	Bm (570)
Maynard & Loosli	$2.78xW^{0.75}$	186.7	154.5	53.8	42.5	324.3
Brody	$3.65xW^{0.73}$	219.1	182.2	65.3	51.9	375.0
Price	$1.3xW^{0.73}$	78.0	64.9	23.3	18.5	133.6

Total Digestible Nutrients (gms)

Source and Estimator		Wm (273)	Wf (212)	Im (52)	If (38)	Bm (570)
		Species and Body Weight (kg)				
Brody	$35.2 \times W^{0.73}$	2113	1763	630	501	3617
S - Price	$22.0 \times W^{0.73}$	1321	1102	394	313	2261
Crampton	$31.8 \times W^{0.75}$	2136	1773	616	487	3710

Metabolic Energy (Mcal) Source Estimator x 1.36 for maintenance

		Wm (273)	Wf (212)	Im (52)	If (38)	Bm (570)
Rogerson	$1.36 \times 104 \times W^{0.73}$	11.55	7.06	2.53	2.01	14.53
Brody	$1.36 \times 70 \times W^{0.73}$	7.77	4.75	1.70	1.35	9.78
Hopcraft & Arman	$1.36 \times 70 \times W^{0.85}$	15.24	9.07	4.07	2.10	20.95

Figure 7.7a and 7.7b show actual intakes and theoretical requirements for DP and TDN/ME for male and female wildebeest. Figure 7.8a and 7.8b show the same for male and impala. Male and female impala data are almost identical, but female wildebeest by virtue of a greater rumen content per unit body weight have values considerably in excess of male wildebeest.

Impala results show no period of the year when protein intake is limiting when compared with the theoretical value of 1.3 gms/kg $W^{0.73}$ given by Elliot & Topps (in Price 1974). But values do drop below the value of 3.65 gms/kg $W^{0.73}$ given by Brody (1945) for the period of the late rains - early dry season (April-July). Adequate dry season protein intake is a result of high quality browse in the diet, impala changing to dicot components in July-August. Energy input (and hence TDN - as energy is directly proportional to TDN) shows a similar pattern, intake dropping during the March to July period. This intake is adequate for maintenance according to Brody's theoretical requirement but only just adequate for 6 months and inadequate for 6 months if Rogersons values for wildebeest apply to impala. Assuming Rogersons value to be inapplicable then the diet has adequate surpluses of both enery and protein for processes of growth, gestation and lactation.

Wildebeest show differences from this pattern, intake levels of both protein and energy being at their lowest during the dry season, July-November. For both nutrients values fall well below the lowest theoretical requirements, those of Price and Brody. During this period animals in this habitat are in negative nutrient balance as regards maintenance processes only. There are no surpluses for growth or lactation. Females are better off than males, due to their greater food input relative to body size, but even so they are protein deficient and energy deficient for 5 months, as compared to 6 and 7 months for males.

The small amount of data for hartebeest/sable show. that dry season intakes are well in excess of theoretical requirements for both protein and energy. This is a result of high quality graze being available after fire in the woodlands. Wildebeest moving into this habitat in the dry season can be assumed to have similar intakes as well.

7.26. Effects of Growth and Pregnancy.

(a) Growth.

Using Moen's (1973) values for the nutritional demands of growth, it is possible to estimate protein requirements over and above those for maintenance alone. Results for wildebeest are discussed here. As the nutritional inputs of lactation to the young animal are unknown, discussion is limited to animals over 9 months of age, i.e. when they are fully weaned (see chapter 8). Chapter 8 discusses growth rates of juvenile wildebeest and shows average daily increments (kg) over 6 month periods of:

Age (males)	Season	Growth increment	Protein Need	Mean Body Wt.
0-6 mos	Wet	0.46 kg/day	73.6 gms/day	60 kg
6-12	Dry	0.16	25.6	115
12-18	Wet	0.29	46.4	155
18-24	Dry	0.13	20.8	190
24-30	Wet	0.22	35.2	220
30-36	Dry	0.09	14.4	260

Moen assumed protein demands of growth were approximately: GR = 0.16 dW. where dW is daily gain in gms.

Intakes for immature animals depend on knowledge of rumen size, which apart from a mean figure of 2.8 kg for 13 animals between 3 and 36 months is not available. For the purposes of this exercise, I assume the following rumen size data:

	Dry	Rains	Dry	Rains	Dry	
Age (mos)	9-12	12-18	18-24	24-30	30-36	(males)
Rumen Size (kg)	2.2	2.8	3.3	3.8	4.2	(adult)

Mean rainy season CPd is 9.43% giving rumen throughput time of 18hrs.
Mean dry season CPd is 5.03% giving rumen throughput time of 60 hours
DP values are 4.5% and 1.4% respectively.

From data on rumen contents, throughput time and digestible protein content, actual protein intake can be determined. From body weight data and using the estimator of 1.3 gms/kg $W^{0.75}$ DP, the maintenance requirement for DP can be calculated. This can be summarised as follows:-

Age (Months)	Body Weight	Season	DP input	DPR (M)	DPR (G)	DPR (M&G)	BALANCE
9-12	120kg	D	13gms	42.8gm	25.6gm	68.4	-
12-18	155	R	168	51.6	46.4	98.0	+
18-24	190	D	19	59.9	20.8	80.7	-
24-30	220	R	228	66.7	35.2	101.9	+
30-36	260	D	24	75.3	14.4	89.9	-

where DPF (M) & DPR (G) are requirements for maintenance and growth respectively, and "Balance" indicates if protein intakes are adequate or not. Note that if Brody's estimator for DPE (M) is used, then the 12-18 months period is marginally in negative balance and the 24-30 month period is marginally in positive balance. The table emphasises that for short grass habitats, rainy season diets are in positive balance, dry season diets are not.

(b) Pregnancy.

Moen (1973) proposed an estimator for protein requirement for gestation of:

$$\text{DPR (p)} = \left(e^{a + bt/c}\right) \div 45$$ in gms per day per kg of foetal birth weight

where a, b, c are constants and t is time into pregnancy in days.

From Moen, a = -3.1206
b = 0.0298
and c is taken as 0.89, the ratio of wildebeest gestation (250 days) to Moen's cattle standard of 280 days.

With a birth weight of 16.1 kg (chapter 8), protein demands during pregnancy can be determined as:

Day	DPR (Pr)	Approximate Date
15	0.03 gm/day	1 April
45	0.07	1 May
75	0.19	1 June
105	0.53	1 July
135	1.45	1 August
165	3.96	1 September
195	10.81	1 October
225	29.53	1 November
250	68.19	Late November.

It can be seen that the nutritional demands of pregnancy are minimal until the last few weeks, demand at full term (day 250) is equivalent to that for body maintenance, 68.2 gms compared to 64.9 gms. This period, (late November and early December) is one of high nutritional input and females will be in positive nutritional balance. Protein demands for pregnancy during the dry season, a period of negative nutritional balance are negligible. The process of lactation has much great demands in term of all nutrients, estimated at 120 gms DP per day at peak lactation in January, February, March, a period of positive nutritional balance, with an adequate surplus for lactation.

7.3 Discussion.

7.31 Gross Dietary Characteristics

7.311. Browse-Graze categories

Jarman (1974) discussed the question of the use of the descriptive terms "browser" and 'grazer" and produced an enlarged classification of feeding style (with five categories, "A-E") based on the species ability to select food items in its diet. Jarman, and Estes (1974), showed that body size greatly influenced the degree of selection. Jarman stressed the fact that several species did not easily fit his classification, sable and waterbuck were immediate examples. Lack of detailed information was one reason for this difficulty of classification. This chapter uses two broad categories for grazing animals, sdlective grazer and coarse grazer (buffalo perhaps being a very coarse grazer). If these differences are added to Jarman's categories then classification becomes easier. A new scheme would then be:-

Jarman Class	New Class	Description
A	A	Entirely browser, very selective, small fixed home range. eg. duiker, suni.
B	B	Either all browser or all graze, very selective, larger home ranges, e.g. kudu, reed buck.
C	C	Flexible feeders, browse and graze, selective, large home range, e.g. impala.
D	D(i)	Grazer, can select parts & browse to some degree, animals of fixed home range, eg. sable, Lichtensteins hartebeest, waterbuck.
	D(2)	Grazer, little selection for dicot or individual part, frequently migratory, select grazing site rather than species or part e.g. wildebeest, zebra.
E	E	Bulk feeder, little selection, e.g. eland, buffalo.

As D(1) animals tend to be smaller than D(2) this scheme fits with the size element in Jarman's and Estes' discussion.

The seasonal use of browse by primarily grazing animals is odd, some species do, eg. impala, sable, cattle waterbuck, buffalo, whilst others do not e.g. wildebeest, hartebeest and zebra. The use of browse by impala is discussed in appendix 9. Use increases as dry seasons increase in severity, but where two rainy seasons exist impala are almost entirely grazers.

Child and Wilson (1964) state that sable and roan in Central Africa were "both mainly grazers that occasionally took browse, grass making up over 90% of the stomach contents". Seven browse species are noted as being used by sable (two only by roan, which seem to select fruits rather than leaves) three of which are used in this study area. Estes & Estes studied sable populations in many areas of Africa. They say of the Giant sable (Hippotragus niger variani Thomas), "Whilst the sable is primarily a grazer, it eats a certain amount of browse at all times of the year and substantial amounts in the dry season. By far the most important is Diplorhyncus condylocarpon", (Estes & Estes 1974). This is similar to the pattern here. These authors make similar statements for populations in Kenya and southern Africa

(Estes & Estes 1969 a&b). Wilson & Hirst (1977) in a recent paper on the ecology of sable and roan in southern Africa mention roan as taking over 50% browse in the diet (whereas in central Africa they rarely browse) and sable in South Africa taking little browse, even when graze is poor, but sable in Rhodesia took close to 80% browse. Clearly great differences exist from area to area: such differences may be genetically or learning process controlled (Westoby 1974).

The use of browse by cattle is discussed by Rees (1973) in Zambia and by de Leeuw (1975) in Nigeria. Buffalo are discussed by Sinclair (1977). No study of hartebeest, wildebeest or zebra has shown evidence of their use of browse plants. (I have seen one record of a single instance of hartebeest briefly feeding on D. condylocarpon in Zambia; Zambia Forest Research Herbarium, Kitwe, Zambia). Why this should be is not clear, especially for Lichtensteins hartebeest, a species of woodlands where seasonal grass biomass can be very low, as after late dry season fires, or the forage quality of available grass can be very low, often less than 2.0% CP in leaves.

Jarman & Jarman (1973) in a study of ungulate diets in Rhodesian woodlands present conflicting evidence. They show impala with a diet consisting of 5% grass and 95% browse over the course of a year. At the height of the rains, grass formed only some 20%. Buffalo in their study were primarily browsers, 54% of the diet being dicotyledons over the course of the year. Strangely grass formed only 20% of the diet in the rains and 74% in the dry season!

7.312. Adaptations to diet.

I know of no other studies that discuss gross external adaptations to diet within the Bovidae. Hoffman (1972) and Hoffman & Stewart (1972) discuss rumen morphology and show structural changes dependent on the amount of browse material in the diet. Estes (1974) discusses the behavioural implications of ungulates in grassland and wooded habitats and concludes the grazing habit evolved from the purely browse habits of primitive ungulates as a response to more open habitats and to greater body size. Jarman (1974) shows that fine selection in diet is not easily possible for large ungulates, which tend to maximise food quantity and not quality.

Cumming (1975) detailed the functional morphology of the head and jaws of warthog and compared this with that of bushpig. Feeding behaviour and morphology are closely related. Dubost (Afr. J. Ecol., 1979) shows a relationship between cephalophine shoulder height and feeding behaviour and habitat selection.

7.313. The concept of selection.

Elfyn Hughes et al, (1964) and Arnold (1964) give general reviews on the process of selection in herbivorous feeding. Several authors have examined plant species selection by African herbivores to show niche separation amongst sympatric species, (detailed in section 7.0).

Grasses, belonging to one plant family (and in African rangelands mainly to three tribes in one family), are an extremely homogenous group in terms of their structural and chemical components. This is very different when compared with non grasses which include several hundred plant families and very diverse chemical constituents, the so called "plant secondary compounds". Many of these compounds are toxic, either completely so or in degree, and browsing animals must exercise selection to avoid toxicity. It is thought such compounds may have evolved as a defence against herbivory (Freeland & Janzen 1974) and so herbivores have had to evolve considerable powers of selection (chemical recognition - acceptance or rejection) to overcome this defence. Field (1976) discusses the presence of such secondary compounds (called palatability factors) in African grasses, Such compounds do occur, but with the exception of aromatic oils in Cymbopogon and Bothriochloa (and possibly tannins in mature Andropogonae) they have little role in determining preference and selection and are non poisonous and mainly tasteless. Braden & McDonald (1970) detail many toxic compounds of tropical posture plants; only one group, the cyanogenetic compounds are found in grasses, and then only at certain seasons, notably when wilting during drought. Ruminal microbes are thought to break down such compounds when present in low quantities.

Physical defences against herbivory are infrequent amongst grasses (e.g. spines, prickles, irritant hairs etc.), although leaf tensile strength could be important in determining the ease of ingestion. The lack of inhibitors or repellents tends to make all grass species inherently available to grazing animals, and if selection for grass species does take place it is probably due to seasonal or growth factors such as height, leaf-stem ratio, or nutrient content and not characteristics specific to the grass species alone.

Determination of grazing selection for grass species is difficult. Techniques involve either tame animals (see Field 1968 and 1970) or the collection of wild animals and examination of rumen or faeces components with prior or subsequent sampling of the sward. Experiments with tame animals are difficult to arrange to represent natural condition. Sward analysis is difficult, and frequently sampled at only low levels for grazing studies. As plant particles can exist in the faeces up to 120 hours and rumen up to 90 hours after ingestion then the sampling of the sward in the vicinity of a shot animal may be grossly misleading. Fistulation techniques with fenced animals may overcome this problem.

Such species selection studies are concerned only with the abundance of the different species in the sward, and rarely with the differences in their growth stage, moisture content or other parameter of palatibility not due to taxonomic differences. A species with 10% abundance in the sward and 20% in the rumen cannot be thought of as being taxonomically selected if that is the only species in a palatable growth stage. Field (1968) states "Persistence of certain species in the diet even when rare in the sward implies considerable selection". This does not clarify what the animal is selecting for - is it that plant species or is it the microsite where the species is found or for a growth stage or other category in which that species is found. For example in the south of the wooded grasslands in this study area, Chloris virgata, Brachearia spp and Sporobolus spp are heavily grazed, but only where they occur on old termitemounds, and not when found under a taller canopy of Heteropogon. Similarly Panicum infestum is 'heavily' grazed, but most heavily under shade trees, (chapter 3). I strongly suggest that animals search for grasses of specific growth stages, greeness or moisture levels etc. and not for grass species A as compared with grass species B. Microsite is thus very important in determining palatability. Microsites tend to get over looked in rapid surveys of available forage when undertaking feeding studies.

Jarman's concept of heterogeneity of plant parts is a valuable idea in this context, as is the idea of coarse and fine grained environments to different species (Levins 1968)..Animals are selecting for optimum food quality within the restraints of energy expenditure in selection and the limitation of gross morphology for such selection. As plant leaves usually have a higher nutritive value than stems, leaves are selected more frequently by animals able to undertake such selection. But a wildebeest for example (a typical leaf selector) would probably choose young green stems of Brachiaria spp over dry rank leaves of Loudeta spp. Is it the plant part that is important, or is it the relative values of the parts that the animal is selecting for? Experimental work on this problem would be valuable.

It is my contention that animals select for nutritional values, eg. crude protein, although there is evidence that other nutrients such as sugars (Bland & Dent, 1962), may influence such selection. All selection for growth stage, site, species, part etc is a manifestation of selection for high concentrations of nutrients.

For several reasons I have been unable to present data on the possibilities of grazing selection for plant species or plant part. Information on crude protein however (fig. 7) does show that selection is taking place for a large part of the year. Only when protein is relatively abundant, i.e. in young growing grasses, does estimated dietary protein equal estimated forage protein, indicating no or little selection. As grasses mature and then decompose, their protein levels drop and selection becomes increasingly important. A new low point of selection is reached at the end of the dry season when protein content is uniformly low and high content forage cannot be selected. This information can be portrayed graphically by using a relative selection index (SI) where:-

$SI = \frac{\text{CP in diet}}{\text{CP in forage}}$ and

$SI < 1.0$ indicates avoidance

$SI = 1.0$ indicates no selection

$SI > 1.0$ indicates selection.

Such a selection index is plotted against calendar month in fig. 7.9 for four grazing species.

7.314. Morphology and selection.

Jarman (1974) shows how increasing body size reduces the possibilities of selectivity in feeding behaviour. Figure 7.2 with the exceptions of kudu and eland agrees with this generalisation, larger animals showing less adaptation towards selective food gathering. Warthog are of interest in that posture is adapted towards diet specialisation by lowering head height not raising it. This enables the animal to feed on the lowest parts of plants, the basal stems and subterranean organs. The warthogs typical feeding stance of reclining on the "elbow" is an extreme modification to this specialisation (Cumming, 1975).

Figure 7.9 shows little difference in the ability to select from above ground grass material for four large herbivores from December to May, the period of high nutritive levels in the forage. From June onwards the two smaller animals with morphological adaptations to diet increase their selectivity by switching feeding behaviour; impala, with a high head posture to browse, and warthog with a low head posture to subterranean organs. By these changes these two species are able to increase dietary inputs above the levels of the larger coarse grazers, zebra and wildebeest. The concept of feeding strategy is discussed further below.

7.315. Grazing succession and selection.

Bell (1969, 1970) and Vesey Fitzgerald (1960, 1969) discuss the ideas of a grazing succession within Africa herbivores. Basically animals which are ill adapted to the utilisation of tall grass forage (the smaller species), are only able to utilise the pasture after the passage of larger species which reduce grass height by grazing (zebra in Serengeti) or by trampling (buffalo in Rukwa). Chapters 4 and 6 have discussed the role of fire in supplanting such a succession in the miombo woodland habitat.

7.32. Dietary Protein.

7.321. Rumen content nitrogen analysis.

Klein (1962) and MacBee (1964) quoted in Moen (1973) are the earliest attempts to describe food quality from rumen chemical analysis. Klein states the method enables a reliable comparison to be made, but a quantitative basis for such a comparison would be valuable. Hall-Martin & Basson (1975) used rumen nitrogen levels, expressed as CP, to compare seasonal changes of dietary protein in giraffe. They concluded that the method does have values as an indicator of dietary nutrient content.

S- Price (1974) and Duncan (1975) discuss the factors preventing the use of a direct relationship between rumen N% and forage CP% as can be done for non ruminants Table 7.4 and figure 7.3 show seasonal changes in rumen and stomach nitrogen for several species. Interspecies and seasonal differences are immediately apparent. Of interest is the higher level of rumen nitrogen for wildebeest shot in the woodland habitat during the dry season. Values here are considerably in excess of those from the wooded grasslands and reflect the high protein content of post burn reg$\overset{er}{e}$rating grassleaf.

July-November Miombo, $\bar{CP} = 16.56$, W. Grasslands $\bar{CP} = 14.03$,

$n = 10$.

$t = 2.48$. Sig. < 0.05.

Assuming the validity of rumen content N analysis as an index of dietary protein content, the results obtained agree well with what is known of different species feeding behaviour.

7.322. Estimation of dietary protein from rumen plant part analysis and from faecal analysis.

The estimation of dietary protein content is of crucial importance to the results of this chapter. As rumen N content analysis cannot be used, and plant part analysis results were not available, figures used are derived from faecal nitrogen regressions based on different species and different diets. Earlier sections have quoted both Price & Duncan as stating protein content of the diet is underestimated by plant part analysis. This is presumably due to the animals ability to select for protein being greater than the ecologist's clipping experiments and also due to differential retention times for different parts (leaf< stem) causing bias in the analysis. Correction factors for different retention times can be applied (Duncan, 1975) but these are difficult to determine.

Duncan found that dietary protein calculated from faecal analysis was in close agreement with values obtained from oesophageal fistulated animals. He attached high confidence to the accuracy of these results, using Bredon et al's(1963) generalised regression equation. Two regression equations were available, those of Bredon et al and those of Arman for Amboseli wildebeest. Section 2.23 discussed the advantages of both methods and concluded that a mean value from both methods was preferable for this study. As results are used on a comparative basis (species, seasons etc.) then a relative value of CPd can be acceptable.

7.33 Food intake

7.331 The grazing exclosures.

Due to the large number of unknowns the grazing exclosure experiments could not give 'accurate' results for daily intake rates. Combination of less important unknowns allowed the solving of simultaneous equations to determine rates for two species, but the method could lead to very large biases. Results obtained however, especially for wildebeest, are of similar orders of magnitude to the results from other methods.

It is of interest to apply the results from other methods to the grazing experiments and look at differences.

Exclosures data were as follows (Table 7.8):-

Late rains I	3.3kg/ha offtake per day	(0.23W, 0.48 I per ha)
Late rains II	5.3kg/ha offtake per day	(0.88W, 0.31 I per ha)
Dry season	2.9kg/ha offtake per day	(0.33W, 0.33 I per ha)

Estimates of food intake are (Table 7.9 & 7.10):

Season	Wildebeest	Impala
Late rains I	2.42 kg/day	0.79 kg/day
Late rains II	2.47 kg/day	0.83 kg/day
Dry season	1.20 kg/day	0.54 kg/day

Wildebeest and Impala figures are computed as 0.7 times the male rate to allow for juveniles in the grazing population. Impala dry season values are computed as 0.5 times the male rate to allow for browse input. Buffalo are assumed to be x 3 the wildebeest rate, zebra x 2 and warthog x 0.7.

Offtakes are therefore (in kg/day):

LR I	Actual (A)	3.3	Computed (C)	1.79	C = 54% A
LR II		5.3		3.76	C = 71% A
Dry		2.9		0.75	C = 26% A

Results are thus very different, and I do not think more exact figures for population offtake rates would make any appreciable difference. Both exclosures were in swards of high annual grass species content, which fragment after growth ceases, especially with trampling. Much of the loss not accounted for by grazing will be by such fragmentation, increasingly so in the dry season.

7.332. Intake rates.

The methods used to compute intake rates shown in tables 7.9 and 7.10 have been discussed in earlier sections. Mean annual rates of 4.2 and 5.5 kg/day (70 and 110 gm/kgW$^{0.73}$/day) for wildebeest and 1.4 and 1.1 kg/day (77 and 77 gm/kgW$^{0.73}$/day) for impala are in agreement with those of hartebeest - 64g/kgW$^{0.73}$/day (Price 1974). Hartebeest data vary from 26.1 gms to 87.5 gms from dry season to rains and wildebeest vary from 26.7 to 93.3 gms (males), results which are very close indeed.

Bines (1971) and Forbes (1970) discuss food intake rates of pregnant and lactating ruminants and show an increased intake during lactation and a decreased intake during late pregnancy. The decrease is a physical limitation due to foetal volume reducing abdominal space for rumen distension. Comparable data are not available as intake rates are controlled by diet quality and these effects cannot be separated from those of lactation. Data on rumen contents weight are limited and variable for individual months. Female rumen weights are low at the time of late pregnancy, but so are those of males so no conclusions can be drawn.

Seasonal intake rates vary by a factor of 3.5 and 3.8 in male and female wildebeest respectively. Low dry season values are due to very slow throughput times. To enhance digestion, rumination time increases with poor quality diets, (Sinclair 1977, Hancock 1954). This will cause a decrease in time available for feeding but feeding rates will be low as rumens at maximum distension will decrease feeding stimuli (Bines 1971). Dry season rumen weights are higher than rainy season values, indicating that input is as high as can be, commensurate with the low throughput times.

7.333. Rumen content weights.

Section 7.231 mentioned a trend towards increased rumen size relative to body size with increasing body weight. Data is available for buffalo from Kruger National Park, South Africa, (Pienaar 1969), dik dik and suni (Hoppe 1977) Zebu cattle, Grant and Thomsons gazelle and suni (Hungate 1959) Cokes hartebeest (Price 1974) and Thomson gazelle (Robinette & Archer 1970).

Data used are dry weight rumen contents expressed as a % of total body weight. Results are shown in figure 7.10, and give a correlation coefficient 'r' of 0.903, n = 12, sig. $p < 0.001$. Note that the value given by Hungate for

Thomson gazelle has been left out as it is very atypical (3.16% body weight). The significance of this trend to larger rumen size is discussed below.

7.34. Feeding and Nutritional Strategies.

Westoby (1974) discussed the concept of feeding strategies in grazing animals. A strategy assumes an objective and, simplistically, the objective of the herbivorous mammals described in this study may be taken as the maximisation of nutrient input within the limitations of available forage and the animals adaptations to feeding. The adaption of feeding strategies, which have been determined by natural selection, will reduce inter-specific competition for food resources and enable the animal to maintain a positive nutritional balance for much of the year and provide nutritional surpluses for reproduction and growth. Emlen (1966) argued that, "natural selection favours the development of feeding preferences that will, by their direction and intensity and within the physical and nervous limitations of the species, maximise the net caloric intake per individual of that species per unit time".

By use of Brody's (1945) interspecies metabolic weight index of $W^{0.73}$ one can express nutrient requirements (eg. protein) as a single figure for all taxonomically related mammals. I have used the figure of 1.36 $gms/kgW^{0.73}/day$ as a maintenance requirement for protein, and shown extra requirements for growth, gestation and lactation.

The available nutrients are determined by the condition, growth stage and type of forage within the different habitats. Although availability varies seasonally and spatially, they can be considered as being equally available at any one time to all motile animals. Different species will have different adaptations though, restricting or increasing their ability to utilise the nutrients in different areas and forage types.

Considering the different animal species in this study area: buffalo, hartebeest, impala, sable, wildebeest, warthog and zebra, and more briefly duiker, eland and kudu, it is of interest to compare the different means (strategies) they adopt to ensure adequate nutrient intake.

As species of different body size have differences in their daily nutrient requirements then differing qualities of diets may satisfy these requirements, for example (using males):

Species	Weight	Daily Protein Requirement	Protein/kg body weight.
Buffalo	570 kg	139.7 gms	0.25 gms
Wildebeest	273	81.7	0.30
Hartebeest	180	60.2	0.33
Impala	52	24.3	0.47
Suni	4	3.7	0.94
Sable	250	76.7	0.31

Small animals have a very much greater protein requirement per unit body weight than larger animals. Further larger animals tend to have larger rumen capacities which, depending on dietary quality, will enable larger intakes to be taken per day. These factors combined mean that larger animals can exist on diets lower in nutritive quality than smaller animals.

Assume a diet of 5% crude protein.
5% CP = 1.3% DP = 60 hours rumen retention time.

Species	Rumen size	Daily food intake	Protein Intake	Intake/ Requirement
Buffalo	16.8 kg	6.72 kg	87.4 gms	63%
Wildebeest	4.2	1.68	21.8	27
Hartebeest	3.7	1.48	19.2	32
Impala	0.9	0.36	4.7	19
Suni	0.06	0.024	0.3	8

Assume a diet of 6% crude protein.

6% CP = 2.04% DP = 48 hours rumen retention time.

Buffalo	16.8	8.4	201.6	144
Wildebeest	4.2	2.1	50.4	62
Hartebeest	3.7	1.85	44.4	74
Impala	0.9	0.45	10.8	44
Suni	0.06	0.03	0.72	19

Thus it can be seen that a diet of some 5-6% crude protein can be assumed adequate for buffalo maintenance requirements, but is only some 15% of the requirements of suni. Using the same method, one finds that:-

Wildebeest require a diet of 7% Crude Protein for maintenance

Hartebeest , " " " " 7% " " " "

Impala " " " " 8% " " " "

and suni " " " "10% " " " "

As the poorest quality forage in the study area (dry season wooded grassland grasses) rarely drops below 5% during the year then buffalo can maintain themselves with only a slight degree of selection for micro-habitat. In terms of evolutionary strategy they have reduced the need for specialised diets by enlarging body size (Jarman 1974) and maximising the rate of food input - large capacity rumen and large jaws adapted for bulk ingestion not selection. Sinclair (1977) accepts a 5% CP value as a minimum maintenance level for buffalo in the Serengeti. As adequate resources are found virtually year round in one spot, buffalo tend not to be migratory but remain within fairly small home ranges. As the dry season progresses, resources become smaller in patch size (microsites) and buffalo group size may decrease as a result.

Browsing animals have access to forage of high quality and by reason of the production of leaf, flower and fruit through the year such forage is rarely of low nutrient content. Browsing animals have adaptations to allow selection of high quality items. With the exception of eland which needs resources in bulk due to its body size and large group size, browsing animals tend to be sedentary in habit with small permanent home ranges, eg. suni, common duiker and kudu.

The protein content of grasses is not limiting during the rainy season, December to May, in the wooded grassland habitat. It is only as grasses mature that nutritive levels fall below maintenance requirements. It is at this stage that grazing animals must change or modify their feeding strategies to achieve positive nutritional balances.

Impala do this by switching to a diet high in browse components, and nutritional input increases as a result. Table 7.12 and figures 7.3 and 7.8 show that protein (and calorific) intake is at a maximum when taking browse during the dry season.

Warthog take increasing amounts of nutrient rich subterranean organs during the dry season. Examination of stomach protein values (table 7.2) shows that intake is maintained at an adequate level through the year.

Wildebeest and zebra use a strategy of changing habitat rather than changing dietary type. As the dry season proceeds both wildebeest and zebra make increasing use of the miombo woodland habitat and the floodplain, where the nutritional level of regenerating grass is high. It is interesting to note that zebra leave the wooded grasslands first (May-June, see chapter 5 and 6). This is perhaps due to their ability to utilise the tall unburnt grasses in the woodlands rather than their inability to utilise the drying grasses of the wooded grasslands. Zebra by virtue of their fermentative caecum are able to exist on lower quality forage than wildebeest, (Bell 1969). It is important to realise that dry season data for wildebeest, which show severe negative nutritional balances, are for animals shot from the wooded grasslands. Previous chapters have shown that the bulk of the wildebeest population does move to the woodlands, it is unfortunate that similar data are not available for these animals. Section 7.321 discusses the data from rumen N analysis and suggests that animals from the woodlands have higher dietary inputs. Wildebeest numbers invading the woodlands change from year to year, depending on the degree and timing of burning and the post burn flush. Wildebeest are unable to utilise the tall unburnt grass. Some years a large proportion of the population may be forced to remain on the wooded grassland. The existence of a period of negative nutritional balance need not be critical to the population, (although juveniles may show higher mortality due to lower body reserves, Sinclair 1977). Adult animals with rainy season surpluses can store fat as a dry season reserve, and many ungulates can utilise body protein as an "emergency" source of energy. The following chapter shows that female wildebeest do lose condition during the dry season (as measured by Kidney fat indices) but that males, with no reproductive load can slowly gain in condition. I emphasise that as methods utilised in this chapter are based on many unproven assumptions figures for nutritional balance are better read as relative values and not absolute values.

Sable, hartebeest and water buck, by virtue of their morphological adaptations are able to exercise considerable selectivity in their food intake. Sable and water buck may supplement their dry season grass intake with variable amounts of browse components. Waterbuck, with preferred habitat close to perennial water presumably have access to 'green' forage throughout the year, (Leuthold 1975). Sable and hartebeest utilise a habitat with fluctuating amounts of high quality forage, depending on the timing of fires and subsequent flush. In years of no fire or late fires, negative nutritional balance may result and animals can lose condition, (discussed in the next chapter for hartebeest, and see plate 6). The lowest levels of nutrients presumably occur during the late rains when perennial grasses have flowered and nutrients are translocated to shoot bases. Sable and hartebeest are able to select individual leaves at this time, Price (1974) considers that the elongated skull of the hartebeest is an adaptation to grazing basal leaves of tall grass plants.

To summarise this section one can state that variations in time and space in the nutritional level of available forage means that herbivorous species have to adopt a range of feeding strategies to achieve optimal nutritional balances. Strategies within the spectrum of herbivores discussed in this study take many different forms: viz:

(1) Consistent use of high quality browse and great selection

for plant species and plant part, eg. suni, duiker, kudu.

(2) Flexibility in feeding behaviour, the ability to use browse when graze becomes deficient in quality (or quantity), eg. impala and warthog.

(3) Flexibility in habitat occupance, the ability to change habitats in order to obtain adequate nutritional inputs, e.g. wildebeest and zebra (taken to extreme levels in the Serengeti migratory populations eg. Bell 1970).

(4) Adaptations to allow selective grazing and partial supplementation with browse components, eg. sable, hartebeest, waterbuck.

(5) Adaptations to larger rumen capacity allowing increased food quantity rather than quality in the diet e.g. buffalo.

As Westoby (1974) points out, the strategic objectives of food selection in large generalist herbivores is to obtain the best mix of nutrients within a fixed total intake. For any animal the amount of food that can be processed is a function of the cross sectional area of the gut whereas metabolic needs are a function of weight. Thus, the larger the animal, the more limiting is the rate at which food can be processed through the gut. Larger herbivores therefore have adopted strategies of using foods which are abundantly available but of low nutritional values. They keep their guts full almost continuously and have developed large rumen capacities and large food gathering organs to achieve this.

Hence it is possible to relate many aspects of herbivore biology to food requirements. Habitat occupance, movement patterns, food selection are all a function of nutritional needs. These needs are, to a large extent, dependent on body size.

7.35. Nutritional strategies and reproduction and growth.

The preceding section showed how different species adopted different feeding strategies to achieve positive nutritional balances for maintenance requirements. Population well being needs more than individual body maintenance; surpluses for growth, gestation and lactation must be available. Previous sections have shown that nutritional inputs do allow surpluses, for wildebeest in the rains, December-May, and for impala during the late dry season and early rains, September-February.

I have shown that the nutritional demands of gestation are minimal apart from the last few weeks, the demands of lactation are very much greater. From the point of view of the nutritional status of the mother, the timing of parturition and hence the onset of lactation is more critical than the timing of conception and the onset of gestation. Obviously though, the timing of conception affects the timing of parturition.

Chapter 8 discusses the timing of reproductive processes but it is immediately obvious from figures 7.7 and 7.8 that herbivorous species do start lactation at the onset of periods of nutritional surpluses. Wildebeest calve in late November and hence peak lactation proceeds from December onwards. Impala with a late dry season surplus calve in late September, (wildebeest with no access to wooded grassland habitat and are restricted to the woodlands, calve in October). Hartebeest and sable with surpluses due to the post burn flush calve in September.

Juvenile animals depend on milk for their post birth growth, but data from chapter 8 do indicate greater growth during periods of nutritional surpluses.

7.36. Mineral Nutritional.

Chapter 4 discusses the mineral content of forage and appendix 5 relates this to the mineral content of animals from this study area. To summarize, animal blood serum levels of calcium, magnesium and copper were similar to those of domestic stock (Worden, Sellars and Tribe 1963). Phosphorus levels in whole blood varied from 15.4 to 6.9mgm/100ml as mean values for several samples of five species investigated. These levels are considerably lower than those accepted as normal for cattle (35-45 mgm/100ml) and would cause phosphorus deficent diseases and impaired reproduction in domestic stock (Moustgard 1959). Appendix 5 concludes that indigenous wild animals must have an adaptation to diets low in phosphorus and they can exist at high reproductive rates on phosphorus contents which are below the minimum requirements for domestic stock.

A recent study of sable and roan populations in southern Africa (Wilson & Hirst 1977) pointed out the low phosphorus content of available forage grasses (0.02-0.05% w/w) and low levels in blood serum (92 ppm). These authors state that phosphorus deficiency may be a factor in the low survival rates of sable on game ranches in South Africa. As forage grasses were extemely low in protein I suggest that gross nutritional stresses are likely to be more important.

CHAPTER EIGHT

POPULATION PARAMETERS

8.0 Introduction

Previous chapters have described the animal population in terms of their numbers, distribution and use of the different vegetation communities. Patterns of use and feeding strategies were shown to vary seasonally and spatially. It is of interest and value to examine "how well" the different animal species "perform" at different seasons and in different habitats, and to compare these measures of performance with populations elsewhere in Africa.

Performance can be considered at the level of the population i.e., "is the population increasing or decreasing numerically?" Or it can be considered at the level of the individual, i.e., condition indices, pathogen levels, reproductive parameters. As the performance of the population is the resultant of the sum of the performance of the individuals in that population, then the question of population increase or decrease is the outcome of several parameters of the individual, (fecundity, longevity, calf survival, etc.). An understanding of the rate of population increase needs an understanding of the life history parameters of the individuals in that population. This chapter starts with an analysis of population growth rates and then examines the parameters of body growth, body condition, reproduction, longevity and pathogen levels.

The concept of performance is discussed further at the end of this chapter and the "performance" of Selous populations compared with that of other African populations. Finally an attempt is made to explain the factors responsible for the zero population growth recorded for wildebeest since 1972.

Most data are available for wildebeest, followed by impala and then hartebeest, zebra and warthog. Little data were collected from the woodland habitats, but some information is available for comparison with animals from the wooded grasslands.

8.1 Methods

8.11 Population performance

Data on population rate of increase is taken from table 5.4 for four species, wildebeest, impala, zebra, warthog. Rate of increase, expressed as '$\bar{r}$', the mean observed exponential rate of increase was calculated by:

$$\bar{r} = \frac{\Sigma Nt - \dfrac{(\Sigma N)\,(\Sigma t)}{n}}{t^2 \pm \dfrac{(\Sigma t)^2}{n}}$$

where N is the natural logarithm of the estimated population size at any one time, with n separate estimates carried out over t years, (Caughley, 1977). The expression is basically a regression equation and averages several years data, without undue weighting being given to the first or last estimate. I know of no other time serial census data for populations of these species, from the Selous or other African miombo woodlands, with which these values could be compared.

8.12. Individual performance

Much of the data presented in this chapter has been collected from post mortem examination of shot animals. Small numbers of the commoner species have been shot as a routine task since the start of the MRC in 1968. Animals were shot for purposes of famine relief, National Festivals and for research programmes. These programmes were intensified with the appointment of a veterinarian to the centre from 1971 - 1974. With experience post mortem examinations were developed into a standard routine.

8.121. General post mortem procedure.

Animals in the field were shot using a .30-06 or .375 rifle, where possible during early or mid morning periods. According to the research programme and to the need to obtain adequate representation of age and sex classes, specific animals would be searched for and sho t, eg. a 2 year old female. Within this category there was no overt selection of individuals, the first animal of that category to be sighted was hunted. It was assumed that collection was not influenced by animal size or condition. On death the animal had its jugular vein severed, (a necessary rite with Moslem staff) and blood samples taken. Ticks and other ecto-parasites were searched for macroscopically and collected, the carcass was numbered and transferred to the base abbatoir.

At the at attoir the animal was weighed (and 2% of nett weight added to compensate for blood loss and fluid loss by evaporation) and measured - body total length, tail length, shoulder height, heart girth, hind foot length and trophy size.

On completion of measurements, the head was removed and skinned, the skull was cleaned and brain case and sinuses opened for parasite collection, and the jaws put aside for later age determination.

The carcass was opened up along the ventral mid line from sternum to sacrum. Endo parasites were searched for as per Sachs & Debbie (1969), and the animal was eviscerated, different organs being removed, weighed and put aside for later examination. On occasions the complete muscle content of the carcass was sliced for cysticerci (measles) examination. The femur was retained for qualitative estimation of marrow condition.

Most data was obtained for wildebeest, less for impala and warthog and little for hartebeest, sable, buffalo and zebra.

8.122. Growth.

Only growth and variation in body weight is considered here. Adequate data was available for wildebeest, and, to some degree impala insufficient immature animals were collected to be able to draw growth curves for other species. Corrected total body weight from post mortem records were used as the raw data.

As wildebeest and impala are restricted seasonal breeders, animals could be separated into age classes of months up to 36 months of age, on the basis of month of collection and tooth replacement categories, (Watson 1967, Spinage 1971). Growth curves of body weight against age in months were drawn for each sex for each species. Daily weight gain averaged over each 6 month rainy season (December to May) and 6 month dry season (June to November) was estimated. The theoretical growth curve, based on Von Bertalanffy's growth equation was determined according to the method of Beverton & Holt (1957) and superimposed on the actual growth curve. Real weight gains could thus be compared with theoretical growth curves for each season.

Mean weights for adults of both sexes were tested for significant differences between seasons, and against published data for other populations. Significance was tested by "t" test and by Tukey's short test for differences between means, (Bliss, 1967 see below).

8.123. Condition.

Indices of condition for African ungulates have been discussed by Riney (1960) using field characters, and by Smith (1970) and Sinclair & Duncan (1972) using body measurements. This study made use of the Kidney Fat Index (KFI), which was determined as $KFI = \frac{\text{Wt. of Renal Fat } \times 100,}{\text{Wt. of both Kidneys}}$

according to the methods of Sinclair & Duncan (1972).

Bone marrow, from midway along the femur was examined subjectively, but in all cases marrow appeared of firm creamy consistency and was never seen reddish or watery. This would indicate high fat content and 'good' condition, as such further analysis of fat content was not undertaken.

Data for KFI were combined for three years as seasonal patterns appeared similar, these values were plotted separately for male and females against calendar month. Wildebeest data was used, difficulty being found in discriminating renal and mesenteric fat in impala. Orthogonal polynomial curves were fitted to the raw data by computer, (Bear, 1971; Duncan, pers. comm.) and computer generated values added to the graph of monthly means.

8.124. Reproduction.

a) Males

Growth in weight of testes and seasonal change in testes weight for wildebeest and impala were the only aspects of the male reproductive cycle investigated. Data used were the weights of both testes (plus epididymus) combined. Testes weights of sexually immature animals were plotted against age in months. Mean testes weights for adults were determined for rainy and dry seasons, and individual weights plotted against calendar month.

b) Females.

All females post-mortemed were categorised as pregnant/non pregnant and lactating/non lactating. Pregnancy was determined by macroscopic examination of uterus and uterine horns only. Lactation was determined by milk or fluid flow from the nipple or slashed mammary tissue. Pregnant animals were further categorised as yearlings (12 - 24 months) or matures, (24 months and older). Embryos were weighed and measured (crown-rump length) and, when possible, sexed. Data were tabulated to show pregnancy rates during the period of visible gestation (May to November) for yearling and mature age classes. Embryo weights were used to investigate synchrony of calving for wildebeest within the period 1971 - 73, according to the technique described by Huggett & Widdas (1955). Lactation data were used to estimate calf survival, as per Spinage (1970) for waterbuck.

8.125. Disease and parasite load.

This topic is being written up in detail elsewhere (Gainer, in preparation). Brief coverage only is given here. As a routine measure, samples of blood sera of shot animals were deep frozen and sent to the Central Veterinary Laboratories in Dar es Salaam, (CVL) or the Kenya Veterinary Laboratories or the East African Veterinary Research Organisation Kenya, for analysis of disease anti-bodies. Anti-bodies specifically tested for were those relating to: Brucellosis, Rinderpest, Foot and Mouth Disease (4 strains), Infectious Bovine Rhinotracheitis IBR, Malignant Catarrhal Fever MCF, Contagious Bovine Pneumonia CBP, Johnes Disease and 'Q' Fever; and for warthog only, African Swine Fever.

The presence of anthrax was confirmed in the study area in 1970, (Gainer, 1972, 1973). Bacterial isolation, culture and serum agglutination techniques showed positive reactions for several found carcasses of wildebeest, impala and for one elephant.

With the exception of anthrax and hoof rot (hoof abscess- a localised bacterial infection, prevalent in wildebeest calves during the rains and causing some deaths) no other disease or pathogenic condition was found to be important in the game animals of the Selous.

Parasites were searched for during the post mortem examination and specimens were identified by the CVL and by Dr. R. Sachs of the Tropeninstitut, Hamburg, Germany.

8.126. Field methods.

(a) Condition.

During the course of the study, animals were subjectively observed as to condition class according to the method of Riney (1960). As very few animals fell in the poorer condition classes, the data were not taken further.

(b) Found skulls.

Staff at the MRC made large collections of found skulls for wildebeest and warthog. These were aged according to the methods of Spinage (1971) and Spinage & Jolly (1974) respectively. Age data were used to determine mean age of death of the adult population (sexes combined) as an indication of longevity. Life table analysis was not attempted for this study.

(c) Calf survival.

Studies on ungulate group size (Rodgers, 1977, attached as appendix 7), included data on calf content of wildebeest breeding herds, with calf number being expressed as a percentage of group size. Although total group size will decrease due to adult mortality and expulsion of immature males and so obscure exact rates of decrease of the calf crop, the results can give some indication of calf survival.

d) Animals found dead

Animals found dead were assessed as to cause of death-predation or non predation. Carcasses seen with predators are discussed elsewhere, (appendix 6). Where deaths were not attributed to predators and decomposition was not advanced, carcasses were subjected to the post mortem procedure described above, but only results of disease examination were used for this study. Subjective estimates of deaths due to anthrax were made from field carcass examinations.

8.2. Results

8.21. Population growth

Values of '$\bar{r}$', mean observed exponential population growth rate, for four species over eight years are as follows:-

Zebra	0.107,	Increasing,	Time to double, 6.5 years
Warthog	0.091,	Increasing,	Time to double, 7.5 years
Wildebeest	0.036,	Increasing-stationary,	Time to double, 19 yrs
Impala	-0.014,	Decrease-stationary,	Time to halve, 50 years

As individual year census figures have a confidence interval of some 25%, no tests of significance were performed on these results. Note that zebra and warthog populations have increased steadily over the study period, whilst wildebeest and impala populations have fluctuated and could be said to be stationary.

8.22. Individual performance.

8.221. Growth in weight.

(a) Wildebeest.

Data from 168 animals were used, 45 mature males, 79 mature females and 44 immatures. Maturity was taken as 36 months and 24 months for males and females respectively. Body weight results are shown in table 8.1. Adult male weights were separated into dry and wet season categories but no significant difference in value was detected, (t = 1.676). Weights of females were not compared because of weight changes due to the conceptus in the dry season. A growth curve was constructed with weights of known age immatures and adult mean weight. Curves are drawn in figure 8.1 for males and females separately. The von Bertalanffy growth equation was calculated using 16.9 kg as calf mean birth weight (average of two full term embryos and 2 one day old calves). The equation was calculated for males only (more data points) and took the form:

$$Wt = W \; (1 - e^{-k(t - t_o)})$$

where Wt - Weight at time t, where t is age in years.

W = Maximum asymptotic weight = 311.7 kg.

k = Specific constant = 0.71.

t_o = Theoretical time at which weight is zero = -0.98 years

This theoretical growth curve is fitted to figure 8.1 for ages up to 36 months. Extrapolation shows that mean adult weight in males is approximated in the fourth year and females in the third year.

An interesting comparison between actual weight increment and theoretical growth increment can be made for six monthly periods from birth, where the first period equates to the rains, the second to the dry season and so on. Rainy season growth during the first three years gives on average 1.31 times the theoretical rate. Theoretical increments were detefmined by calculating six monthly von Bertalanffy values and actual rates read from the curve for each period. Details for each period are shown in table 8.2. Note that the rapid growth rate in the first six months of life may be due to the high protein milk diet of suckling calves. Poor agreement with theoretical growth curves at this stage is typical for African ungulates, (Duncan, 1975).

(b) Impala.

Data from a total of 118 animals were used, 27 adult males, 57 adult females and 34 immatures. Maturity was taken as 36 and 24 months for males and females respectively. Weight data are shown in table 8.1. There is a significant difference between male dry and wet season weights ($t = 3.74$, P 0.01) although mean values are close. A growth curve has been constructed, but as there were large gaps in seasonal data collection theoretical curves were not determined, (figure 8.2).

(c) Other species.

Body weight data for warthog and hartebeest are shown in table 8.1.

8.222. Physical condition.

Results are given for wildebeest only as Kidney Fat Index determination in impala was hindered by greater difficulty in seprating renal from abdominal and mesenteric fat deposits.

Graphs of KFI versus calendar month were drawn for male and female wildebeest for the years 1970, 1971 and 1972. Plots were similar in all years, varying in amplitude but not in general form, so all data were combined. A polynomial curve was fitted to the data. Curves were of the form:-

Females n = 57

$$y = -40.49 + 2.16x - 0.012x^2 - 0.000017x^3$$

Males n = 44

$$y = 28.92 - 0.66x + 0.006x^2 - 0.00001x^3$$

where y is KFI% and x is time from January 1st in days.

These curves together with monthly mean and monthly range of observations are shown in figure 8.3. Curves show distinct patterns for male and female animals. Both sexes start the year with a low KFI of some 10%. Females increase KFI during the rains (despite lactation) reaching a maximum of 110% in May. Non lactating animals (either 2 year olds or adults which have lost a calf) show much higher levels of KFI (table 8.3). In the dry season females slowly use up fat deposits reaching a low point of KFI in December-January, the time immediately after parturition and during heavy lactation. Males have low levels of KFI during the rains but slowly gain fat during the dry seasons, losing fat only right at the end of the dry season in December-January.

How significant are these differences, between sexes and between seasons? Standard error values for the polynomial curves were available but these showed "inflated" results for the later half of the year due to the large size of the cubic coefficient of dx^3 where x is measured in days, e.g. 345 days for mid December. Analysis with time expressed as months would have given better results but computer facilities were limited. As S.E. values were not usable differences between sexes and 3 month seasons were tested by use of a t test for small samples, using individual animal data for each period and sex, (Bailey, 1959). Detailed results are shown in table 8.3, but all between sex and between season comparisons tested were significantly different.

8.223. Reproduction.

(a) Males.

(1) Wildebeest.

Growth in testes weight is shown in figure 8.4 from birth until adult testes weight is reached in the fourth year. Unlike the Serengeti wildebeest, (C.t. albojubatus, Watson, 1969) male wildebeest here show a definite seasonal change in testes activity. After the March-April rut testes weight drops to a low of 60% of their peak weight. Mean testes weights for rains and dry season were:-

Rains 293.3 gms ± 6.26 (S.E.) $n = 10$
Dry 220.6 gms +± 6.55 (S.E.) $n = 16$

These values are significantly different ($t = 8.02$, $P < 0.1\%$). Seasonal fluctuation is shown in figure 8.5.

(2) Impala.

Growth in testes weight is shown in figure 86. Comparable data from Rhodesia (Kerr, 1965) are included in the figure. Like wildebeest, impala testes show a seasonal reduction in weight. Values are:-

Rains 110.3 gms ± 3.73 (S.E.) $n = 9$
Dry 69.3 gms ± 2.86 (S.E.) $n = 12$

Values are significantly different ($t = 7.72$, $P < 0.1\%$). Seasonal fluctuation is shown in figure 8.5.

(b) Females.

(1) Wildebeest.

Of 62 females of 2 years and older examined between May 1st and November 15th all were pregnant, i.e. 100% fecundity. Of 9 yearling females examined 5 were pregnant, i.e.55% fecundity. No evidence of twinning or abnormal pregnancy was noticed. The sexes of 47 embryos were 26 male and 21 female, not significantly different from a 1:1 ratio. Lactation was observed to persist in some animals up to August or some 8-9 months after calving.

Foetal growth rates and the spread of time of parturition and conception can be determined from figure 8.7 for the three years studied. Constants used in deriving this figure were as follows:-

tg = Gestation length = 250 days (Asdell, 1946).

t_o = Constant used to overcome the problem of non linear growth in foetal weight from conception for first period of growth, = $0.2 \times tg$ = 50 days.

a = Specific foetal growth velocity, calculated as 0.128.

Wg = Weight at birth = 16.9 kg. $Wg^{0.33} = 25.66$ gms.

t = Time since conception (in days).

as $W_t^{0.33} = a\,(t - t_o)$ Huggett & Widdas (1951).

therefore $t = Wt^{0.33} + t_o$

and $a = Wg^{0.33}\ \ tg - t_o$.

It is apparent from figure 8.7 that the timing of reproduction is closely synchronised within years and very similar between years. Although sample sizes are small viz: 1970 - 13 foetuses, 1971 - 8 and 1972 - 21, examination of foetal age for extreme points from the line of figure 8.7 gives the following results for calving spread:

1970	13/11	to 4/12	1st calf observed (table 8.4)	12/11
1971	21/11	to 4/12		20/11
1972	25/11	to 11/12		25/11.

No examination of possible correlation between the timing of reproductive activity and physical occurrences such as rainfall or lunar periodicity has been made. Peak calving for all years of the study was judged to be the last week in November, putting the period of peak conception at late March.

(2) Impala.

Of 39 females of 2 years and older examined after the rut, all were pregnant, a fecundity of 100%. Five out of 7 yearlings examined were pregnant, a fecundity of 71%. Of 35 indentifiable embryos 20 were male and 15 female, not significantly different from 1:1 sex ratio; Insufficient data were available for construction of foetal growth curves but from field observations impala showed a restricted calving season peaking from late September to mid October. Dates of observation of first calves are shown in table 8.4.

(c) Other Species

Occassional autopsies of hartebeest and warthog males indicate they also show seasonal loss in testes weight. Fecundity rates for all species examined are high (brief details in table 8.4). All species considered in this study with the possible exception of zebra show restricted calving seasons. Figure 8.8 illustrates the spread of calving and conception periods for several species in this study area.

8.224. Calf Survival

Data came from two sources, one being information on the calf content of breeding herds (appendix 7) and the other from lactation data. Only wildebeest are considered here.

Calf content per breeding herd declines from a maximum of 34.1 per 100 animals in January to a low of 21.9 per 100 animals in October, a drop of 35.8%. But the calf content is biased by mortality amongst other age classes in the breeding herd. Annual means of calf and yearling content are of the order of 30% and 16% respectively indicating a mortality of some 46.7% during this 12 month period. Table 8 in appendix 7 shows a smooth decline in calf content through much of the year, January to September. When data are plotted on a log scale against month there is a strong linear relationship, indicative of constant mortality rates, (Poore, 1970). Only October shows an increased calf loss possibly due to the accumulated affects of the drought.

Lactation data for mature post pregnancy females from between 1st December and 30th June each year were analysed. This period of seven months is taken as the duration of normal lactation. Of 47 females so examined 36 were lactating. Assuming mortality to be constant throughout the year then annual calf mortality per surviving mother can be determined as

$$100 \left(-\frac{36}{47} \times 100 \right) \times \frac{12}{7}, \qquad \text{Spinage (1970).}$$

This gives 40.1%, not appreciably different from 36 and 47% as determined above.

8.225. Longevity.

Age data for 878 wildebeest skulls and 171 warthog skulls are shown in table 8.5. No correction for bias in collection of younger animals is made and so results are given for animals of 2 years old and above. Sexes are not separated. Constants applied in Spinage's (1971) conceptual wear model for ungulates which I have used for age determination of wildebeest age are

$$y_0 = 66 \text{ mm and } n = 21 \text{ years: and}$$

$$y = y_0 \left(1-\frac{t}{n}\right)^{\frac{1}{2}}$$

where y is M1 tooth height, y_0 the theoretical height of M1 with zero wear, t is animal age and n is assumed physiological longevity.

From this data, the mean age of death for adult wildebeest (those having reached 24 months) is 8.34 years and that of adult warthog is 4.39 years. The peak of mortality associated with 6 year old wildebeest may be due to increased predation on males becoming territory holders at this age (table 8.5).

8.226. Diseases and Parasitism.

Results of serum anti-body testing are given in table 8.6 for five viral diseases: Rinderpest, IBR, MCF, Q fever and 4 strains of Foot and Mouth Disease, and three bacterial diseases: CBP, Brucellosis and Johnes Disease. Note that positive titres in serum testing suggest past contact with the disease and are not an indication that the animal is suffering from or acting as reservoir for the disease at the time of death. Trace titres are even less conclusive.

Reference to table 8.6 shows no indication of contact with Rinderpest, CBP or Brucellosis and only trace indications of contact with Foot and Mouth (strain O and Sat 1) in wildebeest.

Foot and mouth disease is a contagious viral disease of ungulates, infection is characterised by vesicular erruptions on mouth and feet. Twenty nine African ungulates are known to be susceptible and mortality may be high as in impala in South Africa, (Anon 1963, Meeser 1962). As no clinical signs of the disease have been seen, and as trace titres only are inconclusive of disease presence (Brooksby, 1969), no definite statement on foot and mouth infection can be made.

Four diseases showed positive titres on serum screening: IBR, MCF, Q Fever and Johnes Disease. IBR is an infectious viral disease of the respiratory and genital tracts of bovines, (Karstad, 1970a). It is thought to be world wide in distribution. No clinical signs were seen in this study and the disease is of unknown significance. MCF is an important viral disease of the respiratory tract of cattle and wild ruminants. It is world wide and has been confirmed in wildebeest in Kenya, where it is apparently endemic but not fatal (Karstad, 1970).

Q Fever is a rickettsial infection and ordinarily non fatal. It is transmissable to man, (Bell 1970). Wild animals appear to recover rapidly from the disease. It is of minor or no significance in wild ungulate populations.

Johne's Disease is a bacillary disease akin to tuberculosis and commonly found in domestic ruminants. Eleven species of ungulate from Serengeti were free of the disease, (Rankin & McDiarmid 1969). The disease is of unknown significance, but it is possible that this is the first instance of the disease being found in wild ungulate populations in Africa.

As was mentioned earlier anthrax is endemic in the study area and has been confirmed for wildebeest and impala (Gainer, pers. comm.). A useful review of the disease in wild animals is given in Choquette (1970), and Pienaar (1961) discusses the diseasein Kruger National Park. Pienaar notes that wildebeest were not affected and impala only scarcely so. Greater kudu are documented as being extremely susceptible but populations here are so low that carcasses could be over-looked. The disease is usually peracute in form, apparently healthy animals dying a few hours after contact. Hence sick live animals are rarely seen. All data in this study are from carcasses, which are rarely taken by scavengers. Ecologically the study area favours the disease, being hot, humid and with alkaline, seasonally flooded soils and a number of small pools to act as disease foci. Personal observation & Gainer, (1974) show most deaths in the rains and among mature wildebeest. In the most severe years (1971 - 1974) we estimated up to 500 wildebeest could be succumbing per year. This is would be 4.6% of the population.

Levels of parasitism, in terms of number of parasite species, % hosts infested and numbers of parasites per host are not high, (Sachs, pers. comm.). Exceptions are the non ruminants, zebra and warthog, and to some extent, buffalo. Table 8.7 gives infestation rates for four separate taxonomic groups of parasite. Details of parasite species are not included in this thesis.

On rare occasions individual animals have been observed to harbour large numbers of parasites, viz:- one hartebeest with heavy infestation of pentastomid larvae (Armillifer sp.) in lymph nodes, one immature hartebeest with a heavy infestation of adult ticks of Boophilus species, and one impala with a higher than usual intestinal nematodes, but also revealing intestinal coccidiosis infection. Frequently wildebeest and impala have revealed no intestinal helminths on macroscopic examination, an unusual observation for wild ungulates. This finding is borne out by low infestation rates of strongyles as determined by faeces egg counts, (table 8.7c)). Egg counts gave significantly higher infestation rates in the rains than in the dry season.

Verminous pneumonia (parasitic lung nodules) is widespread in impala, less so in wildebeest and hartebeest. Insignificant amounts of lung tissue are affected. Tick infestation whilst high in % infected, is low in terms of ticks per host. Muscle cysts similarly are of low density per host.

There is little data of similar form with which to compare levels of parasitism. Sachs (pers. comm.) confirms that these populations show much lower levels of parasitism than those of Serengeti and Lake Rukwa.

8.3. Discussion.

8.31. The Results.

8.311. Population Growth.

Caughley (1977) states that, "Rate of increase measures a populations general well being, describing the average reaction of all members of the population to the collective action of all environmental influences". No attempt has been made to measure "r_m", the innate capacity for increase, or "r_s" the survival - fecundity rate of increase for a stable age population. Rather, "$\bar{r}$" is used, the mean actual rate of increase over a long period. Data expressed in section 8.21 show two species increasing vigorously, zebra and warthog with $\bar{r}$ values of close to 0.1 and two species with very slow or no growth, wildebeest and impala with $\bar{r}$ values of 0.04 and -0.01 respectively. The negative value for impala is so close to zero that it indicates a stationary population rather than a decline. This is borne out by fig. 5.3. It is suggested that deaths due to anthrax are causing the reduced rates of increase. Section 8.226 estimates up to 500 wildbeest a year are succumbing to anthrax, if this figure held from 1972 to 1977 then $\bar{r}$ would be increased by some 50%.

8.312. Body growth.

Recently a number of papers have analysed body growth of African mammals in detail (e.g. Howells & Hanks, 1975 for impala and Smuts 1975, for zebra). These authors have used "mass" instead of "weight", an unnecessary distinction to my mind, and their graphical portrayal of asymptotic weight (Beverton & Holt, 1957) appears erroneous. Although impala and to a lesser extent zebra are seasonal breeders in southern

Africa and a harsh dry season lasts for half the year, no apparent seasonal distinction in growth rate is visible in their data. Figure 8.1 and table 8.2 show this trend for wildebeest in this study (too few data points precluded significance testing) but the impala data being inadequate in several age classes, could not be analysed. Duncan (pers. comm.) suggested a similar trend for topi in the Serengeti National Park. Chapter 7 has shown that available forage nutrient levels are minimal or inadequate for wildebeest in the dry season and this must reduce weight gains.

Wildebeest and impala have different mean weights from other African populations. The study area wildebeest *(C.t. johnstoni)* being significantly larger than northern races *(C.t. albojubatus & C.t. heckii)*, viz:

		Males	Females
C.t. johnstoni	(this study)	273.8kg	213.3kg.
C.t. albojubatus	(Sachs 1967)	201.1***	163.0***
C.t. heckii	(Ledger 1964)	243.3	192.4
C.t. heckii	(Lamprey 1964)	227.2	253(Suspect error in printing)

(asterisks denote the significance level of difference between Selous figures and other data using Tukey's short test for differences between means with range data, Bliss, 1967).

Impala subspecific taxonomy is more controversial (Ansell, 1972). The Selous race is smaller than both the northern (Serengeti) race and the southern African forms, viz:

	Males	Females
Selous impala (this study)	52.3kg	37.9kg
Serengeti (Sachs, 1967)	56.9**	42.1**
N. Tanzania (Lamprey, 1964)	63.8	43.8
Rhodesia (Wankie)(Howells & Hanks, 1975)	56.6	43.2
Rhodesia (Child, 1964)	53.6	40.8

Wildebeest here reach adult weight after 36 months, i.e. in their 4th year (males) and after 24 months (females); data which agrees with the Serengeti findings, (Watson, 1969). Impala are similar with males after 36 months entering the size range of adults and females taking just over 24 months. These figures are less than those of Howell & Hanks (1975) but for a smaller animal and smaller data set.

I know of no published data on seasonal differences in body weights for free ranging African ungulates, comparable with figures from this study.

8.313. Condition.

Data in figure 8.3 show significantly different patterns of fat reserves between sexes and between seasons for each sex. As non lactating females show higher fat values than lactating animals presumably fat reserves reflect the increased metabolic stresses of lactation and the reproductive cycle. Caughley (1977) is critical of the use of fat reserves to indicate a population's "condition", especially as the term "condition" is usually undefined or described in vague terms. "Such indices are useful as long as we know just what it is they index. If one population has a higher "condition" (as measured by an index) than another, how is the difference manifested ecologically". He goes on to state that indices of condition should correlate with demographic vigour as measured by some form of "r".

Sinclair & Duncan (1973) present data for Serengeti wildebeest kidney fat indices. Their results show dry season levels low enough to cause severe fat reduction in bone marrow, Selous data do not show loss of condition to such an extreme degree. Nevertheless, Serengeti wildebeest have shown a very rapid population growth rate this past decade, $r = 0.11$ (1967 total 0.48×10^6, 1977 total 1.3×10^6, Sinclair, 1973 and Grimsdell, pers. comm.). This is very much higher than the Selous population increase, even allowing for anthrax deaths.

In this case condition measured by Kidney Fat Indices does not correlate with demographic vigour. Presumably it would do so if Serengeti marrow fat levels drop any further, as increased phyiological stress could cause death and impaired fertility.

Does the level of Kidney Fat reflect nutritional inputs? To some degree, yes, but this is masked by changes associated with the reproductive cycle. Taking the rainy season to have considerably greater nutritional values than the dry season, then female wildebeest lay down fat in the rains (following heavy lactation) and lose fat during the dry season and early rains (also affected by late pregnancy and early lactation). Males however lose condition in the rains and slowly gain in the dry season, this can be explained by the stresses of territoriality when food intake is lowered and by no reproductive load in the dry season.

Riney (1960) described a visual field technique for assessing ungulate condition based on angularity of the pelvis. Animals in his poorer condition classes were rarely encountered, in this study area, exceptions being hartebeest at the end of the dry season in areas of late burning and no grass flush.

8.314. Reproduction.

(a) Males.

Unlike the Serengeti (Watson, 1969) wildebeest here show a seasonal change in testes weight, peak weight being reached during the rut and period of active territory defence, February to May. Assuming young animals to enter this cycle, they would appear to reach full sexual maturity at the age of 52 months (figure 8.4). This finding agrees with Watson (1969) for C.t. albojubatus.

Serengeti mature wildebeest single testis weight is 153.5 ± 90 gms (mean and standard deviation), agreeing closely with a Selous value of 293.3 ± 19.8 gms (n = 10) for both testes during the rut. However following the rut Selous wildebeest show a significant decline in testes weight, values falling as low as 186 gms in November, figure 8.5. As section 8.221 shows, this decline is significant.

Impala show a similar pattern, figures 8.5 and 8.6. Testes growth in impala agrees closely with data from Kerr (1965), for Rhodesia and impala testes will reach mature weights at about 41 months, to coincide with the March rut. Impala testis weights also decline significantly in the non rutting season, a phenomenon found elsewhere in southern Africa but not in Kenya and northern Tanzania where impala can breed year round (Leuthold, 1970).

For a strictly seasonal breeder it must be disadvantageous to have high levels of testicular activity and consequent behavioural activities throughout the year. Chapter 7 showed adult male wildbeest to have lowered food intake during the rut and this is reflected in the animals body condition, a reduced fat content, (section 8.222). Cessation of spermatogenesis, and presumably reproductive hormonal secretion will allow the male to reduce its territoriality and herding drive during the harsh dry season conditions. This is apparent in the lowered numbers of solitary males (appendix 7).

(b) Females.

High fecundity of adult animals is typical of tropical ungulates, (Caughley 1977, Watson 1969, Sinclair, 1977 etc.) Values as in this study approaching or equalling 100% are not unusual. A much larger sample may show a slightly reduced fecundity in older age classes, but this has a very small effect on overall population dynamics as old age classes form an insignificant proportion of the population. A parameter more meaningful to population growth is fecundity in the subadult classes, those animals calving at 24 months in the case of wildebeest and impala.

Watson (1969) shows a 35% fecundity for wildebeest 2 year olds, n = 29, and Talbot (1963) at an earlier period also in the Serengeti quotes a value of 85%. The Selous figure of 56% is intermediate. There is some evidence that subadult fecundity can be correlated with population density (Laws, Parker & Johnstone, 1974)for elephant). Intensive tsetse control hunting in southern Africa reportedly led to an increase in sub adult fecundity among common duiker, (Wilson & Roth, 1967). Impala show 71% (n = 7) fecundity amongst animals calving at 24 months. Two subadult hartebeest examined were both pregnant. Sex ratios at birth of unity were found for wildebeest and impala, the typical pattern for ungulates (Caughley, 1977).

Calving periods are of considerable interest. Many authors have investigated the seasonality of calving and possible synchronising trigger mechanisms, (Fraser 1968, Sadleir 1970, Spinage 1973, Skinner 1973, and several authors in J. Fert. & Reprod. Symp. 1969). Spinage (1973) states that there is little overt evidence for photo periodic response for populations close to the equator although observations outside the tropics suggest possible long and short day responses for different species. Without photoperiodic synchrony it is likely that climatic factors act as a coarse trigger and there is a possibility of lunar cycles providing the fine tuning (Sinclair 1977, Grimsdell, pers. comm.). Timing of birth seasons can be explained by natural selection forces determining the period of optimum nutritional values for heavily pregnant or lactating females or weaning calves.

Leuthold (1975) makes a convincing argument to explain differing temporal reproductive strategies amongst nine ungulate species in Tsavo National Park. In his case grazing ungulates tend to have unimodal or bimodal birth peaks coinciding with the rains - periods of maximum nutritional value for grasses; whilst browsing animals have no periodicity as nutritious browse: leaf, fruit, flower can be found throughout the year. There is, however, considerable risk of tautology and circular argument within these explanations. Unless we can obtain experimental evidence of birth period being an adaptation to nutritional phenomena, our answers are little more than guess work.

Figure 8.8 illustrates the observed spread of calving for the eastern Selous and this can be compared with monthly rainfall. Based on known gestation time, the period of peak conception for each species is indicated by an asterisk. Wildebeest, impala, hartebeest, warthog, eland, water buck and sable can be seen to have a very restricted breeding period: zebra and buffalo less so but still a distinct unimodal peak. Calving periods for smaller ungulates are not known accurately. Estes (1976) has shown how restricted calving seasons may be accentuated by increased predation of calves born outside the peak period.

As such predation may affect observed calving spread, then quantitative data can be obtained by an examination of foetal growth (using the method of Huggett & Widdas, 1959). Figure 8.7 shows foetal growth for wildebeest for three years plotted against a time axis. There is synchrony both between and within years. A few points fall outside the main scatter; these are pregnancies of sub adults.

Figure 8.8 shows several species calving in the mid dry season, exceptions are buffalo, eland, wildebeest and waterbuck. The dry season here is a time of high grass nutritive values in the woodland habitats following fire induced grass flushes, (chapter 4). Crude protein contents of woodland grasses are higher than rainy season values and considerable browse material - young leaf, fruit and flower is available for animals taking all or part browse, (appendix 8). Calving at this time for woodland animals or animals able to move into the woodlands could be explained by selecting for maximal nutritional values for females undergoing lactational stress. Warthog are not primarily woodland animals, and densities are highest in mid dry season around the flood plain edges and in the wooded grasslands (chapters 5, 6 and unpublished data). Warthog at this time feed on perennial grass and sedge shoots and root bases, a relatively high quality diet. As young warthog are reared in burrows or hole, farrowing in the rains could [illegible] cause piglet mortality due to flooding or cold.

Where wildebeest have no access to short grass habitats and are restricted to the woodlands, they too calve in the mid dry season; e.g. at Madaba some 100 km away from this study area but separated by a dense forest watershed ridge. Isolated herds closer to the study area at upper Nahomba and Kinjekejeke have been observed to calve in early October, and not late November which is the normal time for the study area. For these animals, calving coincides with the flush of short annual/perennial grasses caused by the onset of the rains in late November. These grasses do not flush following burning earlier in the dry season.

Eland calve in late June as calves are abundant in mid-July, and eland exhibit a distinct lying out behaviour (Hillman, pers. comm.). It is difficult to visualise the adaptive significance of such timing as lactating mothers and weaning calves are faced with a long dry season - perhaps the availability of dry season browse components is of importance. Cobb (1976) has documented the great mobility of eland and their apparent ability to move to ares with adequate food resources.

Buffalo calving is in the peak rains, presumably buffalo being a coarse non selective grazer cannot utilise the nutritious but sparse ($<$5cms tall, $<$20gms dry matter/m^2) dry season flush of grass and their calving coincides with bulk vegetation production. Sinclair (1977), reaches similar conclusions.

8.315. Calf Survival.

Spinage (1970) suggests a calf mortality of some 50% is usual for African ungulate populations. Figures for this wildebeest population agree with this estimate. A slightly unusual feature may be the apparent constancy of mortality rate in the first year of life, increased mortality in the first few months being more typical. Methods as used here may be too crude to show such detail.

8.316. Longevity.

Schedules of age specific deaths are not of great interest in themselves, but they can lead to complex population analysis if certain assumptions regarding stable age distributions are met, Caughley (1977). Having no criteria on which to test these assumptions, analysis has not been attempted. Examination of table 8.4 does show for wildebeest a considerable number of animals dying in older age classes and mean age of death of the adult population is 8.3 years. This indicates a considerable longevity, greater for example than Watson (1969) shows for Serengeti wildebeest.

Warthog, although having a similar potential life span, (Spinage & Jolly, 1974, quotes 19 years) have a much greater mortality early in life and adult mean age of death is 4.4 years. Actual longevity per average adult is therefore quite low.

8.317. Disease and parasite load.

Tables 8.5 and 8.6 reveal a low incidence of disease and parasite presence. Anthrax is perhaps the only pathogen of ecological importance, being responsible for an estimate of up to 500 wildebeest deaths per year. Anthrax is of widespread occurrence in Africa and can reach epidemic proportions, as in Kruger National Park for kudu (Pienear 1964). Control is difficult without recourse to expensive measures of burning carcasses, fencing natural water points and supplying artificial water points. The disease became apparent in 1971/72 and there are subjective impressions that its impact diminished in 1976 and 1977, (Mbano, pers. comm. from the Miombo Research Centre).

Parasite loads are low in comparison to Serengeti and Lake Rukwa. Possible reasons for this are the prevelance of dry season fires, the lack of domestic livestock from the wild animals range now and in historical times and the previous low numbers and dispersed nature of the animal populations.

8.32 The Concept of performance.

Ecological performance is a difficult concept and can be measured only against what the species, population or individual is attempting to achieve. This involves postulating the objectives of species or individuals and examining the strategies adopted by them to attain these objectives.

The performance of a species can be measured by its ability to maintain itself numerically. A species expanding or maintaining constant size can be considered to be performing well, a species in decline cannot. In terms of a species there can be no finer criterion of performance, and interspecies comaprisons cannot be made. Finer criteria of performance can be made at the level of the population and population performances within a species can be compared. For example, in this study area, Peter's oribi and cheetah populations are at the extremities of their natural ranges. Population sizes are low and fluctuate and several years may pass between sightings. The populations, in comparison with say oribi in Liwale district or cheetah in Serengeti are not performing well. Wildebeest here with zero population growth can be considered to have a poorer performance than the Serengeti population with a high rate of growth. However, wildebeest in the east Selous with a density of $28/km^2$ cannot be said to perform better than populations in the south Selous with densities below $0.5/km^2$. Both populations may be performing equally well within the limits of available resources.

Explaitation agencies, such as agriculturalists or foresters measure and compare performance by the yield of some stated objective such as grain, wool or timber production. Defining the biological objectives of wild populations is not so simple. The objectives of a population could be stated as self maintenance and, for k-selected organsims such as large mammals, the maintenence of homeostatic ability in fluctuating environments. Strategies towards this objective would be the increase of population size by reproduction and such increases would be damped by intra-specific competition, predators, food availability, disease etc. The population objectives must equal the sum of the objectives of all the constituent individual objectives, unless one considers the intricacies of sociobiological regulation of population size.

The objective of an individual could be considered as the perpetuation of genotypes and increasing the individuals genetic contribution to the population gene pool, i.e., to multiply. Strategies pertinent to this objective would include the successful production and rearing of young through as long a time period as possible. This would entail: high fecundity, early fertility, high calf survival, longevity etc. Gross objectives and strategies are genetically determined, but the factors leading to strategies are more plastic and readily influenced by external and behavioural stimuli, eg. the age of first conception.

As populations in the study area utilise both major habitats (Woodlands and wooded grasslands) is is not feasible to compare performance between habitats. However results in this and the previous chapters stress the dependence of wildebeest and zebra populations on both habitats. The removal of either habitat would cause an immediate deterioration in performance.

Within the limits of this definition of performance, the populations of the major species of this study area are performing adequately. Rates of reproduction, survival and longevity are high in comparison with other populations. This is illustrated below by comparing wildebeest parameters of the Selous and Serengeti populations.

Parameter	Selous	Serengeti
Fecundity (adults)	100%	96%
Fecundity (yearlings)	55%	35%
Longevity (adults)	8.34 years	6 years
Condition (KFI)	Good	Lower
Pathogen level	Low	Higher
But,		
$\bar{r}$	0.04	0.1

The question of why wildebeest population growth is virtually zero in the Selous population when population parameters are high is discussed in the following section.

8.33 Population limitation and performance

Earlier sections have shown that wildebeest and impala populations have close to zero population growth rates and that there has been no significant growth since 1971. Some factor or factors of the environment must therefore be limiting to the growth of these populations. Data for wildebeest are sufficient to hazard a guess at the nature of these factors.

Chapter seven showed, from data collected in 1970 - 1972, that total nutritional inputs for wildebeest were adquate for bodily maintenance and allowed a surplus for population growth - provided that animals utilised the woodland areas during the dry season.

The available evidence shows that they do. Section 8.223 showed that wildebeest body condition was 'good' throughout the year and did not reach the low levels of Kidney Fat Index attained by the Serengeti wildebeest, a population experiencing rapid growth. Disease (apart from anthrax) and parasitic infestation levels appeared unimportant. Finally wildebeest fecundity, as measured by pregnancy rates was at a maximum for adults and a relatively high figure of 0.56 for yearlings.

Production therefore is high, affording opportunities for population growth. What is preventing it? Table 8.10 documents wildebeest population inputs and outputs in the form of a population balance sheet. The population size is shown as 12,000 animals and average proportions of calves, yearlings, male and female adults are known from unpublished field observations. In the light of no knowledge to the contrary, calf and yearling sex ratios are taken as 1:1. Applying known fecundity rates shows an annual calf crop of 4,858. The population is stationary, therefore there should be annual loss to the population (mortality) of approximately 4,858 animals.

Section 8.223 shows a calf loss of close to 50% per year, a figure in accord with other wild ungulate populations. Unpublished, and rather scanty data, suggests a yearling mortality figure of some 25% per year. Half the calves die in the first year giving a recruitment of some 2429 to the yearling class, one quarter of these die giving a recruitment of 1822 to the adult class each year.

A figure of 1822 yearlings recruited is 37.5% of calf production, there being 62.5% juvenile mortality. What happens to the adult population? Appendix 6 gives data on the lion population of the study area, and suggests a minimum lion population size of 120 and shows 34 % of the observed kills to be wildebeest (n = 77). Published data assumes a kill rate of 36 "average" sized animals per "average" lion per year, Schaller (1972). This indicates some 1,469 wildebeest being lost to lion predation per year. Observations suggest the bulk of this will be adult animals. I have no evidence for hyaena predating adult wildebeest and the clan behaviour of hyaena described by Kruuk (1972) for northern Tanzania has not been observed here. Wild dog appear to concentrate on the young of large ungulates and on impala. The very few leopard kills I have observed have been impala or smaller vertebrates. I believe predation on adult wildebeest by carnivores other than lion to be insignificant. I suggested a figure of up to 500 wildebeest dying each year from anthrax. This, with the loss of 1,470 by predation (or more, as 120 lions was a minimum estimate) is sufficient to prevent any possibility of growth in the adult population and would lead to a decline in numbers.

How reliable are these figures? Firstly we know the population to be stationary for the past five years, therefore mortality must balance natality, there being no emigration or immigration. Further, the calf content figure of 30% is a year average (see table 8, appendix 7) and the figure of 3,600 (30% of 12,000) falls very close to the mid-point of the year start figure of 4,860 calves and year end figure of 2,430 calves. Similarly the 16% yearling population is a year average and this figure of 1,920 again lies between the year start and end figures of 2,430 and 1,820. These facts lend credence to the above results.

The population is reproducing at close to maximum levels. If yearling fecundity reached the maximum potential value of 1.0 this would give 960 calves instead of 538. After juvenile mortality of 62.5%, this gives 360 recruits to the adult class and not 202, an increase of 158 which is not going to significantly change the rate of population growth.

Adult mortality factors, predation and anthrax can be classed as density independent. Details of juvenile mortality are unknown, but would include predation (hyaena and wild dog principally - dog densities are high, there being an estimated 100 in the study area, unpublished information), disease (hoof rot & others), loss of mother, and the possibility of dry season stress and starvation. The dry season is the time of weaning and the time of low nutritional inputs if the animals have not moved to the woodlands. Chapter seven mentioned the fact that calves have low levels of resistance (reserves going to body growth, Sinclair 1977) and considerable mortality could be expected. However a constant mortality rate during the first year (chapter eight) would suggest such a factor is not of prime importance.

Of the four species for which serial censuses exist, two, zebra and warthog show a rapid rate of increase and two, wildebeest and impala, have shown no real increase since 1972. It may be a significant that these two species are the most dependant on early burning, wildebeest needing woodland post burn grass flush and impala needing fire to stimulate browse new leaf. The change in landuse in 1973 (chapter nine) and consequent decrease in early burning may well be a significant factor in preventing population growth. The data on calf mortality are taken from the 1971 - 1972 period when early fires were regular, further investigation may well reveal increased dry season calf mortality.

PART THREE

Chapter 9 Final Discussion

Chapter 10 Conclusions

CHAPTER NINE: FINAL DISCUSSION

9.0. INTRODUCTION

Discussion sections of individual chapters have dealt at some length with the methods and results described therein. These results have been compared with similar data from other wildlife areas in Africa. This chapter therefore does not go into detail into any of the results from specific studies or sections. Rather, this attempts to discuss ideas and concepts arising from a consideration of more than one section, i.e. the relationship between land form and vegetation type or vegetation type and animal presence. In addition, this chapter compares the miombo woodland habitat, the Selous Game Reserve and the study area with other African wildlife reserves. These comparisons are both descriptive, as in the concept of scarce resources causing animal concentrations, and quantitative, as in the comparisons of animal biomass density and diversity values. Specific attributes of the miombo habitat are discussed in relation to animal occupance, fire and seasonality for example. Finally the chapter stresses the theme of the thesis, "the divergence of grazing strategy by large herbivores in their utilisation of the different habitats in this study area".

9.1. THE MIOMBO WOODLANDS AS A WILDLIFE HABITAT

The miombo woodlands and the physiognomically and floristically similar Guinea savanna of West Africa form Africa's largest vegetation type. Given the past and present low human populations the habitat is of major importance for wildlife conservation not because of high animal densities, diversities or carrying capacity but because of its vast size. With the difficulties of developing human interests such as logging, pastoralism or agriculture in the miombo, it is likely that the existing wildlife values will remain for the forseeable future. Large areas of miombo woodland have been set aside for permanent wildlife and wilderness conservation in Tanzania, Zambia, Zaire, Angola, Zimbabwe and Mozambique.

Chapter three has described the variety of plant community within the broad habitat type of "miombo woodlands". Much of the variety is dependent on topography, and influenced by historical factors of fire and cultivation. The largest block and, in terms of tree density, the "richest" miombo, is found on the flat central African plateau in Northern Zambia and Western Tanzania. Here completely unbroken homogenous woodland stretches for hundreds of kilometres; streams, valleys and ridges being very rare. This miombo carries very low wildlife densities, even in the absence of human pressures. A recent survey of Western Tanzania, Rukwa Region miombo areas in 1977

(Ecosystems 1978, Rodgers 1978a) showed animal densities in the miombo woodlands of Ugalla-Msima-Mlele to be less than 10% of that in the adjacent grasslands and open woodlands of the Rukwa valley. Overall densities within this 30,000km^2 area averaged 7.0/km^2 with buffalo forming 48% of the total.

Initial studies in the Moyowosi Game Controlled Area gave data on the wildlife occupance ratio between the extensive homogenous woodland and the adjacent Moyowosi floodplains and wooded grasslands (Mutch 1973). After correction for sampling effort these ratios can be expressed as:-

Species	Miombo Woodland		Grassland
Topi	1	:	43.5
Giraffe	1	:	19.0
Buffalo	1	:	18.0
Zebra	1	:	14.0
Warthog	1	:	13.0
Roan	1	:	5.4
Sable	1	:	2.1
Elephant	1	:	1.3
L. Hartebeest	1	:	0.7

It can be seen that only three species, sable, elephant and hartebeest do not avoid the miombo habitats to any significant degree and that roan forms an intermediate type. Densities for these four species combined are less than 1.0km^2. A similar pattern exists in the plateau miombo of Northern Zambia and Mozambique (pers. comm. Zambia Game Department, Mozambique Wildlife Department).

Chapters 2 and 3 stated that the miombo in its present form is a relatively recent habitat type, derived by the action of fire and settlement on forest and thickets following the most recent pluvial period. Endemic vertebrates are few (unlike insect or higher plant species), and include only two large mammal species, sable and Lichtenstein's hartebeest, although two other species reach their maximum densities in the miombo - roan and common duiker. But none of these species attain high densities, certainly not as high as 5.0/km over an annual range. Other species more typical of the open habitats to the north and south can also be found throughout the miombo, e.g. buffalo, eland, elephant, wurthog and zebra, but again do not achieve the densities of their other more open habitats. Other species, notably wildebeest, topi and impala do little more than penetrate the edges, see chapter six. It may be that the time available for the evolution of adaptations suited to the peculiarities of the miombo has been insufficient, but other simpler reasons seem more likely.

There is an apparent relationship between tree canopy cover (tree density) and grass biomass, the higher the cover the lower the biomass, and, to a lesser degree, the shrub growth (pers. observations). The plateau woodlands have deep free draining sandy soils with a very low water table allowing little post burn grass regeneration. These plateau areas have scarce dry season water resources (Rodgers 1978a), and all species listed above with the possible exception of eland are water demanding. These three factors then, low grass standing crop, very little dry season grass regeneration and scarce dry season water serve to reduce game densities to extremely low levels. As most woody species are deciduous and maybe without leaf cover for several months, large specialist browsing herbivores are also uncommon, eg. greater kudu and eland.

Where the homogeneity of plateau woodland is broken by different topographic features providing different vegetation types, then game densities may be very much higher. The Selous, lying below and on the edge of the East and Central African plateau, has a more varied relief, giving rise to greater heterogeneity of habitat and higher animal densities and diversities. This heterogeneity may take very different forms, viz:-

(a) Miombo and Tall Grass Swamp: eg. Kilombero, Moyowosi,
Rukwa, Katavi;
Tanzania. Lakes
Mweru and Bangwelu;
Zambia.

Here species such as buffalo, topi, zebra, puku and lechwe dominate on the grasslands. The ecotone between the grasslands and dense woodlands provides habitat for impala, eland, giraffe, warthog, roan as well as allowing higher densities of sable and hartebeest.

(b) Miombo and Short Grass Scattered Tree Grassland:

eg. East Selous, Ruvuma; Tanzania.
Luangwa, Zambezi; Zambia
Limpopo, Saabi, Lund; Mozambique/
Zimbabwe.

The short grasslands allow high densities of wildebeest, impala, zebra and warthog, the ecotone offers habitat for other species.

(c) Miombo and <u>Acacia-Combretum-Commiphora</u> <u>Bushland</u>

eg. Ruaha, Rungwa; Tanzania.

Elephant, rhino, roan, impala, buffalo densities are very much higher than in adjacent homogenous miombo areas (Rodgers, pers. observations).

(d) Miombo and River Valley and <u>Combretum</u> mbugas.

e.g. South and West Selous, Ugalla:
Tanzania.

The higher water tables, more water, and open grassland areas allow higher game densities.

These differences in habitat heterogeneity do give differences in game density, viz:-

Area	Size(km^2)	Habitat	Large Animal Density	Source
Moyowosi Woodlands	4,000	homogenous miombo	2.0/km^2	1
Ugalla-Msima-Mlele	11,400	homogenous miombo	2.5	2
Ugalla G.R.	6,000	miombo and river valley	5.6	2
Rungwa-Kizigo G.R.	12,500	miombo and bushland	6.0	3
Biharamulo G.R.	780	miombo and Combretum	6.8	4
West Tanzania	31,000,	miombo, valley grassland	7.0	2
Selous G.R.	45,000	miombo, valley grassland	16.0	5
North Rukwa	2,100	grassland, and some miombo	22.5	2
Eastern Selous	16,000	miombo and short grassland	27.6	5

Sources as follows:

1) Mutch (1973), and pers. observation
2) Ecosystems (1978), Rodgers (1978a)
3) Douglas-Hamilton & Rodgers, aerial survey 1977. Unpublished.
4) Rodgers, Ludanga and De Suzo (1978)
5) Douglas Hamilton, Rodgers & Mbano, aerial survey 1976. Unpublished.

Note that for unpublished surveys, computer analysis is as yet incomplete and values are provisional only.

It is clear then that heterogeneity of habitat, where miombo is broken by changing relief, gives greater wildlife densities than homogenous woodland alone. Other factors are involved; adequate water distribution and availability in the dry season, and high water tables allowing post burn grass regeneration, and a history of no or very low human pressures on the land all serve to raise wildlife densities. These factors are discussed in more detail below.

Chapter 2,2 stressed the low nutrient content of miombo soils, and that much of the nutrient store is tied up in the vegetation cover. For agricultural purposes, miombo areas need frequent rotations of cropping and fallow period, with or without additional inputs of fertiliser le (e.g. Allan 1965). Even with some tree clearing and provision of water points animal husbandry is not an easy proposition. Grasses are predominantly coarse sour veld species of low nutritional values for much of the year. More research effort is needed to determine optimum burning and grazing regimes for efficient beef production. Liver-stock densities on improved miombo pastures are low in comparison with other rangeland areas of East and Central Africa. (Pratt & Gwynne, 1977). These difficulties of livestock management apply equally to wildlife management, the miombo is basically infertile and nutrient availability must set a limit to habitat productivity.

9.2 THE SELOUS GAME RESERVE AS A WILDLIFE HABITAT.

Mention has been made of how the Selous Game Reserve gains in wildlife density by the heterogeneity of land form and hence habitat type. Densities of many animal species are higher than most other miombo reserves as a consequence. But this heterogeneity also leads to disparate wildlife distribution and abundances within the reserve. A number of distinct land forms may be recognized, these are:-

(a) The far south: highly dissected and eroded surfaces with remnants of previous flat ridges with deep red sands bearing miombo woodland. The eroded surfaces have shallow rocky soils with sparse grass cover and scattered trees. Dense riverine bush fills the numerous steep stream beds. This whole area is cut by three major rivers, the Luwegu, Mbarangandu and Njenje, and their tributaries. River valleys are broad with wide shallow sand rivers, fringing palm woodland and extensive open alluvial swamps. Elephant, buffalo and waterbuck dominate the valleys, elephant and sable the hills. Hartebeest apparently avoid the dissected terrain. Impala and wildebeest exist at low densities on short grass ridges near the major rivers, eg. Mkoma ya Ngasha.

(b) The south west and north west corners: mountains with elevations in excess of 1200m. and rainfall over 1200mm per annum. Dense forest and thicket remnants still exist and woodland canopy cover values are high. Wildlife densities are low with elephant, buffalo and sable dominating.

(c) The west: flat lowlying land with much alluvium and high rainfall. The Kilombero, Msolwa and Luhombero valleys cross the area. Vegetation varies from open floodplain and swamp to riverine forest to dense miombo. Buffalo, elephant and hartebeest dominate, kudu are absent. Densities are high for woodland habitats, see table 6.2.

(d) The centre: gently undulating miombo-Combretum open woodland with occasional reliot land surfaces as hill massifs, eg. Nandanga Mt. Elephant, buffalo, impala, hartebeest dominate, wildebeest may be found on short grass areas near sand rivers.

(e) The east: the transition from sandstone to pleistocene deposits, typified by the study area. Short grass herbivores dominate on the scattered tree grasslands. Densities are high.

Generalised land form profiles are shown in figure 9.1 and examples of different habitats can be seen in plates 1-6.

It is obvious that the Selous contains a great variety of land form and habitat type and that the eastern Selous including the study area cannot be judged representative of the entire reserve. Whilst the study area contains examples of all habitats within the Selous (with the exception of mountain forests and permanent swamp), the distribution and relative abundance of these habitats produce ecological conditions different from other regions of the reserve. The greatest difference arises from the presence of extensive areas of alkaline river terrace carrying a short grass cover favourable to grazing herbivores.

Some animal species distribution patterns within the reserve are odd, and not easily explained by consideration of habitat preference alone, (Rodgers, unpublished data). Section 9.3 in this chapter makes mention of the Selous as an ecological island and points out the number of small distributional islands along the periphery of the Selous. Puku are limited to a tiny ($< 20km^2$) patch of floodplain on the Kilombero River at Boma ya Ulanga, but exist in large numbers outside the reserve. Their distribution is obviously habitat controlled within this local area, but other apparently suitable habitats are not inhabited, eg. the lake swamp system of the lower Rufiji. Puku have a discontinuous distribution in Central Africa and now occur in only two isolated sites in Tanzania, the Rukwa and Kilombero valleys. As puku must have crossed the Iringa-Mbeya-Njombe forested highlands to reach the Kilombero it is strange that they have not penetrated downstream along the Kilombero to the Rufiji lakes. Perhaps it is simpler to believe they did so and have since become locally extinct. Past high human populations and frequent river course changes could have caused such extiction. Other odd distributions are the giraffe restricted to the North east Selous and not crossing the Rufiji River. Roan and dik dik and ostrich are absent from S.E. Tanzania and do not re appear in coastal Africa until south of the Zambezi. At present the lower Rufiji does not appear to be a major barrier, dry season levels can be as low as 1.2m, and elephant, buffalo and waterbuck easily ford it. Yet the river serves as a barrier between two morphologically distinct races of wildebeest (see plate 8). The southern race has a conspicuous white facial chevron which is absent or very inconspicuous in the north bank and in the Mikumi National Park populations. Kingdon (1972) makes mention of the Rufiji as a barrier to many small mammal species. With one exception of the Mahenge mountains, the Rufiji and Kilombero rivers act as a barrier to black and white colobus monkeys, populations existing in fringing palm-Sterculia forest on the north bank and absent on the south (Rodgers, unpublished information).

Jackal distribution poses another but different problem. Jackal are commonly found close to settlements around the Selous; Kisaki, Utete, Ngarambi, Liwale and Songea. Yet they have been observed within the Selous only three times since 1970, and always within a kilometre or two of the boundary.

The tongue of short grass wooded grassland extending along the eastern boundary can be thought of as an extension of the northern/central Tanzanian savanna into the woodland habitat. Typical savanna animals, wildebeest, zebra and impala are dominant, but another species the giraffe, has been unable to cross a river barrier. Cheetah, a typical short grass predator does occur but is very rare, (see chapter eight). More mobile creatures do take advantage of this extension and the preliminary bird list for the Selous (Matzke & Matzke 1975) lists ten species of savanna bird not previously recorded south of the Central Railway line.

Distribution patterns of the Hippotragines, roan and sable antelope, both typical miombo species can lead to speculation on species origin. Gentry (1968) states the Hippotragines to be essentially African (despite rare fossil finds in India). Sable are found from coastal Kenya south west to Angola and southern Africa but fail to enter West Africa

Roan are found from West Africa south east to Central Tanzania and Southern Africa but fail to enter coastal East Africa, the Usambara to Mbeya to Nyika mountains presumably acting as a barrier. Hemingway (pers. comm.) suggests this may indicate an East African origin for sable and a West African origin for roan.

Plant species distribution patterns have been discussed in detail in Chapter 3.3 and are summarised below.

9.3 THE SELOUS GAME RESERVE AND HUMAN POPULATION PRESSURES.

John Owen was one of the first conservationists to draw attention to the insularity of even the largest of Africa's Parks, " --- few of the worlds parks are large enough to be, in fact, self regulatory ecological units, rather most are ecological islands subject to direct or indirect modification by activities and conditions in the surrounding areas", (Owen 1972). The Selous Game Reserve is Africa's largest wildlife sanctuary and, as a result, has much less of a problem with border pressures than do many smaller areas in densely populated regions e.g. Nairobi National Park. The lack of traditional or recently developed pastoralism has prevented the increasing demand for grazing areas, which for example has virtually overtaken Umba (East Mkomazi) Game Reserve in Northern Tanzania (Rodgers, unpublished records). The low (and decreasing) human populations bordering much of the Selous have not caused the demand for land and the encroachment of reserve space, as has happened, for example, with Maswa Game Reserve bordering the Serengeti (Rodgers & Mbano, 1975, unpublished report to Game Division).

But the Selous was not divorced from human modifying factors in the past. In some areas, it is subject to influence now, and there are indications of much greater influences to come in the future. On a large time scale the Selous owes its existence to the activities of early man clearing and burning the post pluvial thickets and forests. A 45,000km^2 area of coastal thicket would not merit conservation status as a Game Reserve, just as the adjacent 4,000km^2 Kichi hill thickets have low wildlife values (in terms of large mammals).

Within this century much of the Selous was settled, albeit lightly, and by hunters and shifting cultivators, not by more advanced agriculturalists, (Rodgers 1976b; Matzke 1975 and 1977). Their activities whilst being depressant on wildlife presence in areas occupied, especially the larger, gregarious animals, did not extend to all favoured grazing areas or dry season water resources. The human populations' activities in bush clearing and burning would have kept the vegetation in an open state and prevented the spread of thicket. Their burning practice, traditionally early in the dry season, would have created optimum grazing conditions for the woodland animals. But their hunting and cultivation did reduce animal populations, and it is highly likely that populations now are considerably higher than at the time of the great 'Kihamu' or mass evacuation of 1947 (Ionides, Nicholson, Rees, pers. comm.; Kjekshus, 1977). Thus past human settlement has depressed animal populations by both competion for space and water resources and by direct exploitation-hunting. The settlement may also have promoted wildlife populations by burning, thus reducing thicket growth and stimulating dry season grass flushes.

Within the present Selous boundaries there is no human settlement or human-animal competition for land. Direct exploitation of the Selous wildlife populations does exist, as it does in virtually all African reserves, by illegal hunting or poaching. Levels in the 1966-1976 period are considered low however, by comparison with other areas of East Africa. There have been indications of an increase in poaching during the present period of high trophy price in the markets of Eastern Africa. The proposed anti-poaching developments within Tanzania could reduce this recent increase. Even so the 1976 aerial census showed an extremely low elephant carcass - live elephant ratio, an index of mortality used as a measure of poaching. This survey did show areas of poaching activity, which, as is to be expected, were close to human settlement areas. The Rufiji and Ruaha rivers proved to be access routes for such activities.

Figure 9.1 maps the major settlement areas of the 1940s within what is now the Selous Game Reserve. Figure 9.2 documents present border settlement and indicates the sites of heavy poaching pressures, land demand, tourist activity (and future potential) and planned industrial and communication development.

Low poaching levels may be due to: 1) low human populations, 2) the difficulty of access to all but the periphery of the reserve due to terrain, rivers and distance from settlement, 3) the continued existence of wildlife populations outside the Selous and 4) to the degree of supervision of villagers within the new Ujamaa villages of south east Tanzania. I had no knowledge of organised poaching or racketeering in trophies around the Selous during my ten year stay. At Kingupira Game Base, most arrests were for hunting for meat, not trophies. The previous Game Warden at

Liwale recalled an elephant shot and the meat virtually all removed and dried, but the tusks neatly placed on the carcass (Madogo, pers. comm.).

Chapter one discussed the Selous as an ecological unit and pointed out there was little game movement across reserve boundaries with the exception of elephant. Home ranges of most large mammal species appear small and there is little need for movement in terms of resource availability. Populations are continuous for at least 80% of the Selous boundary and in the south densities are as high outside as inside the reserve. An area the size of the Selous cannot be homogenous in respect of wildlife distribution. The Selous does not purport to enclose total populations, rather it attempts to enclose a number of high density wildlife areas and the sub populations which might use these areas. Boundaries were drawn with that objective and by attempting to use natural markers such as ridges, rivers etc. and not artificial lines from A to B. As such boundaries will cut home ranges and small movement areas, but not cut across or separate major resources such as dry season or wet season concentration areas.

Animals leaving the reserve are of course open to exploitation, this is not thought to be significant, expect in the case of elephant, which when in proximity to settlement are at risk from crop protection game scouts. An average of some 2,500 elephant have been shot per year since 1933 on crop protection in south east Tanzania. The Selous must act as a reservoir for such continual culling, (Rodgers 1978c).

As human populations increase, land pressures increase. Much of south east Tanzania is underpopulated and the recent ujamaa village programme has resettled scattered hamlets away from the reserve (Rodgers 1978). On some boundary salients, pressures are increasing, notably in the north west, on what is now Mikumi National Park. Pressures are from pastoralists for grazing land, cultivators for crop land, and major sugar estates for valley land for future sugar cultivation. Villagers in the north east want access to fishing lakes in the Selous and occasional requests for timber exploitation are made. At present such pressures are being resisted by conservationists and by Government.

The Selous is safe from many insular pressures because of its size, but size creates its own problems. If a reserve is small, communication routes could pass around it, but not when the reserve is large. The great mass of the Selous prevents easy communications in south east Tanzania. As a result there are growing demands for access roads from Mahenge to Songea and Mahenge to Liwale. Access roads destroy wilderness, wilderness has kept the Selous in a pristine state and wilderness is one of the Selous' unique values, (Rodgers, 1977b).

Large size can mean large scale resources, and the Selous has one resource in abundance - water, Plans are virtually complete for a major dam across Steigler's Gorge on the Rufiji River (plate 1) giving rise to a 1,600km^2 lake in the centre of the Selous and an 800 MW power station and attendant township. The dam and access road will allow an easy crossing of the Rufiji giving rise to a major trunk road to the south.

It can be argued that land held as conservation estate has to pay its way, ethically, aesthetically, scientifically or economically. The Selous, some 6% of Tanzania's land surface, does not contribute to the economy (although it did before the hunting closure in 1973) and does not pay its costs of upkeep. Its ethical values compete with thirty other areas in Tanzania, its aesthetic values are not utilised and its scientific values are untapped. Cobb (1976) argues for observable utilisation of land as a safeguard for conservation in his discussion of Tsavo National Park. I agree in practical terms for the Selous (Rodgers 1977b) but point out that much of the Selous is not suitable for tourist development. The

Selous Game Reserve's most unique assetts are its size and wilderness, these alone should count heavily in arguments for its continuation.

We have seen how the Selous perhaps benefitted from early settlement albeit at a very low density, how present external settlement pressures are negligible and capable of control, and that it is future development that is the major threat to the Selous in its present form. The large size of the Selous has prevented present disturbance, but is a major factor in causing future disturbance. But its size is essential in some ways, any reduction will cause species loss. Not strictly according to species-area relationships (Diamond and May, 1976) as many species ranges are on the reserve periphery. The loss of the north east would exclude giraffe; the north, black and white colobus; the north west, red colobus, the west, puku, the south, an elephant shrew (Rees, pers. comm.); the south east, Peters oribi; and the east, cheetah. But if the central 50% were to go, no species range would be eliminated. The boundaries of the Selous are more than just the periphery of a large island, they are minature islands themselves.

Management recommendations in this context are given in Rodgers (1978b) and in chapter ten.

9.4 THE EASTERN SELOUS GAME RESERVE STUDY AREA.

Mention has been made of the fact that the east Selous is atypical of the Selous Game Reserve and the miombo habitat in general. It is typical however of a hill - river terrace - flood plain land system which can be found across the woodland formations of Africa. Such systems characteristically carry high wildlife densities and many are conservation reserves. The study area then is relevant more to such reserves than to the greater mass of miombo much of which has less conservation significance..

This section attempts to compare herbivore ecology within this study area with other wildlife areas in Africa. Quantitative comparisons can be made, based on biomass and on faunal diversity, but first a number of facets of the ecology of the Selous need to be discussed in more detail. These are water distribution, the seven month drought, the juxtaposition of two dissimilar habitats - the tall and short grasslands, and finally fire.

9.41 Water, fire, grass and herbivore movement pattern.

One immediate difference between the Selous including the study area and other game areas, both miombo and non miombo is the abundance of water (chapter 2.4). The eastern Selous receives half the rainfall of the western Selous but even so for most years nowhere in the study area is more than 10km from permanent water. In very dry years some of these "permanent" sources may dry in late October and November. Widely distributed dry season water prevents a dry season concentration of water dependent herbivores around scarce water resources, a phenonomen frequently found in Africa's parks and reserves, eg. Tsavo (Cobb, 1976). Within the study area the small hippopotamus population does concentrate in one water hole (Kingupira forest) during the dry season.

Water is but one of many essential resources for large herbivores, another major resource being adequate forage of the correct type (height, growth stage, quality). The majority of herbivores within the study area prefer, or are adapted to, short grass sward. Short grass habitats occupy some 20% of the study area during the rains. This causes a rainy season concentration, where herbivores are concentrated for a relatively scarce food resource - short grass conditions. This condition is unusual in African wildlife ecology as animal populations typically concentrate around scarce water resources in the dry season and disperse during the rains.

Early dry season burning is the key to such dispersion as wildebeest and impala do not leave the short grass habitats until the tall grass woodlands have been burnt. Zebra appear to be less restricted by grass height (chapters 6 & 7). Patch-work burning early in the dry season gives rise to nutritious grass flush on slopes with high water tables and these patches are favoured by grazing animals - including the woodland residents sable and hartebeest. Late dry season burns however are extensive and produce little or no grassflush and, when they cover large areas (as they can do e.g several thousand sq. km in 1976) are catastrophic for grazing animals unable to turn to browse. Chapter 3 suggested that early burning has been the norm in miombo since historical times, but early patch work burning requires man's presence. Previous settlement provided this presence in the past and hunters, legal and illegal, burnt as a matter of policy until 1973 when legal hunting ceased.

With no hunting and decreasing Game Division patrol activity burning has been carried out later in the year, with the unfortunate exception of areas close to the boundary where villagers and Divisional staff burn the short grass habitats. Animal populations are caught in a dilemma, non burning of the woodlands restricts them to the short grass areas, but burning of the short grass areas, which produce no flush being largely composed of annual species, forces them to the tall grass woodlands. Adequate fire policies are essential to the management of tall grass woodland habitats for grazing purposes as ranchers in Central Africa have found out. The Selous has been fortunate in the past that the optimal policy of patchwork early burns was undertaken by hunting safaris, as burning is also essential for game viewing purposes. Now hunters have been excluded from the reserve, the Selous managers must face their responsibilities and undertake an early burning policy, arduous as it is over 45,000 sq. km. Hunters were readmitted to the selous in late 1978, but it will be several years before safaris cover the whole area.

9.42. The importance of fire in the miombo habitat.

Fire is not only of importance in determining herbivore movement patterns as discussed above. Fire directly affects vegetation dynamics and succession, production of browse and graze, and to a certain extent affects herbivore nutrition, condition and timing of reproduction.

Miombo is a fire induced sub-climax vegetation type and, as was detailed in chapter 3, will revert to thicket/forest if fire is excluded for long periods of time. Management for non forest herbivores therefore demands the presence of fire. Chapter 3 also showed the dynamic interrelationship between the miombo (Brachystegia) and the chipya (fierce fire woodland) associations, fire in terms of frequency and intensity being the agent of change. In terms of occupance by large herbivores there is little difference between miombo and chipya (as shown by this study) but the miombo shows far greater diversity in plant species at all physiognomic levels, and probably greater diversities of smaller vertebrates and invertebrates as well. The present heterogenous assemblage of associations, thicket, miombo and chipya has evolved over several thousand years. Evidence indicates that a policy of patch work early burns perpetuates this heterogeneity. Different burning regimes, either no fires or late dry season fires will reduce heterogeneity at both the association and species level (Freson et al 1974).

The study area is well watered, but by streams, springs and seepages, not by permanent rivers. The continuation of these water resources depends on the continuation of the thicket forest cover of the two major watershed ridges, Libungani and Tundu hills. Fire, by slowly removing the dense vegetation cover would increase surface run off and erosion, thereby decreasing ground water supplies and spring flow.

On a shorter time scale fire affects the grass layer - removing coarse growth and stimulating fresh growth. This drastic alteration of habitat causes changes in herbivore habitat utilisation patterns, see chapter 6. Utilisation patterns respond to changes in the availability of nutritious forage, and fire (and heavy grazing pressure and trampling by buffalo) is the main stimulus for dry season growth. With no fires, the lack of adequate rainfall from late May to late November prevents the production of new grass shoots.

Miombo grasses are typically tall coarse tussock Andropogonae of low nutritive value following maturity and flowering. Production of new tissue in these (and the annual species) is restricted to the rainy season. New growth can often be masked if last season's fires did not remove previous coarse stems. No fires for only three to four years can cause a significant depression and masking of grass growth by herbs and shrubs.

Fire is important in allowing short grass grazers access to the woodland and providing adequate dry season forage. Many woodland animals are adapted to the presence of fires, especially as regards the timing of reproductive cycles. Chapters 7 and 8 suggest that parturition and lactation coincide with the period of optimum nutrition. This period is dependent on early season burning and the subsequent grass flush.

9.43 Fauna-flora relationships.

Topography, soil, climate and history have determined the structure and composition of the vegetation of the study area. This vegetation is basically Zambezian in origin (chapter 3.3, White 1965), but a savanna element - the scattered tree grasslands is present with species affinities to coastal East Africa and structural affinities to the Soudanian zone. Forests, whilst of little importance to large herbivores are again primarily coastal. The fauna is likewise composed of two major elements: the Zambezian or woodland: sable, hartebeest and common duiker; and the savanna elements: wildebeest, impala, and zebra. Other species are broadly adapted and found within many faunal zones, eg. elephant, buffalo, bushbuck. A third element - a forest element of red and blue duiker and suni can also be distinguished. Presumably collecting of smaller mammals would more clearly define these elements (Kingdon 1971).

Chapters 6,7,8 and parts of this chapter have highlighted the ecological differences between these elements. Basically the woodland fauna is adapted to tall grass conditions and are selective grazers or grazer/browsers whilst the savanna fauna is adaptdd to short grass and are basically non-selective grazers. There is no gazelle-like species in Central

Africa and its role of small grazing herbivore is partially filled by the impala, whose numerical dominance and ability to use open grassland resembles the Thomson's gazelle rather than the impala of northern Tanzania. Impala thus become the major prey species of cheetah and wild dog, two typical savanna predators.

9.44 Quantitative comparisons.

Two quantitative comparisons are used, biomass density and faunal diversity. Comparisons based on vegetation values are almost impossible to make as floras are so rich that differences in collecting intensity dominant differences in diversity and species number. The Selous has an estimated plant species total of over 2,000, compared with 931 species for another large area, East Tsavo, (Bjornstad 1976). Comparisons made below are based on large mammal populations only.

9.441 Biomass density.

Biomass density data afford a simple method of comparing animal communities, both spatially and temporally, as well as synthesing data on the densities of individual species. Coe et al (1970) amassed considerable biomass data from African game areas and showed significant correlations between biomass and rainfall and primary production. It is of interest to compare Selous miombo data with theirs. These authors give mean body weight data for several species, I have accepted this data for all but three species - wildebeest, hartebeest and impala, where subspecies differences cause considerable weight changes. Table 9.1 gives body weight data and biomass densities for different areas of the Selous. Figures are given for the study area scattered tree grasslands in the rains and the dry season, for the complete study area and for the southern and western areas of the Selous. Data are taken from chapters 5 and 6 and from the preliminary results of the 1976 aerial census.

There is a considerable difference between seasonal biomass density for different seasons in the study area short grass habitat. The very high rainy season value of 13,500 kg/km decreasing by some 58% to 5690 kg/km in the dry season. The woodland area will of course show an opposite but smaller shift due to its greater size. Biomass data based on incomplete population ranges or measured at extremes of seasonal distribution patterns may thus be subject to considerable error. However data for individual or seasonal habitats serve to show their level of use. The figure of 13,500kg/km of animal biomass is some 3.9% of the peak forage standing crop of 350,000kg/km. A proportion which is considerably higher than that of the woodland bahitats, although the heterogeneity of the woodlands prevents the determination of exact figures.

Coe et al (1976) show a significant regression between log biomass density (BD) and log annual precipitation (AP) of:

$$\log BD = 1.552 \log AP - 0.62.$$

This regression is based on data from 24 wildlife areas in Africa but includes only 2 miombo woodland areas, Sengwa and Henderson Ranch, both in Zimbabwe, and both with rainfalls considerably below that of the Selous. Data for the three Selous areas fell below that predicted by the regression line(using rainfall data of 760mm and 1000mm p.a. for the east and south/west) but within the 95% confidence limits.

The low primary productivity and standing crop of the grass layer in miombo habitats (due to long dry seasons and frequently dense tree cover) will reduce the carrying capacity of large herbivores below that predicted by Coe et al's regression. Indeed their regression must have a cut off point, precipitation above 1500mm p.a. frequently leads to forest habitats with lowered mammal biomass. Coe et al (1976) state that comparisons of herbivore biomass and habitat type failed to yield significant predictive equations. But differences in vegetation structure, phenology and production must affect biomass and carrying capacity, obviously the relationship is of a complex dynamic nature and not suited to single variable analysis.

Also of interest in these comparisons is the contribution made by browsing herbivores (or generalist feeders, especially elephant) to the biomass totals. Cobb (1976) draws attention to the domination of the Tsavo animal biomass by elephant, (72% in Tsavo east and 62% in Tsavo west). There is, as would be expected, a relationship between the % contribution by browsers and the relative abundance of grass and non grass components of the vegetation. Available data show the following pattern.

Area	Vegetation	% Browsers	% Elephants
Serengeti (Hendrichs 1970)	Grassland/Savanna	18.6	5.7
E. Selous (WAR)	Wooded Grassland	30.4*	8.9
Ugalla (WAR)	W. Grassland/Woodland	34.1	32.1
S & W. Selous (WAR)	Woodland	64.2	61.2
Tsavo W. (Cobb 1976)	Woodland/Thicket	77.3	61.9
Tsavo E. (Cobb 1976)	Woodland/Thicket	85.8	71.9
Kariba (Jarman 1971)	Woodland/Sparse Grass	87.9**	69.6

* Includes impala as a browser.

** This figure is increased if buffalo is included as a browser, their diet in Kariba contains 55.5% browse components.

As Cobb (1976) and Laws et al (1975) point out, the elephant is a generalist and able to expoit a wide range of habitats, some woody material does appear to be essential though. Its ability to exploit water sources unavailable to smaller animals enables it to utilise areas away from permanent open water. The elephants great weight means that only minor changes in density cause large changes in area biomass estimates. Whilst elephant may be dominant in some miombo areas, eg. Luangwa valley (Caughley 1976), Rungwa/Rucha, South Selous etc. in others it is very much less eg. Moyowosi. Here historical and human factors are probably more important than habitat factors.

9.442. Diversity values.

The concept of ecological diversity is being increasingly used to compare communities, (Pielou 1969) and is frequently used as a measure of ecological richness when considering conservation values (Margalef 1963). Chapter 3.6 of this thesis introduces indices of diversity. H' and equitability E, in a discussion of vegetation diversity. The same indices are used here, viz:

$$H^1 = \sum_{i=1}^{s} - (pi)(\log pi)$$

$$E = H^1/H^1 \max \; \& \; H^1 \max = \log_s$$

"H^1", the Shannon-Weiner Index is a valid tool to compare diversities even though its exact biological meaning and relevance is controversial, Pielou (1969). "E" is a measure of evenness and is the ratio of the observed diversity to the theoretical maximum diversity given the number of species in the community.

Diversity and equitability indices have been calculated for the study area, the Selous, Tsavo and Serengeti. All large mammals including large primates and carnivores have been included. Data came from my own data and from data checked by Drs. Cobb and Grimsdell in the case of Tsavo and Serengeti. Figures for the less common species are often based on guess work, but this is unlikely to affect the results to any significant degree. Results are as follows:

Area.	Species Number. S	Diversity H'	Equitability E
Tsavo	34	1.20	0.78
Selous	37	1.22	0.71
Study Area	31	0.98	0.66
Serengeti	40	0.63	0.39

The low value for the Serengeti reflects the numerical dominance of wildebeest and the presence of several species with very low populations, eg. roan, oryx, colobus etc. Tsavo on the other hand has several species of similar population size and thus no dominance by one or two species.

The Selous is intermediate in position, buffalo and elephant showing partial dominance only (see table 1.2). The Selous for its size is species poor compared with many other smaller areas, this can be attributed to dominance by one vegetation type, the miombo.

ECOLOGICAL STRATEGIES WITHIN THE HERBIVORE POPULATIONS

Chapter 7 of this thesis described feeding strategies of the common herbivore species within the study area. It was seen that strategies were to maximise nutrient input, and that the strategies involved spatial and habitat distribution and diet selectivity. Much of the species biology is tied to the feeding strategy; e.g. movement patterns and the timing of reproductive processes, parturition in many species occurring at the time of maximum nutritional input.

Divergence in feeding strategy is most noticeable during the dry season, the time of reduced vegetation production and widely spread water and forage resources. For the array of predominantly grazing herbivores this would be the time of maximum inter-specific competition for food. Diverging strategies will minimise competition by decreasing the extent of niche overlap.

Maximum dispersion of niche space will occur with a patch work of early burns causing widespread (spatial and temporal) grass and browse flushes of regeneration. Late fires will reduce all resource levels to the extent that competition becomes a major factor and environmental stress, loss of condition and mortality all increase. Early burning with adequate regeneration is suggested as the ecological norm, breeding seasons are closely adapted to peak nutritional inputs which are dependent on burning. No burning and late fires will reduce nutritional levels at critical periods in the species annual cycle.

CHAPTER TEN

CONCLUDING REMARKS

10.1. Introduction.

Ideally research into wildlife ecology, and indeed all scientific disciplines, should have an ultimate objective. This objective may be the advancement of scientific knowledge, as in cases of pure research or, with more applied research, increasing the capability of conserving, managing or utilising the system under study. Studies undertaken in wildlife areas nearly always do have the second objective in mind, indeed it is almost impossible to work and live in a natural area and not have thoughts and ideas on improving conservation status and management efficiency.

It is a sad but true state of affairs in East African conservation however, in that very rarely are the results and conclusion from biological studies incorporated into conservation policy or management activity. A gap does exist between the scientist studying the animals/habitat, and the administrative warden charged with their conservation and management. I have been fortunate in that during my tenure with the Tanzanian Game Division I acted not only as biologist, but also as field warden, as wildlife project developer and was involved in policy decisions in headquarters. It is perhaps natural therefore that one should attempt to translate the conclusions of a biological study into conservation and management terms.

There are two aspects to conservation however, one is the biological basis, concerned with the animal populations and their habitats; the other is the political and economic basis for conservation, concerned with national policy objectives, landuse planning and development pressures. Both aspects are equally important.

10.2. Biological Problems in the Conservation of the Selous Game Reserve.

Caughley (1977) states that conservation consists of promoting growth in declining populations and reducing growth in populations thought to be expanding to deleterious levels. To this could be added the safeguarding of the habitat to allow animal populations to achieve acceptable levels of growth. Prior to being able to undertake these options is the need to know what one is attempting to conserve. The resource must be described:- its composition, numerical status, distribution and functioning. This thesis is an attempt to describe the resources of the east Selous - there is an immediate need for survey and study of the other areas of the Selous, as well as a need for the continuing monitoring of the east.

Assuming for a moment our biological knowledge is adequate to consider conservation policies, what problems are there? In the case of large mammals all populations within the Selous appear to be maintaining an adequate numerical status or increasing. No species is increasing to levels likely to cause major changes or disturbances in the environment. Some species by virtue of their gross geographic distribution maintain very small and possibly nonviable populations in the Selous, eg. red colobus and puku, these species do have adequate populations in areas adjacent to the Selous boundaries (see chapter nine). About other animal species we know virtually nothing.

Furthermore the Selous is large enough and has a habitat diversity great enough to be able to absorb minor changes due for example, to small scale climatic fluctuations without ill effect. One factor though which does exert considerable influence on the habitat and on the animal populations is more critical in that its variability is due to man and not natural cyclical change. This factor is fire. Chapters 3, 4, 6, 7, 8 and 9 have discussed the role of fire in affecting long term and short term vegetation change, grass phenology and nutrient content, animal distribution patterns, animal nutrient inputs, condition levels and reproduction. The thesis concludes that much of the miombo woodland habitat and its resident animal species are adapted to a regime of sporadic early burning in a mosaic pattern. This regime is believed to have been that typical of the Central African woodlands from the latter part of the Pleistocene, and of traditional hunters and cultivators in historical times.

The policy of tourist trophy hunting, which started in the Selous in 1964, also favoured an early burning regime, and the spread of hunting effort all over the Selous by the late 1960s meant that a patch work early burn policy really did exist. Attempts were made in the early 1970s to expand on this simple policy in that the short grass wooded grasslands and riverine and ground water forest were protected from fires by a system of fire breaks and buck burning.

The cancellation of all tourist hunting and the consequent lack of development and maintenance revenue to the Selous meant that hunters/game scouts were no longer reaching all areas of the Selous, graders became unservicable and roads and fire breakers were not maintained. Late dry season fires, covering much larger areas were more typical; with, as an example, an area of over 6,000km^2 north of Nandanga burning in two days in late 1976. These extensive, very hot fires remove all browse and grass growth and soil water levels are in adequate to produce a post burn flush. Effects on vegetation regeneration and animal populations must be catastrophic.

To my mind fire management and additional fire research are essential to the well being of the Selous. Game Division and reserve management authorities must, as a matter of urgency, reduce the frequency and intensity of late season fires.

The question of the utilisation of Selous animal populations is discussed in a later section.

1.3. Political, Economic and Development Problems in the Conservation of the Selous Game Reserve.

1.31. Political problems.

The conservation of any resource must proceed towards a desired objective or policy goal, but unfortunately conservation policies are poorly defined in Tanzania (and most African countries). Game Division policies may be briefly stated as "the perpetuation of the wildlife resource and its wise utilisation for the benefit of the nation". To this general statement may be added another, "the protection of life and property from the activities of wild animals".

Admirable as these sweeping statements may be, there exists no further more detailed policy statement for any of the individual wildlife areas under Game Division's control, including the Selous Game Reserve. There is no written policy document which states the reasons for conserving the Selous or states its importance in overall national conservation policy.

Basic questions of landuse policy are decided by politicians and senior civil servants - economists and administrators, although with Tanzania's policy of regionalisation local people have an increasing voice in what happens in their immediate environs. With very few exceptions, these people - politicians, economists and rural agricultural communities - have virtually no training in conservation problems or an interest in wildlife conservation. Forest conservation in terms of safeguarding soil and water resources is becoming acceptable, but 45,000km^2 for a single wildlife reserve is hard to accept, especially when very few tangible benefits reach national levels let alone the local coffers!

The reserve does exist however, as a large and relatively unspoilt wilderness conservation area. Changes to this state of affairs will only come about by actual decisions of policy change. Pressures for such policy decisions are increasing:- tarmac access roads, hydroelectric dams, permanent townships, stock movement routes etc. Proposers of such land use changes tend to be well armed with facts and statistics to support their case, Game Division has little factual evidence in written policy to back its case for conservation and, for many areas, would find it difficult to readily collect such evidence. The policy decision maker is likely to accept a well supported case for change in the absence of any high level national statement of the conservation values of the Selous. The creation of a permanent township of 15,000 people in the north Selous to support the Stigo dam project is a case in point.

To summarise this section, there is an urgent need to draw up detailed national conservation policies, to state the conservation values of major wildlife areas and have these values endorsed at the highest political levels and to draw the attention of decision makers to these values.

1.32. Economic problems.

In a relatively impoverished and developing country such as Tanzania, it is sometimes difficult to justify the retention and expensive maintenance of a resource, unless it is utilised for the benefit of the country. The Selous, although comprising over 6% of the countries land surface contributes virtually nothing to the national economy, yet acts as a drain on finances in order to maintain its staff and vehicles etc. This dilemma can be answered in two ways: by popularising and selling the concept of non tangible values: aesthetics, education, science, gene pools, land banks, ecological reference centres etc., or by some degree of utilisation of the resource to generate tangible revenues. Game Division has not yet got to grips with the first alternative and in the lack of a definite Selous land use policy has vacillitated in its utilisation efforts; hunting-no hunting, fishing-no fishing, cropping-no cropping.

This chapter is not the place for a debate on the pros and cons of utilisation in a major conservation estate, but it should be stressed that maximum levels of consumptive utilisation are scarcely compatible with the concept of wilderness conservation. On the other hand, the state of the national economy demands that conservation should try to be financially self supporting. A combination of non-consumptive utilisation - viewing tourism, and low impact high return consumptive utilisation - hunting tourism, when considered with the ecological benefits of burning control, would appear to be permissable.

Another consequence of the large size of the Selous is the ability to vary land use policy. Some areas could be heavily utilised, others lightly utilised and still other areas could be set aside as strict nature reserves with no utilisation at all.

1. 1.33. Development problems.

Chapter nine stressed that one of the main values of the Selous is as a total wilderness area (Rodgers, 1978c); any large scale development will therefore reduce this particular set of values. Some degree of development is necessary however, to implement effective conservation; tracks, airstrips and ferries for anti poaching, research, fire management etc are required, as are peripheral bases, incorporating housing and workshops etc.

A decision to utilise Selous resources will mean increased development and a further decrease in wilderness or naturalness values. High density mass tourism for instance, seems to require elaborate hotels and all weather access and viewing roads. Permanent cropping projects also require additional facilities and can have a considerable impact on populations, unless strictly controlled.

The question arises as to what degree of utilisation and development to allow? As mentioned above, the Selous is large enough to allow multiple use planning with different utilisation zones - high density tourism in the scenic north east for example. Such policies must however be rigidly defined and enforced. The recent case of hunting tourism and cropping in what had been declared a viewing and photographic area means one can no longer closely approach an animal, the area will take another five years to recover from what has been described as an oversight.

Offtake levels must be carefully considered. The existence of large populations does not automatically mean there is an annual surplus which can be harvested. Chapter eight of this thesis showed that the wildebeest population of the study area was only just remaining stationary - any offtake would reduce the size of the population, which is already reproducing at close to its maximum rate. Sport hunting tourism has less effect, in that only males are removed. But for rare species such as sable, offtake quotas, whilst they may appear low at four per block for example, may be near the sustainable maximum level.

In conclusion it must be stated that the Selous has managed to exist in its present state not through any miracles of conservation ability but because of the very low level of land and development pressure on the reserve. There were no demands for hydroelectric dams, access roads or revenue generation in the past. These demands are beginning now and the effective conservation of the Selous, as we know it today, is going to need a great deal more biological knowledge, value description and publicity, and political and land use planning argument in the coming five years than we have had to use in the past fifty.

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