The Structure and Dynamics of an Insularized Large Herbivore Community in Lake Nakuru National Park, Kenya

by

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DECLARATION

I, Evans Mwangi, declare that this thesis is my original work and has not been submitted for a degree in any other university

Evans M. Mwangi — 27.6.94

Signature 27/6/94 — Date

We the undersigned declare that this thesis has been submitted for examination with our approval as the University supervisors

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DEDICATION

Dedicated to those who live adjacent to and among wildlife, giving up part of their opportunities to ensure the continued existence of this vital resource.

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ABSTRACT

Lake Nakuru National Park was fenced all round in 1987, making it an ecological island. Its isolation started earlier this century when man began utilizing the catchment for urban development, commercial farming and livestock rearing. The isolation has resulted in loss of migration opportunities, low predation pressure and increased herbivore density. Having been so modified by man, the park is now in dire need for active management which requires that accurate information be readily available on all aspects of its ecology.

This study aimed at understanding the structure of large herbivore populations and their interactions with grazing resources. Field work began in March 1991 involving a series of 12 monthly and six bimonthly surveys along a predetermined road transect network. The method produces reliable density estimates, when strip width is reasonably large. During the surveys, data were gathered on numbers, age structure, sex composition and the spatial distribution of large herbivore species.

The quality and quantity of herbaceous plants were measured on eight study plots after every two months throughout the study. The effects of grazing on species composition and standing crop accumulation were documented on five vegetation exclosures.

Seventeen large herbivore species were found along the transects during the study. Overall herbivore density differed significantly among species and vegetation types, but not among seasons. Of nine species encountered in all surveys, no seasonal differences were found in the density of buffalo (*Syncerus caffer*), Grant's gazelle (*Gazella granti*), impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsonii*), Defassa waterbuck (*Kobus ellipsiprymnus defassa*), warthog (*Phacochoerus aethiopicus*) and zebra (*Equus burcheli*). Only the eland (*Taurotragus oryx*) had density estimates differing significantly among seasons.

Differences were significant among habitats for all species, except the buffalo and eland. Differences in age and sex composition were not significant among seasons for the giraffe, Grant's gazelle and zebra. They were, however, significant for all other species

Detrended Correspondence Analysis (DCA) showed clear seasonal patterns of association between the species, whereby big bodied, bulk and mixed feeders, namely the buffalo, eland, Grant's gazelle, rhinoceros and zebra were grouped into one large and distinct cluster.

Two predominantly grazer species with a preference for short grass, the Thomson's gazelle and warthog, fell into a smaller but nevertheless distinct cluster. This clustering was more diffuse for dry than wet season data, suggesting greater habitat selectivity and increased ecological separation of the herbivore species during dry periods, when availability of vital resources is more localized.

This finding was further supported by DCA based on vegetation types, which placed open habitats together in the dry seasons, as was the case for wooded or bushed habitats. Data for waterbuck fell in neither of the clusters, possibly because, being the most numerous large herbivore species in the park, it competitively displaced other species.

Herbaceous plant standing crop differed significantly between wet and dry seasons, and among vegetation types. The differences were more pronounced on grazed than ungrazed plots. Standing crop was correlated with rainfall accumulated over the eight days preceding sampling, indicating the need for proper timing of field measurements. It was highest after the long rains in 1991, thereafter decreasing to a minimum in the middle of a dry season in February 1992.

The analysis of nutritive value of 23 most common grass and sedge species indicated clear seasonal fluctuations in percent protein content, with some species falling below the theoretical minimum required for maintenance by animals during the dry season. The temporal fluctuations in availability and nutritive value of food are profoundly manifested in periodic losses of body condition among the park's large herbivores.

Herbaceous standing crop inside vegetation exclosures remained consistently higher than outside after the first few months of sampling, fluctuating with two annual cycles. Relative abundances of green and dry material differed over time inside all the exclosures, these being the same throughout the study outside three of the five exclosures. Ratios of different plant parts differed with time both inside and outside all the exclosures.

Species composition showed only marginal changes, with the most common grass species, among them *Themeda triandra* and *Hyparrhenia lintoni*, slightly declining in importance over the two years of field work. This study discusses the implications of ecological isolation to the interactions between plant and animal species and puts forward some recommendations for the management of wildlife resources in the park.

This study recommends a prescribed burn management programme, emphasizing the removal of each season's production to stimulate fresh growth. It suggests that some woody habitats be opened up to enable the park continue accommodating its remarkably large grazer community, alongside an expanding black rhinoceros population. Depending on habitat attributes and management priorities, it is recommended that the populations of constituent herbivore species be manipulated to fit within inherent environmental constraints.

CHAPTER 1. GENERAL INTRODUCTION

In recent times, conservationists have assumed that strict protection of selected areas can maintain biodiversity, leading to the establishment of national parks as the dominant approach to conservation. The number of protected areas in Kenya has increased considerably since the establishment of Nairobi National Park in 1946. By 1992, the country had gazetted 26 national parks and 29 reserves.

In the East African savanna, national parks and reserves represent the last relatively large scale remnants of the tremendous variety of mammals of the Pleistocene epoch, between 10,000 and 2.5 million years ago. Some of these parks and reserves are too small in size, however, and their boundaries were fixed without due regard for the year round needs of large herbivores (Myers 1972).

Due to human activities and land use practices within and around protected areas, natural communities have become increasingly reduced and fragmented over different time scales in many parts of the world. A large portion of the Kenya's wildlife habitat was lost between 1950 and 1985 (Mugabe 1993). This reduction in habitat areas has resulted in severe pressures on the remaining space.

Insularization is the term used for this phenomenon in which the fragmentation of a previously single geographic range results into small habitat isolates or virtual ecological islands. The most severe degree of insularization has been documented in the temperate regions and tropical woody savannas, mainly resulting from the extensive development of agriculture and forestry. Studies based on satellite imagery and aerial photographs have indicated the loss of up to 50% of rain forest in Madagascar between 1950 and 1985 (Myers 1988).

In East Africa, a rapid human population increase and changes in people's lifestyles over the last 50 years, have resulted in increased competition for resources and unprecedented human wildlife conflicts. In an attempt to ameliorate these conflicts, some protected areas are partially or completely isolated from surrounding lands by the construction of physical barriers, such as deep trenches and fences. The barriers are meant to contain and restrain animals within parks, and to protect man and his property from wildlife damage. Ultimately, these developments present new challenges to the management of protected areas and wildlife.

Concern for the effects of insularization on species richness and the diversity of biological communities is not new. Scientists have long observed the relationships between ecological isolation and the rates of immigration and extinction. The equilibrium theory of island biogeography predicts that the number of species on a real island or a similarly isolated area is a result of a dynamic equilibrium between immigrations and extinctions (MacArthur and Wilson 1963). Immigration rate is seen as a decreasing function, and extinction rate as an increasing function, of the size of the island. The theory predicts an equilibrium at the intersection of the two rate functions (Rey 1984).

The number of species of a particular group of organisms, for example mammals or birds, in island systems increases approximately as the fourth root of the land area and the probability of extinction for any species decreases with increasing population size. Large areas accommodate potentially more individuals per species, thereby reducing their probability of extinction. In addition, areas far apart from each other are not within reach of immigrants. These premises have been shown to hold true on real islands and other less well defined ecological isolates, such as clumps of trees in the middle of a grassland (*op cit.*).

On the basis of various rough assumptions, it has been estimated that 11% of the species of large mammals may be lost from East African national parks in 50 years, and up to 44% after 500 years (Soule 1980, Wilcox 1980). By virtue of their low population densities, birds and mammals are among the taxa most likely to disappear from isolated fragments.

There is convincing evidence that many parts of East Africa are undergoing rapid impoverishment of animal species. For example, the Mkomazi Game Reserve in Tanzania contained 43 large mammal species in 1952, four of which had disappeared by 1977 (Shaw 1985). Miller (1978) estimated that the reserve would eventually lose up to 21 species before reaching an equilibrium in about 300 years. Following a similar argument, it was estimated that Nairobi National Park would lose over 80% of its species within a few centuries, and the Serengeti would lose about 70% in about 1500 years (Soule *et al.* 1979).

The fragmentation of ecosystems leads to a reduction in total habitat area, which causes local extinctions through primary effects on population sizes. With increased isolation, the influence of large mammals on habitats becomes more pronounced. That elephants play a profound role in opening up woodlands and forests for example, has been recognized for a long time. Not until they are forced to live in unnaturally high densities, because of insularization and other causes, does their capability to destroy habitats become real cause for worry.

Fragmentation also causes the redistribution of the remaining area into disjunct components. It usually results in a juxtaposition of natural areas and man made habitats, thereby reducing dispersal opportunities. The ultimate result is an increase in the probability of local species extinction, which is known to depend on both area and population size (Quin *et al.* 1989).

For some species, loss of habitat means loss of space available as home range or territory, and species may even disappear from fragments far exceeding their minimum home range sizes. Another consequence of fragmentation is a reduction in habitat heterogeneity and therefore loss of microhabitats. Patchily distributed species or those that utilize a wide variety of microhabitats are particularly vulnerable under such circumstances.

The space between any two ecological isolates may form a formidable barrier to colonization, and human created landscapes can contribute directly to extinction within the isolates. In addition, populations of certain species within isolates can build up due to sealing of previous migration routes, leading to potentially deleterious processes and irreversible changes on the ecosystem. For example, plant-herbivore and predator-prey interactions can be radically disrupted by changes in the composition of plant and animal communities. The movement of migratory animals across and beyond park boundaries can be critical to wildlife populations (Buechner 1987).

Wildlife conservation and management authorities in East Africa are now faced with the task of establishing a network of scaled down functional units within the existing national parks system. This is easier said than done, however, given that only a few parks comprise what may be referred to as self supporting ecosystems. There is overwhelming evidence that wildlife of East Africa's parks and reserves depend on resources located outside, for at least part of the year. Good examples are provided by Amboseli (Western 1973) and Nairobi National Parks (Casebeer 1970), both of which occupy only small dry season concentration areas, with animal populations dispersing into the much wider neighbouring areas during wet seasons.

Seasonal movements of wildbeest and zebra in response to water supply have been reported in many other East African wildlife areas, for example the Ngorongoro Conservation

Area (Estes and Small 1981) and Tarangire ecosystem (Kahurananga 1981). Clearly, there is need to reconcile land use practices outside such parks with wildlife requirements.

The theory of island biogeography as initially proposed by MacArthur and Wilson (1963, 1967) has found wide application in predicting extinction levels on isolated parks and designing protected areas (Diamond and May 1981). It is becoming increasingly clear, however, that island biogeography models are too coarse grained to explain trends of species loss in specific circumstances. Their predictive ability for extinction rates and faunal equilibria in isolated wildlife preserves is questionable, at least in the savanna (Western and Ssemakula 1981). Factors contributing to this lack of a simple species area relationship include the effects of habitat heterogeneity and primary productivity on animal species richness.

Western and Gichohi (1993) identified segregation effects as possible causes of non insularization losses of diversity in East African savanna parks. They argued that even without any significant loss in land area, the establishment of a park itself sets off a series of events that bring about relatively slow impoverishment. Continued existence of many national parks and reserves as viable conservation units will depend on sound management of constituent wildlife resources and concerted efforts towards restoration of damaged habitats.

CHAPTER 2. LITERATURE REVIEW

All species appear to have the innate capacity to increase from generation to generation, which raises the need to disentangle the environmental and biological factors that hold it in check over the long run. Consequently, an understanding of the patterns of abundance and rarity of species has important applications and implications in conservation biology and elsewhere (May 1989). In East Africa, it has been suggested that changing environmental conditions could affect the ability of large mammal populations to adapt successfully to periodically recurring wet and dry conditions (Miller 1979).

The term herbivore applies to a large variety of animals, ranging from the largest of mammals, like the elephant, to insects and zooplankton. The number of mammalian herbivore species is rather small when compared to insects for instance. Out of the more than 1.4 million species of living organisms already described, only about 4000 are mammals, a small proportion indeed when compared to about 750,000 insect species. Annelids and Nematodes contain about 12000 species each (Wilson 1988).

The abundance of herbivores in the grassland savannas of eastern and southern Africa greatly exceeds that found almost anywhere else in the world (Botkin *et al.* 1981). This reaches 280 kg/ha, nearly 10 times that estimated for the North American prairies prior to colonization (*op cit.*). It has been observed that net primary production and animal production are exponentially related to rainfall (Coe *et al.* 1976, Western 1991).

Many studies have been conducted in an attempt to describe large mammal distribution patterns in different East African ecosystems (for example, Lamprey 1963, Stewart and Zaphiro 1963, Western 1973, Rodgers 1980). Many others aimed at understanding the factors that regulate these populations, in particular, precipitation (Coe *et al.* 1976, East 1984, Western 1991), food (Sinclair 1974, 1979) and competition (Sinclair and Norton-Griffiths 1982, Dublin *et al.* 1990). Thus a large body of data has been accumulated to enable a clear understanding of East African large mammal dynamics.

Following the pioneering works of Robert MacArthur and others, a good deal has been done both to elucidate the patterns of relative abundance of species and mechanisms producing them (MacArthur and Wilson 1967). Biotic communities have become progressively reduced in area as a direct result of human activities throughout the world, resulting in increased fragmentation of wildlife habitats (Spellerberg 1991). As the areas of natural communities become smaller and the fragments increase in number, there is an increasing incidence in the number of isolated plant and animal populations

Fragmentation and reduction in the area of natural communities affect population size and dispersion, both of which lead to extinctions (Spellerberg 1991). Loss of habitat heterogeneity is another product of insularization and those species with patchy distributions or those which utilize a range of microhabitats are especially vulnerable to losses in mosaics of habitats (Wilcove *et al.* 1986). Other long term effects of insularization include the increase in numbers of invasive species and higher levels of heavy metals (Spellerberg 1991).

Insularization has occurred over different temporal and spatial scales in all parts of the world. For example, current losses of tropical rain forests are estimated at about 76000 Km^2 per year (Malingreau and Tucker 1988, Spellerberg and Hardes 1991). A planned systematic and scientific assessment of the rates, extent and effects of insularization has not been attempted anywhere in the world (Spellerberg 1991).

Some attempts have been made, however, to monitor insularization in restrospect. Several notable wildlife monitoring programmes have been initiated in African national parks. Fixed point photographic stations and aerial counts of 12 species of large mammals have been used for monitoring purposes in the Kruger National Park since 1975 (Huntley 1988) and a few cases can be cited in East Africa. For example, an intensive ecological monitoring programme has been sustained in the Amboseli ecosystem since 1967 and regular game counts have been done in both Lake Nakuru and Nairobi National Parks since the 1960s.

Most of the insularization experienced in natural communities so far has been attributed to the extensive development of agriculture and forestry. Temperate closed forests have suffered the greatest cumulative area losses of 32-35%, followed by woody savannas (Repetto and Gillis 1988) The effects of insularization are manifested in short term effects on wildlife, caused by the resultant fragmentation and isolation, as well as long term effects resulting from disturbances on the remnant communities (Verner *et al.* 1986).

Insularization has both ecological and genetic implications and reduced genetic variability has long been recognized as a feature of small and isolated populations (Brakefield 1991). The remaining patches of the Brazilian Atlantic forest, for example, may contain populations of many species that are too small to ensure that genetic variability is maintained (Fonseca 1985).

The rules governing the maintenance of fitness in individuals and populations, and the biological principles upon which they are based. form the fundamental basis of conservation biology (Soule 1986). Populations have demographic and genetic thresholds below which no adaptive random forces operate (Soule 1985). In general, certain processes are considered responsible for reduced variability in small isolated populations, namely, inbreeding, genetic drift. the bottleneck and founder effects (Miller 1979).

Inbreeding increases the proportion of homozygotes in a population, thereby increasing the incidence of recessive variants. The most serious short term effect of this is inbreeding depression. which involves a decline in fecundity, juvenile survival or both (Shaw 1985, Ralls *et al.* 1986). In spite of lack of data from natural populations, studies of captive and experimental animals consistently confirm the ubiquity and magnitude of its effects (Ralls and Ballou 1983).

Genetic drift is the change in gene frequency that results in each generation, from the random sampling of alleles in a panmictic population. Its effects are particularly noticeable in small genetically isolated populations. In the rhinoceroses of Africa and India (Merenlender *et al.* 1989) and cheetahs in captivity (O'Brien *et al.* 1985), genetic variability has been measured and shown to be very small. Genetic drift can overwhelm natural selection in small populations. which can then suddenly succumb to demographic stochasticity in spite of individual robustness (Soule 1986). The implications of this are that such populations may not be able to adapt to changing environments.

The bottleneck and founder effects occur in very reduced populations or where a few individuals establish a population in a new area and in both cases, a few individuals are passing on a small fraction of genetic material from the original population. Outbreeding can also entail costs, as is the case for instance. where individuals require to disperse over unfamiliar environments in search for mates (Ralls *et al.* 1986). It may also involve genetic costs. as when fecundity or viability declines following intraspecific hybridization (Templeton 1986).

Nature reserves have been seen as last havens for wildlife and important locations for research and monitoring (Jenkins and Bedford 1973, Cairns 1981). Most protected areas are remnants of what used to be much larger biotic units. Despite their establishment, loss of species and changes in species composition continue to take place (Western and Gichohi 1993) Parks often represent patches of protected habitat with more or less dramatic changes in environmental features at the edges (Jansen 1983, Harris 1984, Schonewald-

Cox and Bayless 1986). Newmark (1987) attributed post establishment losses of mammals in North American national parks to habitat loss and active elimination of fauna on adjoining lands.

In most cases, animals are free to move back and forth across park boundaries, resulting in a net influx or outflow of individuals (Schonewald-Cox and Bayless 1986). The direction and magnitude of net animal movements may have serious impacts on wildlife populations living within a park (Buechner 1987). When the conservation of a species depends on immigration from external source pools, lack of immigration rather than an excess of emigration could pose conservation problems, especially likely when migratory species are concerned (Whitecomb *et al.* 1981). Pest species could invade a park from outside (Buechner 1987), or the lack of emigration may result in overpopulation by otherwise acceptable species (White and Bratton 1980).

Park boundaries themselves vary in their permeability (Stamps *et al.* 1987), and environmental gradients may affect net movement across park boundaries (Schonewald-Cox and Bayless 1986). Work on species diversity of invertebrates has shown that where a small fragmented protected area is surrounded by a structurally more diverse vegetation, invertebrate diversity was greater than where such an area is surrounded by a structurally less diverse vegetation (Webb *et al.* 1984).

Ehrlich and Murphy (1987) discussed the importance and value of monitoring populations in remnant communities as well as the difficulties involved. They suggested that such monitoring programmes can contribute towards an understanding of population dynamics and processes. They further emphasized the value of population genetic studies, in light of their important application in the management of isolated populations.

In addressing the important issue of conservation of biological diversity, the IUCN recently recommended that a global system of biological diversity monitoring stations devoted to the study of certain key indicator species be established (IUCN 1989). The amount and quality of information available about the species contained in these protected areas vary for several reasons. In Africa, and almost certainly elsewhere, lack of monitoring in national parks can be attributed to a general lack and high turnover of qualified staff. Other problems abound with reference to continuity and compatibility of methods (Spellerberg 1991).

This case study of Lake Nakuru National Park provides an opportunity to understand the implications of insularization to wildlife management. The park was surrounded with an electric fence in 1987, making it the first such ecological island in East Africa. Events leading to its complete isolation started earlier this century when man began utilizing the catchment for urban development, commercial farming and livestock rearing.

The park is characterized by high herbivore densities. Large mammal populations have increased steadily since its isolation, probably due to low predation pressure, decrease in poaching, the direct effect of confinement and, more recently, the introduction of year round water supply. For example, the numbers of three most common herbivore species, namely waterbuck (*Kobus e. defassa*), impala (*Aepyceros melampus*) and warthog (*Pharcochoerus aethiopicus*), more than doubled between 1978 and 1990.

With the establishment of a rhino sanctuary in the park, various proposals were put forward regarding the introduction of other wildlife species, some of which had become locally extinct earlier this century. Large populations and loss of dispersal opportunities as a regulation mechanism, could lead to over exploitation and the eventual degradation of the park. This situation indicates a need for intensive management of the ecosystem's entire resource spectrum. Such management depends on availability of data on various ecological factors and processes including animal and plant communities. In the absence of any migrations, animal populations need to be closely monitored and controlled whenever necessary.

Past studies in the Rift Valley indicated the prevalence of low levels of some key minerals, particularly copper and cobalt, in the soil (Hudson 1944, Chamberlain 1957, 1959, Maskall 1987). Suboptimal levels of copper and cobalt were reported in the blood of several wild and domestic bovine species from one of the ranches that finally became incorporated into the park, especially after a prolonged dry season (Robin Long, *Pers. comm.*, Howard 1964, Clausen 1970). There is evidence to link this mineral deficiency to the frequent loss of body condition encountered among the ungulates of the park.

A recent study on the Feral Donkey (*Equus asinus*) in Australia showed that females in a high density population ingested a species poor, mineral deficient diet. The animals also had lower levels of stored minerals, when compared to those living at lower density (Freeland and Choquenot 1990). At heavy grazing pressure, high quality plants are selectively consumed, forcing herbivores to feed on a species poor, high fibre diet that stimulates increased secretion of mineral rich saliva (Doyle *et al.* 1982). Such diets also act as gastrointestinal irritants, causing the secretion of copious quantities of mineral rich mucous (Freeland and Choquenot 1990). The result is that herbivores at high population density are likely to lose condition faster, and subsequently exhibit higher mortalities, as pasture conditions deteriorate.

The situation is compounded by other factors of the vegetation and the animal behaviour. Higher levels of nutrition may be achieved by greater selectivity in feeding, with the animals taking proportionately more of the higher quality plant parts (Owen-Smith 1982). Further, at lower protein levels, the activity of rumen micro organisms is inhibited, leading to low protein and energy assimilation (Sinclair 1974). Thus an apparent abundance of forage may still be accompanied by a more subtle nutritional deficiency. Ecological isolation and associated increases in wildlife biomass density can affect the distribution and availability of food resources.

Since the ecological responses exhibited by wildlife populations in the park could be directly influenced by the management actions in force, it is essential that the full implications of isolation be understood before any far reaching actions can be recommended. The conservation of biological diversity in increasingly smaller areas and under intensifying pressures requires knowledge about the status of resources therein (Jenkins 1988).

The pressures exerted on the ecological resources of the park can only be expected to increase with time. There is therefore a need for more knowledge about numbers, condition, genetic health, distribution and ecological relationships within and between species and communities. The park's insularization has presented an unprecedented opportunity to study ecological isolation and develop scientifically sound techniques for restoration before further fragmentation and isolation occurs elsewhere in the East African savanna.

This study forms an essential component of a wider effort towards achieving the overall objectives of generating information needed for management of the park ecosystem. Armed with such data, ecological catastrophes that would result from decisions made on the basis of insufficient information will be avoided and more sound planning strategies facilitated.

In realization of the critical need to maintain Lake Nakuru National Park as a viable and functional ecosystem, this study was designed to test the hypothesis that the structure and composition of plant and animal communities of the Nakuru region have changed over the last century, and may necessitate some management in order to reestablish a number of species and ecological processes.

I therefore undertook to achieve the following objectives:

i. To document the ecological history of Lake Nakuru National Park and catchment basin;

ii. To determine the temporal and spatial distribution patterns and structure of large herbivore populations in the park;

iii. To determine plant herbivore interactions and the response of one key species, the Defassa waterbuck, to seasonally fluctuating food resources and

iv. To establish and evaluate various management needs and propose ecologically sound ways of managing large herbivore populations in the park.

CHAPTER 3. THE STUDY AREA

3.1. Introduction

Lake Nakuru National Park lies in the eastern arm of the Great Rift Valley, between the longitudes 36° 03' and 36° 07' E, and latitudes 0° 18' and 0° 30' S. It is located about 156 km north of Nairobi and only about 4 km south of Nakuru town centre (Figure 1). Mean annual rainfall is about 823 mm (Kutilek 1974) which is by no means uniformly distributed. The park straddles an area between the 760 mm and 1015 mm isohyetes, at an average altitude of 1750 m asl (Kakuyo 1980).

Rainfall is bimodal, with two wet seasons from March to May and October to December, separated by two dry seasons from June to September and January to March. April is generally the wettest month, but exceptionally heavy rains in October and November are not unusual. The rainfall patterns for stations within the area over the study period are presented in Figure 2.

The park lies on recent alkaline lavas deposited less than 70 million years ago during the Tertiary-Quaternary period, with major soil groupings formed from sedimentary lacustrine ash deposits (McCall 1967). To the east and south east of the lake is Lion Hill, covered with numerous rock outcrops and a large expanse of an almost pure stand of *Euphorbia candelabrum*. The western side is also dominated by cliffs and rock outcrops which at one point almost reach the water's edge. These are largely basaltic in formation, constituting part of the west wall of the eastern Great Rift Valley (Vaucher 1973).

3.2. The lake

Lake Nakuru occupies about 42 km^2 at the lowest point in a wider catchment basin of approximately 1800 km^2. The recent geological history of the catchment is characterized by intense volcanic activity. The lake is one of seven in the Kenyan portion of the Rift Valley, each unique in its own way, marking the low depression points in the surrounding land. The maximum depth ever recorded was 2.75 m during a wet season (Mavuti 1975). As a result of gradual leaching of volcanic soils from surrounding areas, the lake water has a high mineral concentration with a pH of 10.5, and conductivity oscillates from 9000 to 160,000 µS (Vareschi 1982).

Figure 1. Outline map of Kenya, showing the location of Lake Nakuru National Park, in relation to other features in the Rift Valley.

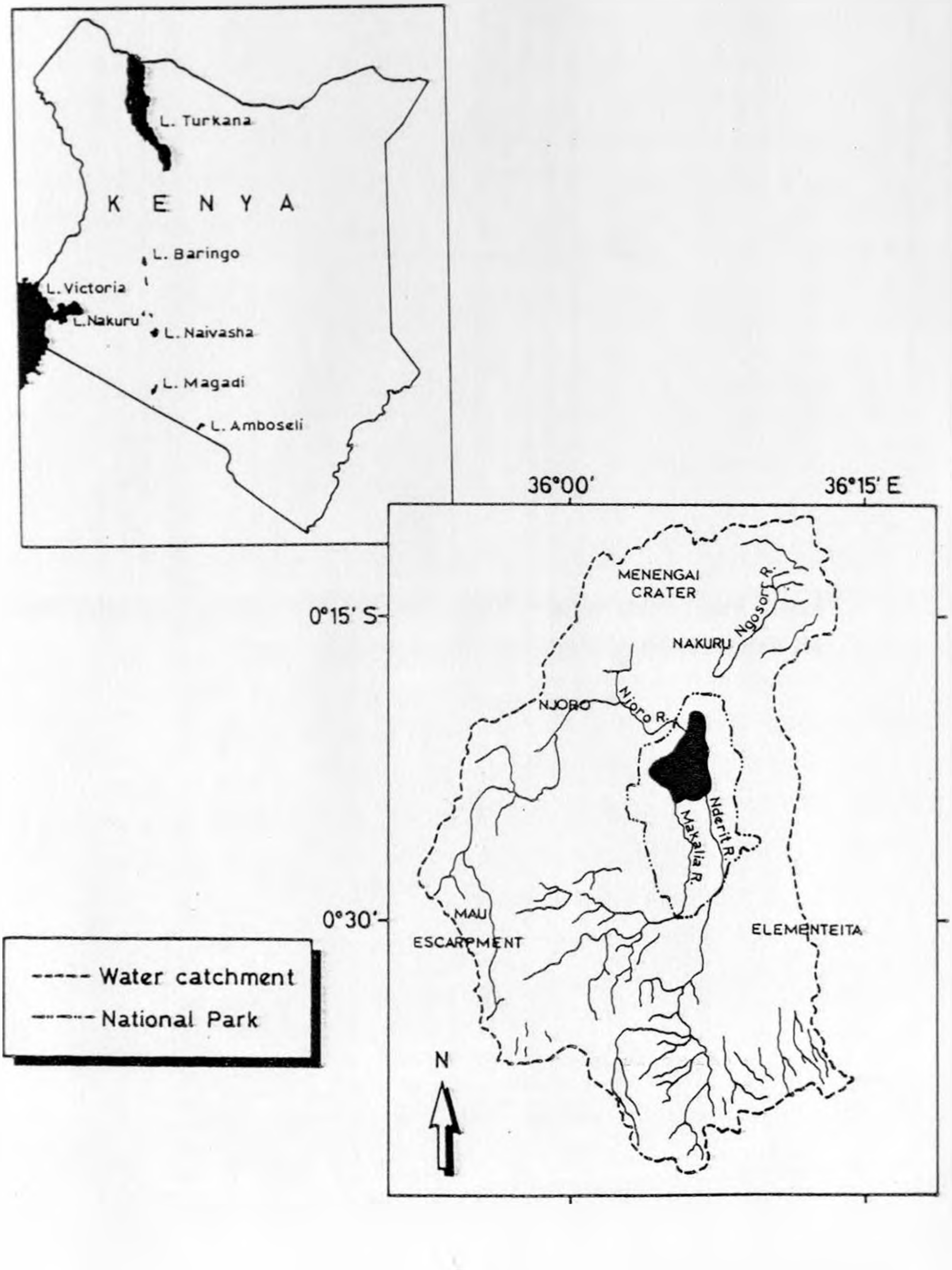
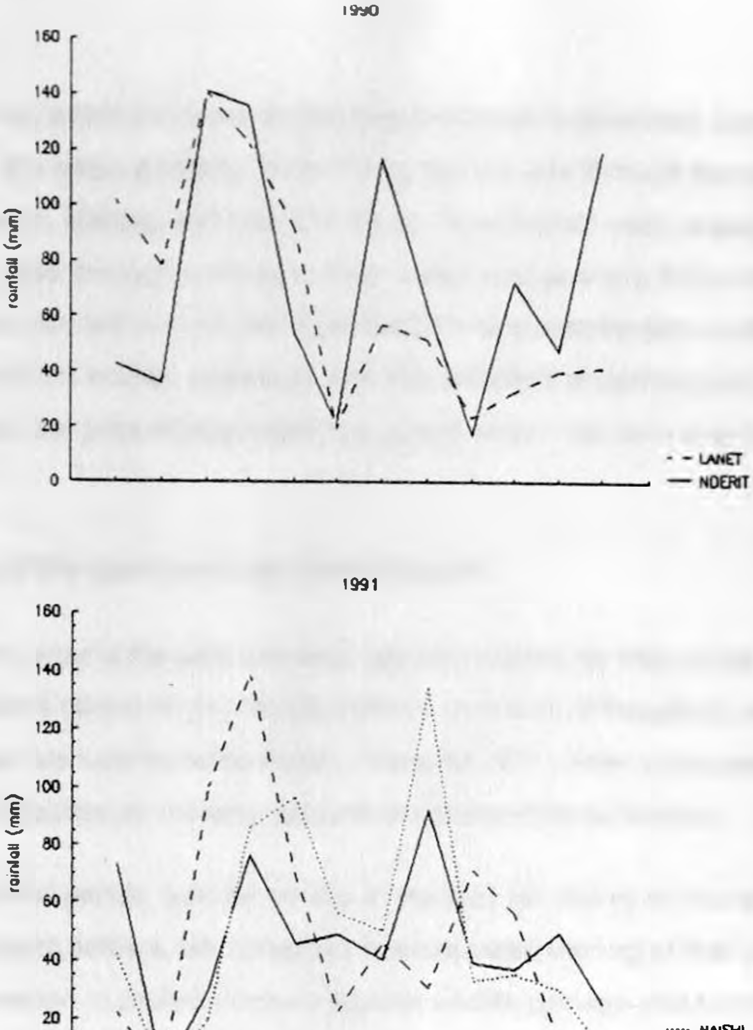

L. Turkana
K E N Y A
L. Baringo
L. Victoria
L.Nakuru
L. Naivasha
L. Magadi
L. Amboseli
36°00'
36°15' E
0°15' S
0°30'
MENENGAI CRATER
Ngosorr R.
NAKURU
NJORO
Njoro R.
Nderit R.
Makalia R.
MAU ESCARPMENT
ELEMENTEITA
N
----- Water catchment
-·-·-·- National Park

Figure 2. Total monthly rainfall for Naishi, Lanet and Nderit stations for the years 1990 to 1992 (records for Naishi were not available for the year 1990).

FIGURE 2


1990
1991
1992
rainfall (mm)
0
20
40
60
80
100
120
140
160
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
month
NAISHI
LANET
NDERIT

The main way by which water leaves the lake is through evaporation. Lack of an outlet contributes to the lake's alkalinity. Water flows into the lake through the rivers Njoro along the western shoreline, Makalia and Nderit to the south and south east, respectively. The lake also receives water through a series of fresh water springs along the northern and eastern shorelines. It is also fed through direct precipitation and subsequent runoff. With a continued rapid increase in the human population and intensification of farming and industrial activities around the lake, the park management has raised serious concern over the quality of this runoff.

3.3. History of the park and catchment basin

The area in and around the park has been greatly modified by man in the last century. It has been an important centre for human populations over tens of thousands of years, and many prehistoric sites are located in the vicinity (Horrobin 1971). Prior to the onset of colonialism, the area was inhabited by nomadic pastoralists and shifting cultivators.

During the colonial period, land ownership in the area fell mainly in the hands of farming and ranching European settlers, who engaged in widespread fencing of their properties. The fences were erected to protect property against wildlife damage and to control the spread of diseases on the farms (Cone and Lipscomb 1972). Fencing and shooting initiated limitations in the numbers and movements of wildlife in the area and are implicated in the extinction of the Nakuru hartebeest (*Alcelaphus buselaphus cokii x jacksoni*) (Kutilek 1974).

Percival (1924) reported the African elephant (*Loxodonta africana*) and black rhinoceros (*Diceros bicornis*) among the wildlife species that migrated to the Nakuru Elmenteita region from the Laikipia plateau. Other species that undertook seasonal migrations in the area included the common zebra (*Equus burcheli*) and Thomson's gazelle (*Gazella thomsoni*) (Percival 1928).

The park was established in 1961, initially for the protection of its prolific birdlife. Originally, only the southern two thirds of the lake and a narrow shore woodland belt were accorded protection under the Colonial National Parks. The area under protection was increased by the gazettement of the whole lake as a park in 1968, and the inclusion of land purchased from surrounding farmers and ranchers in 1974. This expanded the boundaries to cover the present area of 188 km^2.

The park is surrounded mainly by agricultural and ranching properties, which contribute up to 60% of the lake's total catchment area (Linger *et al.* 1981). A high voltage electric fence, surrounding the whole park, was erected in 1987. The fence together with some human activities have effectively transformed the park into a terrestrial island.

The areas around Lake Elmenteita and Nakuru have provided traditionally important haunts for grazers for as long as available records indicate. Meinertzhagen (1957) reported large herds of Jackson's hartebeest (*Alcelaphus buselaphus jacksoni*), Thomson's gazelle, Grant's gazelle (*Gazella granti*), and a few bohor reedbucks (*Redunca redunca*) between Nakuru Railway Station and the lake, during a dry spell in 1904.

During the same period, the Gilgil - Elmenteita region was reportedly full of Masai and their livestock with little game, among them the Thomson's gazelle, zebra and ostrich (*Struthio camelus*). The Thomson's gazelle became most numerous during southward migrations at the end of the rains when grass in the Rift Valley north of Nakuru grew very long. Grass remained short around Lakes Elmenteita and Nakuru, occasioning the movement of grazer species (Percival 1928). Eliot (1905) saw the country near Elmenteita so "literally covered with Thomson's gazelles that it appeared sandy yellow".

In 1903. The Rift Valley, especially around Lakes Naivasha, Elmenteita and Nakuru, was described in superlative terms regarding the wildlife residing there. The climate was pleasant, grass never grew long and `burr clover' were plentiful. As a result, many Thomson's and Grant's gazelles could be found between Lakes Elmenteita and Nakuru (Simon, 1962).

According to Chapman (1908), one of the best places for seeing concentrations of game was at the confluences of Rivers Nderit and Makalia with Lake Nakuru, an area of perhaps no more than 500 Acres, and dotted with single or clumped trees and thick riverine forests. The area was reportedly swarming with herds of ungulates. Even crocodiles could be found in the Nderit River. Lions were abundant on the plateau, where francolin and guinea fowl were also plentiful. Quails were so many that "half a dozen would spring up at every step".

In the broken bush country north west of Nakuru, rhinoceros, lion and buffalo were common. In this area was also a common boundary between the Jackson's and Nakuru hartebeest and these could be seen in separate herds within a few hundred yards of each other (Simon 1962). A herd of eland was present in and around Menengai Crater.

On a predawn march from Nakuru to Elmenteita, Percival (1924) saw plenty of zebra in thousands, "miles long as far as the eye could see." There were also many zebra bones that the party suspected were due to lions. Hippopotami (*Hippopotamus amphibius*) were numerous on the two lakes, especially Elmenteita where a small grass covered island afforded adequate shelter. Lake Nakuru, being more open, was more vulnerable. Near both lakes were many defassa waterbuck, impala, Bohor reedbuck, dik dik (*Rhrynchotragus spp*), duiker (*Sylvicapra spp*) and steinbuck (*Raphicerus campestris*).

Percival correctly observed that the Rift Valley would be the first to suffer as Kenya's human population increased, as most land was suitable for settlement and wildlife was sure to be driven out. He therefore discouraged the subdivision of land. The history of the park is marked by the introduction of species whose survival could not be guaranteed elsewhere.

In June 1977, 21 Rothschild's giraffes (*Giraffa camelopardalis rothschildi*) were translocated from Lewa Downs Farm near Kitale in western Kenya, where much habitat had been lost to human settlement. Two months later, two individuals escaped without trace and one female died soon after, but these were replaced by the birth of three calves within two years of the translocation (Kakuyo 1980). That nucleus population had increased to over 170 animals by 1990.

The project was considered a success story, in the light of two disastrous attempts to translocate the Rothschild's giraffe to Maralal in 1963 and 1968. In Maralal, animals either failed to survive the translocation operation or disappeared within the year of release (Evans 1970).

In June 1987, 19 Black rhinoceroses were translocated into the park from Solio Ranch in Central Kenya, with a view to forming a viable breeding population. It was hoped that while enjoying maximum protection within a sanctuary, this nucleus population would generate a stock for reintroduction into areas where the species has been virtually eradicated by heavy poaching in the last few decades. Several more have been moved in since, and two white rhinoceroses (*Ceratotherium simum*) have also been translocated. The white rhinoceroses have since bred and several cases of successful breeding were recorded among black rhinoceroses in the first six years of the project.

3.4. Vegetation

The vegetation of the park has been classified into broad categories on the basis of physiognomy and species composition (Curry-Lindahl 1971, Kakuyo 1980, Mutanga 1989). The major vegetation groupings are presented in Figure 3. The foreshore gently slopes into the water all round the lake, with an area and species composition that change constantly due to fluctuations in lake level. The western and southern shores are dominated by *Sporobolus spicatus*, a salt resistant grass, interspersed in places by rarer grasses and sedges. The alluvial and waterlogged soils of the south eastern end of the lake are dominated by a dense mat of the sedge *Cyperus laevigatus*.

There are two distinct types of grasslands in the park. Those to the south and west of the lake are characterized by *Hyparrhenia spp* and *Chloris gayana*, while those to the north have a more diverse species composition, the most common grasses being *Themeda triandra* and *Cynodon nlemfluensis*.

Woodlands are dominated by *Acacia xanthophloea*, sometimes with dense undergrowth of shrubs such as *Pluchea baquaertii*, *Senecio petitianus* and *Abutilon mauritanium*. Where the acacias form a dense canopy, ground cover also consists of creepers such as *Commicorpus plumbaginous* and several shrubs, predominantly *Justicia whytei* and *Toddalia asiatica*. The park contains a part of Kenya's dry forest, dominated by *Olea hochstetteri* and *Croton dichogamus*.

The cliffs and escarpments contain unique vegetation types, with *Tarchonanthus camphoratus* contributing significantly to woody plant cover. Associated with the hills are some glades, mainly consisting of the grasses *Cynodon nlemfluensis* and *Pennisetum squamalatum*. The more gentle hill sides contain scattered trees of several *Acacia spp*, mixed with shrubs, notably *Psiadia arabica* and *Aspilia mossambicensis*.

One conspicuous vegetation type consists of a dense stand of *Euphorbia candelabrum* occupying much of the eastern half of Lion Hill. In the recent past, this vegetation type has become interspersed with trees of other species, notably *Teclea simplicifolia* and *Obetia pinuatifolia*.

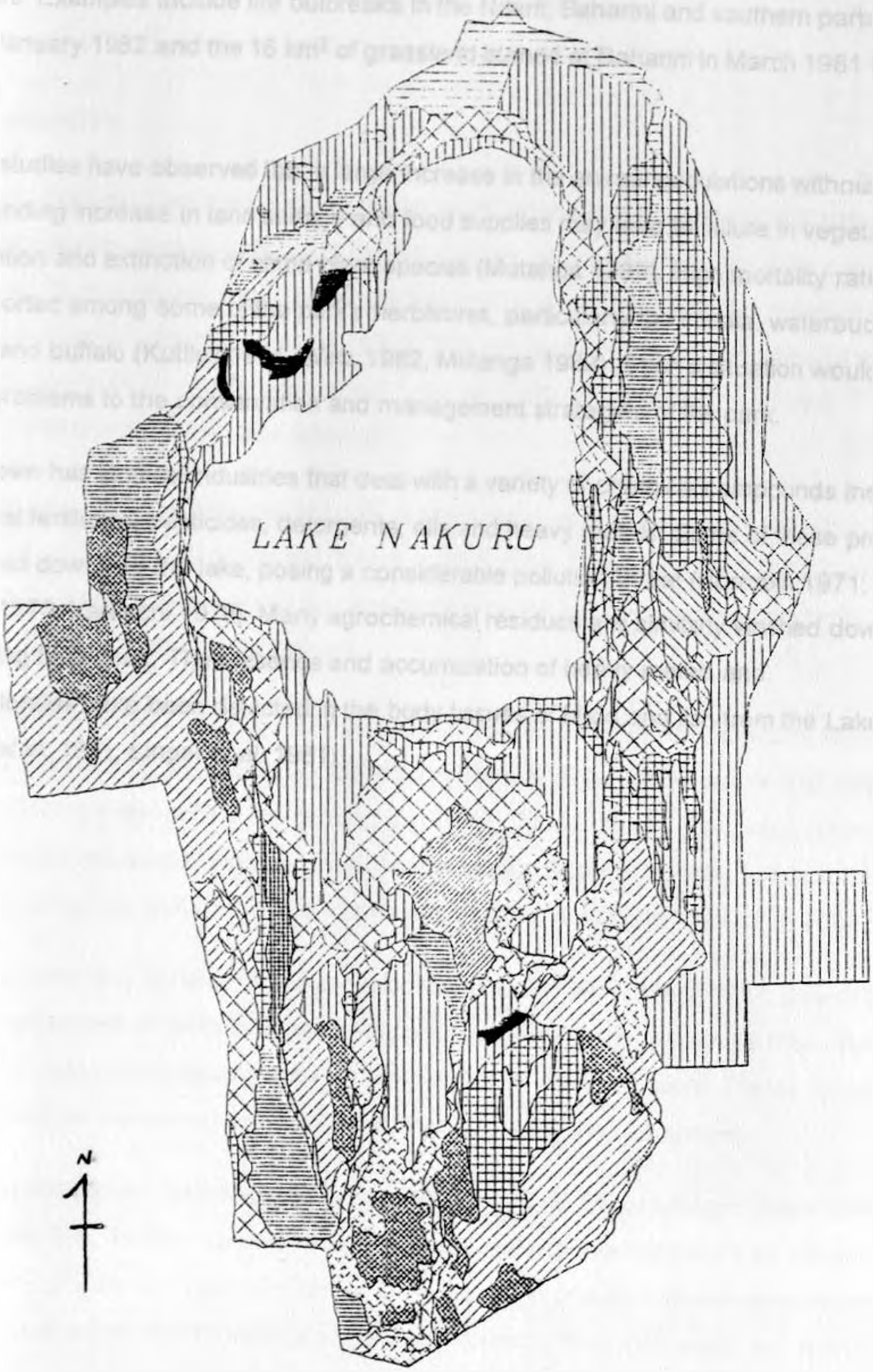
Like all savanna ecosystems, the plant communities in Lake Nakuru National Park have coevolved in the presence of fire, herbivory and management. The direction of plant succession, to a large extent, is determined by levels of these factors. Incidences of

Figure 3. Annotated map of Lake Nakuru National Park, showing the main vegetation groupings.

LEGEND

‖‖	Undifferentiated Open grassland
▩	Chloris gayana/Cynodon nlemfuensis grassland
■	Chloris gayana / Digitaria abyssinica grassland
☰	Chloris gayana / Cynodon nlemfuensis / Acacia gerrardi wooded grassland
⬚	Cynodon nlemfuensis / Acacia xanthophloea wooded grassland
▦	Chloris gayana / Cynodon nlemfuensis wooded grassland with Acacia gerrardi and Acacia seyal
⊞	Tarchonanthus camphoratus bushland
▤	Tarchonanthus camphoratus / Euphorbia candelabra / Acacia xanthophloea wooded bushland
▧	Tarchonanthus camphoratus / Euphorbia candelabra bushland
⊠	Acacia xanthophloea / Pluchea bequertii bushed woodland
⊠	Acacia xanthophloea closed woodland
▨	Acacia xanthophloea forest
▧	Euphorbia candelabra forest

VEGETATION MAP OF LAKE NAKURU NATIONAL PARK



SOURCE OF INFORMATION

Map adapted from J.G Mutangah, 983

ecologically harmful uncontrolled fire outbreaks have been recorded frequently by the park managers. Examples include fire outbreaks in the Nderit, Baharini and southern parts of the park in January 1982 and the 16 km^2 of grassland burned at Baharini in March 1981 (Park records).

Several studies have observed that a large increase in the animal populations without a corresponding increase in land surface and food supplies may lead to failure in vegetation regeneration and extinction of some plant species (Mutanga 1989). High mortality rates have been reported among some of the park's herbivores, particularly the impala, waterbuck, warthog and buffalo (Kutilek 1974, Wirtz 1982, Mutanga 1989). Such a situation would pose serious problems to the conservation and management strategies of the park.

Nakuru town has several industries that deal with a variety of chemical compounds including agricultural fertilizers, pesticides, detergents, oils and heavy metals. Some of these products are washed down into the lake, posing a considerable pollution threat (Horrobin 1971, Vaucher 1973, Vareschi 1978). Many agrochemical residues are similarly washed down from surrounding farmlands. The presence and accumulation of heavy metals and organochlorides have been detected in the body tissues of birds and fish from the Lake (DeJaux *et al.* 1981, Linger *et al.* 1981).

CHAPTER 4. LARGE HERBIVORE POPULATION DENSITIES

4.1. Introduction

The Nakuru National Park's large mammal community has undergone major changes in both species composition and diversity over the last century, and particularly since the park was established. Their numbers and movements became severely limited by the activities of early European farmers and hunters (Kutilek 1974). This resulted in the local extinction of several species, for example, the Nakuru hartebeest, Masai giraffe (*Giraffa camelopardalis masaicus*) and cheetah (*Acinonyx jubatus*).

Others like the Lion (*Panthera leo*) are only present today as a result of reintroduction. The Rothschild's giraffe population started from a small number introduced from Lewa Downs Farm in 1977. More recently, areas surrounding the park have been settled by a large population of mainly subsistence farmers.

Since the initial inclusion of a terrestrial component into the park in 1968, the total area available for occupation by wildlife has undergone several major alterations. In 1973 the park was expanded from about 63.5 km^2 to nearly 170 km^2 (Kutilek 1974). This was further increased by the addition of land bought from surrounding farmers in 1974, to encompass an area of approximately 202 km^2. It was further adjusted to the present 188 km^2 in 1981.

The park became fully isolated by the construction of an electric fence in 1987. Due to these changes, total counts of animals done in the park have been within a variable area, making it impossible to assess population trends on the basis of absolute numbers. Trends reported here are based on the density and relative abundance of the various species.

A direct association has been recognized between annual rainfall and large African herbivore biomass. Coe *et al.* (1976) examined both published and unpublished data from wildlife and pastoral areas of East and Southern Africa. Over the range of data available, they found a curvilinear relationship with an inflection between 800 and 900 mm of rainfall per year. The data fitted a highly significant least squares log-log regression of herbivore biomass on rainfall.

Using data from 114 ecosystems throughout Africa, Western (1991) looked at how large herbivore abundance varied with annual precipitation. He concluded that total production increases with rainfall, mixed wildlife livestock systems are more productive than protected areas and that wildlife production is lower outside protected areas as a result of competitive displacement by livestock. He also found that double rainfall regimes are more productive in terms of large herbivore biomass than single rainfall areas.

Species diversity itself increased with rainfall to a peak at about 600 mm, thereafter gradually dropping off. The relationships between total large herbivore production and rainfall were described by the following log - log regression equations: $y = -0.27 + 2.68x$ and $y = -2.24 + 2.13x$ for single and double rainfall systems, respectively.

The term habitat describes the sum total of the physical and chemical conditions surrounding a single species or group of species. It is therefore a concept of distribution in space and time. Patterns of habitat occupancy indicate the relative degree of preference for species within a community. From a management point of view, the number of species occupying a given habitat and the time spent there are important in determining the conservation value of such habitats.

Populations in optimal habitats would be expected to have relatively dumped fluctuations while a species at the edge of its range is likely to be occupying very little suitable habitat (Flowerdew 1987). Populations in sub optimal habitats would thus be subject to wide fluctuations, oscillating with temporal changes in habitat quality. Knowledge of such patterns is essential in enabling the formulation of proper park management policies.

4.2. Methods

4.2.1. Large mammal density

Many ecological studies aim at establishing the number of animals present in an area at a given time and various techniques are available for use in different circumstances. These have been reviewed extensively in literature (Seber 1982, 1986, 1992, Krebs 1989). For each study, the specific technique applied depends on a number of considerations.

Ground counts are a common source of information used for management. They may be done by searching through an entire area, or along transects of fixed or variable width. Counting from a vehicle enables the investigator to stop as necessary and make accurate counts and other observations on behaviour, age and sex structures (Norton-Griffiths 1978). Besides being impractical for large areas, the efficiency of ground counting techniques is severely curtailed by such factors as roughness of terrain and the non random nature of animal distribution.

Aerial censuses have the distinct advantage of being fast which means that relatively large areas can be covered within a short time. They require expensive equipment like aircraft and cameras, however, and highly qualified personnel. Aerial surveys often produce incomplete counts as a result of visibility bias (Marsh and Sinclair 1989, Seber 1992). In areas with dense vegetation, their accuracy can be seriously compromised especially for small and cryptic animals.

In this study, data for animal numbers and distribution were collected on a series of transects laid along the existing road and track network, measuring a total of 102 km. This technique was chosen because it allowed the sampling of relatively large areas within a short time, and has low requirements in terms of manpower and equipment. Transects were selected prior to the beginning of study, along roads traversing the major vegetation types and representing the main habitats for large mammals. The network was also laid out so as to ensure as much spatial representation as possible, care being taken to avoid criss crossing roads or ones running too close together (Figure 4a).

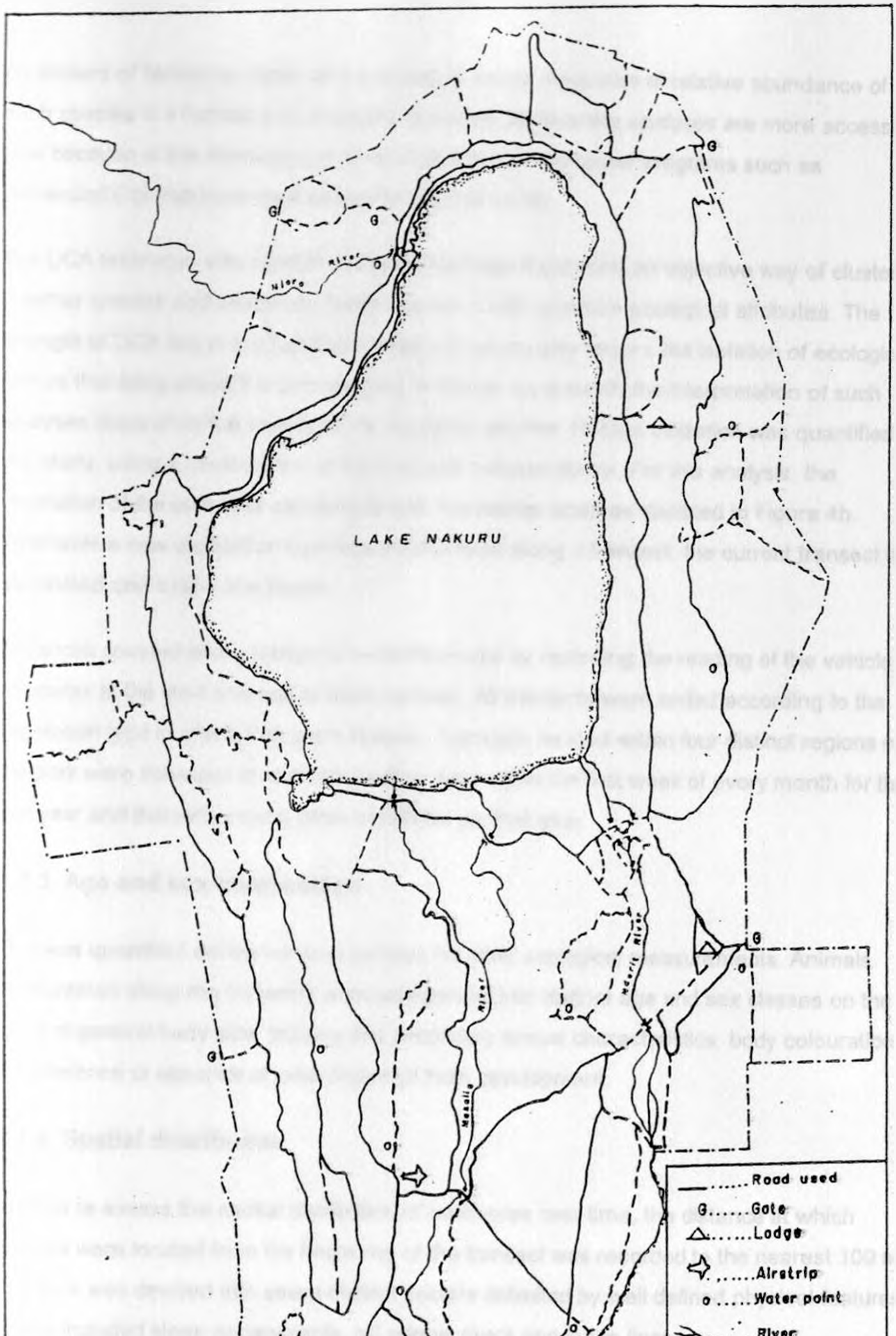
All counts were conducted by two observers, one also serving as a driver and the other as a recorder, beginning between 6.30 and 7.00 a.m. Counts were done by slowly driving along the road and recording the species, number, age and sex of all large herbivores found within a predetermined strip width on either side of the road, ranging from 25 to 100m.

4.2.2. Habitat occupancy

To maintain mixed ungulate populations in an area without detriment to either habitat or animals, it is essential that an insight be gained into the habitat needs, habitat use and potential interspecific competition among the animals (Scogings *et al*. 1990). Simple qualitative techniques express habitat occupancy in terms of the proportion of animals present in each habitat type over a given time interval. The concept can be improved by including a comparison of observed with expected habitat use according to habitat availability (Hirst 1975). Coefficients of association and indices of selection may also be calculated (Scogings *et al*. 1990).

More quantitative analysis of animal habitat relationships can be achieved with the use of multivariate analysis techniques. Studies using such techniques do not require information

Figure 4a. Map of Lake Nakuru National Park, showing the road and track network (the bold lines indicate the road transects used in this study).


LAKE NAKURU
Njoro
Makalia
River
Nderit River
G
o
..... Road used
G ..... Gate
...... Lodge
...... Airstrip
o ..... Water point
.... River
.... Road not used
0
2
3 km.

on amount of habitat available and a record of simple measures of relative abundance of each species in a habitat type is usually sufficient. Multivariate analyses are more accessible now because of the development of rapid and flexible computer programs such as Detrended Correspondence Analysis (DCA) (Hill 1979).

The DCA technique was used in this study because it provided an objective way of clustering together species and season by habitat samples with common ecological attributes. The strength of DCA lies in the fact that it does not necessarily require the isolation of ecological factors that bring about the emerging associations. As a result, the interpretation of such analyses depend on the investigator's biological wisdom. Habitat utilization was quantified in this study, using a combination of the methods outlined above. For this analysis, the vegetation of the park was categorized into five habitat types as depicted in Figure 4b. Whenever a new vegetation type was encountered along a transect, the current transect was terminated and a new one began.

Distances covered along transects were measured by recording the reading of the vehicle's odometer at the start and end of each transect. All transects were coded according to the vegetation type in which they were located. Transects located within four distinct regions of the park were surveyed in four consecutive days within the first week of every month for the first year and thereafter every other month for another year.

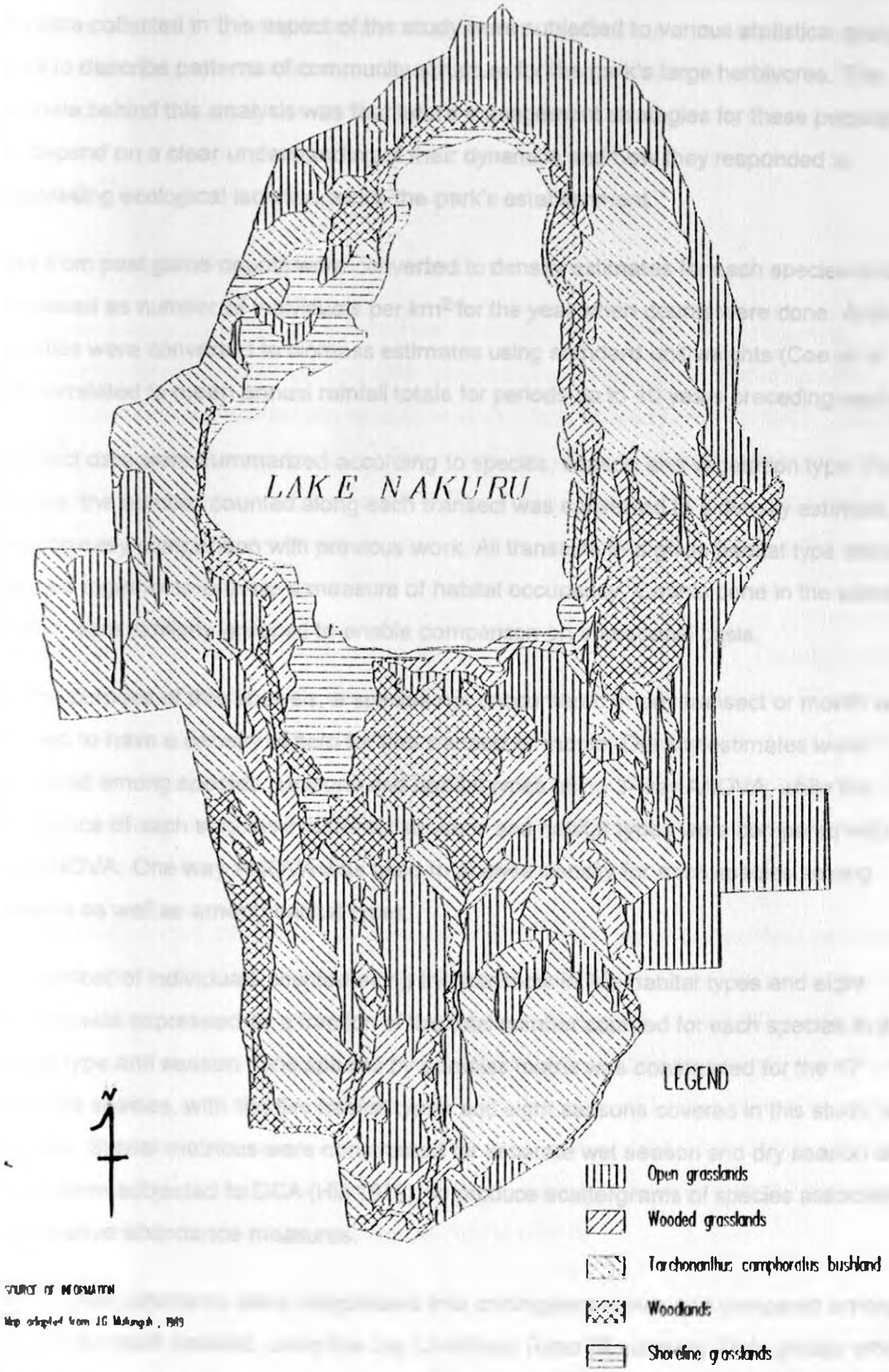
4.2.3. Age and sex composition

This was quantified during transect surveys for other ecological measurements. Animals encountered along the transects were categorized into distinct age and sex classes on the basis of general body size, primary and secondary sexual characteristics, body colouration, the presence or absence of, and degree of horn development.

4.2.4. Spatial distribution

In order to assess the spatial distribution of herbivores over time, the distance at which animals were located from the beginning of the transect was recorded to the nearest 100 m. The park was devided into seven distinct sectors delimited by well defined physical features. These included steep escarpments, hill edges, rivers and fence lines.

Figure 4b. Map of Lake Nakuru National Park, showing the five habitat types used to quantify utilization patterns during this study.



SOURCE OF INFORMATION
Map adapted from J.G. Mutangah, 1989

4.2.5. Data analysis

The data collected in this aspect of the study were subjected to various statistical analyses so as to describe patterns of community structure for the park's large herbivores. The rationale behind this analysis was that future management strategies for these populations will depend on a clear understanding of their dynamics and how they responded to progressing ecological isolation, since the park's establishment.

Data from past game counts were converted to density estimates for each species and expressed as number of individuals per km^2 for the year when counts were done. Animal densities were converted to biomass estimates using standard unit weights (Coe *et al.* 1976), and correlated to mean annual rainfall totals for periods up to 10 years preceding each count.

Transect data were summarized according to species, season and vegetation type. For each species, the number counted along each transect was converted to a density estimate, allowing easy comparison with previous work. All transects in a given habitat type were then grouped together to provide a measure of habitat occupancy. Counts done in the same season were similarly grouped to enable comparison on a seasonal basis.

For the purpose of this analysis, a species not encountered in any transect or month was deemed to have a density of zero for that transect or month. Density estimates were compared among species, seasons and habitat types using 3-way ANOVA, while the occurrence of each species in different seasons and habitat types were compared with 2-way ANOVA. One way ANOVA was used to analyse density for each species among seasons as well as among habitat types.

The number of individuals counted along the transects in five habitat types and eight seasons was expressed as a fraction of the total number counted for each species in a habitat type and season. One species by samples matrix was constructed for the 17 herbivore species, with the five habitat types and eight seasons covered in this study, as the samples. Similar matrices were constructed for separate wet season and dry season data. These were subjected to DCA (Hill 1979), to produce scattergrams of species associations from relative abundance measures.

Age and sex structures were compressed into contingency tables and compared among seasons for each species, using the Log Likelihood Ratio (G statistic). Only groups whose age and sex class composition were positively identified in the field were included in this analysis. The number of animals counted on each transect or part of transect within a given sector were devided by strip area to obtain a density estimate for each species in a sector for each month. Months falling in the same season were again grouped together for this analysis. One way ANOVA was used to compare seasonal patterns of density in the seven sectors for every species.

4.3. Results

4.3.1. Past population trends

The defassa waterbuck was the park's most dominant large herbivore, contributing consistently more biomass than any other species over all the years when data were available. Average density for the species was 41.7 individuals per km^2 in 1973. This later fell drastically in subsequent years, to 7.0 individuals per km^2 in 1979 and then increased steadily to 31.2 individuals per km^2 in 1990. The buffalo (*Syncerus caffer*) and Grant's gazelle populations showed similar patterns, with the upward trend continuing through to the most recent counts (Figures 5a to 5c).

Mean density remained low for the warthog, impala and zebra until 1978. Counts done after 1986 showed a steady increase in population density for all the three species (Figures 5d to 5f). The reverse was true for density trends exhibited by Thomson's gazelle and bushbuck (*Tragelaphus sylvaticus*) (Figures 5g and 5h). The density of Rothschild's giraffe and eland (*Taurotragus oryx*) also showed noticeable upward trends, while the Bohor reedbuck declined after 1973.

Using a mean annual rainfall of 823 mm p.a. (Kutilek 1974), herbivore biomass predicted for Nakuru on the basis of the biomass rainfall relationship is about 9328.3 kg per km^2. Total herbivore biomass density has twice increased above this value since 1970, reaching about 11221.2 kg km^{-2} in 1973 and 9510.3 kg km^{-2} in 1990. It remained below levels predicted on the basis of mean rainfall received over two years, between 1974 and 1986 (Figure 6). Herbivore biomass was positively correlated to mean annual rainfall for periods up to three years, for counts done after 1986 when migrations were not possible, with the highest correlation being over the two years preceding the counts.

Figure 5a. Population density of waterbuck (No. km^{-2}) for the years 1970 to 1992.

Figure 5b. Population density of buffalo (No. km^{-2}) for the years 1970 to 1992.

Figure 5c. Population density of Grant's gazelle (No. km^{-2}) for the years 1970 to 1992.

FIGURE 5 a

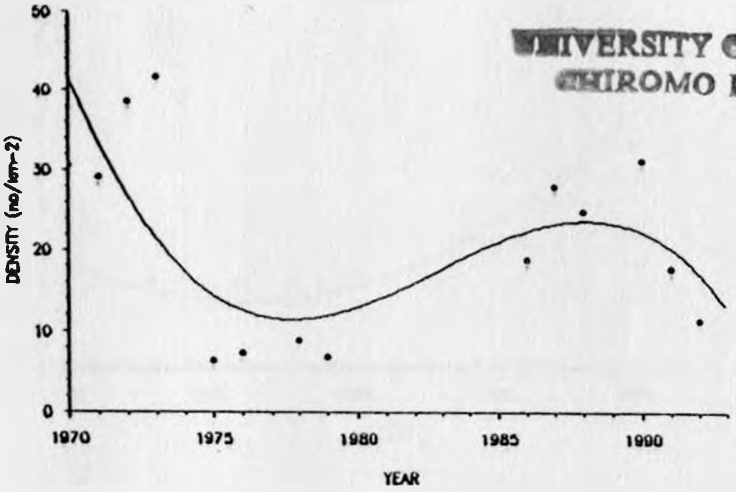


FIGURE 5 b

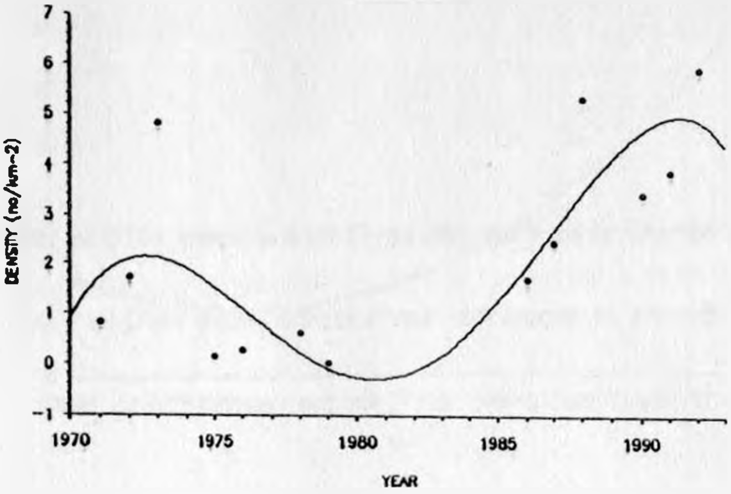


FIGURE 5 c

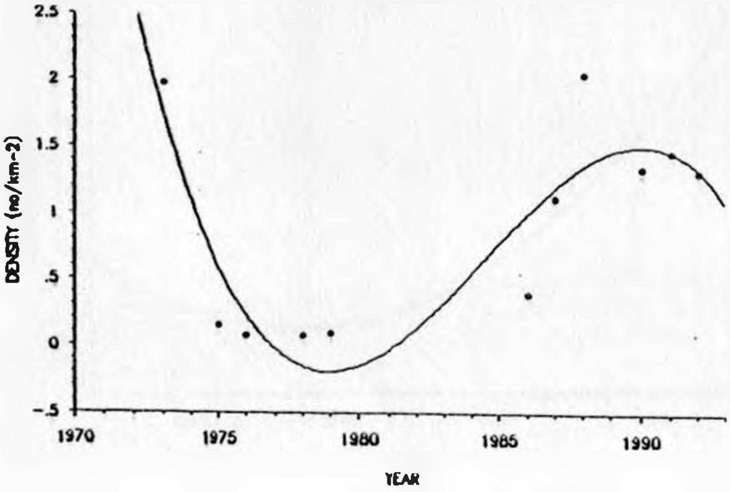


Figure 5d. Population density of warthog (No. km^{-2}) for the years 1970 to 1992.

Figure 5e. Population density of impala (No. km^{-2}) for the years 1970 to 1992.

Figure 5f. Population density of zebra (No. km^{-2}) for the years 1970 to 1992.

FIGURE 5 d

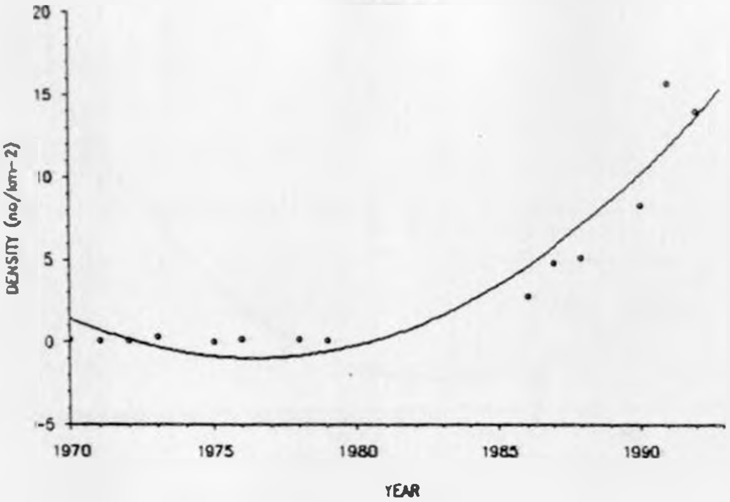


FIGURE 5 e

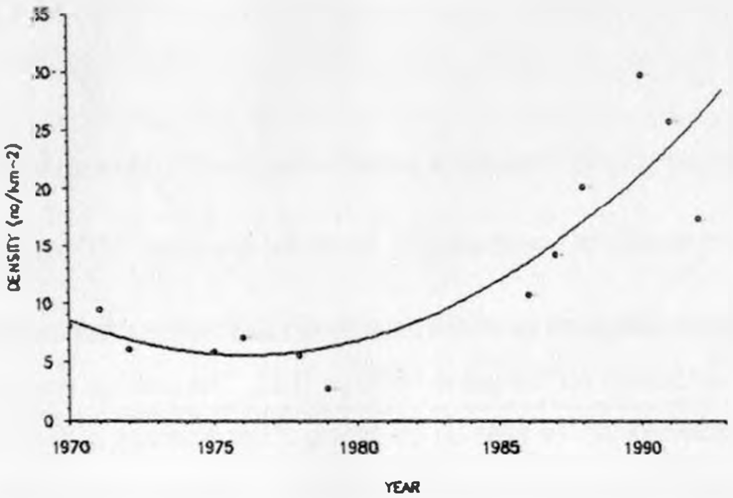


FIGURE 5 f

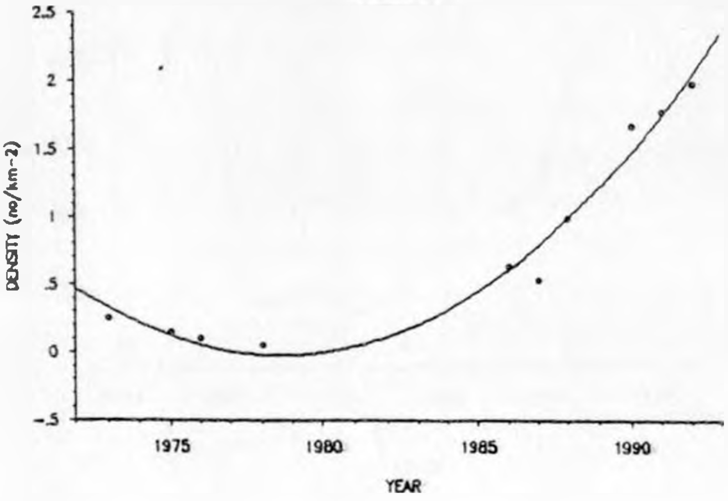


Figure 5g. Population density of Thomson's gazelle (No. km^{-2}) for the years 1970 to 1992.

Figure 5h. Population density of bushbuck (No. km^{-2}) for the years 1970 to 1992.

Figure 6. Standing large herbivore biomass density in Lake Nakuru National Park (kg km^{-2}), based on game count records for the years 1970 to 1992. The dashed line represents the annual production expected for the area on the basis of the biomass rainfall relationship for double rainfall regimes, using mean annual precipitation over two year periods (after Wester 1991).

FIGURE 5 g

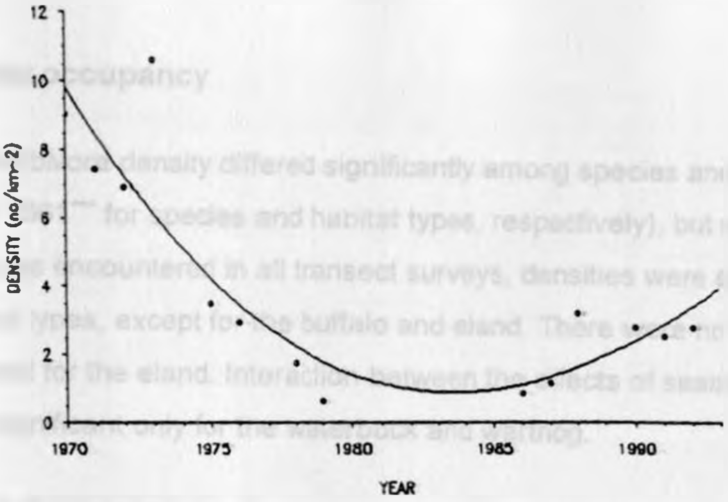


FIGURE 5 h

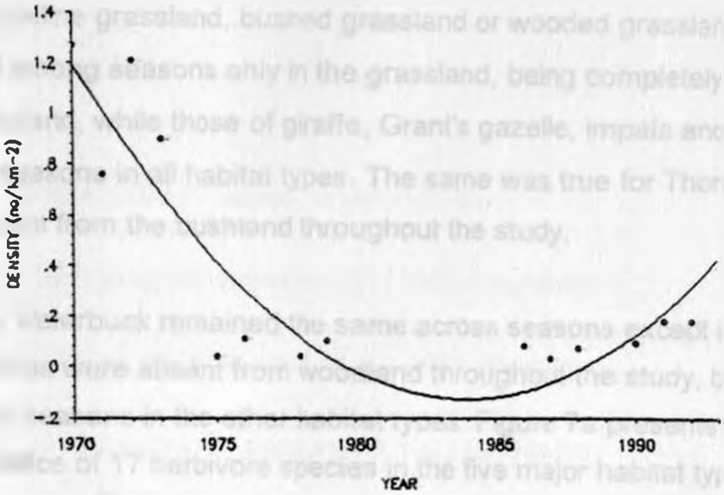
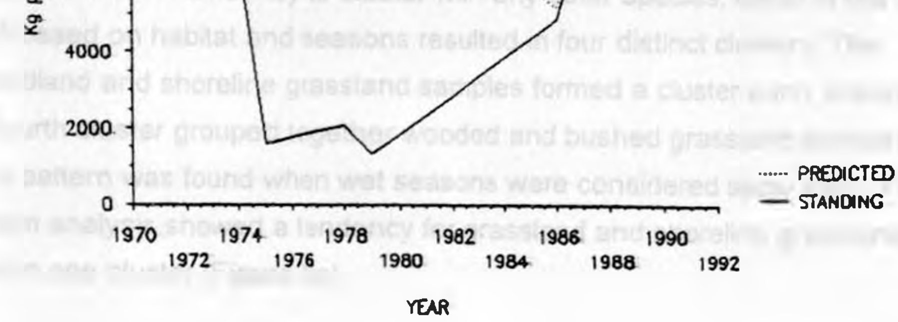


FIGURE 6



4.3.2. Habitat occupancy

The overall herbivore density differed significantly among species and habitat types ($F_{16,4,7}$ = 109.993^{***}, 21.661^{***} for species and habitat types, respectively), but not among seasons. Of the nine species encountered in all transect surveys, densities were significantly different among habitat types, except for the buffalo and eland. There were no differences among seasons except for the eland. Interaction between the effects of season and habitat type on density was significant only for the waterbuck and warthog.

A comparison of occupancy by these species in different seasons is presented in Tables 1a to 1i. The density of buffalo differed among seasons in the woodland, but not in the grassland, shoreline grassland, bushed grassland or wooded grassland. The occurrence of eland differed among seasons only in the grassland, being completely absent from the shoreline grassland, while those of giraffe, Grant's gazelle, impala and warthog were the same across seasons in all habitat types. The same was true for Thomson's gazelle, being altogether absent from the bushland throughout the study.

Occupancy by waterbuck remained the same across seasons except in the wooded grassland. Zebras were absent from woodland throughout the study, but occurred in similar densities for all seasons in the other habitat types. Figure 7a presents the results of DCA on relative abundance of 17 herbivore species in the five major habitat types and eight seasons covered in the study. Two distinct clusters resulted, one grouping the eland, Grant's gazelle, rhinoceros, buffalo, zebra, impala and giraffe, all of which are either big bodied, bulk or mixed feeders. A second one grouped together two predominantly grazer species, the Thomson's gazelle and warthog. When wet season samples were considered separately, the large cluster remained relatively unchanged, as did the second one comprising the Thomson's gazelle and warthog (Figure 7b).

DCA on dry season samples resulted in much less clustering of species (Figure 7c). The waterbuck data showed no tendency to cluster with any other species, either in the wet or dry seasons. DCA based on habitat and seasons resulted in four distinct clusters. The grassland, woodland and shoreline grassland samples formed a cluster each, irrespective of season. The fourth cluster grouped together wooded and bushed grassland samples (Figure 8a). The same pattern was found when wet seasons were considered separately (Figure 8b), while dry season analysis showed a tendency for grassland and shoreline grassland samples to fall in one cluster (Figure 8c).

Key to season codes used in Tables 1a through 4h

season 1 = pre 1991 long rains; season 2 = 1991 long rains;

season 3 = pre 1991 short rains; season 4 = 1991 short rains;

season 5 = pre 1992 long rains; season 6 = 1992 long rains;

season 7 = pre 1992 short rains; season 8 = 1992 short rains;

Table 1a. Buffalo population density (No. km^2, mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ $P<0.05$; ** ⇒ $P<0.01$; *** ⇒ $P<0.001$).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	5.9±2.3	1.1±0.8	2.6±1.5	143.5±107.5	6.8±2.3
2	6.9±4.4	0.9±0.6	4.8±3.3	6.1±3.7	11.9±7.2
3	7.1±5.0	0.3±0.3	0.6±0.5	13.4±7.7	15.5±8.4
4	10.2±6.3	0.3±0.3	4.9±2.9	15.0±15.0	2.6±2.6
5	6.9±3.4	9.1±2.9	2.5±1.3	10.3±4.5	10.4±4.6
6	5.1±3.4	0.2±0.2	3.7±1.7	8.4±5.6	7.6±5.6
7	16.8±16.3	2.3±2.3	13.5±13.5	12.3±12.3	7.2±4.9
8	11.1±10.2	3.4±2.1	6.2±3.8	6.2±5.6	1.6±1.3
F VALUE	(7,82) 0.343 NS	(7,64) 2.662 *	(7,64) 1.135 NS	(7,82) 1.64 NS	(7,136) 0.424 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.904	NS
habitat	(4)	2.091	NS
interaction	(28)	1.124	NS

Table 1b. Eland population density (No. km^2, mean± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ $P<0.05$; ** ⇒ $P<0.01$; *** ⇒ $P<0.001$).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	0.0	2.4±2.4	0.0	0.0	3.3±2.6
2	20.0±13.9	0.0	0.0	0.0	6.3±6.3
3	0.3±0.3	0.0	0.0	0.0	4.6±4.2
4	3.7±3.7	0.0	0.0	0.0	0.0
5	0.2±0.2	0.6±0.6	0.0	0.3±0.3	1.3±0.8
6	0.5±0.5	0.0	0.0	1.2±1.2	0.4±0.3
7	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0
F VALUE	(7,82) 2.273 *	(7,64) 0.538 NS	(7,64) -	(7,82) 0.555 NS	(7,136) 0.664 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	2.073	*
habitat	(4)	1.483	NS
interaction	(28)	1.181	NS

Table 1c. Giraffe population density (No. km^{2}, mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ P<0.05; ** ⇒ P<0.01; *** ⇒ P<0.001).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	0.0	0.0	0.2±0.2	0.0	0.3±0.3
2	25.4±25.5	0.0	0.9±0.6	0.0	0.0
3	0.0	0.1±0.1	2.1±2.1	0.6±0.6	0.0
4	0.0	0.0	0.0	0.3±0.3	0.0
5	0.0	2.0±1.7	0.0	0.0	0.0
6	0.3±0.3	0.0	0.0	0.0	0.0
7	0.0	0.3±0.3	0.0	0.0	0.3±0.3
8	0.0	0.0	0.3±0.3	0.0	0.0
F VALUE	(7,82) 1.153 NS	(7,64) 0.47 NS	(7,64) 0.81 NS	(7,82) 0.748 NS	(7,136) 1.248 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.970	NS
habitat	(4)	2.536	*
interaction	(28)	1.087	NS

Table 1d. Grant's gazelle population density (No. km^{2}. mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ P<0.05; ** ⇒ P<0.01; *** ⇒ P<0.001).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	4.8±2.8	0.0	0.0	0.0	4.7±2.0
2	12.4±6.7	0.0	0.0	0.0	2.8±1.5
3	2.9±1.6	0.0	0.0	2.8±2.8	3.8±2.2
4	5.5±4.0	0.0	0.0	0.0	11.2±6.5
5	5.4±2.0	0.5±0.4	0.8±0.8	1.5±1.5	9.1±3.6
6	2.5±1.1	0.0	0.8±0.5	0.0	6.5±3.7
7	7.2±4.5	0.0	0.0	0.0	2.8±1.9
8	6.6±6.6	0.0	0.3±0.3	0.0	2.6±2.6
F VALUE	(7,82) 0.808 NS	(7,64) 0.677 NS	(7,64) 0.355 NS	(7,82) 0.525 NS	(7,136) 0.584 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.498	NS
habitat	(4)	7.695	***
interaction	(28)	0.473	NS

Table 1e. Impala population density (No. km^{2}, mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis. NS ⇒ non significant result; * ⇒ $P<0.05$; ** ⇒ $P<0.01$; *** ⇒ $P<0.001$).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	84.7±36.3	76.3±18.5	21.7±8.9	29.5±15.8	150.6±26.2
2	103.3±30.8	23.0±12.6	25.0±10.3	21.4±19.4	180.8±27.7
3	27.8±10.6	42.3±23.4	11.9±8.4	62.1±52.0	188.4±40.6
4	114.0±46.2	31.2±17.7	5.6±1.9	40.0±40.0	278.3±81.2
5	73.8±19.7	105.7±33.0	54.9±15.2	55.0±15.7	105.0±22.3
6	113.7±36.1	42.2±11.3	16.2±7.4	18.7±6.6	222.4±49.8
7	70.4±41.1	5.8±5.0	54.7±46.0	12.6±7.8	236.7±100.7
8	98.0±65.4	18.6±10.8	16.3±13.9	13.1±7.4	208.8±102.9
F VALUE	(7,82) 0.648 NS	(7,64) 1.473 NS	(7,64) 1.535 NS	(7,82) 0.643 NS	(7,136) 1.645 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.484	NS
habitat	(4)	24.53	***
interaction	(28)	1.186	NS

Table 1f. Thomson's gazelle population density (No. km^{2}, mean ± SE) in different seasons and habitat types (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ $P<0.05$; ** ⇒ $P<0.01$; *** ⇒ $P<0.001$).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	10.2±4.3	0.0	6.7±4.0	0.0	11.7±3.9
2	14.4±13.4	0.0	4.0±3.3	0.0	4.9±2.7
3	17.4±11.8	0.5±0.5	7.2±4.8	0.0	7.4±3.8
4	17.4±17.4	0.0	8.5±8.5	0.0	4.4±3.1
5	11.1±4.9	0.0	8.6±2.5	0.0	5.4±1.5
6	11.4±8.5	0.0	10.4±5.5	0.0	7.5±4.1
7	4.1±4.1	0.0	10.2±6.9	0.0	6.6±6.6
8	0.0	0.0	5.0±5	0.0	0.1±0.1
F VALUE	(7,82) 0.267 NS	(7,64) 1.161 NS	(7,64) 1.213 NS	(7,82) -	(7,136) 0.747 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.473	NS
habitat	(4)	8.314	***
interaction	(28)	0.294	NS

Table 1g. Waterbuck population density (No. km^2, mean± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis. NS ⇒ non significant result; * ⇒ P<0.05; ** ⇒ P<0.01; *** ⇒ P<0.001).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	79.7±26.7	76.7±33.5	111.7±44.5	8.2±4.1	66.9±17.0
2	102.2±46.4	35.8±15.6	76.5±23.8	2.1±1.5	116.8±54.0
3	27.2±9.0	35.0±15.0	192.1±47.8	5.2±3.2	75.4±17.9
4	79.9±25.2	43.3±33.1	242.9±48.9	0.3±0.3	80.8±20.4
5	43.3±13.1	76.2±13.5	107.5±26.8	6.6±2.6	15.0±3.5
6	47.8±18.9	56.2±24.4	77.0±34.1	4.6±2.7	34.8±15.7
7	38.4±30.7	9.6±6.8	176.1±81.9	10.9±10.9	5.1±3.6
8	13.8±9.7	98.8±50.1	138.6±97.4	0.0	8.0±4.3
F VALUE	(7,82) 1.173 NS	(7,64) 0.891 NS	(7,64) 1.342 NS	(7,82) 0.658 NS	(7,136) 3.133 **

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	1.958	NS
habitat	(4)	18.985	***
interaction	(28)	1.611	*

Table 1h. Warthog population density (No. km^2, mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis, NS ⇒ non significant result; * ⇒ P<0.05; ** ⇒ P<0.01; *** ⇒ P<0.001).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	73.6±18.6	22.9±7.0	229.7±59.9	11.1±4	36.0±8.1
2	66.3±17.9	5.5±3.2	90.7±18.6	2.3±1.5	32.5±11.2
3	57.9±20.3	13.0±4.3	212.2±67.7	11.5±8.9	49.8±16.4
4	83.9±38.4	6.5±3.9	179.9±54.9	0.7±0.7	22.8±8.8
5	74.7±20.2	21.4±4.4	354.1±84.0	18.1±7.6	25.3±4.5
6	70.9±27.9	13.0±3.3	113.9±26.1	0.5±0.3	26.4±7.7
7	33.1±22.8	4.3±3.2	101.6±40.8	5.0±3.4	15.7±5.6
8	47.1±27.0	13.7±5.9	46.1±15.6	0.0	34.6±15.5
F VALUE	(7,82) 0.24 NS	(7,64) 1.616 NS	(7,64) 2.048 NS	(7,82) 1.174 NS	(7,136) 0.962 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	4.449	NS
habitat	(4)	49.757	***
interaction	(28)	2.242	***

Table 1i. Zebra population density (No. km^2, mean ± SE) in different seasons and habitat types. (Degrees of freedom in parenthesis. NS ⇒ non significant result, * ⇒ $P<0.05$; ** ⇒ $P<0.01$; *** ⇒ $P<0.001$).

SEASON	GRASSLAND	WOODLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
1	0.0	0.0	0.0	0.0	14.6±6.4
2	7.9±4.3	0.0	2.8±1.9	0.0	32.0±30.1
3	5.7±5.7	0.0	0.0	0.0	9.1±5.2
4	7.6±7.6	0.0	0.0	0.0	8.3±4.6
5	6.1±4.2	0.0	1.4±1	0.6±0.6	12.6±4.6
6	0.6±0.6	0.0	0.0	0.0	34.3±19.4
7	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	2.4±2.4	0.0	24.0±21.9
F VALUE	(7,82) 0.659 NS	(7,64) -	(7,64) 1.105 NS	(7,82) 0.353 NS	(7,136) 0.599 NS

2-WAY ANOVA

SOURCE OF VARIATION		F VALUE	
seasons	(7)	0.568	NS
habitat	(4)	5.776	***
interaction	(28)	0.342	NS

Figure 7a. Results of DCA on the relative abundance of 17 large herbivore species encountered in the five habitat types during the eight seasons during the study.

Figure 7b. Results of DCA on the relative abundance of 17 large herbivore species encountered in the five habitat types during four wet seasons during the study.

Key to species codes for Figures 7a to 7c

BB	bushbuck
BF	buffalo
BRB	Bohor reedbuck
DD	dikdik
DK	duiker
ED	eland
GF	Rothschild's giraffe
GG	Grant's gazelle
IM	impala
MRB	mountain reedbuck
OS	ostrich
RH	black rhinoceros
TG	Thomson's gazelle
WB	waterbuck
WH	warthog
WP	wild pig
ZB	zebra

FIGURE 7 a

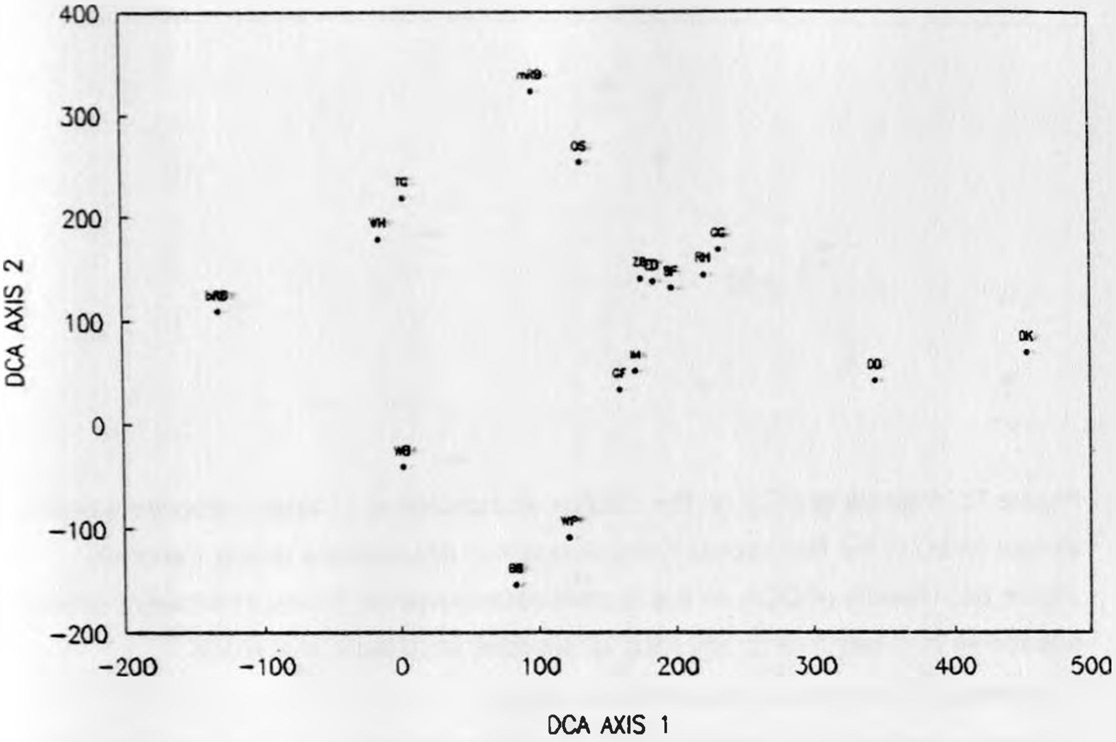


FIGURE 7 b

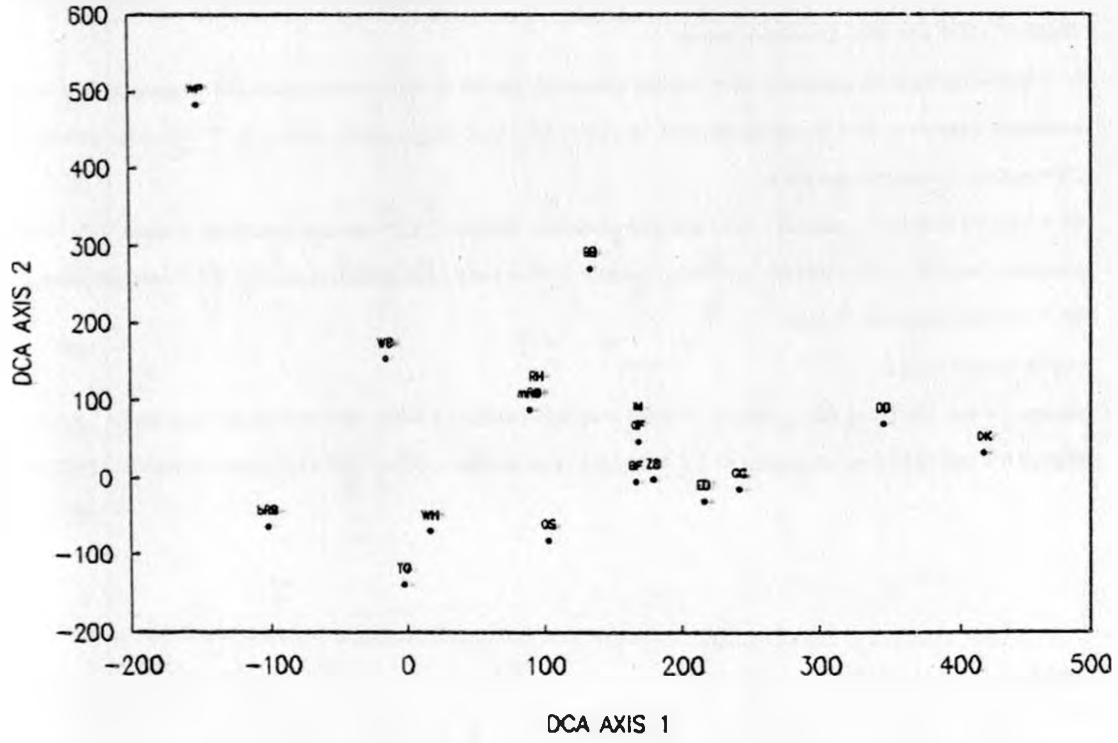


Figure 7c. Results of DCA on the relative abundance of 17 large herbivore species encountered in the five habitat types during four dry seasons during the study.

Figure 8a. Results of DCA on the relative abundance for 17 large herbivore species in a season by habitats matrix, covering all seasons included in this study.

Key to habitat by season combinations used in Figures 8a to 8c

A1 = grassland, season 1; A2 = grassland, season 2; A3 = grassland, season 3; A4 = grassland, season 4; A5 = grassland season 5; A6 = grassland, season 6; A7 = grassland, season 7; A8 = grassland, season 8

B1 = woodland, season 1; B2 = woodland, season 2; B3 = woodland, season 3; B4 = woodland, season4; B5 = woodland season 5; B6 = woodland, season 6; B7 = woodland, season 7; B8 = woodland, season 8

C1 = shoreline grassland, season 1; C2 = shoreline grassland, season 2; C3 = shoreline grassland, season 3; C4 = shoreline grassland, season 4; C5 = shoreline grassland, season 5; C6 = shoreline grassland, season 6; C7 = shoreline grassland season 7; C8 = shoreline grassland, season 8

D1 = bushed grassland, season 1; D2 = bushed grassland, season 2; D3 = bushed grassland, season 3; D4 = bushed grassland, season 4; D5 = bushed grassland, season 5; D6 = bushed grassland, season 6; D7 = bushed grassland, season 7; D8 = bushed grassland, season 8

E1 = wooded grassland, season 1; E2 = wooded grassland, season 2; E3 = wooded grassland, season 3; E4 = wooded grassland, season 4; E5 = wooded grassland, season 5; E6 = wooded grassland, season 6; E7 = wooded grassland, season 7; E8 = wooded grassland, season 8

Key to season codes

season 1 = pre 1991 long rains; season 2 = 1991 long rains; season 3 = pre 1991 short rains; season 4 = 1991 short rains season 5 = pre 1992 long rains; season 6 = 1992 long rains; season 7 = pre 1992 short rains; season 8 = 1992 short rains

FIGURE 7 c

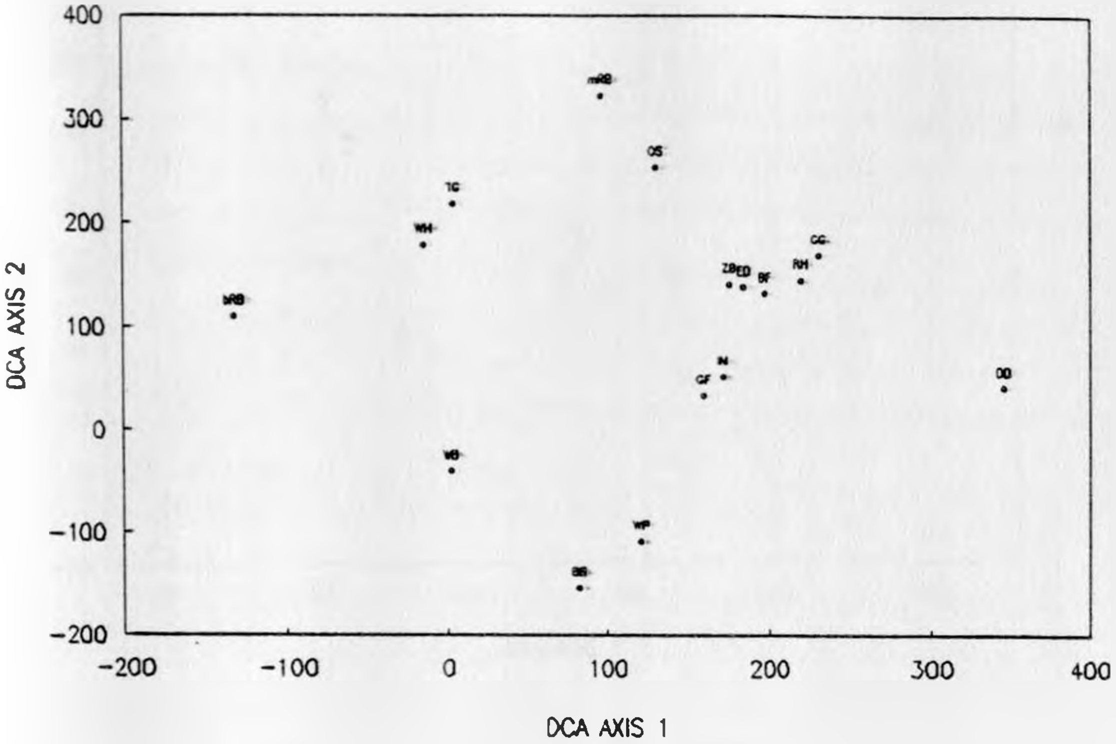


FIGURE 8 a

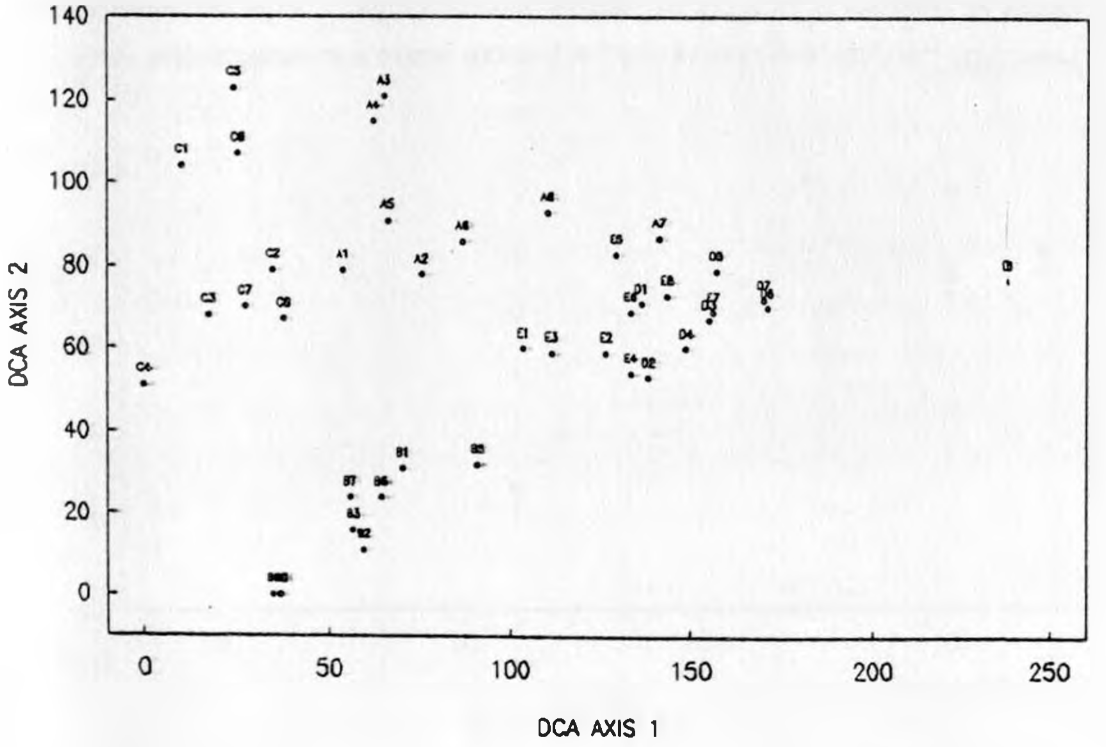


Figure 8b Results of DCA on the relative abundance for 17 large herbivore species in a season by habitats matrix, covering the four wet seasons included in this study.

Figure 8c. Results of DCA on the relative abundance for 17 large herbivore species in a season by habitats matrix, covering the four dry seasons included in this study.

FIGURE 8 b

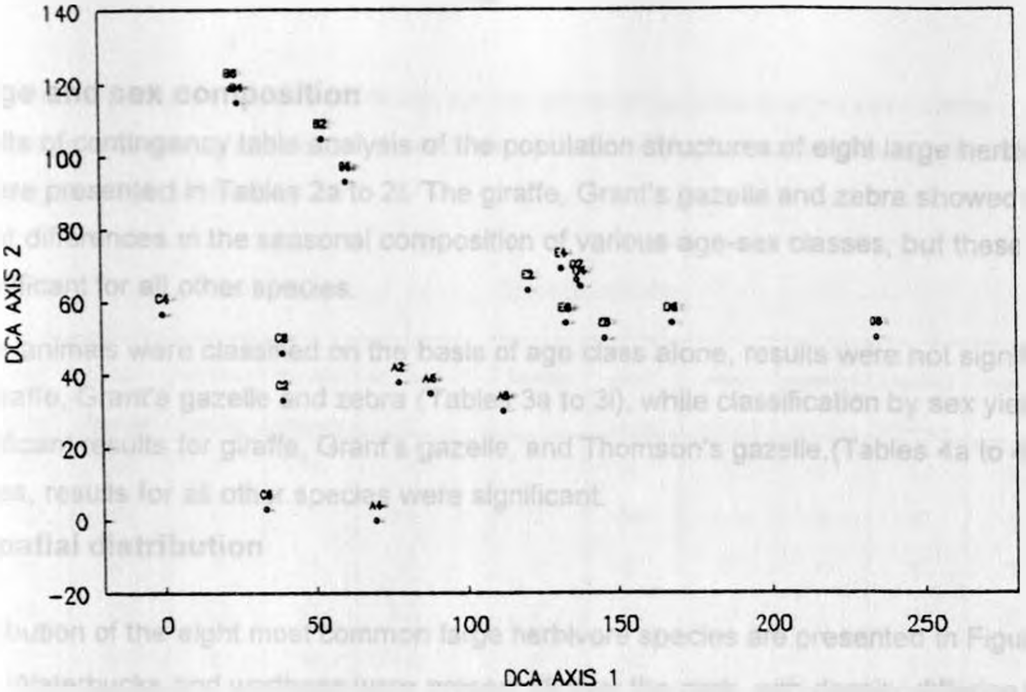
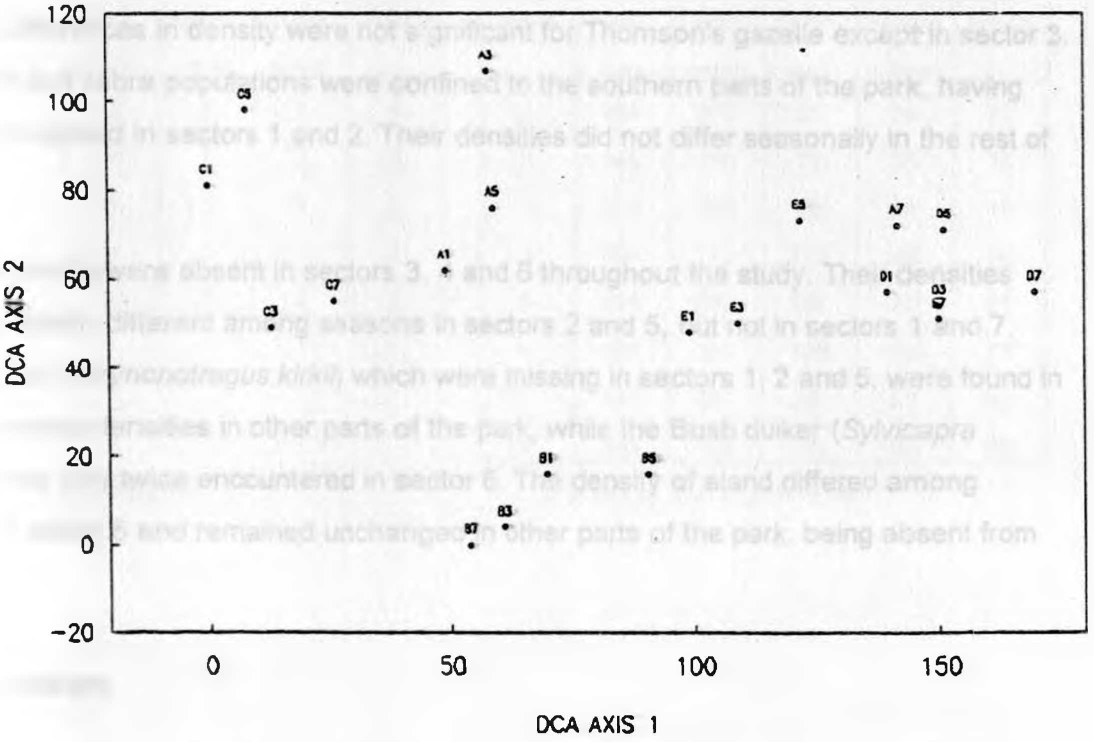


FIGURE 8 c



4.3.3. Age and sex composition

The results of contingency table analysis of the population structures of eight large herbivore species are presented in Tables 2a to 2i. The giraffe, Grant's gazelle and zebra showed no significant differences in the seasonal composition of various age-sex classes, but these were significant for all other species.

When the animals were classified on the basis of age class alone, results were not significant for the giraffe, Grant's gazelle and zebra (Tables 3a to 3i). while classification by sex yielded non significant results for giraffe, Grant's gazelle, and Thomson's gazelle.(Tables 4a to 4i). In both cases, results for all other species were significant.

4.3.4. Spatial distribution

The distribution of the eight most common large herbivore species are presented in Figures 9a to 9h. Waterbucks and warthogs were present all over the park, with density differing with seasons only in sectors 5 and 6 for waterbuck and sector 1 for warthog. Impalas were distributed all over the park, with densities being significantly different among seasons only in sectors 1 and 6.

The density of buffalo did not differ among seasons in any of the seven sectors, while Grant's gazelles were absent from sector 2 and their density remained unchanged in other parts of the park. Differences in density were not significant for Thomson's gazelle except in sector 3. The giraffe and zebra populations were confined to the southern parts of the park, having never been sighted in sectors 1 and 2. Their densities did not differ seasonally in the rest of the park

Bohor reedbucks were absent in sectors 3, 4 and 6 throughout the study. Their densities were significantly different among seasons in sectors 2 and 5, but not in sectors 1 and 7. Kirk's dikdiks (*Rhrynchotragus kirkii*) which were missing in sectors 1, 2 and 5, were found in similar seasonal densities in other parts of the park, while the Bush duiker (*Sylvicapra grimmia*) was only twice encountered in sector 6. The density of eland differed among seasons in sector 5 and remained unchanged in other parts of the park, being absent from sector 2.

4.4. Discussion

The examination of long term population trends shows the defassa waterbuck to be an important component of the large herbivore community, contributing more biomass density and thus probably exerting greater feeding impacts than any other herbivore species in the

Tables 2a to 2h. Frequencies of animals of different age and sex classes in samples of the various large herbivore species at different times during the study (G values accompanying each table denote log likelihood ratio for contingency table analysis).

Table 2a. Buffalo

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	37	29	2	11	11
2	84	40	4	7	11
3	59	53	3	11	19
4	79	79	17	17	26
5	72	41	8	9	12
6	66	47	7	9	14
7	58	114	9	14	35
8	87	81	2	3	10

G = 94.57, D.F.= 28, P<0.001

Table 2b. Giraffe

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	4	3	1	1	2
2	18	21	8	5	3
3	8	8	1	5	1
4	11	27	5	3	2
5	10	7	1	1	2
6&7&8	7	8	2	1	1

G = 16.14, D.F.= 20, P>0.5 NS

Table 2c.Grant's gazelle

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1&2	14	11	1	1	1
3&4	38	40	1	2	3
5	38	46	5	2	2
6	20	24	3	1	3
7&8	43	26	5	4	2

G = 12.65, D.F= 16, P>0.5 NS

Table 2d. impala

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	262	256	39	36	33
2	445	346	73	35	35
3	402	438	76	86	45
4	604	782	174	106	99
5	464	585	102	70	51
6	403	642	105	92	77
7	437	567	59	53	53
8	448	552	85	62	76

G = 140.32, D F = 28, P<0.001

Table 2e. Thomson's gazelle

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	31	52	2	2	8
2&3&4	36	69	1	2	6
5	51	106	5	5	9
6	36	76	13	2	7
7	40	75	2	7	9
8	31	55	5	10	9

G = 32.55, D.F.= 20, P<0.05

Table 2f. waterbuck

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	263	339	59	79	29
2	295	520	82	86	15
3	330	520	77	55	7
4	435	750	65	107	26
5	258	425	28	23	8
6	233	419	19	15	18
7	196	312	9	6	32
8	217	399	13	20	39

G = 309.35, D.F.= 28, P<0.001

Table 2g warthog

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1	74	98	6	15	81
2	125	183	24	26	17
3	240	308	19	25	2
4	306	423	25	32	1
5	385	431	22	12	60
6	222	238	22	26	38
7&8	159	209	32	36	1

G = 418.07, D.F.= 24, P<0.001

Table 2h. zebra

SEASONS	ADULT MALES	ADULT FEMALES	SUBADULT MALES	SUBADULT FEMALES	JUVENILES
1&2&3	2	6	1	1	2
4	17	50	4	7	2
5	11	32	2	5	5
6	19	44	3	5	4
7&8	33	41	4	2	1

G = 21.1, D.F.= 16, P>0.1 NS

Tables 3a to 3h. Frequencies of animals of different age classes in samples of the various large herbivore species at different times during the study (G values accompanying each table denote log likelihood ratio for contingency table analysis).

Table 3a. buffalo

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	66	13	11
2	124	11	11
3	111	14	19
4	158	34	26
5	113	16	12
6	112	16	14
7	172	23	35
8	168	5	10

G = 42.0, D.F. =14 P< 0.001

Table 3b. giraffe

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	7	2	2
2	39	12	3
3	16	5	1
4	38	8	2
5&6	15	3	1
7&8	19	1	3

G = 8.27, D.F.= 10, P>0.5 NS

Table 3c. Grant's gazelle

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1&2	25	1	1
3	54	1	1
4	127	7	7
5	84	7	2
6	44	4	3
7&8	68	9	2

G = 9.97, D.F.= 10, P>0.25 NS

Table 3d. impala

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	518	75	33
2	791	107	35
3	840	161	45
4	1386	280	99
5	1049	172	51
6	1045	197	77
7	1004	112	53
8	1000	147	76

G = 53.46, D.F.= 14, P<0.001

Table 3e. Thomson's gazelle

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	16	2	4
2	100	2	6
3	185	6	8
4	157	1	13
5	157	9	9
6	112	16	7
7	115	9	9
8	86	15	9

G = 46.42, D.F.= 14, P<0.001

Table 3f. waterbuck

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	603	139	29
2	815	168	15
3	850	131	7
4	1185	172	26
5	684	51	8
6	652	34	18
7	508	15	32
8	616	33	39

G = 278.18, D.F.= 14, P<0.001

Table 3g. warthog

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	172	21	81
2	307	50	17
3	547	44	2
4	729	57	1
5	816	35	60
6	460	49	38
7&8	368	67	1

G = 398.28, D.F.= 12, P<0.001

Table 3h. zebra

SEASONS	ADULTS	SUB ADULTS	JUVENILES
1	4	1	3
2	11	3	2
3	9	1	2
4	67	11	2
5	43	7	5
6	63	8	4
7&8	73	6	1

G = 20.69, D.F.= 12, P>0.05 NS

Tables 4a to 4h. Frequencies of animals of different sex classes in samples of the various large herbivore species at different times during the study (G values accompanying each table denote log likelihood ratio for contingency table analysis).

Table 4a. buffalo

SEASONS	MALES	FEMALES	JUVENILES
1	39	40	11
2	88	46	11
3	61	64	19
4	96	96	26
5	80	50	12
6	73	55	14
7	67	128	35
8	89	84	10

G = 56.4, D.F.= 14, P<0.001

Table 4b. Giraffe

SEASONS	MALES	FEMALES	JUVENILES
1	4	5	2
2	26	25	3
3	9	12	1
4	16	30	2
5	10	7	2
6&7	11	7	1
8	3	14	3

G = 16.1, D.F.= 12, P>0.1 NS

Table 4c. Grant's gazelle

SEASONS	MALES	FEMALES	JUVENILES
1&2	14	11	1
3	27	28	1
4	63	71	8
5	43	48	2
6	23	25	3
7&8	47	30	2

G = 8.6, D.F.= 10, P>0.5 NS

Table 4d. impala

SEASONS	MALES	FEMALES	JUVENILES
1	301	292	33
2	518	381	35
3	478	524	45
4	778	888	99
5	566	655	51
6	508	734	77
7	496	620	53
8	533	614	76

G = 80.9, D.F.= 14, P<0.001

Table 4e. Thomson's gazelle

SEASONS	MALES	FEMALES	JUVENILES
1	7	12	4
2	39	64	6
3	69	121	8
4	45	113	13
5	56	110	9
6	50	78	7
7	42	82	9
8	36	65	9

G = 11.9, D.F.= 14, P>0.5 NS

Table 4f. waterbuck

SEASONS	MALES	FEMALES	JUVENILES
1	323	419	29
2	377	606	15
3	406	575	7
4	500	857	26
5	286	448	8
6	252	434	18
7	205	318	32
8	230	419	39

G = 92.44, D.F.= 14, P<0.001

Table 4g. warthog

SEASONS	MALES	FEMALES	JUVENILES
1	80	113	81
2	149	208	17
3	259	332	2
4	331	455	1
5	407	443	60
6	245	264	38
7&8	190	245	1

G = 344.95, D.F = 12, P<0.001

Table 4h. zebra

SEASONS	MALES	FEMALES	JUVENILES
1	1	4	3
2	5	9	2
3	2	7	2
4	21	57	2
5	13	37	5
6	22	49	4
7	12	11	1
8	61	74	1

G = 37.34, D.F = 14, P<0.001

Figure 9a. Seasonal distribution of waterbuck in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Key to season codes used in Figures 9a through 9h

season 1 = pre 1991 long rains; season 2 = 1991 long rains;

season 3 = pre 1991 short rains ;season 4 = 1991 short rains;

season 5 = pre 1992 long rains; season 6 = 1992 long rains;

season 7 = pre 1992 short rains; season 8 = 1992 short rains;

Fig 9a

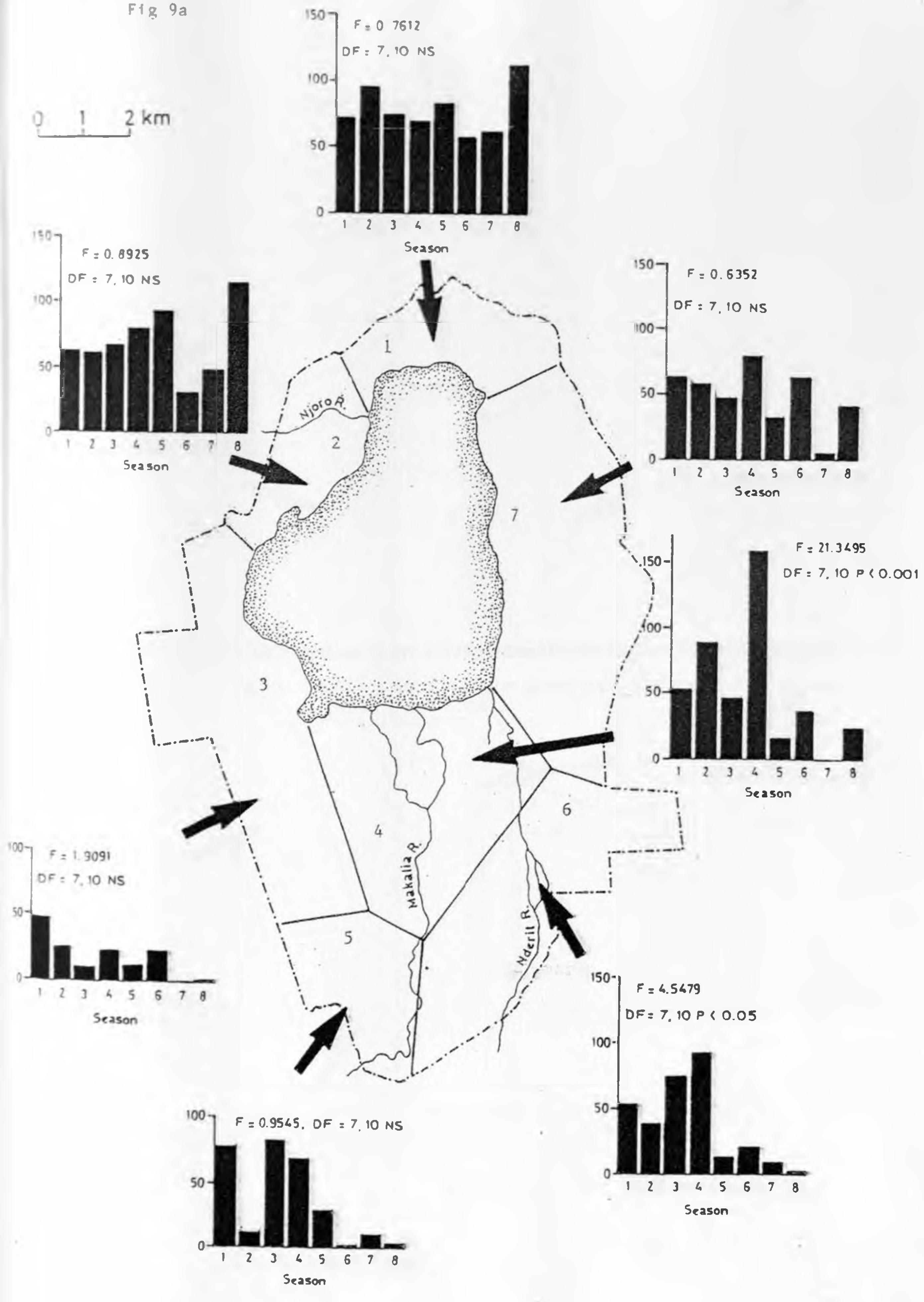

0 1 2 km
150
100
50
0
F = 0 7612
DF : 7, 10 NS
1 2 3 4 5 6 7 8
Season
F = 0. 8925
DF : 7, 10 NS
Season
F = 0. 6352
DF : 7, 10 NS
Season
F = 21.3495
DF : 7, 10 P < 0.001
Season
F = 1. 9091
DF : 7, 10 NS
Season
F = 0.9545, DF = 7, 10 NS
Season
F = 4.5479
DF = 7, 10 P < 0.05
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9b. Seasonal distribution of warthog in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9b

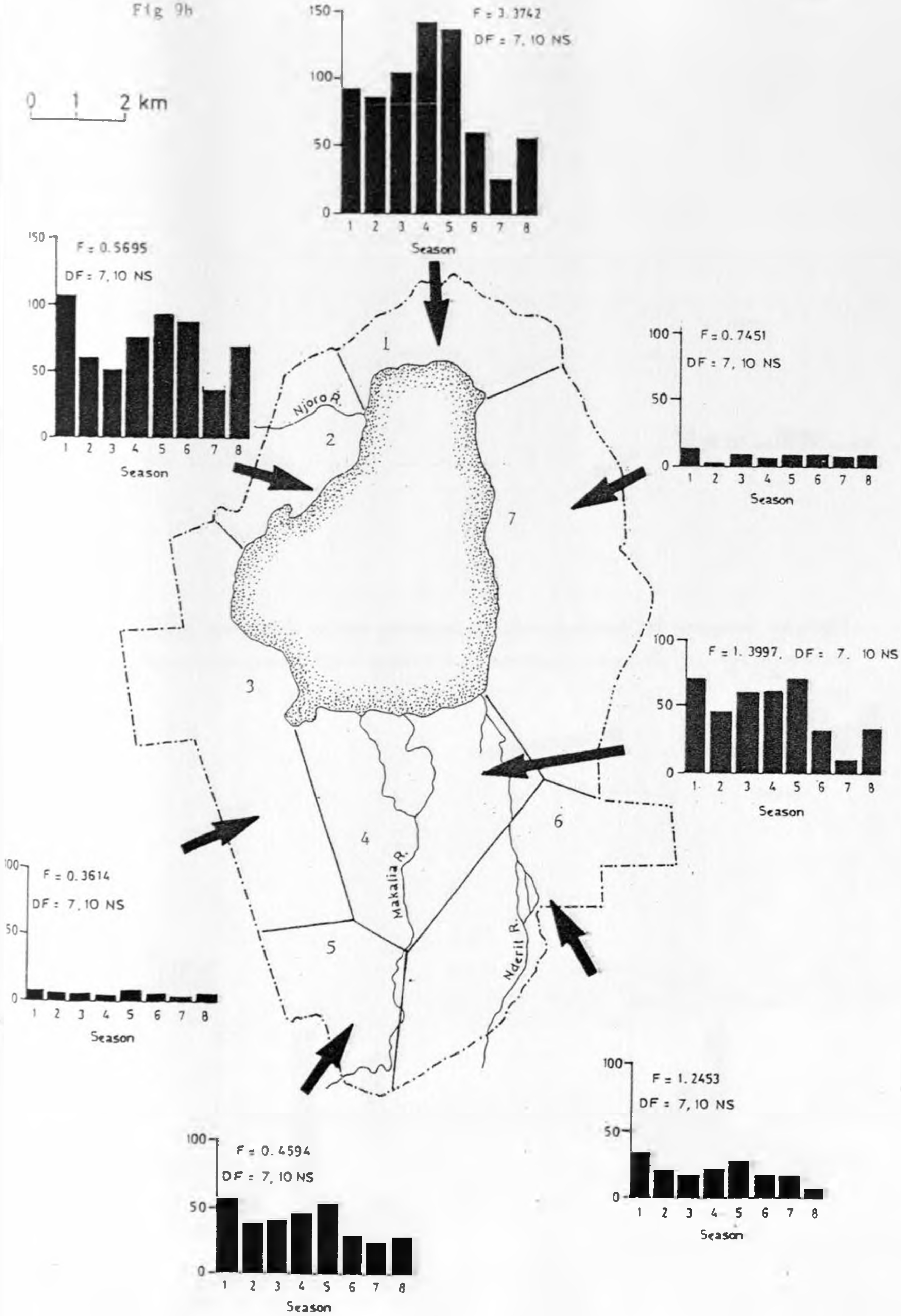

0 1 2 km
150
100
50
0
F = 3.3742
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
150
100
50
0
F = 0.5695
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
100
50
0
F = 0.7451
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
100
50
0
F = 1.3997, DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
100
50
0
F = 0.3614
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
100
50
0
F = 0.4594
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
100
50
0
F = 1.2453
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9c. Seasonal distribution of impala in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig. 9c

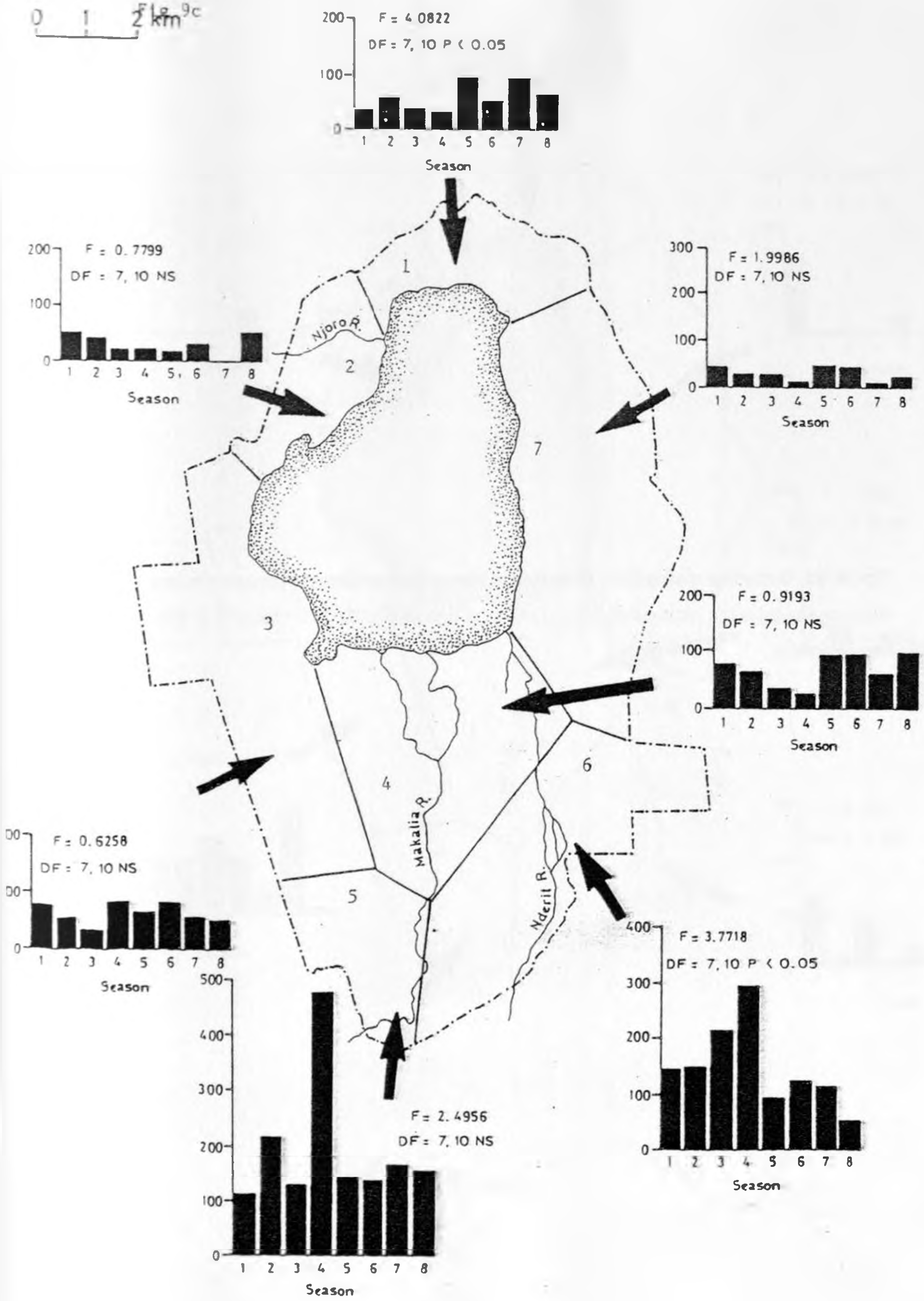

0 1 2 km
200
100
0
F = 4 0822
DF = 7, 10 P < 0.05
1 2 3 4 5 6 7 8
Season
200
100
0
F = 0. 7799
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
300
200
100
0
F = 1. 9986
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
1
2
Njoro R.
7
3
200
100
0
F = 0. 9193
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
4
6
Makalia R.
Nderit R.
5
0
F = 0. 6258
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season
400
300
200
100
0
F = 3. 7718
DF = 7, 10 P < 0.05
1 2 3 4 5 6 7 8
Season
500
400
300
200
100
0
F = 2. 4956
DF = 7, 10 NS
1 2 3 4 5 6 7 8
Season

Figure 9d. Seasonal distribution of buffalo in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9d

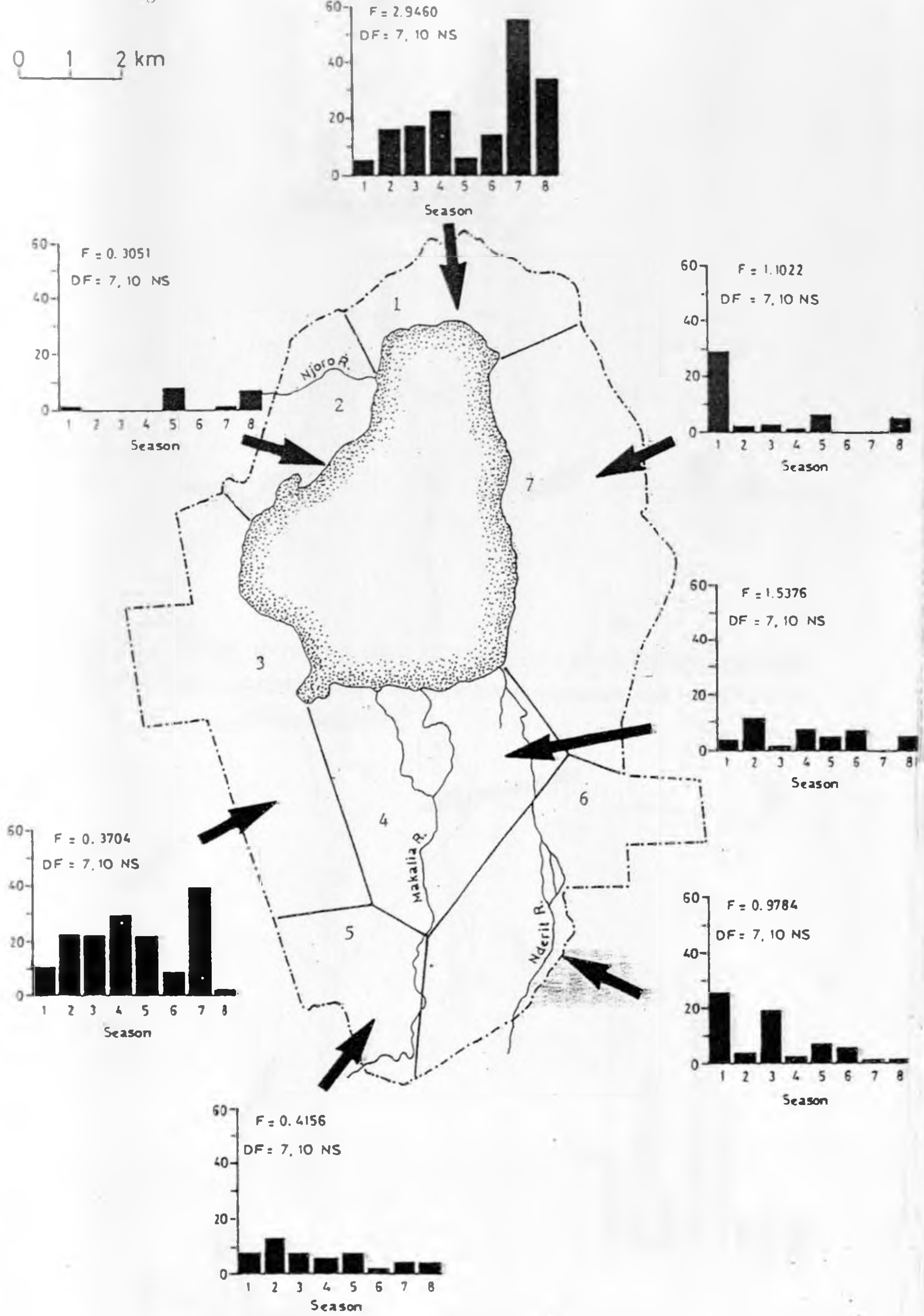

0 1 2 km
60
40
20
0
F = 2.9460
DF: 7, 10 NS
1 2 3 4 5 6 7 8
Season
F = 0. 3051
DF: 7, 10 NS
Season
F = 1.1022
DF = 7, 10 NS
Season
F = 1.5376
DF = 7, 10 NS
Season
F = 0. 3704
DF = 7, 10 NS
Season
F = 0. 9784
DF: 7, 10 NS
Season
F = 0. 4156
DF: 7, 10 NS
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9e. Seasonal distribution of Grant's gazelle in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9e

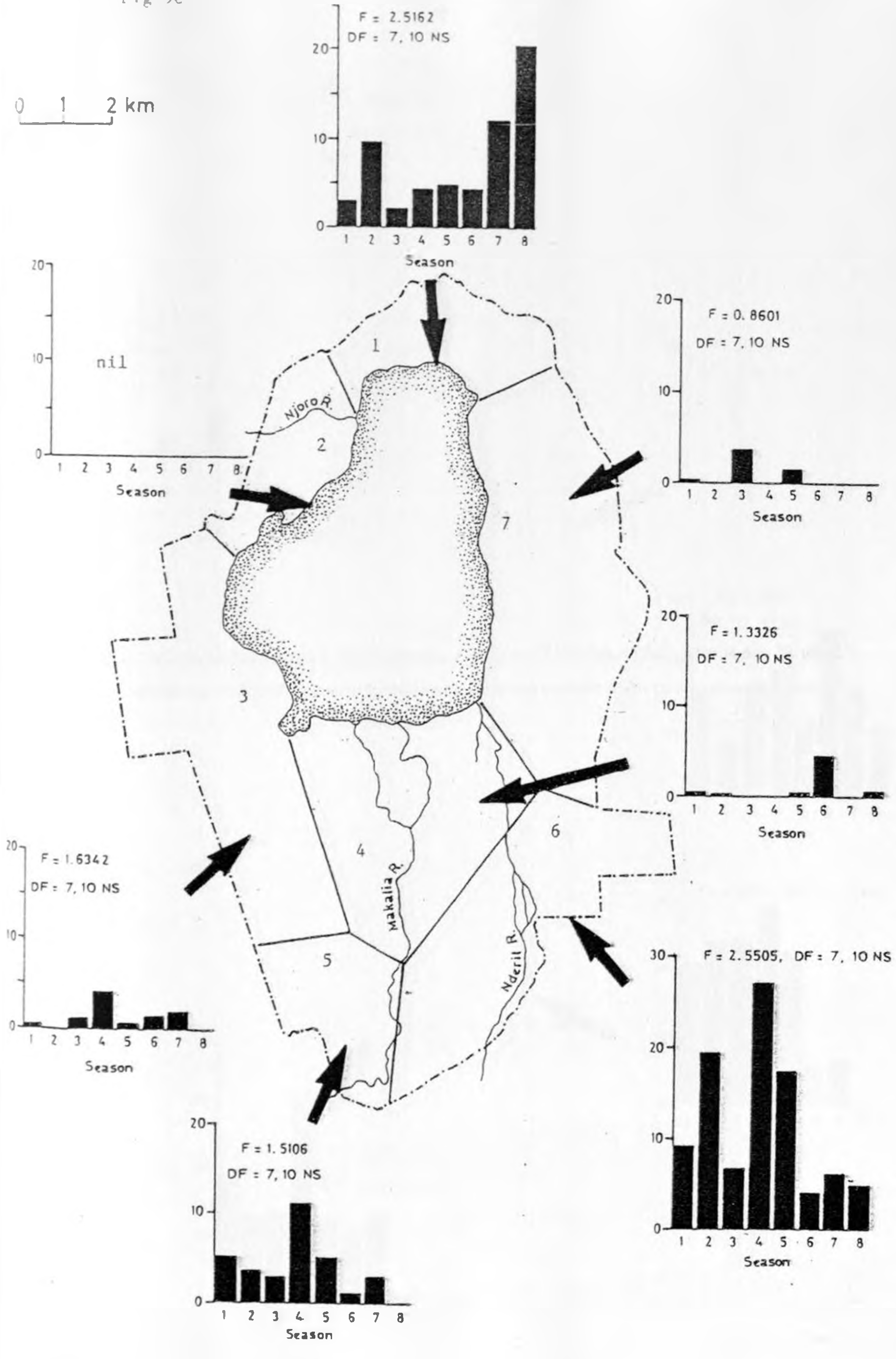

F = 2.5162
DF = 7, 10 NS
0
10
20
1 2 3 4 5 6 7 8
Season
0 1 2 km
nil
0
10
20
1 2 3 4 5 6 7 8
Season
F = 0.8601
DF = 7, 10 NS
0
10
20
1 2 3 4 5 6 7 8
Season
F = 1.3326
DF = 7, 10 NS
0
10
20
1 2 3 4 5 6 7 8
Season
F = 1.6342
DF = 7, 10 NS
0
10
20
1 2 3 4 5 6 7 8
Season
F = 2.5505, DF = 7, 10 NS
0
10
20
30
1 2 3 4 5 6 7 8
Season
F = 1.5106
DF = 7, 10 NS
0
10
20
1 2 3 4 5 6 7 8
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9f. Seasonal distribution of Thomson's gazelle in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9f

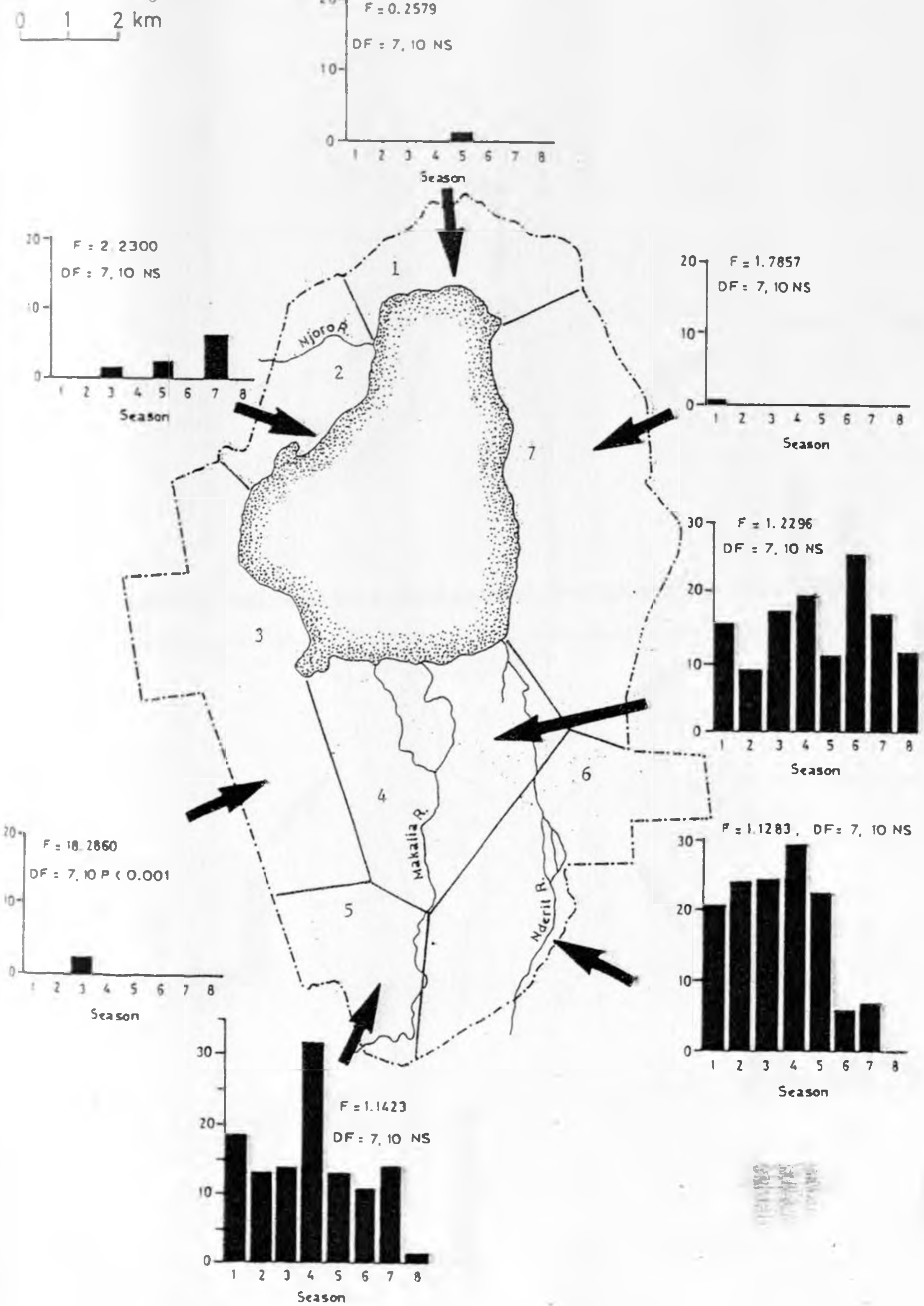

0 1 2 km
F = 0.2579
DF = 7, 10 NS
F = 2.2300
DF = 7, 10 NS
F = 1.7857
DF = 7, 10 NS
F = 1.2296
DF = 7, 10 NS
F = 1.1283, DF = 7, 10 NS
F = 18.2860
DF = 7, 10 P < 0.001
F = 1.1423
DF = 7, 10 NS
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9g. Seasonal distribution of Rothschild's giraffe in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9g

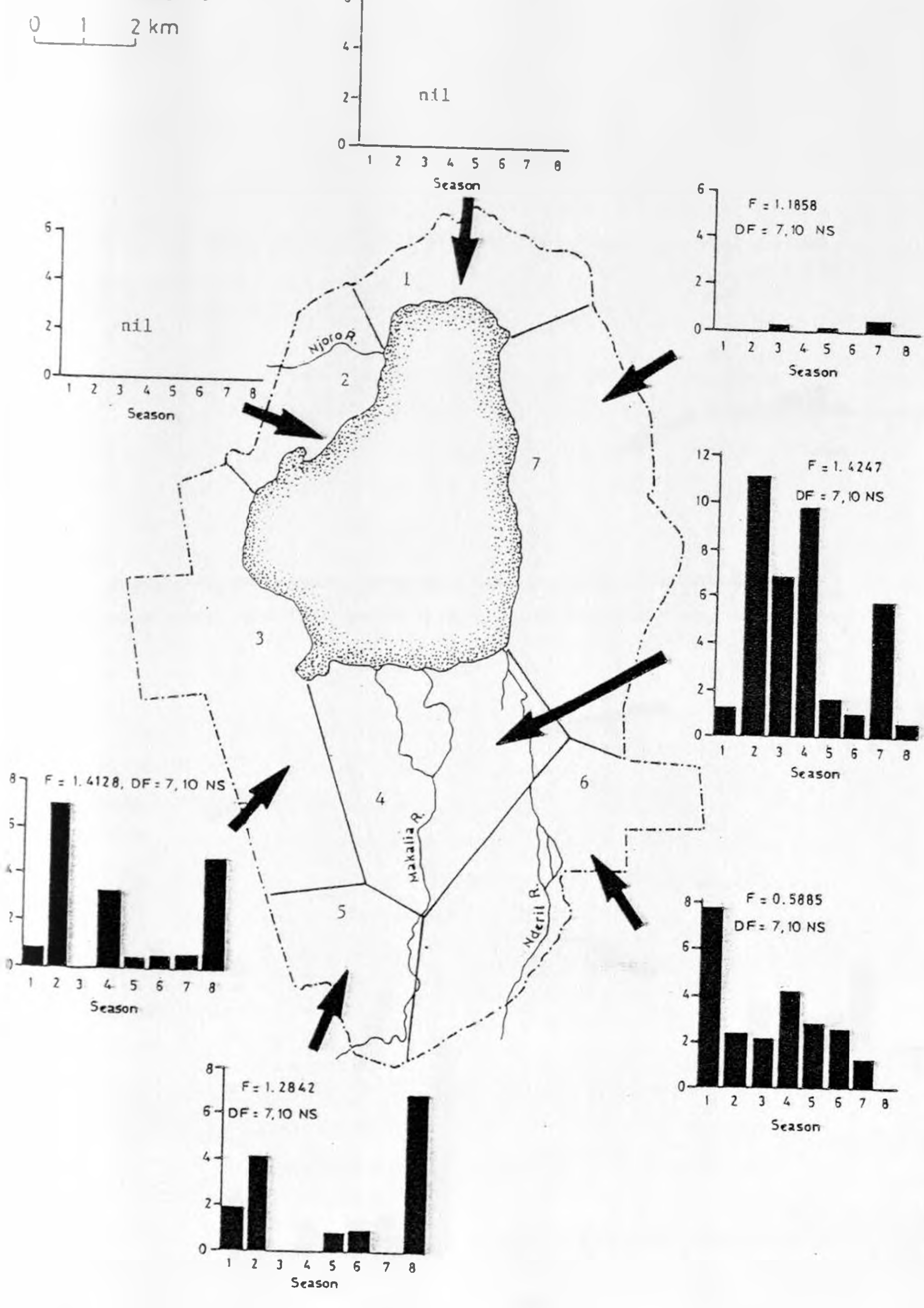
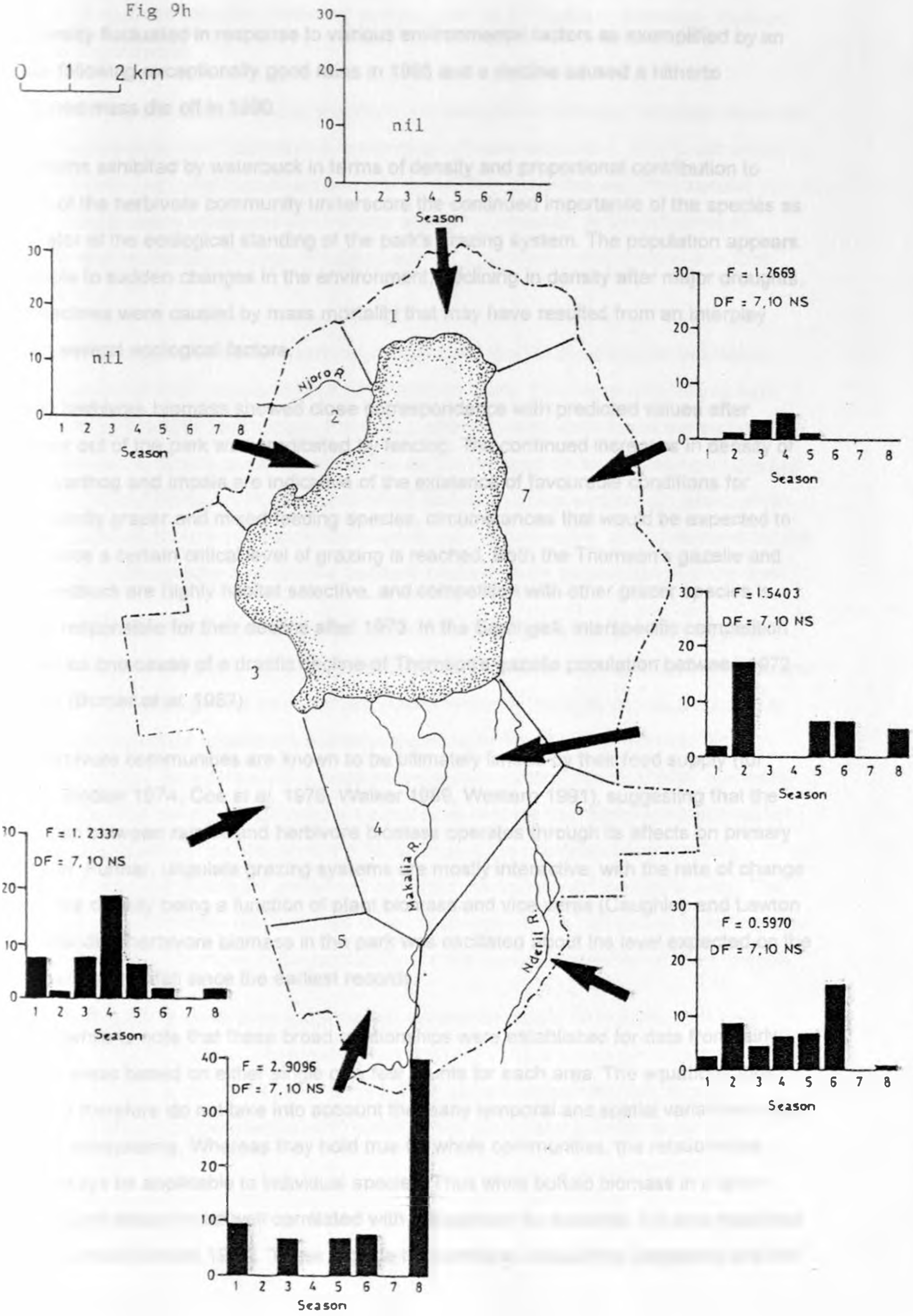

0 1 2 km
nil
1 2 3 4 5 6 7 8
Season
nil
1 2 3 4 5 6 7 8
Season
F = 1.1858
DF = 7,10 NS
1 2 3 4 5 6 7 8
Season
F = 1.4247
DF = 7,10 NS
1 2 3 4 5 6 7 8
Season
F = 1.4128, DF = 7,10 NS
1 2 3 4 5 6 7 8
Season
F = 0.5885
DF = 7,10 NS
1 2 3 4 5 6 7 8
Season
F = 1.2842
DF = 7,10 NS
1 2 3 4 5 6 7 8
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.

Figure 9h. Seasonal distribution of zebra in the seven sectors of the park (figures accompanying each histogram depict results of oneway ANOVA on density in the areas represented).

Fig 9h


0 1 2 km
30
20
10
0
nil
1 2 3 4 5 6 7 8
Season
30
20
10
0
nil
1 2 3 4 5 6 7 8
Season
F = 1.2669
DF = 7,10 NS
30
20
10
0
1 2 3 4 5 6 7 8
Season
1
2
3
4
5
6
7
Njoro R.
Makalia R.
Nderit R.
F = 1.5403
DF = 7,10 NS
30
20
10
0
1 2 3 4 5 6 7 8
Season
F = 1.2337
DF = 7,10 NS
30
20
10
0
1 2 3 4 5 6 7 8
Season
F = 0.5970
DF = 7,10 NS
30
20
10
0
1 2 3 4 5 6 7 8
Season
F = 2.9096
DF = 7,10 NS
40
30
20
10
0
1 2 3 4 5 6 7 8
Season

park. Density fluctuated in response to various environmental factors as exemplified by an increase following exceptionally good rains in 1986 and a decline caused a hitherto unexplained mass die off in 1990.

The patterns exhibited by waterbuck in terms of density and proportional contribution to biomass of the herbivore community underscore the continued importance of the species as an indicator of the ecological standing of the park's grazing system. The population appears susceptible to sudden changes in the environment, declining in density after major droughts. These declines were caused by mass mortality that may have resulted from an interplay between several ecological factors.

Standing herbivore biomass showed close correspondence with predicted values after movement out of the park was eradicated by fencing. The continued increases in density of buffalo, warthog and impala are indicative of the existence of favourable conditions for predominantly grazer and mixed feeding species, circumstances that would be expected to change once a certain critical level of grazing is reached. Both the Thomson's gazelle and Bohor reedbuck are highly habitat selective, and competition with other grazer species is probably responsible for their decline after 1973. In the Serengeti, interspecific competition was cited as one cause of a drastic decline of Thomson's gazelle population between 1972 and 1985 (Borner *et al.* 1987).

Large herbivore communities are known to be ultimately limited by their food supply (for example Sinclair 1974, Coe *et al.* 1976, Walker 1989, Western 1991), suggesting that the relationship between rainfall and herbivore biomass operates through its effects on primary production. Further, ungulate grazing systems are mostly interactive, with the rate of change in herbivore density being a function of plant biomass and vice versa (Caughley and Lawton 1981). Standing herbivore biomass in the park was oscillated about the level expected on the basis of annual rainfall since the earliest records.

It is worthwhile to note that these broad relationships were established for data from fairly disparate areas based on either single or a few counts for each area. The equations thus developed therefore do not take into account the many temporal and spatial variations within individual ecosystems. Whereas they hold true for whole communities, the relationships cannot always be applicable to individual species. Thus while buffalo biomass in a given area has been shown to be well correlated with precipitation for example, it is also regulated by other factors (Sinclair 1974). These include the nutritional state of the vegetation and the effects of interactions between coexisting species such as competition, predation pressure and social organization.

In evolutionary terms, it appears that stability in populations should occur at levels where the risks of overpopulation and starvation are minimized (Flowerdew 1987). This is still subject to much discussion, as many factors are involved in stabilizing populations. Thus natural selection acts at many levels and with varying degrees of intensity. At the influence of stochastic environmental or human mediated events, a population may exist in a multiple stable state.

Sinclair (1981) suggested that an example of such a situation is shown by the wildebeest (*Connochaetes taurinus*) population in Kruger National Park. They were originally at high density and regulated by food supply. A culling programme was instituted at the same time that an increase in rainfall reduced suitable habitat for the species, by increasing long grass areas. The population had to break up into small groups on areas with shorter grass which made the population more vulnerable to predation. After seven years, culling stopped but the population did not increase as expected because predation was stabilizing it at a low level.

The population structures reported in this study varied in temporal stability from species to species. Except for the giraffe, Grant's gazelle and zebra, all the other species showed some degree of flux in their age and sex structure. These temporal changes can be attributed to the increased incidence of juveniles in some species at certain times of the year. For example, warthogs gave births with a peak between January and March, slightly preceding the long rains. The waterbuck also had a distinct peak in births coinciding with the onset of rainy seasons. Mason (1990) reported similar findings in the wildebeest and warthog populations of Kruger National Park, where parturition coincided with the wet season. The differences could also have resulted from temporal changes in the distribution of various age sex classes, causing changes in the probability of them being detected along the transects.

The community under study is totally enclosed, preventing movements across the park boundaries. Thus fluctuations observed in the density of various species in a habitat type are indicative of temporal changes in level of use. Such patterns are greatly influenced by prevailing conditions of the environment, including the quality and quantity of various resources.

Results of this study indicate some distinct preferences for the five major habitat types. In a study of eight ungulate species in the Umfolozi Game Reserve, Melton (1987a) found the common waterbuck (*Kobus e. ellipsiprymnus*) to have preference for the widest range of habitat types, which was inconsistent with results from most previous studies (Lamprey 1963, Hanks *et al.* 1969, Spinage 1970). In fact, Hirst (1975) found the waterbuck to be the most stenoecious of five grazer species that he studied in South Africa. This study produced results similar to Melton's, whereby waterbuck were found in unchanging densities over the entire habitat spectrum, except the wooded grassland whose importance varied with seasons.

The waterbuck also displayed some degree of ecological segregation from other species. Their presence at high density in any habitat type or area led to the competitive exclusion of most other grazers. Asymmetric competition for resources was suggested as the ultimate cause of population decline in the common waterbuck in Umfolozi Game Reserve (Melton 1987a). Melton (1978) proposed an hypothesis that with a high stocking rate, nutritious grass in the waterbuck's preferred habitat becomes grazed too short, forcing the species to use habitats with tall and often poor quality grasses.

This study provides evidence for competition between the park's grazers. The Thomson's gazelle and warthog were both found in close association throughout their range. Both are low grazers, likely to benefit from the presence of bulk feeders like the zebra. The warthog however displays a peculiar behaviour that intensifies during the dry seasons. They dig up grass rhizomes, as well as bulbs, tubers and corms from other plants from below the soil surface with the snout. This broadens the warthog's niche and introduces some degree of ecological segregation between the two species. It is a widespread behavioural adaptation that becomes particularly important to the survival of warthogs during drought (Mason 1990).

Both the buffalo and eland, despite being grazers, are big bodied and need to range over large areas in order to meet their dietary requirements. In this study, the two species were found to exhibit little habitat selectivity. Given the small size of the park, and lack of migration, large buffalo herds stayed in one area for protracted periods, grazing it down accordingly, and then shifted to another area in response to food depletion. The buffalo was the only species to be consistently found in the dense *Tarchonanthus camphoratus* bushland, though the larger part of the population preferred open and wooded grasslands. Similar observations were made on the zebra population that however preferentially avoided the woodland. Being non-ruminant bulk feeders, the zebras were able to utilize areas with tall and relatively low quality grass south of the lake.

Of all the species encountered in this study, the black rhinoceros and giraffe were the only exclusive browsers. The rhinoceros population was low, at just 32 animals at the end of fieldwork. Most of these had been recently translocated into the park and were therefore rather elusive, preferring to remain in dense bush and woodland. The giraffes were the only potential competitors, though the intensity of this could not be adequately assessed in this study. It can be expected however that with the prevailing conditions, the park still has sufficient woody cover to support the two species at current population levels. Both browse at different heights and thus experience considerable ecological separation. The interaction between the two species needs to be closely watched in the future, as they cannot continue to increase without more intense competition ensuing.

Rosenzweig (1985) argued that in a single species case, only the best and therefore most preferred habitats will be selected at low population density. Selectivity should then decrease at higher densities in order to maximize the returns of all habitat types. This suggests that habitat selection patterns are expected to change predictably as important resources become scarce. Further, habitat selection has survival value and evolution would hardly have left it to chance.

Food varies in quality and quantity between seasons and habitats. In Nakuru, this variation forced some species to utilize habitats of relatively low value during the dry season. There is general agreement that large herbivore populations are regulated by food supply (Western 1991), but not without considerable debate. Phillipson (1973) concluded that both vertebrate and invertebrate herbivores in the Serengeti consumed only 18% of annual primary production suggesting the absence of food limitation. However, Sinclair (1975) took into account the times of food shortage and abundance and concluded that herbivores are food limited for part of the year. This is enough to regulate numbers in a density dependent manner, as shown for the buffalo (Sinclair 1974).

The line transect counts used in this study have a great inherent variability when based on small samples and narrow strips (Burnham *et al.* 1985, Bothma *et al.* 1990). They may be an effective and relatively cheap way of estimating animal density, however, in which strip width need not be fixed (Anderson *et al.* 1979).

CHAPTER 5 FOOD QUANTITY AND NUTRITIVE VALUE

5.1. Introduction

Large herbivore communities can exert a major impact on vegetation, thereby altering the structure and composition of communities and affecting their own food supply (Cumming 1982, East 1984, Ben-Sahar 1991). High levels of grazing and browsing could lead to radical changes in the balance between grass and woody vegetation. Ultimately, the intensity of these plant herbivore interactions could determine the course of plant succession.

Thus a clear understanding of the structure and dynamics of any plant herbivore system can only be achieved through a complete analysis of the underlying interactive processes (see section 6.1). Analytical models of grazing suggest that the process is characterized by complex dynamics, but empirical data for evaluating these models are rare (McNaughton 1985).

There is general consensus in contemporary ecology that food supply is a major extrinsic factor in regulating large herbivore populations through reproductive stress and juvenile mortality. Others may include disease and predation, by acting directly on both survivorship and fecundity (McNaughton and Georgiadis 1986, Freeland and Choquenot 1990).

Key factor analysis of mortality in wildebeest suggested malnutrition of both newborn calves and adults to be a major negative feedback mechanism, regulating the Serengeti population (Sinclair 1979). Fowler (1981) reported similar findings for the Serengeti buffalo, where the availability of a long time series of data enabled him to examine the stages at which regulatory mechanisms became important. The regulatory factors exerted their effects at levels very near the upper limit of population density. Such information is essential for enlightened management (*op cit.*).

Grass leaves offer high crude protein, exceeding 15 to 20 percent of dry matter when young, which declines rapidly as they grow. Dicotyledonous herbs and woody plants offer generally higher and seasonally more constant levels of protein in leaf tissues (Owen-Smith 1982). Protein content, rather than digestible energy, is considered crucial to grazers because tropical grasses tend to drop below the 5 % crude protein level, regarded as the critical value necessary for maintenance by herbivores, during the dry season (Sinclair 1974, 1977, Owen-Smith 1982, McNaughton 1979).

African ungulates also store little body fat compared with temperate zone species. If energy was limiting during the dry season, one would expect greater fat reserves to be stored, since this is the most efficient energy storage tissue. Instead, African ungulates metabolize muscle tissue under sub maintenance dry season conditions (Duncan 1975). In this study, I used herbaceous plant standing crop as an indicator of food supply, and percent crude protein content of grasses as an indicator of quality.

5.2. Methods

5.2.1. Determination of plant standing crop

The estimation of plant biomass is central to many ecological investigations, enabling the assessment of such factors as ecosystem productivity and grazing pressure. It is also the basis upon which other resources like energy and nutrients are evaluated. Above ground plant standing crop may be measured directly by a variety of harvest techniques. The clipping and sorting involved in such techniques, however, make them both destructive and laborious (Frank and McNaughton 1990). Consequently, a number of non destructive labour intensive techniques have been developed.

The indirect measurements are calibrated to clipped plots and allow for sampling to be done on the same plot many times over, with only minor disturbances. This also eliminates the spatial variation that would otherwise be added to the temporal variation being measured (Jonasson 1988). One such technique is the canopy intercept method used in this study. It relates standing crop to the number of contacts a pin makes when passed through vegetation.

Possible sources of error inherent in this technique include the effect of plant growth form, whereby the probability of contact with different plant parts is a function of both pin diameter and size of the parts (Frank and McNaughton 1990). If pin diameter is reduced to an infinitesimal point, the resultant error would approach zero, although this cannot not be done without regard for pin rigidity (*op cit.*). Caldwell *et al.* (1983) developed a fibre optic system for use with the canopy intercept technique that has several advantages over the traditional pin method. Throughout this chapter and the next, the term biomass is used to imply standing crop. It includes both live plant materials and those at various stages of drying up, before detachment.

5.2.2. Pin frame calibration

A formula for converting pin frame hits into standing crop estimates was developed by calibrating the frame against dry weight from clipped plots, during the period of peak growth in June 1991. Thirty plots each measuring 1m x 1m, were selected in a wide range of standong crop levels. Two plots each were located in areas of low, medium and high staning crop. in each of the five main vegetation types. The plots were sampled with the pin frame and the number of times that each pin came into contact with different plant parts recorded. All above ground herbaceous plant materials within the square meter were clipped and kept in well labeled paper bags. They were then dried to constant weight in an oven at 80°C.

The number of hits per pin in all 30 plots were regressed against dry weight of herbaceous plant material. and the resulting significant relationship was used to calculate subsequent estimates on the permanent plots.

5.2.3. Establishment of study plots

The herbaceous plant standing crop was measured on eight permanent vegetation plots located in the four main grazer habitats within the park. Two study plots were established in open grasslands, one at the northern end and the other at the southern end of the park. These are referred to in the text as plots 1 and 2, respectively. Two others, referred to as plots 3 and 4 were set up in shoreline grasslands at the northern and southern ends of the lake. Plot 5 was set up in the bushed grassland while plots 6, 7 and 8 were established in wooded grasslands, one to the north and two to the south, respectively.

For each plot, a replicate was established at an area with similar topography and vegetation characteristics. All replicates were chosen within about 200m of each other, denoted by A and B in the text, figures and tables accordingly. These were marked with metal pegs and four line transects established, radiating from the centre of the plot.

To establish each baseline. a three digit random number was generated on a scientific calculator, giving a compass direction along which the baseline would extend. To avoid lines lying too close together, whenever two adjacent compass bearings generated were within

30° of each other, the entire set was discarded and the whole process repeated. Five permanent sampling points were established along each line and used throughout the study.

5.2.4. Standing crop measurements

All the permanent plots were sampled with a 10 point pin frame, with the pins inclined at an angle of 33° to the vertical, in the third week of every other month throughout the study. During each sampling, the number of times that each pin came into contact with herbaceous plants were counted. Each contact was categorized as leaf, stem or flower, and whether it was green or dry.

5.2.5. Determination of nutritive value

Food quality was measured by chemical analysis of grass samples taken during sampling of the permanent vegetation plots. A sward of grass comprising both leaves and stems was obtained from the most common and identifiable species. The samples were placed in appropriately labelled paper bags and oven dried to crispness at 80°C. They were then ground into fine particles and analysed for percent Nitrogen content by the Kjeldahl procedure. The percent Nitrogen in each sample was multiplied by a conversion factor of 6.25 to obtain percent crude protein content.

5.2.6. Data analysis

Data obtained from this part of the study were analyzed with the aim of establishing the temporal changes in herbaceous standing crop as an indicator of fluctuations in food availability. This was achieved by usie of a mathematical relationship developed through calibration on clipped plots.

The number of times that each pin came into contact with herbaceous plants (hits per pin) was used to estimate the amount of standing crop at a sampling point. To reduce subjectivity in delimiting seasons, mean cumulative rainfall totals for three stations inside the park were calculated for periods of up to 30 days, beginning on the day preceding the commencement of each sampling. These figures were correlated against mean standing crop for that sampling session.

The resulting correlation coefficients were subjected to polynomial regression of increasing order and the best fitting curve obtained. This was used to establish the point at which standing crop and rainfall were most strongly correlated and therefore when standing crop was best a function of prevailing environmental conditions. The mean cumulative rainfall figure associated with that point was treated as an index of aridity and used as a cutline for wet and dry seasons. Any samples taken when cumulative rainfall fell below this aridity index were classified as dry season samples, the converse being true for data from any session with a value equal or higher.

Standing crop data for months falling within the same season were grouped together to enable the analysis of seasonal patterns. Plots in the same vegetation type were similarly combined for comparison of types. The differences in amount of standing crop over time and among vegetation types were analysed by 2-way ANOVA. Standing crop measurements were compared between replicate plots and between dry and wet months, using paired t-test.

The proportion of leaf, stem and flower hits to the total in different months were transformed into arcsines and subjected to one-way ANOVA. The resulting statistically significant group means were further subjected to the Student Newman Keuls multiple range test to find out exactly which groups differed from each other. The crude protein content for 23 most common grass species were subjected to arcsine transformation and analysed for temporal variation by one way ANOVA.

5.3. Results

5.3.1. Plant standing crop vs rainfall relationship

The relationship between plant standing crop and cumulative rainfall is presented in Figure 10. It was best described by a third order polynomial regression, with the following mathematical expression:

$y = 0.304 + 0.065x - 0.006x^2 + 0.0001x^3$, where y = correlation coefficient between standing crop and cumulative rainfall and x = number of days prior to sampling.

Figure 10. A third order polynomial fit describing the relationship between standing herb standing crop and amount of rainfall received over 30 days preceding sampling.

Figure 11. Regression of standing crop on number of hits per pin, based on calibration on clippings from 30 x 1m quadrats, each samped with 30 pins.

FIGURE 10

$y=0.304+0.065x-0.006x^2+0.0001x^3$

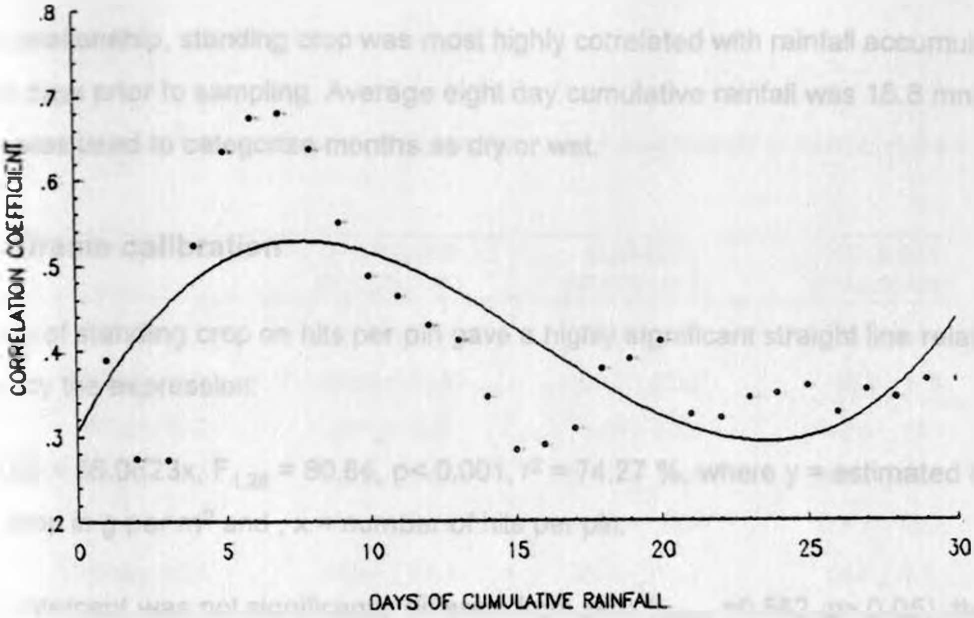
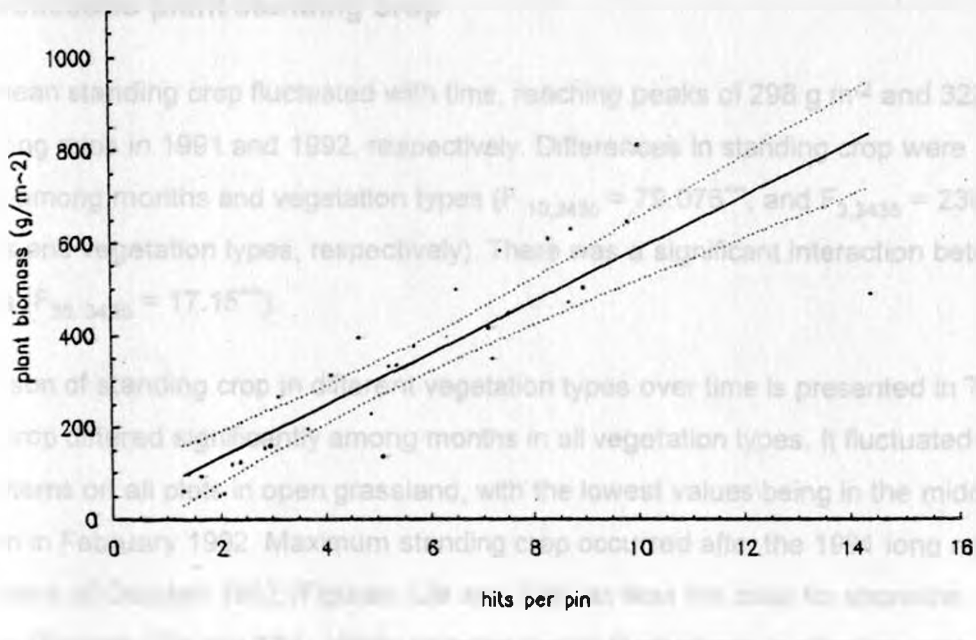


FIGURE 11

R sq = 73.9%; F=378.9; d.f.=1,29; P<0.001



From the relationship, standing crop was most highly correlated with rainfall accumulated over eight days prior to sampling. Average eight day cumulative rainfall was 15.8 mm, hence the figure was used to categorize months as dry or wet.

5.3.2 Pin frame calibration

Regression of standing crop on hits per pin gave a highly significant straight line relationship described by the expression:

$y = 22.2195 + 56.0823x$, $F_{1,28} = 80.84$, $p < 0.001$, $r^2 = 74.27$ %, where y = estimated dry standing crop in g per m^2 and , x = number of hits per pin.

Since the intercept was not significantly different from zero ($t_{28(2)} = 0.562$, $p > 0.05$), the parameter estimates were used to calculate a second regression with a zero intercept, described by the expression:

$y = 59.1037x$, $F_{1,29} = 378.9$, $p < 0.001$, $r^2 = 73.98$ % (Figure 11).

5.3.3 Herbaceous plant standing crop

Overall, mean standing crop fluctuated with time, reaching peaks of 298 g m^{-2} and 322 g m^{-2} after the long rains in 1991 and 1992, respectively. Differences in standing crop were significant among months and vegetation types ($F_{10,3435} = 79.076^{***}$, and $F_{3,3435} = 238.623^{***}$ for months and vegetation types, respectively). There was a significant interaction between the factors ($F_{30,3435} = 17.15^{***}$).

A comparison of standing crop in different vegetation types over time is presented in Table 5. Standing crop differed significantly among months in all vegetation types. It fluctuated with similar patterns on all plots in open grassland, with the lowest values being in the middle of a dry season in February 1992. Maximum standing crop occurred after the 1991 long rains and the short rains of October 1992 (Figures 12a and 12b), as was the case for shoreline grasslands (Figures 12c and 12d). While showing similar fluctuations in standing crop, plots on bushed grassland had consistently higher standing crop than the rest throughout the study (Figure 12e). The same patterns were found on wooded grassland plots which, however, showed distinctively higher peaks after the 1992 long rains than at any other time (Figures 12f to 12h).

Table 5. Comparison of herbaceous standing crop in the four main grazing habitats by months. (g per m^2, mean ± SE).

MONTH	GRASSLAND	SHORELINE GRASSLAND	BUSHED GRASSLAND	WOODED GRASSLAND
Mar 1991	75.2±9.1	105.5±2.9	111.0±2.3	93.3±3.0
May 1991	209.6 ± 14.1	145.6 ± 10.8	309.9 ± 23.6	180.3 ± 9.5
July 1991	284.8 ± 19.2	231 ± 12.8	710.4 ± 43.3	247.4 ± 13.1
Oct 1991	231.6 ± 19.7	228.6 ± 14.4	585.7 ± 30.6	240.4 ± 14.7
Dec 1991	190.5 ± 16.7	209.1 ± 12.6	433.2 ± 18.4	175.7 ± 10.8
Feb 1992	112.2 ± 12.1	125.6 ± 10.1	303.6 ± 17.4	86.6 ± 6.6
Apr 1992	116.9 ± 11.0	140.4 ± 11.0	201.4 ± 18.9	172.9 ± 13.9
Jun 1992	241.4 ± 15.2	193.2 ± 10.4	314.7 ± 16.0	397.4 ± 26.1
Aug 1992	226.1 ± 13.9	224.0 ± 11.6	614.5 ± 29.5	353.6 ± 19.8
Oct 1992	283.0 ± 22.4	223.0 ± 13.2	383.4 ± 16.0	288.4 ± 20.5
Dec 1992	240.5 ± 18.5	169.0 ± 9.9	447.6 ± 22.3	253.4 ± 19.7
F VALUE	12.116, D.F.=10,829, P<0.001	15.633, D.F.=10,869, P<0.001	57.084, D.F.=10,429 P<0.001	38.28, D.F.=10,1309, P<0.001

Figure 12a. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 1A and 1B, in the open grasslands at Baharini in the northern part of the Park.

Figure 12b. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 2A and 2B, in the open grasslands at Nderit in the southern part of the Park.

Figure 12c. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 3a and 3B, in the shoreline grasslands west of Njoro River mouth at the north western end of the lake.

Figure 12d. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 4A and 4B, in the shoreline grasslands between Makalia and Nderit River mouths at the southern end of the lake.

Figure 12e. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 5A and 5B, in the bushed grasslands south of Baboon Cliffs

Figure 12f. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 6A and 6B, in the wooded grasslands west of Njoro River.

Figure 12g. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 7A and 7B, in the wooded grasslands between Makalia and Nderit Rivers.

Figure 12h. Changes in standing crop (mean ± SE, plotted against time of sampling) on replicate plots 8A and 8B, in the wooded grasslands west of Makalia River.

(the bold lines represent replicate A while the dashed lines represent replicate B)

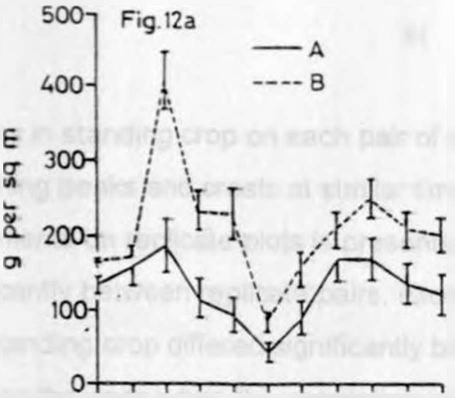


Fig.12a

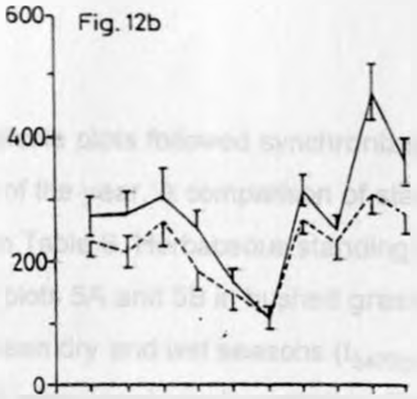
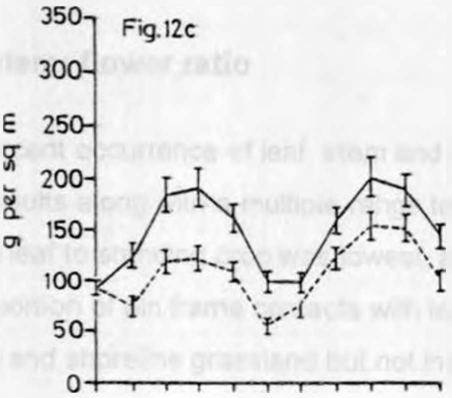


Fig.12b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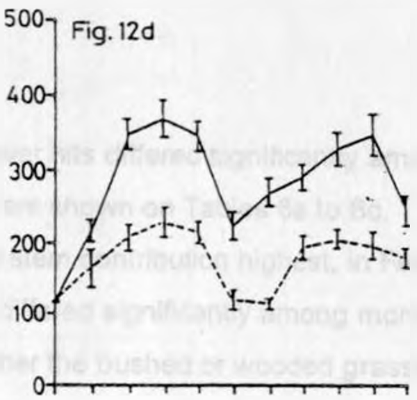


Fig.12d

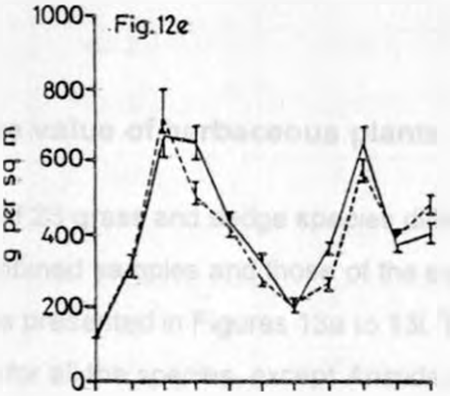


Fig.12e

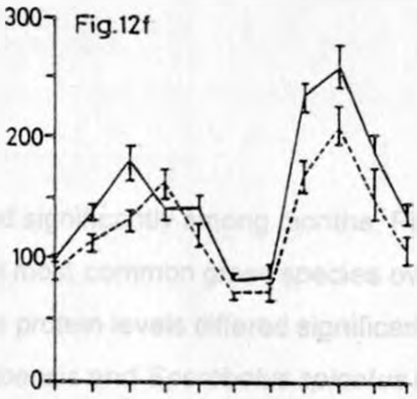


Fig.12f

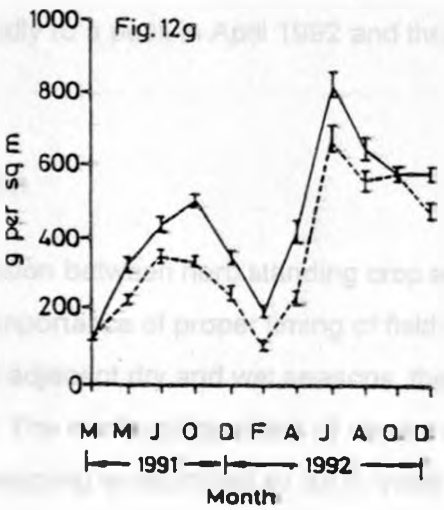


Fig.12g

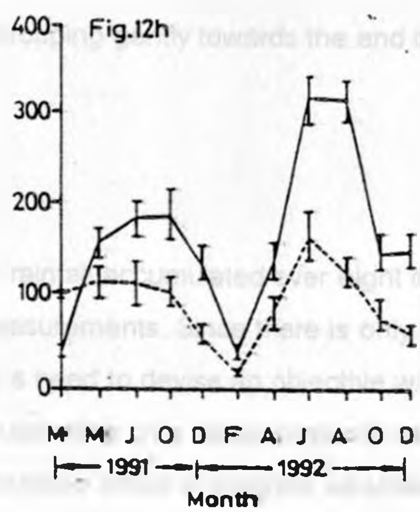


Fig.12h

The fluctuations in standing crop on each pair of replicate plots followed synchronized patterns, reaching peaks and crests at similar times of the year. A comparison of standing crop measurements on replicate plots is presented in Table 6. Herbaceous standing crop differed significantly between replicate pairs, except plots 5A and 5B in bushed grassland. Overall herb standing crop differed significantly between dry and wet seasons ($t_{3477(2)} = 11.03^{***}$), as was the case when the vegetation types were considered separately (Table 7).

5.3.4. Leaf: stem: flower ratio

Overall, the percent occurrence of leaf, stem and flower hits differed significantly among months. The results along with a multiple range test are shown on Tables 8a to 8c. Contribution of leaf to standing crop was lowest, and stem contribution highest, in February 1992. The proportion of pin frame contacts with leaf differed significantly among months in the grasslands and shoreline grassland but not in either the bushed or wooded grassland. Proportions of stem and flower contacts were different among months for all vegetation types.

5.3.5. Nutritive value of herbaceous plants

Nutritive value of 23 grass and sedge species differed significantly among months. Protein contents of combined samples and those of the eight most common grass species over the study period are presented in Figures 13a to 13i. The protein levels differed significantly among months for all the species, except *Aristida adoensis* and *Sporobolus spicatus* (Table 9). Protein levels in combined samples were lowest between October 1991 and February 1992, rising rapidly to a peak in April 1992 and then dropping gently towards the end of the study.

5.4. Discussion

The high correlation between herb standing crop and rainfall accumulated over eight days underlines the importance of proper timing of field measurements. Since there is only a thin cutline between adjacent dry and wet seasons, there is need to devise an objective way of delimiting them. The confounding effect of climate on standing crop measurements can only be reduced if sampling is organized so as to avoid the ripple effect of inherent weather conditions.

Table 6. Comparison of herb standing crop (g per m^2) on replicate plots over the study period.

(Degrees of freedom for t-test are in parenthesis).

PLOTS COMPARED	MEAN ± SE	t VALUE	P
1A	129.5 ± 8.4	6.52	<0.001
1B	210.7 ± 9.2	(219)	
2A	278.8 ± 12.3	3.21	<0.01
2B	226.9 ± 10.5	(219)	
3A	151.6 ± 5.0	6.95	<0.001
3B	107.2 ± 3.9	(219)	
4A	285.0 ± 7.9	11.07	<0.001
4B	176.1 ± 5.8	(219)	
5A	409.8 ± 15.9	0.78	>0.5 NS
5B	392.8 ± 14.9	(218)	
6A	152.9 ± 5.0	3.66	<0.001
6B	128.1 ± 4.5	(219)	
7A	454.7 ± 15.0	4.92	<0.001
7B	354.4 ± 13.9	(219)	
8A	167.4 ± 8.5	7.27	<0.001
8B	92.9 ± 5.8	(219)	

Table 7. Comparison of herb standing crop between dry and wet seasons (g per m^2). (Degrees of freedom for t-test are in parenthesis)

		mean ± SE	t VALUE	P
Overall	Dry	186.4 ± 4.4	11.03 (3477)	< 0.001
	Wet	257.5 ± 4.1		
Grassland	Dry	174.1 ± 8.6	4.72 (838)	< 0.001
	Wet	227.2 ± 6.7		
Shoreline grassland	Dry	167.2 ± 6.2	2.64 (478)	< 0.01
	Wet	187.3 ± 4.5		
Bushed grassland	Dry	358.4 ± 17.0	3.01 (638)	< 0.01
	Wet	425.9 ± 13.9		
Wooded grassland	Dry	149.0 ± 5.7	11.18 (1318)	< 0.001
	Wet	268.5 ± 7.4		

Table 8a. Proportion of overall pin frame contacts with leaf in different months; figures in parenthesis represent a numerical code for each sampling session as follows: 1 = July 1991, 2 = October 1991, 3 = December 1991, 4 = February 1992, 5 = April 1992, 6 = June 1992, 7 = August 1992, 8 = October 1992 and 9= December 1992. (ANOVA on arcsine transformed data, $F_{(8,135)}\ 2 = 3.029$, $p<0.01$; * denotes pairs significantly different at P=0.05, Student Newman Keuls test).

Month	% Hits	(4)	(3)	(2)	(1)	(5)	(8)	(7)	(6)	(9)
Feb 1992 (4)	72.8									
Dec 1991 (3)	81.5	*								
Oct 1991 (2)	82.3									
Jul 1991 (1)	83.0									
Apr 1992 (5)	83.0									
Oct 1992 (8)	85.0	*								
Aug 1992 (7)	85.7	*								
Jun 1992 (6)	86.3	*								
Dec 1992 (9)	89.9	*								

Table 8b. Proportion of overall pin frame contacts with stem in different months; figures in parenthesis represent a numerical code for each sampling session as follows: 1 = July 1991, 2 = October 1991, 3 = December 1991, 4 = February 1992, 5 = April 1992, 6 = June 1992, 7 = August 1992, 8 = October 1992 and 9= December 1992. (ANOVA on arcsine transformed data, $F_{(8,135)}\ 2 = 3.029$, $p<0.01$; * denotes pairs significantly different at P=0.05, Student Newman Keuls test).

Month	% Hits	(7)	(6)	(9)	(8)	(1)	(5)	(2)	(3)	(4)
Aug 1992 (7)	6.0									
Jun 1992 (6)	6.8									
Dec 1992 (9)	7.2									
Oct 1992 (8)	8.5									
Jul 1992 (1)	13.7									
Apr 1991 (5)	13.7									
Oct 1991 (2)	13.9									
Dec 1991 (3)	15.5	*								
Feb 1992 (4)	24.6	*	*	*	*		*	*	*	

Table 8c. Proportion of overall pin frame contacts with flower in different months; figures in parenthesis represent a numerical code for each sampling session as follows: 1 = July 1991, 2 = October 1991, 3 = December 1991, 4 = February 1992, 5 = April 1992, 6 = June 1992, 7 = August 1992, 8 = October 1992 and 9= December 1992. (ANOVA on arcsine transformed data, $F_{(8,135)\ 2} = 7.138$, $p<0.0001$; * denotes pairs significantly different at P=0.05, Student Newman Keuls test).

Month	% Hits	(4)	(3)	(9)	(1)	(5)	(2)	(8)	(6)	(7)
Feb 1992 (4)	1.5									
Dec 1991 (3)	2.0									
Dec 1992 (9)	2.1									
Jul1991 (1)	2.8									
Apr 1992 (5)	2.8									
Oct 1991 (2)	3.1									
Oct 1992 (8)	5.4	*	*	*						
Jun 1992 (6)	6.5	*	*	*	*	*	*			
Aug 1992 (7)	7.6	*	*	*	*	*	*			

Figure 13a. Overall protein content (mean ± SE) in 23 grass species over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13b. Protein content (mean ± SE) in *Aristida adoensis* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13c. Protein content (mean ± SE) in *Aristida keniensis* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

FIGURE 13 a
ALL SAMPLES

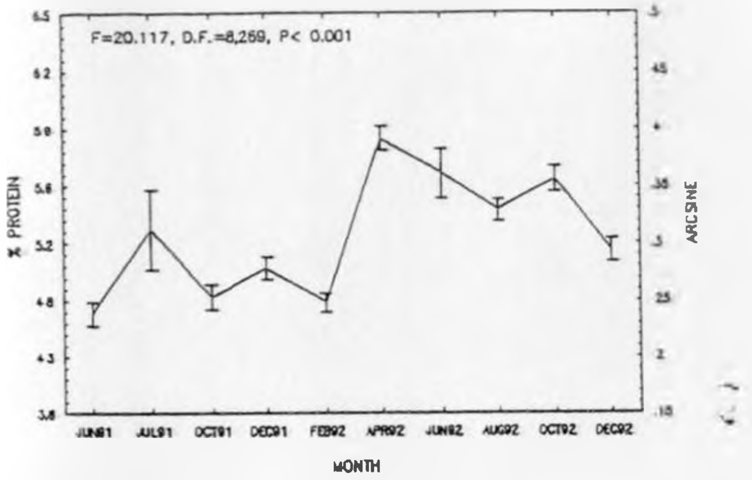


FIGURE 13 b
Aristida adoensis

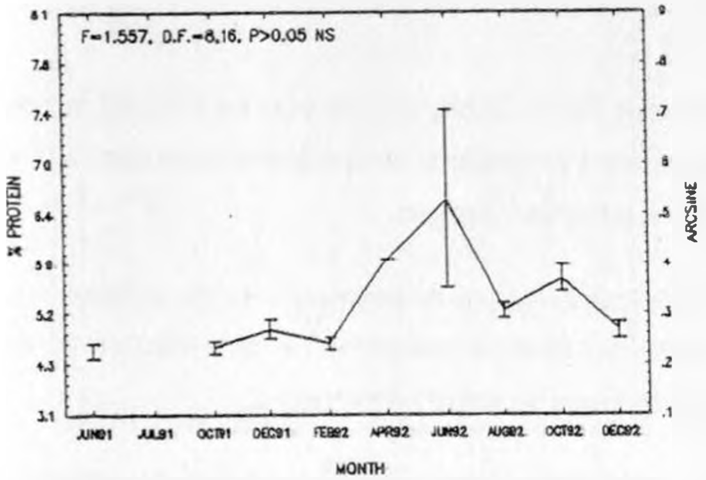


FIGURE 13 c
Aristida keniensis

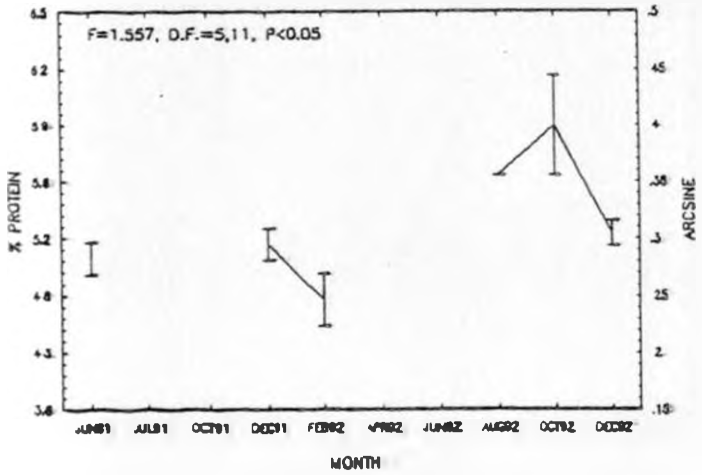


Figure 13d. Protein content (mean ± SE) in *Chloris gayana* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13e. Protein content (mean ± SE) in *Cynodon dactylon* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13f. Protein content (mean ± SE) in *Cynodon nlemfluensis* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

FIGURE 13 d
Chloris gayana

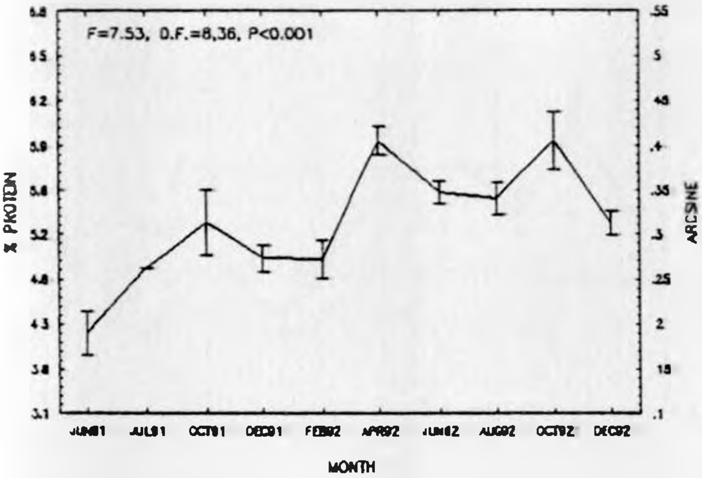


FIGURE 13 e
Cynodon dactylon

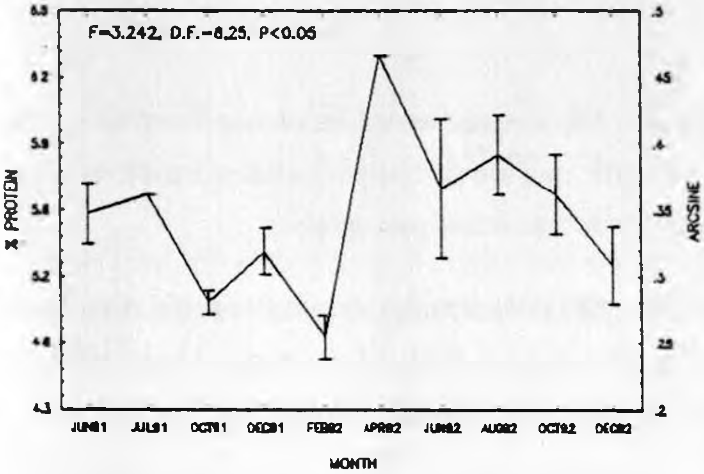


FIGURE 13 f
Cynodon nlemfuensis

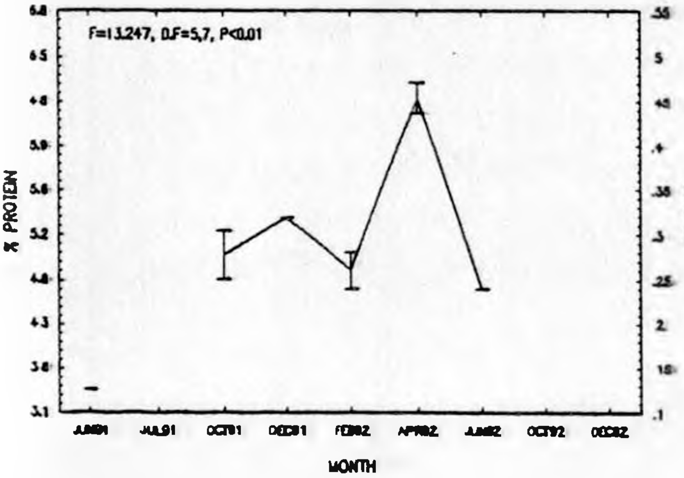


Figure 13g. Protein content (mean ± SE) in *Hyparrhenia lintoni* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13h. Protein content (mean ± SE) in *Sporobolus spicatus* over the different months covered in the study, the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages.

Figure 13i. Protein content (mean ± SE) in *Themeda triandra* over the different months covered in the study. the line and error bars are plotted from arcsine transformed data with values for the left y axis being expressed as actual percentages

FIGURE 13 g
Hyparrhenia lintoni

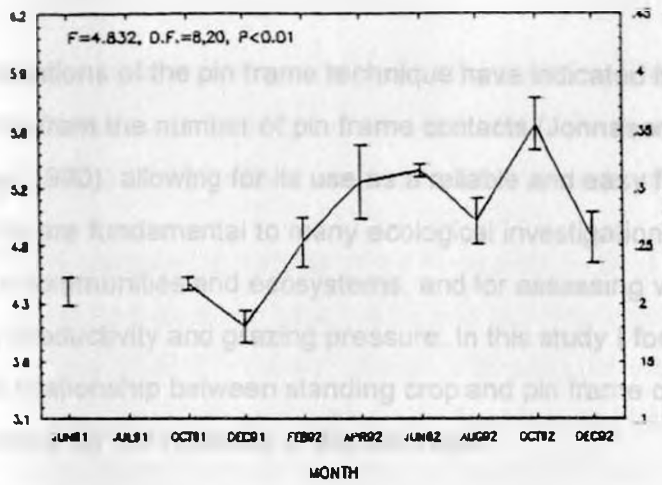


FIGURE 13 h
Sporobolus spicatus

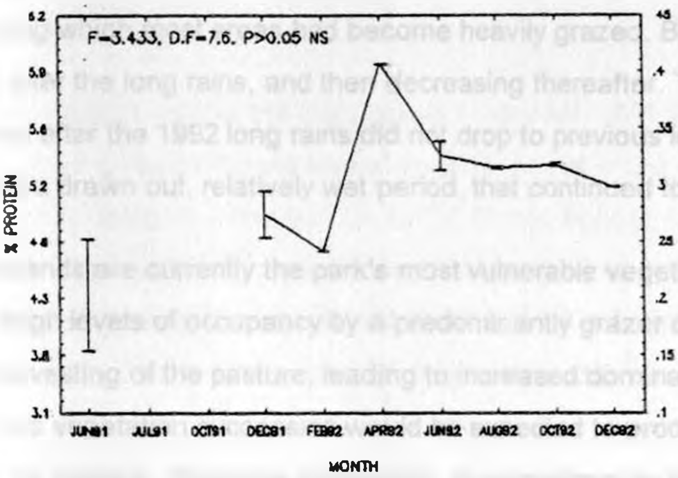
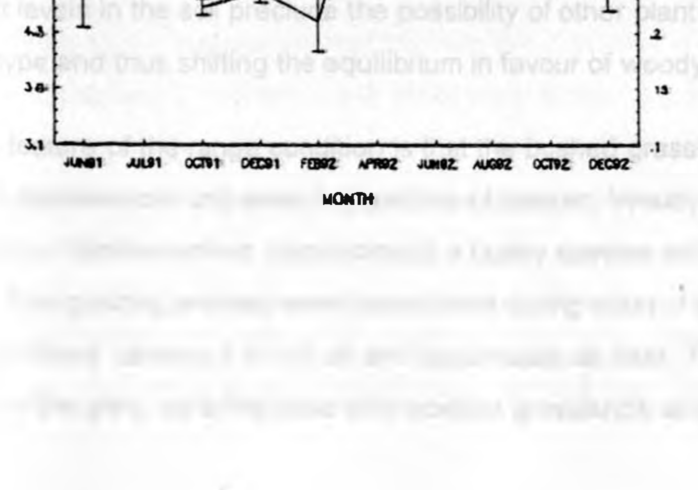


FIGURE 13 i
Themeda triandra



Several evaluations of the pin frame technique have indicated its high power for predicting standing crop from the number of pin frame contacts (Jonnason 1988, Frank and McNaughton 1990), allowing for its use as a reliable and easy field tool. Estimates of plant standing crop are fundamental to many ecological investigations. They are widely used to characterize communities and ecosystems, and for assessing various ecological processes like primary productivity and grazing pressure. In this study I found a strong, highly significant straight line relationship between standing crop and pin frame contacts, thereby providing further evidence for the reliability of the technique.

More than any other factor, precipitation played the single most important role in causing the cyclic changes observed in herb biomass. This study began at the end of a prolonged dry season during which most areas had become heavily grazed. Biomass was low, later increasing after the long rains, and then decreasing thereafter. The large biomass accumulated after the 1992 long rains did not drop to previous levels because the park experienced a drawn out, relatively wet period, that continued to the end of the study.

Open grasslands are currently the park's most vulnerable vegetation type, in terms of habitat alteration. High levels of occupancy by a predominantly grazer community may lead to selective harvesting of the pasture, leading to increased dominance by less palatable plant species. Thus vegetation succession would be expected to proceed towards conditions less favourable for grazers. Shoreline grasslands, characterized as they are by a few salt resistant species of the families Graminae and Cyperaceae, are also under considerable pressure.

This habitat type is limited in spatial extent but heavily utilized by some of the dominant grazer species, notably the waterbuck, warthog and Thomson's gazelle. It is also amenable to flooding as the lake level periodically rises and falls and indeed, occupies an area known to have been completely inundated after heavy rains in 1961. Under current circumstances, the high salt levels in the soil preclude the possibility of other plant species invading this vegetation type and thus shifting the equilibrium in favour of woody plants.

One salient feature of the range condition is that the bushed grasslands contained the highest herb biomass per unit area, irrespective of season. Woody canopy in this habitat type is dominated by *Tarchonanthus camphoratus*, a bushy species with typically low browser preference. Few grazing animals were found there during most of the study. Grass remained relatively unutilized, causing it to dry up and accumulate as litter. The vegetation type is widespread in the park, as is the case with wooded grasslands which are, however, more structurally diverse. Wooded grasslands provide a bigger mosaic of microhabitats, enabling a greater variety of herbivore species to utilize them. This causes a rapid rate of biomass offtake by herbivores and therefore, lower quantities accumulating than in the other areas.

Onyeanusi (1989) reported an offtake of 9.4 % on plots located along local migration routes in the Masai Mara. In that study, large herbivores removed upto 88.2 % of green biomass in the dry season, and 20.6 % in the wet season, indicating the intensity with which large herbivores are capable of influencing their own food supply. It can be argued that any changes in the structure, composition and spatial extent of the most preferred habitat types would lead to major shifts in the balance and integrity of ecosystem processes. If the area under open grassland is reduced through bush encroachment, the park will become increasingly unfavourable for grazer species.

Such a change would compel the management to try and alter the course of plant succession to encourage different animal species, perhaps one of the most challenging tasks facing resource managers today (Luken 1990). In this respect, it will be imperative that the Kenya Wildlife Service (KWS) consider the direction in which habitat changes would be most desirable. Notably, the park is currently designated as a sanctuary for both the black and white rhinoceroses. The former is a browser while the latter is a predominant grazer, for whom Nakuru does not form part of its immediate former range.

In addition, the park contains a sizeable giraffe population, having increased from 19 in 1973 to over 170 at present. Current trends are towards more woody habitats, to the benefit of an increasing browser community. Decisions on whether or not to redirect this trend will be guided by KWS priorities, but it will be essential that the kind of habitats that result be considered. Towards this end, it will be important to address the issue of what population sizes the park is capable of sustaining. In the long run, any habitat changes have important implications on an area's biodiversity.

Differences between dry and wet season biomass are indicative of imminent, albeit temporary, food shortages. Indeed, some areas were almost grazed bare late in the dry seasons, thereby compelling animals to move to poorer and less preferred habitats. When coupled with generally low protein values, these factors exposed the herbivores to the danger of poor nutrition.

Similar seasonal changes in herb quality have been reported for Masai Mara Game Reserve and Nairobi National Park (Boutton *et al.* 1988, Kinyamario and Macharia 1992). The cycles of abundance and scarcity were a clear indication of temporal variability in grazing levels within the park's major habitats. Localized spatial and temporal declines in herbivore food availability, similar to ones found in this study, have been reported in the Serengeti Mara ecosystem (McNaughton 1985, Onyeanusi 1989).

A close look at the contribution of different plant parts to total biomass over time gives deeper insight into the dynamics of herbivore food supply. As expected, leaves were more available during wetter months. This was because much leaf had been lost through death and preferential harvesting by herbivores during dry months. In his study of the Serengeti buffalo, Sinclair (1974) found the amount of available leaf to have declined towards the end of the dry season to such an extent that its contribution to the diet fell to a very low level.

Grazers are usually able to satisfy their qualitative food requirements year round, but are subjected to seasonal deficiencies in quality (Owen-Smith 1982). Changes in biomass availability and leaf to stem ratio are easily manifested in rather subtle attenuating effects on food supply. Under nutrition is considered an important factor influencing the dynamics of many African herbivores (McNaughton and Georgiadis 1986). Seasonal changes in the quality and nutritive value of grasses and forbs in East African grasslands are sufficiently large to affect the resident herbivore populations (Boutton *et al.* 1988).

Seasonal fluctuations in food quality may be implicated in the periodic loss of body condition among the park's herbivores. A few months prior to the beginning of this study, large numbers of waterbuck had died and many more were emaciated, leading to much concern being raised about the health of the entire large herbivore community. Other species, including the buffalo, impala and warthog, also lost condition and the situation was only reversed by the arrival of 1991 long rains.

Investigations into the possible causes of waterbuck mortality revealed no significant disease or parasite factors. Many individuals showed clear evidence of nutritional stress, including poor body coat and muscular degeneration. Postmortem examination of both dead and culled animals further revealed severe mobilization of fat reserves. In addition, all the animals examined had rumens full of ingesta, indicating that they probably consumed enough food, but of inadequate nutritive quality. These results were similar to others reported in earlier studies on impala (Howard 1964). The region has long been known to be deficient in minerals, particularly copper and cobalt, and provision of mineral supplements is a common practice in the management of both livestock and wildlife populations in the area. Mineral supplementation will become increasingly important for the park's wildlife, as they can no longer move to salt licks that may have otherwise existed elsewhere.

The impacts of herbivory on the herb layer now require closer monitoring and assessment. It is also important to keep a close watch on changes in the plant community structure and ratio of green to dry material, which have a major influence on pasture feeding value and hence animal productivity. Productivity of both domestic and wild herbivore systems depends on the quantity of herbage harvested and the efficiency with which animals digest and use nutrients. It has been found from studies of livestock systems that when pasture is available in increasing quantity, intake increases asymptotically (Thompson and Poppi 1990).

The nutritional deficiencies reported here are subject to major confounding factors, main among them being the animals' physiology and behaviour. Ruminant animals have bacteria in the reticulorumen which alter the state in which many nutrients are absorbed. Different foods have different digestibilities and the best feeding strategy is for a herbivore to select food that can be digested within the retention times permitted by the size and activity of their microbial fermentation systems (Howe and Wesley 1988).

Carbohydrates are fermented to yield volatile fatty acids which are then absorbed and used by the animal as energy substrates. Some of the plant proteins in the rumen may be inefficiently captured by bacteria, resulting in less protein reaching the small intestines than was consumed. There may also be a protein gain across the rumen through recycling of urea to the rumen and subsequent utilization by bacteria.

The findings of this study indicate the kind of management actions needed to ensure the continuity of Lake Nakuru National Park as an ecologically viable protected area. Granted that the park experienced increased isolation over many years, it reached a pinnacle when the entire perimeter was fenced. Ecological isolation necessitates the adoption and constant use of various methods of pasture assessment, akin to those used by livestock managers. Many such techniques are available, ranging from visual assessment to capacitance meters and reflectance indices (Lucas and Thompson 1990). There is need to continuously monitor the pasture condition in order to facilitate timely decisions on appropriate management actions.

CHAPTER 6. EFFECTS OF GRAZING ON THE HERB LAYER

6.1. Introduction

Many early studies in the African savanna concentrated on animals, with surprisingly little being known about the plants. One of the salient, and biologically interesting, features of these ecosystems is the existence at high densities of a great diversity of large mammals (Keast 1969, McNaughton and Georgiadis 1986).

Several pioneering studies in East Africa documented a variety of feeding patterns among herbivore species and emphasized the role of vegetation zonation in shaping animal communities (Vesey-Fitzgerald 1960, Lamprey 1963). A series of classic studies were conducted in the Serengeti, in the mid to late 1970's, designed to obtain information on vegetation dynamics, the nature of plant herbivore relations and ecosystem processes of the earth's last vast unmanaged grazing system (McNaughton 1985).

Grasses represent the pinnacle of grazing tolerance (Youngner and McKell 1972), and grazing ecosystems with large mammals are believed to have characterized between one third and half of the earth's terrestrial surface until the last century. The grasses in these areas differ markedly from those evolved in areas lacking large herbivores (Mack and Thompson 1982). The coevolution of mammalian herbivores with grasses and forbs has received much treatment in the literature (McNaughton 1985).

Inferences as to the time of grass emergence in evolution are made largely from a remarkably complete mammalian fossil record. Evidence indicates increased hypsodonty in the dentition of both equid and ruminant herbivores in the last 7 million years, after the Tertiary period, when grasses became both widespread and abundant. The morphology of both rhizomatous and caespitose grasses reflects the two extremes to which grasses have evolved, in response to continuously high against low selection pressure by large congregating mammals (Mack and Thompson 1982). Some of the once extremely abundant large herbivores, such as the bison (*Bison bison*) in North America and Saiga (*Saiga tartarica*) in Eurasia, preceded the vegetation that supported them into near extinction as domestic livestock and cultivation expanded rapidly (McNaughton 1985).

The savanna grassland environment is characterized by continuous stochastic fluctuations of rainfall, grazing, nutrient availability and fire, which generate pulses in primary productivity. These pulses result in a potentially rich but temporary and spatially unpredictable food resource for grazers. The migratory habits of many grazers are instrumental in their effective exploitation of this constantly shifting resource base, enabling them to dominate the landscape. Grazers influence the amount, rate of production and quality of food available to them (Edroma 1981, Owen-Smith 1982), thus carrying capacity is not fixed independently of the animals. They also influence the composition and diversity of the vegetation (McNaughton 1983).

Grazing plays a pivotal role in shaping plant communities in both qualitative and quantitative terms. It causes alterations in habitat structure and affects micro climate for other species. Defoliation has a profound affect upon plant physiological processes, with constant reallocation of resources to the growth, development and maintenance of various tissues in response to grazing pressure. It has multiple effects beyond the mere reduction of plant biomass. For example, it reduces the amount of transpiration surface, thereby conserving soil moisture, which regulates the extent to which vegetation is stimulated by grazing (Crawley 1983).

There is ample evidence that ungrazed tropical grasslands are often limited by nutrients, even at low levels of rainfall. Nutrient cycling through dung and urine is considered a major contributor to the stimulatory effect of grazing on growth, emphasizing the importance of large mammals in the dynamics of grassland ecosystems (Harper 1977, Botkin *et al.* 1981, Crawley 1983).

In addition to animals trampling on vegetation as they feed, they compact the soil, creating germination conditions and characteristic plant communities different from those in the original sward. Heavy grazing on arid lands alters the surface properties of soil to such an extent that the vertical profile of soil water distribution is altered in favour of deep rooted plants. Grasses are replaced by woody plants as a result (Walker *et al.* 1981). Less palatable grass species were shown to exhibit greater resistance to simulated grazing than more palatable ones in the Ruwenzori National Park (Edroma 1981).

Attempts to understand plant herbivore dynamics are handicapped by the existence of multiple factors that influence the functioning of ecosystems. Fluctuations in plant numbers may have nothing to do with herbivore feeding, just as herbivore numbers may change independently of their food plants. Other factors such as weather, fire, disease and intraspecific competition may singly or interactively influence growth of both plants and animals. When there is mutual dependence between plants and herbivore numbers, there are numerous theoretically possible outcomes (Caughley and Lawton 1981, Crawley 1983). In this chapter, I present the fundamental basis for what, it is hoped, will be a long term monitoring programme of the park's grazing system.

6.2. Methods

6.2.1. Establishment of grazing exclosures

Impacts of grazing on the herbaceous plant layer were observed on five permanent exclosures, each measuring 10m x 10m, established at the beginning of the study. All exclosure plots were selected in areas of fairly uniform habitat, and fenced off with cedar poles and chain link, in order to keep out large herbivores. Two exclosures were constructed in open grasslands, one at Baharini in the north, and the other at Nderit at the south eastern end of the park. One exclosure each was put up in the bushed and wooded grasslands west of Baboon Cliffs and south of the lake, respectively.

Of the four exclosures established in an earlier study in 1987, three had become overgrown with woody plants and only one, located south of Naishi Sub Headquarters, was sampled in this study. These will be referred to in subsequent sections as Baharini, Nderit, Baboon cliffs, New Naishi and Old Naishi, respectively, while the older one will be referred to as Old Naishi.

Three parallel baselines were established in each exclosure, one running right through the middle and the others located half way between the mid line and the opposite edges. Three random sampling points, each 1m x 1m were established along each line, care being taken to avoid the metre segment adjacent to the fence. An equal sized plot was chosen adjacent to and outside each exclosure and three baselines established by extending the lines from inside the exclosure. Sampling points were similarly selected and these were used throughout the study.

6.2.2. Herbaceous Standing crop and species composition

The standing crop at each sampling point was estimated with a 10 point pin frame, and the number of contacts with leaf, stem and flower, and whether they were green or dry, recorded in the third week of every other month throughout the study. In addition, the grass or forb species in contact with each pin were recorded during the sampling in May 1991 and June 1992.

6.2.3. Data analysis

The pin frame readings at each point were converted to standing crop estimates using the equation developed through calibration (see section 5.3.2). Standing crop estimates inside and outside exclosures were subjected to 2 way ANOVA procedures to test for differences among exclosures and months. Differences in herb standing crop among months were analysed by one-way ANOVA, while those between inside and outside the exclosures were compared using the paired t-test.

The relative abundance of green and dry plant parts at different times were analysed by the Wilcoxon paired sample test while percent frequencies of pin frame contacts with leaf, stem and flower at different times of the study were analysed by the Kruskal - Wallis test. The species richness, importance values, similarity and diversity indices of each exclosure were calculated for the two years covered in the study (Krebs1989). Shannon - Wiener indices of each exclosure were compared between the two years using t-test (Magurran 1988).

The purpose of these analyses was to quantify effects of grazing on the accumulation of plant materials, as an indication of possible changes if grazing levels changed. It also aimed to describe the effects of grazing on herbaceous plant species diversity.

6.3. Results

6.3.1. Standing crop

Overall standing crop measurements differed significantly among months and exclosures with a significant interaction between the factors ($F_{9,850}=32.274$. $p<0.001$. $F_{4,850}=37.918$, $p<0.001$ and $F_{36,850}=21.265$ $p<0.001$ for months, exclosures and interaction, respectively). The same was true when separate analyses were done for standing crop present inside and outside each exclosure. Figures 14a to 14e show the standing crop inside and outside the five exclosures at different times during the study.

The four new exclosures showed a steady increase in standing crop at the beginning, after which it fluctuated with two annual cycles, both inside and outside. Standing crop remained consistently lower outside than inside all the exclosures after the first few samplings. Two notable cases were the plots in wooded grassland, whereby standing crop increased rapidly in cycles inside the New Naishi exclosure, thereafter steadily declining after the first rise and rapidly after the second (Figure 14d).

The increase was slight outside the exclosure at the beginning, followed by a decline and then a steep rise after February 1992. This later fell rapidly after June 1992. Standing crop differed significantly between inside and outside, except in June 1992 ($t_{(2)16}$=0.1, p>0.9). Standing crop was initially low in the old Naishi exclosure but increased slightly both inside and outside up to October 1991. It later decreased and then rose rapidly after April 1992, remaining at a peak inside but declining slightly on the outside towards the end of study (Figure 14e).

Differences were significant between inside and outside except in the months of May and July 1991, and April and August 1992. Standing crop levels differed for all months between inside and outside in the Baharini, Nderit and Baboon Cliffs exclosures.

6.3.2. Green : dry parts and leaf : stem ratios

The relative abundance of green and dry plant parts in different months are presented in Tables 9a to 9e. These differed significantly between the months inside all the exclosures. They also differed outside the exclosures at Baboon cliffs and Nderit, but not anywhere else. Similar results were found for the relative abundance of leaf, stem and flower in the herb standing crop, being significantly different both inside and outside all exclosures. Ratios of leaf to stem to flower hits for the five exclosures are presented in Tables 10a to 10e.

Figure 14a. Changes in standing crop (mean ± SE, plotted against time of sampling) at the Baharini exclosure (the bold line depicts standing crop inside while the dashed line depicts standing crop outside).

Figure 14b. Changes in standing crop (mean ± SE, plotted against time of sampling) at the Nderit exclosure (the bold line depicts standing crop inside while the dashed line depicts standing crop outside).

Figure 14c. Changes in standing crop (mean ± SE, plotted against time of sampling) at the Baboon Cliffs exclosure (the bold line depicts standing crop inside while the dashed line depicts standing crop outside).

Figure 14d. Changes in standing crop (mean ± SE, plotted against time of sampling) at the New Naishi exclosure (the bold line depicts standing crop inside while the dashed line depicts standing crop outside).

Figure 14e. Changes in standing crop (mean ± SE, plotted against time of sampling) at the Old Naishi exclosure

(the bold line depicts standing crop inside while the dashed line depicts standing crop outside)

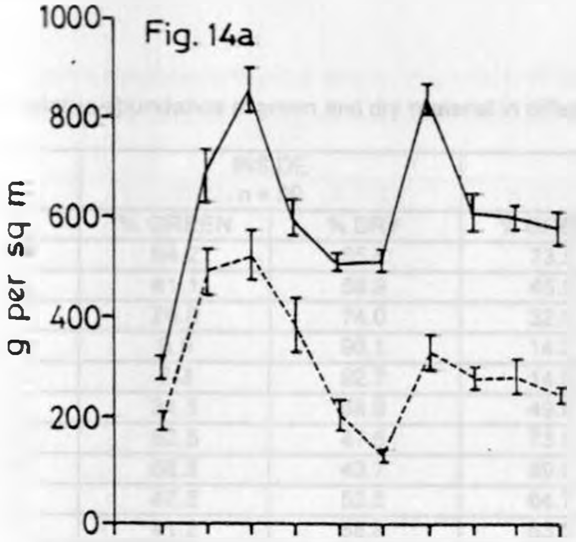


Fig. 14a

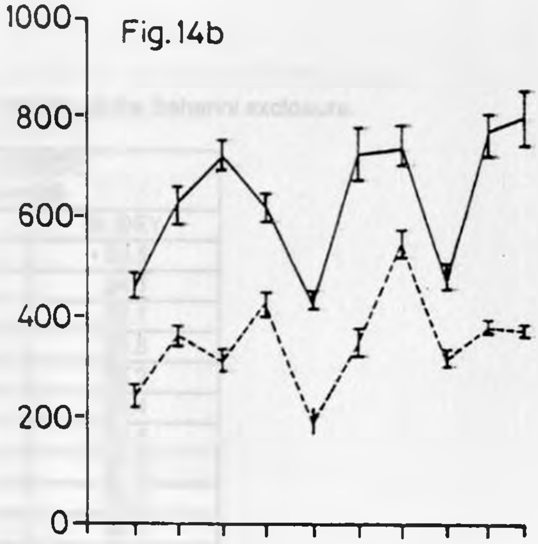


Fig. 14b

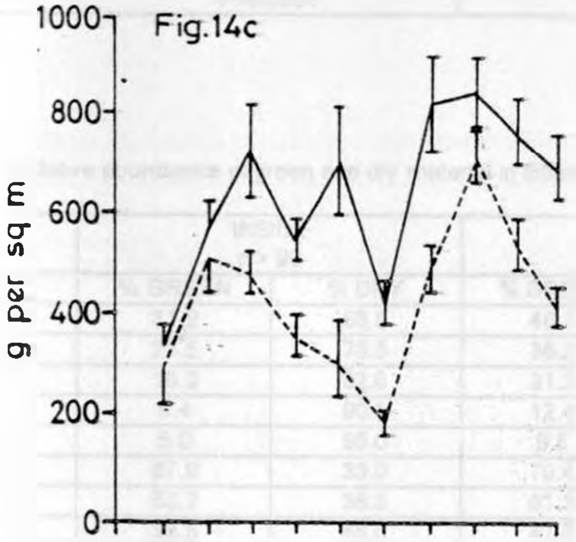


Fig. 14c

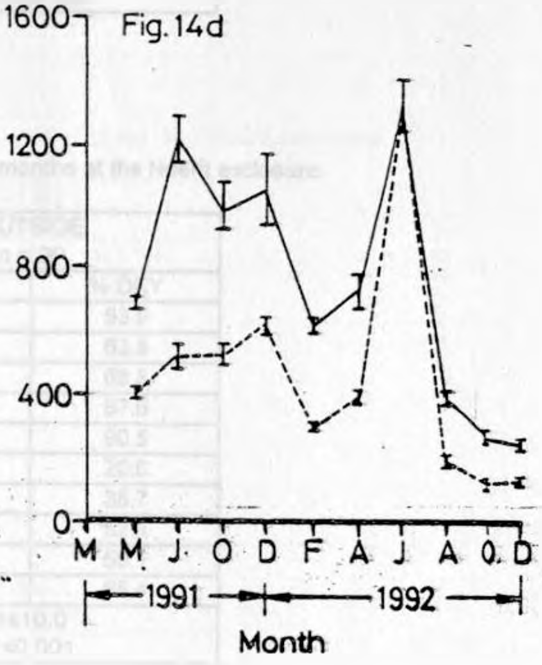


Fig. 14d

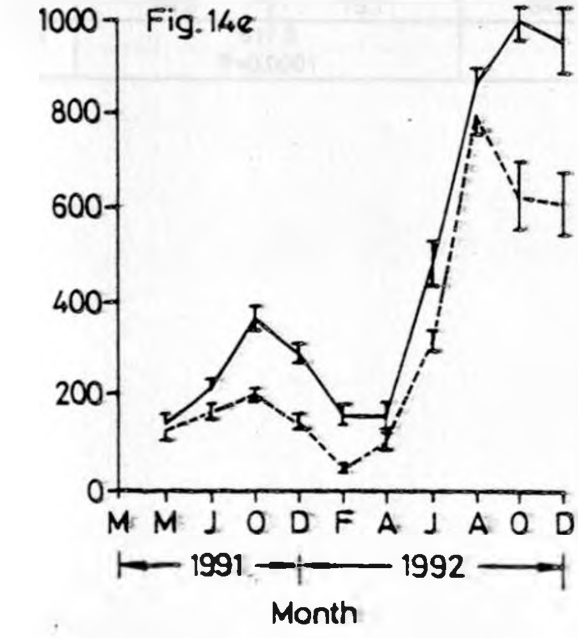


Fig. 14e

Table 9a. Relative abundance of green and dry material in different months at the Baharini exclosure.

	INSIDE n = 99		OUTSIDE n = 99	
MONTH	% GREEN	% DRY	% GREEN	% DRY
May 1991	64.2	35.8	73.5	26.5
Jul 1991	41.1	58.9	45.9	54.1
Oct 1991	26.0	74.0	32.9	67.1
Dec 1991	9.9	90.1	14.2	85.8
Feb 1992	7.3	92.7	14.8	85.2
Apr 1992	31.1	68.9	49.6	50.4
Jun 1992	52.5	47.5	73.5	26.5
Aug 1992	56.3	43.7	69.8	30.2
Oct 1992	47.5	52.5	64.7	35.3
Dec 1992	41.2	58.8	63.5	36.5
WILCOXON T	799.0 P<0.0001		2195.0 P<0.36 NS	

Table 9b. Relative abundance of green and dry material in different months at the Nderit exclosure.

	INSIDE n = 99		OUTSIDE n = 99	
MONTH	% GREEN	% DRY	% GREEN	% DRY
May 1991	31.2	68.8	46.1	53.9
Jul 1991	21.5	78.5	36.2	63.8
Oct 1991	18.0	82.0	31.2	68.8
Dec 1991	9.4	90.6	12.4	87.6
Feb 1992	5.0	95.0	9.5	90.5
Apr 1992	67.0	33.0	79.4	20.6
Jun 1992	63.7	36.3	61.3	38.7
Aug 1992	33.5	66.5	47.7	52.3
Oct 1992	28.5	71.5	49.9	50.1
Dec 1992	24.3	75.7	34.6	65.4
WILCOXON T	517.5 P<0.0001		1410.0 P<0.001	

Table 9c. Relative abundance of green and dry material in different months at the Baboon Cliffs exclosure

	INSIDE n = 99		OUTSIDE n = 99	
MONTH	% GREEN	% DRY	% GREEN	% DRY
May 1991	71.1	28.9	60.5	39.5
Jul 1991	36.7	63.3	35.1	64.9
Oct 1991	27.8	72.2	31.3	68.7
Dec 1991	14.7	85.3	21.9	78.1
Feb 1992	4.7	95.3	7.6	92.4
Apr 1992	46.5	53.5	52.3	47.7
Jun 1992	75.6	24.4	73.8	26.2
Aug 1992	72.4	27.6	75.6	24.4
Oct 1992	34.1	65.9	39.0	61.0
Dec 1992	24.9	75.1	29.9	70.1
WILCOXON T	1401.5 P<0.001		1620.5 P<0.01	

Table 9d. Relative abundance of green and dry material in different months at the New Naishi exclosure

	INSIDE n = 99		OUTSIDE n = 99	
MONTH	% GREEN	% DRY	% GREEN	% DRY
May 1991	49.4	50.6	61.7	38.3
Jul 1991	44.3	55.7	30.5	69.5
Oct 1991	31.6	68.4	31.2	68.8
Dec 1991	17.4	82.6	20.9	79.1
Feb 1992	14.2	85.8	17.0	83.0
Apr 1992	52.0	48.0	71.8	28.2
Jun 1992	60.8	39.2	64.9	35.1
Aug 1992	76.4	23.6	73.3	26.7
Oct 1992	44.6	55.4	43.8	56.2
Dec 1992	63.5	36.5	75.7	24.3
WILCOXON T	1620.0 P<0.01		1964.5 P>0.10 NS	

Table 9e. Relative abundance of green and dry material in different months at the Old Naishi exclosure.

	INSIDE n = 99		INSIDE n = 99	
MONTH	% GREEN	% DRY	% GREEN	% DRY
May 1991	71.7	28.3	81.9	18.1
Jul 1991	68.0	32.0	69.2	30.8
Oct 1991	73.9	26.1	60.4	39.6
Dec 1991	57.4	42.6	39.4	60.6
Feb 1992	19.5	80.5	31.4	68.6
Apr 1992	67.5	32.5	79.3	20.7
Jun 1992	88.2	11.8	87.8	12.2
Aug 1992	50.9	49.1	40.6	59.4
Oct 1992	49.2	50.8	30.0	70.0
Dec 1992	37.3	62.7	39.3	60.7
WILCOXON T	1623.0 P<0.01		2107.5 P>0.26 NS	

Table 10a. Relative abundance of plant parts in the Baharini exclosure over different months during the study.

	INSIDE n=81			OUTSIDE n=81		
MONTH	% LEAF	% STEM	% FLOWER	% LEAF	% STEM	% FLOWER
Jul 1991	80.5	10.4	9.1	82.6	11.9	5.5
Oct 1991	74.1	10.5	15.4	73.5	10.5	16.0
Dec 1991	85.3	13.4	1.2	82.3	17.0	0.7
Feb 1992	62.4	18.9	18.7	61.9	31.1	6.9
Apr 1992	80.4	10.3	9.3	79.0	20.0	1.0
Jun 1992	72.9	13.0	14.1	89.6	7.7	2.7
Aug 1992	73.0	8.6	18.4	78.2	8.9	13.0
Oct 1992	80.1	8.8	11.1	79.1	11.3	9.7
Dec 1992	87.0	5.6	7.4	90.2	3.9	5.9
KRUSKAL-WALLIS H'	19.391 P<0.001			21.849 P<0001.		

Table 10b. Relative abundance of plant parts in the Nderit exclosure over different months during the study.

	INSIDE n=81			OUTSIDE n=81		
MONTH	% LEAF	% STEM	% FLOWER	% LEAF	% STEM	% FLOWER
Jul 1991	74.1	24.8	1.2	69.9	25.4	4.7
Oct 1991	81.8	16.2	2.0	70.1	21.2	8.7
Dec 1991	71.2	28.4	0.3	64.9	34.6	0.5
Feb 1992	61.7	37.3	1.0	54.2	43.8	2.0
Apr 1992	82.7	16.4	0.9	88.7	11.3	0.0
Jun 1992	83.9	11.6	4.5	81.5	12.1	6.4
Aug 1992	96.0	1.8	2.3	86.0	3.2	10.7
Oct 1992	95.4	3.2	1.4	80.0	4.0	16.0
Dec 1992	92.4	3.8	3.8	77.9	6.9	15.2
KRUSKAL-WALLIS H'	24.038 P<0.0001			21.691 P<0.001		

Table 10c. Relative abundance of plant parts in the baboon Cliffs exclosure over different months during the study.

	INSIDE n=81			OUTSIDE n=81		
MONTH	% LEAF	% STEM	% FLOWER	% LEAF	% STEM	% FLOWER
Jul 1991	90.0	8.7	1.3	88.5	10.7	0.8
Oct 1991	81.7	8.4	9.9	88.3	7.2	4.5
Dec 1991	88.9	9.5	1.6	91.6	7.5	0.9
Feb 1992	87.8	7.6	4.6	87.3	11.7	1.0
Apr 1992	93.7	4.3	1.9	92.5	7.2	0.3
Jun 1992	81.3	7.4	11.4	84.2	5.9	9.9
Aug 1992	80.2	6.3	13.5	78.3	5.4	16.2
Oct 1992	83.5	9.4	7.1	77.8	11.0	11.2
Dec 1992	88.5	6.5	5.0	87.3	5.4	7.3
KRUSKAL-WALLIS H'	19.874 P<0.0001			20.529 P<0.0001		

Table 10d. Relative abundance of plant parts in the New Naishi exclosure over different months during the study.

	INSIDE n=81			OUTSIDE n=81		
MONTH	% LEAF	% STEM	% FLOWER	% LEAF	% STEM	% FLOWER
Jul 1991	87.3	10.5	2.2	86.6	12.4	1.0
Oct 1991	90.6	8.5	0.9	83.7	13.3	3.0
Dec 1991	91.8	8.0	0.2	79.1	20.3	0.6
Feb 1992	93.4	6.3	0.3	48.6	51.4	0.0
Apr 1992	88.5	11.3	0.3	84.3	15.7	0.0
Jun 1992	70.8	19.1	10.1	70.6	17.8	11.6
Aug 1992	80.8	9.6	9.6	79.7	15.5	4.8
Oct 1992	63.7	19.8	16.5	64.0	25.3	10.8
Dec 1992	80.1	9.9	9.9	85.7	11.8	2.5
KRUSKAL-WALLIS H'	21.137 P<0.0001			24.849 P<0.0001		

Table 10e. Relative abundance of plant parts in the Old Naishi exclosure over different months during the study.

	INSIDE n=81			OUTSIDE n=81		
MONTH	% LEAF	% STEM	% FLOWER	% LEAF	% STEM	% FLOWER
Jul 1991	77.5	19.3	3.3	88.5	8.6	2.9
Oct 1991	64.1	18.2	17.7	72.4	20.6	7.0
Dec 1991	48.3	46.8	4.8	66.1	32.6	1.4
Feb 1992	41.9	48.7	9.4	53.5	43.7	2.8
Apr 1992	81.2	16.6	2.2	93.1	5.0	1.9
Jun 1992	84.9	13.1	2.0	89.7	7.9	2.4
Aug 1992	91.7	7.3	1.0	90.7	6.7	2.6
Oct 1992	96.0	3.8	0.2	92.9	7.0	0.1
Dec 1992	92.4	7.6	0.1	93.2	6.7	0.1
KRUSKAL-WALLIS H'	20.948 P<0.0001			24.968 P<0.0001		

6.3.3. Species composition

The species composition and importance values for the five exclosures are presented in Tables 11a to 11e, while the corresponding species richness, Shannon-Wiener and Sorensen indices are presented in Tables 12a and 12b.

The more common grass species, among them *Themeda triandra*, *Hyparrhenia lintoni* and *Cymbopogon caesius* slightly declined in importance in the absence of grazing. Four of the species encountered inside the exclosure in 1992, but not in 1991, were forbs and one was a sedge (Table 11a). The same was true for the Baboon Cliffs exclosure where five out of eight species found inside in 1992 but not the previous year were forbs and three were grasses (Table 11b).

Over the two years of sampling, species composition in the exclosures showed only marginal changes between inside and outside. All diversity indices differed significantly between inside and outside, except in Baharini in 1991 ($t_{(2)6}=1.35$, $p>0.2$) and Baboon Cliffs in 1992 ($t_{(2)22}=1.47$, $p>0.1$) (Tables 12a and 12b).

6.4. Discussion

The plant herbivore interphase is characterized by dynamic processes, whereby plants suffer tissue damage from herbivory and in turn, respond in evolutionary time by developing anti herbivore features. Many observations in the fields of agronomy, forestry and range management emphasize various direct plant responses to herbivory, including compensatory growth and assimilate reallocation (Owen-Smith 1982).

Plant responses to herbivory are, however, controlled by an interplay of many complex factors, for example genetics, growth stage, the actual tissues eaten, level of herbivory and the modifying effects of the environment (McNaughton 1979). The removal of plant parts by grazing and browsing ungulates is both selective and specific to animal size. These characteristics have long been recognized as major contributors to the ecological segregation of coexisting herbivore species (Lamprey 1963, Bell 1970). They were the guiding light in the recognition of the grazing succession described for East African fauna by various authors (Vessey-Fitzgerald 1960, Bell 1970, McNaughton 1979).

Table 11a. Species composition and Importance Values for the Baharini exclosure.

INSIDE	1991	1992
SPECIES	I. V.	I. V.
Themeda triandra[1]	0.3499	0.2889
Hyparrhenia lintoni[1]	0.2311	0.1570
Chloris gayana[1]	0.1490	0.3697
Eragrostis superba[1]	0.1274	0.1264
Aristida adoensis[1]	0.0410	0.0126
Fimbriastis humilis[2]	0.0367	0.0008
Hypoestis verticillaris[3]	0.0259	
Saturea biflora[3]	0.0216	
Digitaria abbysinica[1]	0.0130	
Cynodon nlemfluensis[1]	0.0022	
Cyperus obtusiflorus[2]	0.0022	
Brachiaria semiundulata[1]		0.0016
Hirpicium diffusum[3]		0.0008
Senescio spp[3]		0.0016
Senescio discifolius[3]		0.0008
Bulbostylis boeckeleriana[2]		0.0400

OUTSIDE	1991	1992
SPECIES	I. V.	I. V.
Themeda triandra[1]	0.5625	0.3044
Chloris gayana[1]	0.1281	0.2408
Cynodon nlemfluensis[1]	0.0875	
Aristida adoensis[1]	0.0531	0.0809
Saturea biflora[3]	0.0406	0.0829
Fimbriastis humilis[2]	0.0219	0.0154
Hapachne shimperi[1]	0.0188	0.0039
Hypoestis verticillaris[3]	0.0188	0.0058
Eragrostis superba[1]	0.0125	0.0539
Helichrysum glumaceum[3]	0.0125	
Brachiaria semiundulata[1]	0.0094	0.0597
Hyparrhenia lintoni[1]	0.0094	0.0424
Cymbopogon caesius[1]	0.0063	
Digitaria abbysinica[1]	0.0063	
Fuerstia africana[3]	0.0063	
Commelina africana[3]	0.0031	
Lippia javanica[4]	0.0031	
Chloris virgata[1]		0.0231
Senescio spp[3]		0.0077
Polygala petitiana[3]		0.0193
Digitaria ternata[1]		0.0328
Aristida keniensis[1]		0.0058
Commelina benghalensis[3]		0.0116
Bulbostylis boeckeleriana[2]		0.0096

[1]⇒ grasses; [2]⇒ sedges and rushes; [3]⇒ forbs; [4]⇒ semi shrubs.

Table 11b. Species composition and Importance Values for the Nderit exclosure.

INSIDE	1991	1992
SPECIES	I. V.	I. V
Hypoestis verticillaris[3]	0.2849	0.1293
Cynodon dactylon[1]	0.1844	
Archyranthes aspera[3]	0.1173	0.1875
Sida ovata[3]	0.0838	0.0156
Commelina benghalensis[3]	0.0726	0.0355
Justicia striata[3]	0.0670	0.0014
Plectranthus cylindraceus[3]	0.0335	0.0185
Digitaria abbysinica[1]	0.0279	0.0455
Aerva lanata[3]	0.0223	0.0440
Cyperus stuhlmanii[2]	0.0223	0.1676
Setaria verticillata[1]	0.0223	0.0099
Tagetes minuta[3]	0.0223	0.0384
Erlangea cordifolia[3]	0.0168	
Abutilon fruticosa[4]	0.0112	
Chenopodium opulifolium[3]	0.0112	
Cynodon plectostachyus[1]		0.2457
Asystacia schimperi[3]		0.0057
Crotalaria brevidens[3]		0.0028
Chenopodium album[3]		0.0043
Digitaria scaralum[1]		0.0384
Bidens pilosa[3]		0.0099

OUTSIDE	1991	1992
SPECIES	I. V.	I. V.
Cynodon dactylon[1]	0.3450	0.0330
Archyranthes aspera[3]	0.2100	0.3429
Justicia striata[3]	0.1100	0.0022
Digitaria abbysinica[1]	0.0950	0.0088
Cyperus stuhlmanii[2]	0.0650	0.0527
Setaria verticillata[1]	0.0650	0.0374
Tagetes minuta[3]	0.0350	0.0330
Commelina benghalensis[3]	0.0300	0.0352
Hypoestis verticillaris[3]	0.0150	0.1165
Leucas masaiensis[3]	0.0100	
Celosia anthelmintica[3]	0.0050	
Chloris virgata[1]	0.0050	
Coccinia trilobata[3]	0.0050	
Erucastrum arabicum[3]	0.0050	0.0088
Cynodon plectostachyus[1]		0.2418
Eragrostis tenuifolia[1]		0.0176
Asystacia schimperi[3]		0.0066
Bidens pilosa[3]		0.0022
Digitaria scaralum[1]		0.0549
Sida ovata[3]		0.0066

[1]⇒ grasses; [2]⇒ sedges and rushes; [3]⇒ forbs; [4]⇒ semi shrubs.

Table 11c. Species composition and Importance Values for the Baboon Cliffs exclosure.

INSIDE	1991	1992
SPECIES	I. V	I. V
Digitaria abbysinica^1	0.3384	0.4265
Chloris gayana^1	0.2023	0.1298
Cymbopogon caesius^1	0.1891	0.0611
Themeda triandra^1	0.0662	0.2461
Andropogon schirensis^1	0.0473	
Tagetes minuta^3	0.0359	0.0373
Commelina benghalensis^3	0.0265	0.0089
Commelina africana^3	0.0189	0.0447
Priva curtisiae^3	0.0189	
Erlangea cordifolia^3	0.0133	
Cyperus stuhlmanii^2	0.0095	0.0007
Aristida adoensis^1	0.0076	
Solanum incanum^4	0.0076	0.0037
Chlorophytum bakeri^3	0.0057	0.0052
Sida ovata^3	0.0057	
Sporobolus fimbriastis^1	0.0038	
Fuerstia africana^3	0.0019	
Oldenlandia scopulorum^3	0.0019	
Cynodon dactylon^1		0.0030
Hyparrhenia lintoni^1		0.0164
Hypoestis verticillaris^3		0.0022
Bidens pilosa^3		0.0015
Setaria verticillata^1		0.0119
Hibiscus aponeurus		0.0007

OUTSIDE	1991	1992
SPECIES	I. V.	I. V.
Chloris gayana^1	0.5501	0.2681
Digitaria abbysinica^1	0.2116	0.4139
Themeda triandra^1	0.1470	0.1750
Cynodon nlemfluensis^1	0.0245	0.0181
Tagetes minuta^3	0.0134	0.0125
Commelina africana^3	0.0089	0.0014
Solanum incanum^4	0.0089	0.0014
Cyperus stuhlmanii^2	0.0067	0.0111
Hibiscus aponeurus^4	0.0067	0.0069
Sporobolus fimbriastis^1	0.0067	
Chlorophytum bakeri^3	0.0045	
Cymbopogon caesius^1	0.0045	0.0444
Archyranthes aspera^3	0.0022	
Commelina benghalensis^3	0.0022	
Pentanisia ouranogyne^3	0.0022	
Sporobolus pyramidalis^1		0.0194
Monsonia angustifolia^3		0.0167
Commelina benghalensis^3		0.0069
Cynodon dactylon^1		0.0042

^{1}⇒ grasses; ^{2}⇒ sedges and rushes; ^{3}⇒ forbs; ^{4}⇒ semi shrubs

Table 11d. Species composition and Importance Values for the New Naishi exclosure.

INSIDE	1991	1992
SPECIES	I. V.	I. V.
Cynodon dactylon^{1}	0.9869	0.9995
Archyranthes aspera^{3}	0.0085	0.0005
Cyperus stuhlmanii^{2}	0.0047	

OUTSIDE	1991	1992
SPECIES	I. V.	I. V.
Cynodon dactylon^{1}	0.9703	0.9677
Digitaria abbysinica^{1}	0.0203	0.0078
Dichrocephala integrifolia^{3}	0.0047	
Cyperus stuhlmanii^{2}	0.0031	0.0073
Solanum incanum^{4}	0.0016	0.0034
Sida ovata^{3}		0.0061
Archyranthes aspera^{3}		0.0118
Commelina africana^{3}		0.0020

$^{1}\Rightarrow$ grasses; $^{2}\Rightarrow$ sedges and rushes; $^{3}\Rightarrow$ forbs; $^{4}\Rightarrow$ semi shrubs.

Table 11e. Species composition and Importance Values for the old Naishi exclosure.

INSIDE	1991	1992
SPECIES	I.V.	I. V.
Cynodon dactylon^{1}	0.8071	0.5820
Sporobolus fimbriastis^{1}	0.1186	
Cyperus stuhlmanii^{2}	0.0229	0.2205
Aristida keniensis^{1}	0.0171	
Digitaria abbysinica^{1}	0.0114	0.1649
Pentanisia ouranogyne^{3}	0.0100	
Senescio discifolius^{3}	0.0057	
Sida ovata^{3}	0.0043	
Chlorophytum.bakeri^{3}	0.0014	
Commelina africana^{3}	0.0014	0.0088
Asystacia schimperi^{3}		0.0018
Monsonia angustifolia^{3}		0.0132
Setaria pumila^{1}		0.0088

OUTSIDE	1991	1992
SPECIES	I. V.	I.V.
Cynodon dactylon^{1}	0.6390	0.5206
Digitaria abbysinica^{1}	0.0775	0.1562
Sporobolus fimbriastis^{1}	0.0749	
Cyperus stuhlmanii^{2}	0.0695	0.1429
Sida ovata^{3}	0.0561	
Pentanisia ouranogyne^{3}	0.0294	
Aristida keniensis^{1}	0.0267	0.0206
Chloris virgata^{1}	0.0080	
Chlorophytum bakeri^{3}	0.0080	0.0097
Commelina africana^{3}	0.0080	0.0218
Erlangea cordifolia^{3}	0.0027	0.0412
Setaria pumila^{1}		0.0412
Monsonia angustifolia^{3}		0.0254
Hapachne shimperi^{1}		0.0048
Aristida adoensis^{1}		0.0036
Brachiaria semiundulata^{1}		0.0061

$^{1}\Rightarrow$ grasses; $^{2}\Rightarrow$ sedges and rushes; $^{3}\Rightarrow$ forbs; $^{4}\Rightarrow$ semi shrubs.

Table 12a. Species richness and Shannon Wiener indices for the five exclosures in the two years of study (figures in parenthesis denote degrees of freedom).

YEAR	EXCLOSURE	SPECIES RICHNESS S	SHANNON WIENER INDEX H'	T-TEST FOR H'
1991	Baharini (inside)	11	1.77	1.35 (6)
	Baharini (outside)	17	1.65	p>0.2 NS
	Nderit (inside)	15	1.22	2.84 (62)
	Nderit (outside)	14	1.95	P<0.01
	Baboon Cliffs (inside)	18	1.97	8.41 (5)
	Baboon Cliffs (outside)	15	1.36	P<0.001
	New Naishi (inside)	3	0.08	2.40 (1034)
	New Naishi (outside)	5	0.16	P<0.02
	Old Naishi (inside)	10	0.75	7.59 (23)
	Old Naishi (outside)	11	1.36	P<0.001
1992	Baharini (inside)	11	1.50	12.58 (43)
	Baharini (outside)	17	2.13	P<0.001
	Nderit (inside)	17	2.18	3.16 (54)
	Nderit (outside)	16	1.99	P<0.005
	Baboon Cliffs (inside)	16	1.67	1.47 (22)
	Baboon Cliffs (outside)	14	1.59	P>0.1 NS
	New Naishi (inside)	2	0.004	9.11 (2120)
	New Naishi (outside)	6	0.19	P<0.001
	Old Naishi (inside)	7	1.10	10.07 (28)
	Old Naishi (outside)	13	1.58	P<0.001

Table 12b. Sorensen indices comparing species composition on the exclosures in 1991 and 1992.

	SORENSEN'S INDEX S'		
EXCLOSURE	BETWEEN YEARS	BETWEEN PLOTS	
		1991	1992
Baharini (inside)	0.55	0.0	0.0
Baharini (outside)	0.57		
Nderit (inside)	0.56	0.62	0.79
Nderit (outside)	0.52		
Baboon Cliffs (inside)	0.56	0.67	0.73
Baboon Cliffs (outside)	0.76		
New Naishi (inside)	0.40	0.5	0.5
New Naishi (outside)	0.73		
Old Naishi (inside)	0.44	0.86	0.6
Old Naishi (outside)	0.58		

Most studies of biomass offtake by herbivores are based on comparisons between peak biomass inside fences and the residual outside. Peak biomass in areas protected from large herbivores is an unreliable indicator of net production as it takes no account of plant mortality (Deshmukh and Baig 1983), but provides the only comparable data for most studies (Deshmukh 1984).

McNaughton (1985) suggested that a more realistic approach would be to consider the ratio of amount consumed to actual net productivity. In terrestrial ecosystems, most of the net primary production remains unutilized at the end of the growing season and subsequently enters the detritus pathway. The experimental exclusion of herbivory prevents the possibility of grazing stimulation (McNaughton 1979). Fencing itself has effects on vegetation that are both unpredictable and difficult to control.

The variations in standing biomass over time as observed in this study are indicative of the complex forces that influence patterns of primary production. Grazing by vertebrate herbivores has a dominant influence on the rate of biomass accumulation. A conspicuous feature of the fluctuations was the nearly synchronous increases and decreases both inside and outside all the exclosures. When the herb layer dried up, some plant parts either shrunk and crumbled or fell off altogether, leading to an overall decline in the standing biomass. A considerable amount of litter accumulated inside the exclosures, little or none at all being found outside.

The first long rains were followed by at least a two fold increase in biomass inside the exclosures. Similar increases, albeit of a lower magnitude, were experienced outside the exclosures over the same period. That is as far as the simple concordance went, however, and a closer analysis of rates reveals a more complicated situation. The fluctuations in amount of standing biomass inside exclosures reflected a slight spatial and temporal imbalance in rainfall distribution within the park.

The exclosures were set up at a time when virtually the whole park was dry to the extent that even the identification of species was impossible. Good rains were later received with a peak in April 1991, but these were distributed unevenly, being more in the north than the south. Herbage biomass inside the exclosures in these areas responded accordingly, initially increasing at a faster rate in the Baharini and Baboon Cliffs exclosures than the Nderit and Old Naishi, located at the northern and southern parts of the park respectively.

A second rainfall peak was received between August and September 1991, whereby Lanet station in the north received less precipitation than the other two stations to the south. The result was reduced net primary productivity inside the exclosures to the north when compared to the case after the previous rainfall peak. One exception was the new Naishi exclosure, located as it was in an area with unique soil and hydrological properties that enabled the grass there to exhibit a higher net primary productivity than elsewhere after the first rainfall peak, and a drop in biomass after the second.

A similar but less pronounced imbalance occurred in 1992, when the south once again received higher average precipitation in April and May. The rains also arrived earlier in the south than in the north. This was followed by prolonged off season rainfall over the whole park, having two peaks in August and October in the north, and August and December in the south. Increase in biomass inside exclosures consequently began earlier in the south than in the north, all reaching new peaks between June and August. It thereafter decreased until the end of the study in all exclosures, except at Nderit where an increase occurred after the August rainfall peak. The old Naishi exclosure, having reached an all time high in October 1992, experienced only a marginal decline towards the end of the study.

A look at the ratios of green to dry plant matter, and the contribution of leaf and stem to standing herb biomass is similarly telling. In the absence of grazing, a large amount of dead but standing plant material rapidly accumulated within the exclosed plots. The same happened outside in only two of the exclosures, one of which was located in an area of low grazer preference. In a similar study, Onyeanusi (1989), found that exclosures accumulated more green biomass than free grazing plots in the Masai Mara, during the wet season, while the situation was reversed during the dry season.

The leaf to stem ratio was subject to cyclic fluctuations in response to climatic changes, bringing about the observed trends inside exclosures. An additional factor was the selective removal of leaves and young shoots by grazers outside the exclosures. There is presumptuous evidence from earlier studies that large herbivores actively select the seasonally more variable leaf at the expense of the less nutritious stem (Sinclair 1974, McNaughton 1985).

Species composition at the exclosures did not change measurably during the time covered by the study, as indicated by the various diversity and similarity indices. For example, although the Shannon-Wiener indices inside and outside the Baharini exclosure differed in 1991 but not in 1992, species richness remained the same over the two years, probably because of compensatory changes in forb species composition. All the three forbs that invaded the Baharini exclosure within the first year had low importance values, indicating that they were still in the early stages of encroachment.

The findings of this study indicate that with changing grazing regimes expected as the park's large herbivore community gets increasingly isolated, habitats will certainly change in a determinate way. Like heavy grazing which exposes habitats to the danger of bush encroachment, low grazing pressure is likely to result in competition between grasses and forbs. Forb species are preferentially removed from the pasture by herbivores because of their comparatively higher nutritive value (Owen-Smith 1982). They also differ in palatability and some have potentially woody growth habits which if not checked by adequate levels of grazing can lead to reduced grass cover.

CHAPTER 7. THE WATERBUCK PROBLEM

7.1. Introduction

The defassa waterbuck has remained dominant over other large mammal species since the earliest days of the park's existence. It has been the focus of many past investigations, largely because the area contains the highest density of the species recorded anywhere. The population displays a highly dynamic pattern of frequent and widespread loss of body condition. It sometimes culminates in the death of large numbers of individuals, as happened in 1990. Many previous studies attempted to isolate disease agents suspected to be responsible for the periodic loss of body condition and inordinate mortality. Other factors investigated included mineral levels in the soils and plant tissues (Chamberlain 1959, Maskall 1987).

That soils in the region are deficient in certain minerals has been recognized for a long time, and research began into the problems experienced with livestock when the area was under large scale ranching (Clausen 1970, Robin Long *pers. comm.*). In addition, fears were expressed that wildlife species could be suffering from contagious diseases dangerous to livestock. A disease survey was carried out in the impala population in 1968, during which serum samples were tested for antibodies against a suite of animal diseases, including blue tongue, brucellosis, bovine pleuropneumonia, malignant catarrhal and rinderpest.

Analyses were also done on parasite loads and in both cases, results were mostly negative (Clausen 1970). Postmortem results indicated that the impalas were suffering primarily from cobalt deficiency and secondarily from hypocupremia, conditions widely reported in cattle on neighbouring ranches.

At the time, other wildlife species appeared to be free from the conditions, but the waterbuck later showed an increasing tendency towards intermittent poor health and mass mortality. This provided the inspiration for more recent studies, which however did not consider the alternative and purely ecological explanation for the observed emaciation and mortality.

In this study, I examined individuals in different parts of the park over the first year of field work, and later conducted an experiment to investigate the relationship between population density and body condition in the second year. The experiment was timed to begin at the end of a dry season, when most individuals were weak and emaciated. Internal body structures, including kidney, heart, omentum and bone marrow were examined in individuals at varying degrees of emaciation and the rate of recovery monitored in selected portions of the population. Such assessment of physical condition is desirable as it facilitates the evaluation of current or past management practices (Smith 1970).

7.2. Methods

7.2.1. Body condition in the whole population

Waterbucks in different parts of the park were observed over a period of one year and the age and sex recorded for each individual encountered (see section 4.3.3 for age and sex criteria). A body condition score was assigned to each individual, depending on visually discernible body characteristics, such as poor body coat, prominence of ribs and the hip bone. Healthy looking animals were given a score of 1 while the weakest ones scored 5, with those in intermediate stages obtaining the scores in between. These observations were made on animals resident at the northern, southern and south eastern parts of the park, subsequently referred to as zones 1, 2 and 3 in the text, respectively.

7.2.2. Body condition in experimental groups

Two experimental plots, comprising fairly stable waterbuck groups, were chosen for the experiment. All individuals in both plots were counted, aged, sexed and assigned body condition scores at the beginning of the experiment. Similar observations were made on both plots every month for the next five months and again in October 1992 and January 1993. The number of waterbucks on one plot designated as the experimental plot, was reduced by about 20 % while those on the other were left intact as a control.

7.2.3. Blood characteristics

During the population reduction exercise, animals were immobilized with a single shot on the brain. About 20 ml of fresh blood was collected from an animal immediately it fell. This was done by inserting an 18 mm needle into a major blood vessel and sucking into a vacutainer pretreated with Ethylenediaminetetracetic Acid (EDTA) to forestall coagulation. The samples were stored at 4° C in a cool box and transported to the laboratory for analysis.

Haemoglobin content (HB) was measured with a haemoglobinometer while White Blood Cell counts (WBC) and Packed Cell Volume (PCV) were done with an electronic coulter counter. Red Blood Cell counts (RBC) were done on a coulter particle counter.

7.2.4. Data analysis

The data were analyzed with the aim of quantifying spatial and temporal patterns of body condition loss in the waterbuck population, and its possible causes. The number of individuals attaining the same score during an observation period was expressed as a fraction of the total number observed in any given zone or plot. The resulting proportions were subjected to Kruskal-Wallis non parametric one-way ANOVA to test for group differences among body scores and months of sampling. The haemoglobin content, red blood cell and white blood cell counts were compared among animals falling in three health categories, using one way ANOVA, while the same test was used to compare packed cell volume (PCV) on arcsine transformed data.

7.3. Results

7.3.1 Body condition in whole population

The relative frequency of animals in varying states of body condition differed significantly over months (Kruskal-wallis test, $H = 72.115$, d.f. = 4, $p<0.001$). The differences were also significant when the three zones were considered separately ($H = 24.922$, d.f. = 4, $p<0.001$; $H = 24.347$, d.f. = 4, $p<0.001$; and $H = 24.666$. d.f. = 4, $p<0.001$ for zones 1, 2 and 3, respectively). Apparently healthy animals were most frequent during the long rains, with those attaining a score of 1 or 2 accounting for between 61% and 93% of individuals resident in the three zones between May and July 1991. The contribution of animals scoring 4 or 5 ranged between 9% and 24% of the population in the three zones in January 1992.

The frequencies of individuals of five age-sex classes in the three zones and in varying states of body condition, over the months of the study, are presented in Tables 13a to 13e. When each was expressed as a proportion of the total number of individuals examined for the month, the resulting relative frequencies differed significantly among the condition scores for all zones and age-sex classes, except sub adult males in zones 2 and 3, and juveniles in zone 2.

Table 13a. Frequency of adult male waterbucks in varying states of body condition (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	ZONE 1				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	3	81	24	7	0
May 1991	6	48	22	3	0
Jul 1991	11	42	22	9	0
Nov 1991	1	19	21	5	0
Dec 1991	1	38	27	8	0
Jan 1992	1	20	36	22	0

[H_{scores} = 25.524, D.F. = 4, P<0.001]
[H_{months} = 0.092, D.F. = 5, P>0.9 NS]

	ZONE 2				
	SCORE				
	1	2	3	4	5
Mar 1991	6	23	3	1	0
May 1991	15	27	7	0	0
Jul 1991	55	55	6	2	0
Nov 1991	5	56	23	8	0
Dec 1991	1	26	29	9	0
Jan 1992	1	18	21	5	2
May 1992	0	7	14	1	0

[$H = _{\text{scores}}$ 23.294, D.F = 4, P<0.001]
[H_{months} = 0.310, D.F. = 6, P>0.9 NS]

	ZONE 3				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	10	28	9	1	0
May 1991	5	22	20	2	0
Jul 1991	31	36	11	0	0
Nov 1991	2	27	43	21	2
Dec 1991	1	21	28	14	2
Jan 1992	0	12	42	15	0
May 1992	9	14	44	11	2

[H_{scores} = 20.903, D.F. = 4, P<0.001]
[H_{months} = 0.47, D.F. = 6, P>0.9 NS]

Table 13b. Frequency of adult female waterbucks in varying states of body condition (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	ZONE 1				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	10	54	23	7	0
May 1991	27	92	22	0	0
Jul 1991	19	59	25	2	0
Nov 1991	14	39	51	9	0
Dec 1991	1	113	57	10	0
Jan 1992	0	45	110	30	1

[H_{scores} = 23.68, D.F. = 4,P<0.001]
[H_{months} = 0.098, D.F. = 5, P>0.9 NS]

	ZONE 2				
	SCORE				
	1	2	3	4	5
Mar 1991	3	16	3	0	0
May 1991	6	14	6	0	0
Jul 1991	105	35	10	1	0
Nov 1991	6	73	14	2	0
Dec 1991	1	30	28	3	0
Jan 1992	0	2	5	0	0
May 1992	4	27	24	4	0

[H_{scores} = 22.269, D.F. = 4, P<0.001]
[H_{months} = 0.42, D.F. = 5, P>0.9 NS]

	ZONE 3				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	17	75	40	10	0
May 1991	2	20	15	2	0
Jul 1991	33	68	13	2	0
Nov 1991	11	78	101	28	3
Dec 1991	3	59	62	26	2
Jan 1992	0	52	141	54	7
May 1992	0	13	46	8	2

[H_{scores} = 29.435, D.F. = 4, P<0.001]
[H_{months} = 0.06, D.F. = 6, P>0.9 NS]

Table 13c. Frequency of sub adult male waterbucks in varying states of body condition. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	ZONE 1				
	SCORE				
MONTH	1	2	3	4	5
May 1991	6	12	2	0	0
Jul 1991	5	9	14	0	0
Nov 1991	0	4	3	1	0
Dec 1991	0	2	2	1	0
Jan 1992	0	2	11	1	0

[H_{scores} = 16.519, D.F = 4, P<0.01]
[H_{months} = 0.113, D.F. = 5, P>0.9 NS]

	ZONE 2				
	SCORE				
	1	2	3	4	5
May 1991	12	13	6	0	0
Jul 1991	11	3	0	0	0
Nov 1991	2	9	4	0	0
Dec 1991	0	0	0	0	0
Jan 1992	0	0	0	0	0
May 1992	0	0	0	0	0

[H_{scores} = 7.72, D.F = 4, P>0.1 NS]
[H_{months} = 10.631, D.F. = 6, P>0.05 NS]

	ZONE 3				
	SCORE				
MONTH	1	2	3	4	5
Jul 1991	5	8	3	0	0
Nov 1991	0	3	5	3	0
Dec 1991	2	2	5	0	0
Jan 1992	0	1	6	1	1
May 1992	0	0	0	1	0

[H_{scores} = 6.484, D.F. = 4, P>0.1 NS]
[H_{months} = 1.302, D.F. = 6, P>0.8 NS]

Table 13d. Frequency of sub adult female waterbucks in varying states of body condition. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	ZONE 1				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	21	46	15	3	0
May 1991	26	45	16	0	0
Jul 1991	3	13	9	1	0
Nov 1991	5	13	5	1	0
Dec 1991	0	7	6	0	0
Jan 1992	0	2	4	0	0

[H_{scores} = 22.497, D.F = 4, P<0.001]
[H_{months} = 0.661, D.F. = 5, P>0.9 NS]

	ZONE 2				
	SCORE				
	1	2	3	4	5
Mar 1991	0	14	0	0	0
May 1991	3	10	2	0	0
Jul 1991	8	8	0	0	0
Nov 1991	1	7	2	0	0
Dec 1991	0	2	0	0	0
Jan 1992	0	0	0	0	0
May 1992	0	0	0	0	0

[H_{scores} = 14.472, D.F = 4, P<0.01]
[H_{months} = 7.431, D.F. = 6, P>0.2 NS]

	ZONE 3				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	23	48	27	0	0
May 1991	2	7	4	1	0
Jul 1991	2	8	6	0	0
Nov 1991	2	16	18	5	0
Dec 1991	2	7	5	0	0
Jan 1992	0	4	2	2	1
May 1992	0	0	1	1	0

[H_{scores} = 19.112, D.F = 4, P<0.001]

[H_{months} = 0.127, D.F. = 6, P>0.9 NS]

Table 13e. Frequency of juvenile waterbucks in varying states of body condition. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	ZONE 1				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	12	3	3	1	0
May 1991	7	10	2	0	0
Jul 1991	2	1	0	0	0
Nov 1991	3	1	0	0	0
Dec 1991	4	0	2	0	0
Jan 1992	0	0	0	0	0

[H_{scores} = 15.105, D.F. = 4, P<0.01]
[H_{months} = 4.669, D.F. = 5, P>0.4 NS]

	ZONE 2				
	SCORE				
	1	2	3	4	5
Mar 1991	6	12	1	0	0
May 1991	4	1	0	0	0
Jul 1991	13	0	0	1	0
Nov 1991	0	1	1	0	0
Dec 1991	0	1	0	0	0
Jan 1992	0	0	0	0	0
May 1992	0	0	0	0	0

[H_{scores} = 7.231, D.F = 4, P> 0.05 NS]
[H_{months} = 6.256, D.F. = 6, P>0.3 NS]

	ZONE 3				
	SCORE				
MONTH	1	2	3	4	5
Mar 1991	20	25	7	0	0
May 1991	0	1	0	0	0
Jul 1991	1	0	0	0	0
Nov 1991	1	1	2	0	0
Dec 1991	1	0	0	0	0
Jan 1992	0	6	0	0	0
May 1992	0	0	0	0	0

[H_{scores} = 7.817, D.F = 4, P>0.05 NS]
[H_{months} = 4.898, D.F. = 6, P>0.5 NS]

The proportional composition of individuals with varying degrees of emaciation differed among months for the whole park (H = 14.694, d.f. = 6, p<0.05). They were also different for zone 2 (H = 16.076, d.f = 6, p<0.05), but not for zones 1 and 3 (H = 1.849, d.f. = 5 p>0.8; and H = 2.472, d.f. = 6, p>0.8 for the two zones, respectively). Contribution of animals in apparently good body condition differed significantly among months (H = 18.905, d.f. = 6, p<0.01). When separate age-sex classes were considered, the relative proportion of healthy individuals differed among months for sub adult males and females, but not any other class.

7.3.2. Body condition on control and experimental plots

Tables 14a to 14e show the frequencies of individuals of five age-sex classes and body condition scores, at different times on both the control and experimental plots. Overall, the population composition on both plots differed significantly among the various degrees of emaciation (H = 54.402, d.f. = 4 p<0.001), as was the case when either the control or experimental plots were analysed separately (H = 25.6362, d.f. = 4 p<0.001; H = 29.287, d.f. = 4 p = <0.001, for the control and experimental plots, respectively). These did not differ significantly among months overall, and on either the control or experimental plot.

When adults and sub adults were analysed together irrespective of sex, relative frequencies were significantly different among body scores overall, and for both the control and experimental plots.

The frequencies were different for both males and females overall and on the control plot. They were also different for females on the experimental plot, but not for males (H = 9.153 df = 4 p>0.05).

When the different age-sex categories were analysed separately, relative abundance of adult males differed significantly among body condition scores for both the control and experimental plots (see tables for statistics). The same were different for sub adult females, but not for either the adult females or sub adult males on the experimental plot. Only juveniles differed significantly among body scores on the control plot.

The occurrences of adults in different state of health differed among months overall (H = 26.566 df = 4 p<0.001) and on the control plot (H = 15.638 df = 4 p = 0.05), but not on the experimental plot. These were not significant, overall or on either plot, among months for sub adults. They were also not significant among males or females. When grouped

Table 14a. Frequency of adult male waterbucks in varying stages of emaciation over months. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	CONTROL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	17	32	0	0	0
May 1992	10	5	0	0	0
Jun 1992	27	65	1	0	0
Jul 1992	35	58	28	5	0
Aug 1992	14	24	0	0	8
Oct 1992	38	60	1	1	19
Jan 1993	25	86	0	7	21

[$H_{\text{scores}} = 12.986$, D.F = 4, $P<0.05$]
[$H_{\text{months}} = 11.665$, D.F. = 6, $P>0.05$ NS]

	EXPERIMENTAL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	1	2	0	0	1
May 1992	3	31	0	0	1
Jun 1992	38	69	3	6	14
Jul 1992	25	40	16	1	0
Aug 1992	27	66	0	0	29
Oct 1992	46	106	0	2	43
Jan 1993	23	58	0	4	36

[$H_{\text{scores}} = 10.503$, D.F = 4, $P<0.05$]
[$H_{\text{months}} = 11.454$, D.F. = 6, $P>0.05$]

Table 14b. Frequency of adult female waterbucks in varying stages of emaciation over months. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	CONTROL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	30	36	0	1	0
May 1992	26	32	0	1	0
Jun 1992	74	141	0	6	0
Jul 1992	50	69	26	5	0
Aug 1992	32	54	0	0	0
Oct 1992	47	96	2	0	4
Jan 1993	27	91	1	1	2

[H_{scores} = 4.614, D.F = 4, P>0.3 NS]
[H_{months} = 7.566, D.F. = 6, P>0.2 NS]

	EXPERIMENTAL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	7	34	1	4	4
May 1992	17	44	0	3	2
Jun 1992	44	71	6	6	0
Jul 1992	99	93	38	1	0
Aug 1992	30	57	0	1	0
Oct 1992	28	67	0	0	2
Jan 1993	25	64	0	4	6

[H_{scores} = 4.441, D.F = 4, P>0.3 NS]
[H_{months} = 14.241, D.F. = 6, P<0.05]

Table 14c. Frequency of sub adult male waterbucks in varying stages of emaciation over months. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	CONTROL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	60	61	0	2	1
May 1992	83	141	0	3	0
Jun 1992	48	72	0	3	0
Jul 1992	0	0	0	0	0
Aug 1992	51	112	1	3	0
Oct 1992	31	120	0	2	0
Jan 1993	38	89	0	1	1

[H_{scores} = 4.778, D.F = 4, P>0.3 NS]
[H_{months} = 5.81, D.F. = 6, P>0.4 NS]

	EXPERIMENTAL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	35	111	3	6	3
May 1992	44	59	2	2	2
Jun 1992	15	14	1	0	0
Jul 1992	3	0	0	0	0
Aug 1992	35	68	0	1	0
Oct 1992	11	42	0	1	0
Jan 1993	28	90	0	3	2

[H_{scores} = 3.796, D.F = 4, P>0.4 NS]
[H_{months} = 10.988, D.F. = 6, P>0.05 NS]

Table 14d. Frequency of sub adult female waterbucks in varying stages of emaciation over months. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	CONTROL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	25	19	0	1	0
May 1992	14	29	0	2	0
Jun 1992	9	13	0	0	0
Jul 1992	1	6	1	2	0
Aug 1992	2	5	0	0	0
Oct 1992	3	4	0	0	0
Jan 1993	4	2	0	0	0

[H_{scores} = 11.811, D.F = 4, $P<0.05$]
[H_{months} = 2.852, D.F. = 6, $P>0.8$ NS]

	EXPERIMENTAL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	14	60	0	3	1
May 1992	15	16	1	0	1
Jun 1992	1	0	0	0	0
Jul 1992	3	0	0	0	0
Aug 1992	3	2	0	0	0
Oct 1992	0	1	0	0	0
Jan 1993	6	13	0	0	0

[H_{scores} = 11.926, D.F = 4, $P<0.05$]
[H_{months} = 4.597, D.F. = 6, $P>0.5$ NS]

Table 14e. Frequency of adult juvenile waterbucks in varying stages of emaciation over months. (figures enclosed in square brackets represent the resuts of Kruskal-Wallis test for differences in relative proportion among scores and months, accordingly).

	CONTROL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	7	15	0	0	0
May 1992	0	9	0	0	0
Jun 1992	0	0	0	0	0
Jul 1992	14	1	0	0	0
Aug 1992	0	0	0	0	0
Oct 1992	0	0	0	0	0
Jan 1993	0	0	0	0	0

[H_{scores} = 10.59, D.F = 4, P<0.05]
[H_{months} = 7.024, D.F. = 6, P>0.3 NS]

	EXPERIMENTAL PLOT				
	SCORE				
MONTH	1	2	3	4	5
Apr 1992	1	8	0	0	0
May 1992	2	5	0	0	0
Jun 1992	0	0	0	0	0
Jul 1992	12	0	0	0	0
Aug 1992	0	0	0	0	0
Oct 1992	0	0	0	0	0
Jan 1993	0	0	0	0	0

[H_{scores} = 21.136, D.F = 4, P<0.001]
[H_{months} = 5.677, D.F. = 6, P>0.4 NS]

according to age sex classes, relative frequencies were different among months for adult females on the experimental plot ($H = 14.241$, $df = 6$ $p<0.05$) but not for any other class.

7.3.3. Blood characteristics

Table 15 displays the blood characteristics of 18 waterbucks sampled during the culling exercise in April 1992. Red blood cell counts, expressed as number per microlitre of whole blood, differed significantly among individuals grouped into three health categories. Both haemoglobin content and PCV differed significantly among the three categories but not white blood cell counts. Animals in relatively good condition (score 1 or 2) had RBC counts and haemoglobin concentration significantly different from those in poor condition (score 4 or 5). ($t_{10(2)} = 2.967$, $p<0.05$; $t_{10(2)} = 4.217$, $p<0.001$; $t_{9(2)} = 2.88$, $p<0.05$ for HB, RBC and PCV, respectively).

7.4. Discussion

A clear temporal pattern emerged in the health of the waterbuck population, depicting a definite relationship between occurrence of animals in poor health with fluctuations in the quality and quantity of food resources. Healthy animals were most abundant during and immediately after rains, when herbage was available in adequate quantities. Rains also led to improvement in the nutritive value of grasses and an increased proportion of comparatively more nutritious dicot leaves.

Dicotyledonous plants are known to provide a richer and seasonally less variable source of protein (Owen-Smith 1982). The situation deteriorated with the advancement of dry seasons, so that by January 1992 less than 30% of the whole population could be described as healthy. There was also a spatial dimension to the problem, manifested in the tendency for unhealthy animals to be more frequent to the north and south east of the park than the southern part, designated in this study as zone 2. It would be instructive to observe, however, that the southern region offered the additional benefit of having year round fresh water supply.

The vegetation of the area is mainly wooded grassland, with a proportionately higher amount of dicotyledonous herb biomass in the undergrowth than the north, for example, which ensured a relatively more nutritious and seasonally more constant food resource. The findings of this study strongly implicate high population densities in the regular loss of body condition and eventual death of waterbucks in the park. Nearly 25% of animals found at the

Table 15. Blood characteristics of 18 waterbuck specimens taken from the experimental plot in April 1992 (F values below each collumn compare the three health categories).

SERIAL #	BODY CONDITION	PCV %	HB g / dl	RBC # / μ lt	WBC # / μlt
1	GOOD	38	13.3	9.12	4.2
2	GOOD	26	9.7	7.3	3.8
3	GOOD	37	11.7	9.5	5.2
4	GOOD	17	6.9	5.37	7.5
5	GOOD	41	14.8	9.9	4.7
6	FAIR	32	12	8.38	10.4
7	FAIR	15	5.7	7.74	3.9
8	FAIR	42	14.1	9.2	5.2
9	FAIR	35	10.8	7.05	5.7
10	FAIR	18	6.8	6.24	2.7
11	FAIR	16	5.8	4.84	4.7
12	POOR	27	10.8	6.58	8.4
13	POOR	6	2	1.99	4.1
14	POOR	-	5	3.43	2.1
15	POOR	10	3.8	3.46	4.1
16	POOR	11	4.4	2.83	3.1
17	POOR	26	9.8	5.8	4.9
18	POOR	11	4.1	3.39	6.4
MEAN ± SE	GOOD FAIR POOR	(31.4 %) (25.7 %) (14.3 %)	(11.3 ± 1.3) (9.2 ± 1.5) (5.7 ± 1.2)	(8.2 ± 0.8) (7.2 ± 0.6) (3.9 ± 0.6)	(5.1 ± 0.6) (5.4 ± 1.1) (4.7 ± 0.8)
one way ANOVA		$F_{2,14} = 4.146$ $P<0.05$	$F_{2,15} = 4.322$ $P<0.05$	$F_{2,15} = 11.153$ $P<0.01$	$F_{2,15} = 0.172$ $P>0.8$ NS

south eastern end of the park, mainly within a localized high density concentration at the Ndere swamps were in poor health at the height of a dry spell in January 1992. At higher densities, the animals exert more pressure on the available resources, thereby causing a change in the relative abundance of the various plant parts.

Being mainly a grazer, the waterbuck is likely to be adversely affected by seasonal variations in the quality and quantity of the herb layer. A situation arises where animals living at high population density have to utilize large quantities of poor quality food. They also spend more time feeding during times of scarcity, thereby incurring relatively higher energetic costs, as compared to those existing at lower densities.

The main factors influencing waterbuck density and distribution are water, topography and food (Spinage 1974, 1982). The relationship found in this study between population density and body condition could operate through a mechanism involving the availability, or otherwise, of good quality food. Although animals can obtain sufficient nutrition even with protein levels similar to those observed in the herb layer during the course of this study (Sinclair 1974), the situation becomes compounded by various other factors of the vegetation.

Higher levels of nutrition may be achieved by greater selectivity in feeding, with the animals taking proportionately more of the better quality plant parts (Owen-Smith 1982) and at lower protein levels, the activity of rumen micro-organisms is inhibited, leading to reduced protein and energy assimilation (Sinclair 1974). Thus even an apparent abundance of forage is still rendered inadequate by persistent and sometimes less noticeable nutritional deficiencies. Indeed, virtually all the animals removed from the experimental plot had their fore stomachs full of ingesta and that they could be in such poor health could only suggest an interplay of factors that has defied previous attempts to explain.

A similar study was carried out on a declining population of the common waterbuck in the Umfolozi Game Reserve in South Africa, whereby nutritional stress was isolated as a key factor in increasing adult mortality during part of the year (Melton and Melton 1982). In that study, there was an apparent asynchrony between adult and juvenile mortality, suggesting that age specific mortality was subject to different or a combination of factors (Melton 1987b). Tick infestation was suspected to be a possible main cause of juvenile and yearling mortality (Melton and Melton 1982, Melton 1987b). Elliot (1977) reported high juvenile mortality of waterbuck in Kenya which she believed was related to low rainfall and poor nutrition.

An examination of the patterns of emaciation depicted by the waterbuck population under study suggests that the phenomenon does not appear to afflict any age class substantially more than others. But a closer look at the distribution of unhealthy individuals reveals an important fact, that adults displayed a tendency to degenerate to a greater degree than younger animals, with this tendency being more pronounced in females than in males.

It is also worthwhile to note that when the park experienced mass die off in 1990, the greater proportion of deaths was among adults, with lactating females being worst affected (Personal observation). This may have brought about large scale, though undetected juvenile mortality, a commonly observed density dependent factor limiting many ungulate populations (Freeland and Choquenot 1990, Melton 1987b, Sinclair 1979).

In an area traditionally recognized for low mineral levels, lactation exerts additional constraints upon females, likely to accelerate their regression at high populations densities (Freeland and Choquenot 1990). In a study of wildebeests in the Serengeti plains, lactating females were observed to select pasture growing on calcium rich soils (Kreulen 1975). Other reports documented the negative effects of poor nutrition on gestating females and young (e.g. Verme and Ozoga 1980, Thorne *et al.* 1976).

The negative effects of low mineral intake are further confounded by other foraging related losses of minerals critical to growth and maintenance. At high grazing pressure, consumption of a species poor, high fibre diet stimulates the secretion of mineral rich saliva (Doyle *et al.* 1982). High fibre diets also act as gastrointestinal irritants, resulting in the epithelial secretion of mineral rich mucous.

Other peripheral factors have been suggested as possible causes of mortality in the park's waterbuck population, notably territorial behaviour among adult males. It is generally believed that male ungulates hold territories in the best habitats whose superiority in terms of resource availability attracts females, and that individuals living outside these areas are therefore relegated to inferior habitats (Leuthold 1977).

Generalizations about the effect of territoriality on population regulation are, however, complicated by the flexible nature of their boundaries and the confirmed existence of floaters (Shaw 1985). In an earlier study of a section of the same population reported in this study, Wirtz (1981) reported the presence of up to three satellite males who had access to more than one territory.

Over the entire period of my study, I never witnessed any cases of serious territorial defense although encounters culminating in the death of at least one of the contestants have been reported in the Aberdares National Park (Anonymous 1974). It still remains unclear, however, what role territorial behaviour plays in determining the condition of waterbucks in the park, existing as they do in a low density, and at times virtual absence, of large predators. This study therefore provides one of the very few where a population seems to be limited by nutritive factors in the absence of significant predation.

Indeed, the results from the full necropsies carried out on 40 individuals during a parallel study indicated some degree of exposure of the waterbuck to low quality diet (KWS Reports). Some of the animals examined were observed to have their coronary, renal and bone marrow fat deposits heavily gelatinized, and mesenteric fat almost absent.

Such a mobilization of body fats suggests that the population had undergone severe nutritive stress during the ensuing dry season. Animals in poor body condition also had varying degrees of tick infestation, especially around the ears and eyes. The relatively lower haemoglobin level, red blood cell counts and packed cell volume found among such animals were indicative of mild anaemia, which if sufficiently advanced could lead to physiological malfunctions and death.

CHAPTER 8. CONCLUDING REMARKS

8.1. General discussion

The wildlife resource in most of Africa is viewed as suffering from a perpetual threat posed by a combination of pastoral, agricultural and forestry activities (Anderson and Grove 1987). To the trio, one would add the socio-political considerations of conservation policy. On a balance of opinion, these factors seem to have weighed heavily in the minds of planners when the idea of fencing the park was mooted.

The conservation problems facing the Park differ diametrically from those experienced elsewhere in East Africa. For example, the exclusion of livestock, a thorny issue in virtually all other parks in the region, was effectively accomplished without much ado. The fence has managed to keep movements of wild animals outside the park in check, save for primates that periodically raid surrounding farms, but these are being effectively contained by several methods. Thus the park faces few risks of renewed wildlife human conflicts in the foreseeable future.

The most far reaching consequence of ecological isolation on the large mammal populations of the park is their confinement within a rigid perimeter. The area enclosed falls far short of encompassing a complete self sustaining ecosystem. The mammal community under study was the product of a series of compression stages, spanning over several decades, during which the part of the Rift Valley now occupied by the park became progressively altered to its present status as a virtual ecological island.

The examination of a series of aerial photographs indicates that since 1948, land use in the area has changed from natural vegetation to an alternation of managed pasture with large scale cultivation. Interpretation of more recent satellite images shows an accelerated rate of change since 1974. The land adjacent to the western boundary of the park, being better watered than other areas, had been placed under small scale agriculture by 1986. Inside the park itself, the removal of livestock and other human activities promoted a reversion to natural vegetation, with a strong successional force towards more woody cover.

As these processes took place, the size of the park increased in stages through the addition of land bought from surrounding farmers and ranchers. The availability of more space and lack of competition from livestock allowed wildlife to disperse. The result was an initial decline in the density of some species. The newly acquired land had previously been maintained under low pasture, which promoted the proliferation of many grazer species. In spite of increasing grazing pressure, it would appear that the removal of human factors led to an accumulation of tall grass in some places, while other areas experienced bush encroachment, resulting in the progressive loss of open grasslands.

The habitat changes described above affected large herbivore species in two distinct and rather antagonistic ways. The warthog, a species with a preference for short grass, was present in almost undetectable numbers between 1973 and 1978. During this period, the park underwent its first major expansion.

The subsequent phenomenal increase in the warthog population may be attributed directly to availability of low pasture after 1978, caused by localized heavy grazing by increasing populations of waterbuck and buffalo. Thomson's gazelles were present in large numbers in the years before the park's establishment but declined steadily after 1973. I suggest that with an increase in the amount of tall grass during this period, the species moved to more favourable habitat on neighbouring ranches. There are indications that the Thomson's gazelle population is increasing, and its distribution expanding, inside the park. At the beginning of this study, the species was found almost exclusively in the southern half, but gradually spread to the north.

In the absence of any significant browsing, woody cover increased steadily over the years. Most of the riverine and flood plain vegetation is characterized by dense stands of *Acacia xanthophloea*, sometimes having almost closed canopies or dense undergrowth. Tree regeneration is evident in extensive areas, particularly at the fringes of existing woodlands. The most notable browser is the Rothschild's giraffe, having been introduced in 1973 in an effort to save a small and threatened remnant population of the subspecies from human advancement in western Kenya. It occupied a niche previously held by the masai giraffe whose population had gone locally extinct, having been effectively driven out by man.

Owing to suitable habitat, the Rothschild's giraffe rapidly increased in numbers, posing the only veritable competition to the recently reestablished population of black rhinoceroses. Current conservation objectives are to encourage a build up of the rhinoceros population within the sanctuary to generate stock for reintroduction into other areas where the species has been drastically reduced. Put together, these two species will radically shift the balance between grazers and browsers, with attendant effects on habitats. Already, the giraffe is exerting noticeable pressure on the woodlands through browsing and debarking, itself a possible early warning of a possible eventual tree loss. Intense competition between giraffe and rhinoceros has been reported in Oljogi Ranch, Laikipia (Fred Waweru, *pers. comm.*).

Of the 17 large herbivore species regularly encountered in the park during this study, the waterbuck, impala and the warthog maintained the highest densities over the period for which data are available. All three species approached or exceeded 20 individuals km^{-2} at different times. Because of their dominance over other large herbivores, they assumed an important role in determining the course of events in ecological terms, one that is becoming increasingly critical as habitats change.

8.2. Recommendations for management

In light of the findings reported in this study, three main issues need to be given attention with regard to the management of the park in the short term. Firstly, an unrelenting increase in large herbivore populations, or even their continued existence at high density alone, has definite implications to the future and integrity of habitats. Heavy grazing in a situation of increasing woody cover can only promote localized destruction of open areas.

The availability of good quality herbage displays both spatial and temporal patterns of abundance and scarcity, leading to clear patterns of habitat occupancy by herbivores. The shoreline grasslands are utilized by the waterbuck and warthog with strikingly higher frequency than other open habitats. Consequently, the herb layer in that habitat type never attained any meaningful quantities in terms of height and standing crop. This happened alongside the large scale accumulation of low quality grass in localized places throughout the park.

Management efforts should be made towards encouraging greater and more equitable utilization of the entire habitat spectrum. A prescribed burn management programme should be instituted, emphasizing the removal of each season's production, and thereby allowing for fresh growth.

The second consideration relates to the new role that the park now plays as a safe haven for both the black and white rhinoceros. The success of this venture depends on a sustained ability of the sanctuary to accommodate increasing populations of both species. There is need to encourage any habitat change that favours the species, which would mean allowing for controlled tree regeneration. That calls for the maintenance of a rather delicate balance between bush encroachment and the opening up of habitats, emphasizing known rhinoceros food plants. In this case, attention needs to be given to the question of what number of grazers and browsers that would be considered desirable for the park. I suggest that those woody habitats of little importance to the black rhinoceros be considered for opening up. This would enable the park to continue accommodating its remarkably large grazer community, alongside an expanding rhinoceros population.

The third and increasingly crucial consideration revolves around the health status of the park's herbivores. Whenever environmental stresses build up, the waterbuck population responds by showing a rapid loss of body condition. Large numbers of the species display detectable signs of ill health, including muscular degeneration and a dull body coat with easily removable hair. This is followed in a nearly predictable way by emaciation of the impala population, with some individuals developing an arched shape in the pelvic region. Individuals in this state of health walk with extreme difficulty. The warthog and buffalo eventually follow in this sequence of emaciation as the dry season advances. Due to their relatively high densities, these species combine to create an unpleasant sight for visitors.

The sequence of events described above quite understandably causes much concern to the park managers, as questions are raised over its causes and possible steps to redress the problem. I have discussed the complexity of this problem in earlier sections of this report. Whatever the ultimate causes, there is little doubt that the park's large mammal populations need to be maintained at ecologically sustainable levels.

In thinking about the optimum population size for any species in an area, it is essential to consider the number that any given environment is capable of holding. Many models have been developed for population growth, envisaging the existence of a globally stable equilibrium point, christened the carrying capacity. This value is thought of as a shifting equilibrium, determined by many factors among them food, space and predators (May 1981). Communities of indigenous herbivores are regulated in their numbers by density dependent limiting factors of their environment (Lamprey 1983).

Carrying capacity is a controversial value indeed, owing to its elusiveness in natural populations, and the difficulties involved in attempting to uncouple the factors that influence its magnitude and stability. Mathematical intricacies aside, it would be practical to use the biomass rainfall relationship as a rough guide in establishing the numbers of the various species the ecosystem is capable of sustaining on a long term basis.

From results of game counts done between 1970 and 1992, the park has displayed its ability to hold large herbivore biomass at about the levels predicted on the basis on annual precipitation. Twice during that period, it contained a biomass density at levels higher than what would be expected for a double rainfall savanna ecosystem. This was due to a build up of populations following expansion of the park and gradual confinement. Recognizing that the actual composition of the community will have to depend on habitat attributes and management priorities, the number of constituent species ought to be manipulated to fit within inherent environmental constraints.

In foregoing paragraphs, I have laid emphasis on the need for intensive management of the park's plant and animal communities. In particular, a population control programme is recommended, aimed at ensuring the long term existence of a healthy and ecologically sustainable plant herbivore system. In this respect, future conservation policy will necessarily have to change in favour of intervention.

While problems outside the park appear to have been ameliorated to an admirable degree, those inside assumed more challenging proportions. What stands out now is that the park can only continue to exist with a significant amount of scientific input, almost reminiscent of zoo management. For example, the low predation levels in the park are due to active elimination by man when most of the land was under cattle ranches and the introduction of more predators may be considered as a check to herbivore populations. This would call for careful evaluation of their potential role beforehand, given that the effectiveness of predation in controlling prey populations is still subject to much controversy in wildlife management (Shaw 1985).

8.3. Areas of future research

The management suggestions outlined above will only be possible with the availability of quantitative information on many scientific issues. Foremost in this respect is the need for a long term ecological monitoring programme encompassing all aspects of the park's ecology. Data should be collected on animal numbers and distribution, at least twice a year, as well as seasonal measurements of herbaceous plant biomass and tree regeneration. In view of the park's rising popularity among tourists, visitor impacts on habitats need to be evaluated from time to time.

More intense research is needed in the areas of social organization, population genetics and habitat quality, all of which have important bearing on the health of the park's mammals.

Other areas of concern include an investigation of the predator - prey system, foraging strategies and quality of lake water and its implications to flamingoes and other birdlife.

8.4. Conclusion

In the foregoing parts of this thesis, I have provided detailed analyses of the plant herbivore interactions in what is expected to be an irreversibly isolated ecosystem. Different sections have been devoted to reconstructing the ecological history of the lake's watershed, describing spatial and temporal variations in animal distribution within the park and the responses of one key herbivore species, the waterbuck to environmental fluctuations. Finally I have forwarded concrete proposals for successful management of the park's wildlife resources, in the belief that these will be applicable in other ecosystems that may become similarly isolated.

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10. APPENDICES

Appendix 1. Results of clinical diagnosis done on waterbuck individuals in varying stages of health, during a parallel study on animals culled from the experimental plot in April 1992.

SERIAL #	SEX	BODY SCORE	CLINICAL NOTES
1	Male	4	Abomasum, Jejunum and Ileum:- nematodes; Heart:- flabby with gelatinization of coronary fat and sarcosysts.; Liver:- necrotic foci, cell degeneration, inflammation., Spleen:- atrophied, red pulp shrunken.
2	male	4	Abomasum, Jejunum and Ileum and colon:- nematodes.
7	male	4	Lungs:- emphysematous, thickening of interalveolar septae; Heart:- hydropericardium; Liver:- proliferation of bile ducts.
8	female	4	Colon:- nematodes., Liver:- fibrotic cords, generalized cellular degeneration.
9	female	4	Abomasum:- nematodes., Heart:- flabby with pericardial fluid., Liver:- focal necrosis with cymphocytic infiltration., Kidneys:- congestion of the medulla.
10	female	5	Abomasum:- nematodes., Liver:- focal necrosis, cymphotic infiltration, bile duct proliferation.
11	female	4	Ileum:- nematodes., Liver:- necrosis, biliary hyperplasia., Tongue:- sarcocysts.
13	female	4	Ileun and colon:- nematodes., Gallbladder:- distended with bile., Kidney:- renal fat gelatinization., Liver:- capsule thickened, focal necrosis, hemorrhage, bile duct hyperplasia., Lungs:- thickening of interalveolar septum, atelectasis., Heart:- vessel congestion.
14	female	4	Heart:- fusion of pericardium and epicardium, petichial haemorrhage, gelatinization of coronary fat., Liver:- atrophied.
15	male	5	Heart:- hypertrophied, sarcocysts., Liver:- hyperplasia of biliary system., Lungs:- thickening of interalveolar septae.
18	female	2	Liver:- congestion., Lungs:- interalveolar septal thickening.
19	female	2	Colon and caecum:- nematodes., Lungs:- mottling, thickening of interalveolar septum., Liver:- lympocytic cuffing, haemorrhage, hyperplasia of biliary duct epithelium., Heart:- sarcocysts in muscles.
20	female	3	Lungs:- mottling of diaphragmatic lobes.
21	female	5	Colon:- nematodes., Liver:- darkening., Gallbladder:- distended with dark green bile., Heart:- flabby, hydropericardium, gelatinization of coronary fat., Spleen:- enlarged.
22	female	5	Colon and caecum:- nematodes., Kidneys:- hemorrhage., Liver:- Mottling of diaphragmatic lobes.
23	female	5	Colon and Caecum:- nematodes., Liver:- darkened, capsular thickenning, portal cirrhosis, hemosiderosis., Gallbladder distended; Lung:- red hepatization., Kidney:- renal fat gelatinization., Heart:- Hydropericardium and coronary fat gelatinization., Spleen:- atrophy, red and white pulp shrunken.
25	male	4	Colon and caecum:- nematodes; Liver:- reddened., Kidneys:- congestion, of coronary fat with hemorrhage., Heart:- flabby, white flakes, gelatinization of coronary fat, eccymosis., Spleen:- enlarged; Muscles:- muscular cysts

Appendix 1 continued

25	male	5	Colon:- worm nodules., Liver:- necrotic foci, portal cirrhosis, cellular degeneration., Gallbladder:- lot of bile., Kidney:- gelatinization of renal fat., Heart:- hydropericardium., Spleen:- enlarged.
29	female	5	Kidneys:- petichial to eccymotic hemorrhage., Tracheae:- petichial hemorrhage., Heart:- gelatinization of coronary fat, focal lymphocytic infiltration, myocardial degeneration., Spleen:- white and red pulp shrunken. Liver:- portal cirrhosis.
30	female	5	Liver:- necrotic, gelatinization of renal fat; Heart: gelatinization of coronary fat; Liver:- granulomatous inflammation, oesinophils, neutrophils and lymphocytes.
31	female	5	Liver:- focal necrosis,. Kidneys:- petichial hemorrhage, renal fat gelatinization., Heart:- coronary fat gelatinization, congestion of the coronary vessels., Spleen:- atrophy., Liver:- necrotic foci, bile duct over activation, epithelial giant cells.
36	female	2	Heart:- hydropericardium.
37	female	2	Muscles:- muscular cysts.
45	male	3	No clinically important observation.
46	male	2	Colon:- nematodes., Liver:- parasite migratory scars.
47	male	3	Heart:- hydropericardium, haemorrhage., Liver:- parasite migratory scars. granulomatous inflammation, haemorrhage.
48	female	3	No clinically important observation
50	female	5	Liver:- necrotic foci with white patchy lines., Kidney:- renal fat gelatinization.
52	female	5	Colon and caecum:- nematodes., Kidney:- renal fat gelatinization., heart:- coronary vessel congestion. Muscle:- cysts in shoulder muscle.
53	female	2	Heart:- hydropericardium., Muscle:- muscular cysts., Adrenal glands:- hypertrophy.
54	female	2	Liver:- eccymotic haemorrhage., Adrenal glands:- hypertrophy., Lungs:- mottling.
55	female	3	Kidneys:- necrotic areas with fluid filled cysts., Heart:- hydropericardium.
56	female	4	Liver:- cellular degeneration., Kidney:- renal fat gelatinization., Heart:- hydropericardium, hypertrophy of ventricles, myocardium with splashy hemorrhage, epicardial thickening, congestion of vessels, muscular dystrophy shown in myocardial fibres., Lungs:- atelectasis, interalveolar septal thickening with inflammatory cells.
57	female	3	Small intestines:- nodular worm., Lungs:- red hepatization, atectasis, mixture of blood and fibrin.
58	female	3	Kidney:- renal fat gelatinization, Muscles:- cysts
59	female	5	Spleen:- enlarged., Kidney:- renal fat gelatinization.
60	female	3	Lungs:- mottling of diaphragmatic lobes., Kidney:- renal fat gelatinization., Heart:- hydropericardium.

Appendix 2. Results of parasite egg counts done on waterbuck faecal samples, taken during a parallel study on animals culled from the experimental plot in April 1992.

SERIAL #	SEX	BODY SCORE	STRONGYLE EGGS	STRONGYLOIDES EGGS	COCCIDIAN EGGS	TRICHURIS EGGS
1	Male	4	- ve	- ve	- ve	- ve
2	male	4	- ve	- ve	- ve	- ve
3	male	3	- ve	- ve	- ve	- ve
7	male	4	- ve	- ve	- ve	- ve
8	female	4	- ve	- ve	- ve	- ve
9	female	4	- ve	- ve	- ve	- ve
10	female	5	- ve	- ve	+ ve	- ve
11	female	4	- ve	200	- ve	- ve
13	female	4	- ve	- ve	- ve	100
25	male	4	- ve	- ve	- ve	- ve
52	female	5	- ve	- ve	- ve	- ve
53	female	2	- ve	- ve	- ve	- ve
54	female	2	- ve	- ve	- ve	- ve
55	female	3	- ve	- ve	- ve	- ve
56	female	4	- ve	- ve	- ve	- ve
58	female	3	- ve	- ve	+ ve	- ve

Appendix 3. Identification of ticks collected from waterbucks culled from the experimental plot in April, 1992.

SERIAL #	BODY SCORE	SPECIES IDENTIFIED
13	4	*Rhipicephalus pravus*
23	5	*Rhipicephalus pravus*
26	5	*Rhipicephalus appendicalatus*, *Rhipicephalus pravus*
28	5	*Rhipicephalus pravus*
29	5	*Rhipicephalus appendicalatus*
31	5	*Rhipicephalus evertsi*, *Rhipicephalus appendicalatus*
32	2	*Rhipicephalus pravus*, *Rhipicephalus appendicalatus*
33	1	*Rhipicephalus pravus*, *Rhipicephalus appendicalatus*
35	3	*Rhipicephalus pravus*
37	2	*Rhipicephalus appendicalatus*
38	5	*Rhipicephalus pravus*, *Rhipicephalus appendicalatus*
46	2	*Rhipicephalus pravus*
52	4	*Rhipicephalus appendicalatus*
53	2	*Rhipicephalus appendicalatus*
54	2	*Rhipicephalus appendicalatus*
55	3	*Rhipicephalus pravus*
56	3	*Rhipicephalus appendicalatus*
60	3	*Rhipicephalus appendicalatus*