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THE EFFECTS OF LARGE HERBIFORES
OF THE ECOSYSTEM OF
QUEEN ELIZABETH NATIONAL PARK, UGANDA

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THE EFFECTS OF LARGE HERBIVORES ON THE ECOSYSTEM OF QUEEN ELIZABETH NATIONAL PARK, UGANDA

By

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Dedicated to my parents,

PILIPO OJOK and LUCIRA AJOK,

who taught me the meaning of conservation

and appreciation and respect for nature.

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ABSTRACT

THE EFFECTS OF LARGE HERBIVORES
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Game counts in previously studied areas of Queen Elizabeth National Park, Uganda, during November 1981 to June 1983 showed that populations of large and medium-sized ungulates were lower than counts made in 1956/57 and 1963-67. For big game species such as elephant (Loxodonta africana) and buffalo (Syncerus caffer), the decline was attributed to recent large-scale poaching.

The variability of animal counts from month to month was high but showed no marked trend over the course of the study . Censuses of individual species seemed to be influenced by such factors as body-size, wariness, herding characteristics and mobility, the ability of observers to see all the animals present, as well as the size of the population.

Census results showed no significant seasonal differences. This supported the general impression that animals in the park do not undertake large-scale seasonal movements.

Hippopotamus (Hippopotamus amphibius) have returned to the Mweya Peninsula in large numbers following a cropping scheme between 1958 and

1967 during which they were virtually eliminated from the area. Their increase has been at the expense of the other ungulate species. The increased abundance, high biomass and diversity of various large-mammal species which occurred during and immediately after the cropping of hippopotamus have been lost.

In the Craters region, the present study disclosed that a woodland which in 1968 was losing trees due to widespread elephant damage was regenerating abundantly. Although species composition of the woodland had remained virtually the same, major shifts had occurred in the relative abundance of species. The most significant was that of Acacia gerrardii which in 1968 constituted only 21.3% of the trees in the woodland had by 1982 increased to 82.4%. Two other species, Bridelia scleroneuroides Olea africana, which were as abundant as A. gerrardii in the earlier survey have declined greatly and were no longer important components of the vegetation.

The respective roles of fire and elephant in controlling this woody vegetation was examined. On account of a gradient of decreasing mature-tree density with increasing distance from disturbing influences along the park border, it was concluded that elephant rather than fire were the primary factor in controlling woody vegetation. In Murchison Falls National Park, Uganda, observations on experimental plots from which elephant, but not fire, have been excluded support such a conclusion. The pattern of tree distribution seemed likely to have developed as a result of differential use of the range by ungulates in response to poaching and harrassment along the park border.

Thicket clumps constituted an important resource to wildlife providing food, shelter, shade and concealment for a wide range of fauna. An increase in thickets was attributed to their release from frequent fires and heavy browsing. In heavily-grazed areas such as the banks of the Kazinga Channel and the Mweya Peninsula, the absence of fire (due to inadequate fuel to support them) allows thickets to flourish. It was concluded that thicket clumps originate from a nucleus of a single bush in the grassland. The bush has to be a vigorous species in order to persevere and survive frequent fires and persistent defoliation.

Of three grassland types, namely the short, medium-height and tall grasslands, standing-crop plant biomass was highest in the tall and lowest in the short. The differences were attributed both to grazing and precipitation. The intensity of grazing was highest in the short grassland where between 60% and 90% (with an average of 75.6%) of standing-crop biomass was consumed by herbivores compared with only 26.5% in the medium-height grassland. Light grazing enabled the maintenance of good vegetative cover but resulted in accumulation of litter and the risk of hot fires. Heavy grazing severely reduced grass cover and resulted in bare soil patches. It is, no doubt, a major factor in inducing bush-invasion and habitat deterioration in some areas of the park.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

1.1. Introduction

The Queen Elizabeth National Park (QENP) in southwestern Uganda was created by an Act of Parliament in 1952. Until the 1970s it supported the highest biomass of wild ungulates anywhere in the world (Petrides & Swank 1965; Field & Laws 1970; Leuthold & Leuthold 1976). Intense poaching during the 1970s led to a sharp decline in the population of many species (Eltringham & Malpas 1976, 1980; van Orsdol 1979; Malpas 1980).

The massive decline in animal populations seriously interrupted the dynamic equilibrium between animals and vegetation. The magnitude and extent of the consequences are not fully understood and may not be for some time. Some effects are already apparent, however, and involve a profuse regeneration of trees and increase in bush cover.

This regeneration reverses a declining trend blamed (Field 1971) on elephant (_Loxodonta africana_). It is rapidly turning large areas of previously open grassland into dense woodland (Yoaciel & van Orsdol 1981). Park authorities are concerned about possibly-adverse effects of grassland reduction on grazing animals.

In many African national parks, changes in landscape have been attributed to the effects of elephant and fire (Buechner & Dawkins 1961; Laws 1970; Laws, Parker & Johnstone 1970, 1975). Because the interactions between elephant and fire are complex, blame for the changes cannot be attributed to one without considering the other. Until recently both elephant and fire were common in Queen Elizabeth National Park. With the elephant virtually eliminated from large areas of the park, the situation offered a unique opportunity to assess the effectiveness of fire as an agent of habitat change and to determine the relative importance of both fire and elephant in controlling woody vegetation.

One aspect of the changes in habitat involves the spread of thickets. The increase has been particularly rapid along the shores of Lake George, Lake Edward and the Kazinga Channel where grazing by large numbers of hippopotamus (Hippopotamus amphibius) keeps the grass short and thin, and precludes the occurrence of grass fires. In areas where fires are frequent, the spread of shrubs appears to be modest or under control. These observations suggest that grazing enhances the ability of a thicket to spread while fire restricts it. Understanding the processes involved could provide the information necessary to formulate an economic program that would reverse the spread. The authorities have attempted clearing bush on a limited scale on Mweya Peninsula using hand tools, but abandoned the project because it was slow and too costly.

Although there are large populations of hippopotamus in the waters of the lakes and the Channel, there is a decreasing gradient of grazing pressure on uplands as distance from these bodies of water increase (Lock 1967, 1972). Changes in grassland species composition as well as in biomass and productivity are observed along the gradient. An attempt was made to determine the above-ground production of dry matter and the intensity of grazing at varying distances from water.

1.2. Study objectives

The aims of this study were to:

1. Establish the present status of the large-herbivore populations (in terms of abundance, distribution and population structure), assess the extent of changes in abundance over the last decade and project the outlook for the forseable future;

2. Determine the above-ground production of dry matter and obtain mean values for the rate of grazing along a gradient of grazing intensity;

3. Document changes in vegetation, especially the regeneration of Acacia species in the Craters highlands and the spread of thickets on Mweya Peninsula; and

4. Assess the effectiveness of fire as an agent of habitat change in the absence of elephant and determine the relative importance of both elephant and fire in suppressing the regeneration of trees.

1.3. Thesis outline

The thesis is organized in seven chapters each of which explores a different topic. Each topic is presented in a methods-results-discussion format. A brief introduction to the issues and the context in which the study was done is made in Chapter 1 which also outlines the objectives of the study.

Chapter 2 describes the Queen Elizabeth National Park, the reserve in which the study was done and presents a brief overview of its climate, geology, vegetation and fauna. Human and wildlife history relating to the park, its relationship to other natural resources in the region and current threats to its continued existence are outlined. Areas selected for animal censuses and for the study of tree regeneration are described.

Chapter 3 deals with the status, distribution and population structure of large herbivores. Details of census methods are given and results are presented and discussed. The age structure and sex ratio of each population, as well as the abundance of large mammals in three habitats are analyzed. The findings of the study are compared with those of the past, and a long-term trend for one of the areas is discussed. The outlook for each species is briefly outlined.

Chapter 4 deals with tree regeneration in the park. A brief description of the regenerating woodland is given and the method used to determine tree density in the woodland is also described. The composition of the woodland, the spatial distribution of plant species and the importance value of the major trees are given. The effects of elephant and fire on regeneration of the woodland are evaluated and their relative importance in controlling woodland development determined.

Chapter 5 deals with the abundance and expansion of thickets in the park. Methods used to investigate the expansion are presented. The results of investigation, including the origin and development of thicket clumps are reported. Present density, size and rate of expansion of thicket clumps in two different types of grassland, are given and the roles of fire, grazing and trampling on vegetation are assessed. Probable causes of thicket expansion are discussed.

Chapter 6 explores changes in species composition as well as in height and productivity of grasslands at varying distances from the shoreline, corresponding to a gradient of decreasing grazing pressure by hippopotamus. Biomass of grass in grazed and ungrazed plots was analyzed and compared between plots and areas to assess the intensity of grazing in different areas. The effects of fire on species composition and productivity in ungrazed grasslands of the Mweya Peninsula are discussed. The ditched exclosure used to keep animals out of the plot is described.

Chapter 7 concludes the study. Its major findings are summarized and an attempt is made to pull the different components into a coherent overview.

CHAPTER 2

QUEEN ELIZABETH NATIONAL PARK AND THE GAME CENSUS AREAS

2.1. The Queen Elizabeth National Park

2.1.1. Geology and topography

The park is 1978 sq km in area and is situated between longitudes 29° 39'E and 30° 19'E and latitudes 0° 43' S and 0° 15'N, and is situated on the floor of the western arm of the Great Rift Valley of East Africa (Figs. 2.1 & 2.2). The landscape is dominated by the Rwenzori Mountains (the fabled Mountains of the Moon) which lie immediately to the north of the park and include glacier-capped peaks that reach 5119 m above mean sea level. Elevations in the park vary from 913 m at lake levels to 1378 m at Kyamatumu in the Craters highlands.

Associated with the early Pleistocene volcanic activity that gave rise to the Rwenzoris is a series of at least 78 explosion craters which occur in an area of about 155 sq km in the park north of Kabatoro village. These craters are thought to have been formed some 10,000 years ago in violent explosions of gas and steam accompanied by a vast belching of volcanic ash and dust which settled over the area as the basis of a rich, alkaline volcanic soil. The noxious gases and ash are believed to have exterminated some of the Nilotic fauna such as the Nile crocodile (*Crocodylus niloticus*) and Nile perch (*Lates niloticus*) whose fossilized remains have been found in the area (Beadle 1965). A number of the volcanic craters contain saline lakes, and at least two support a

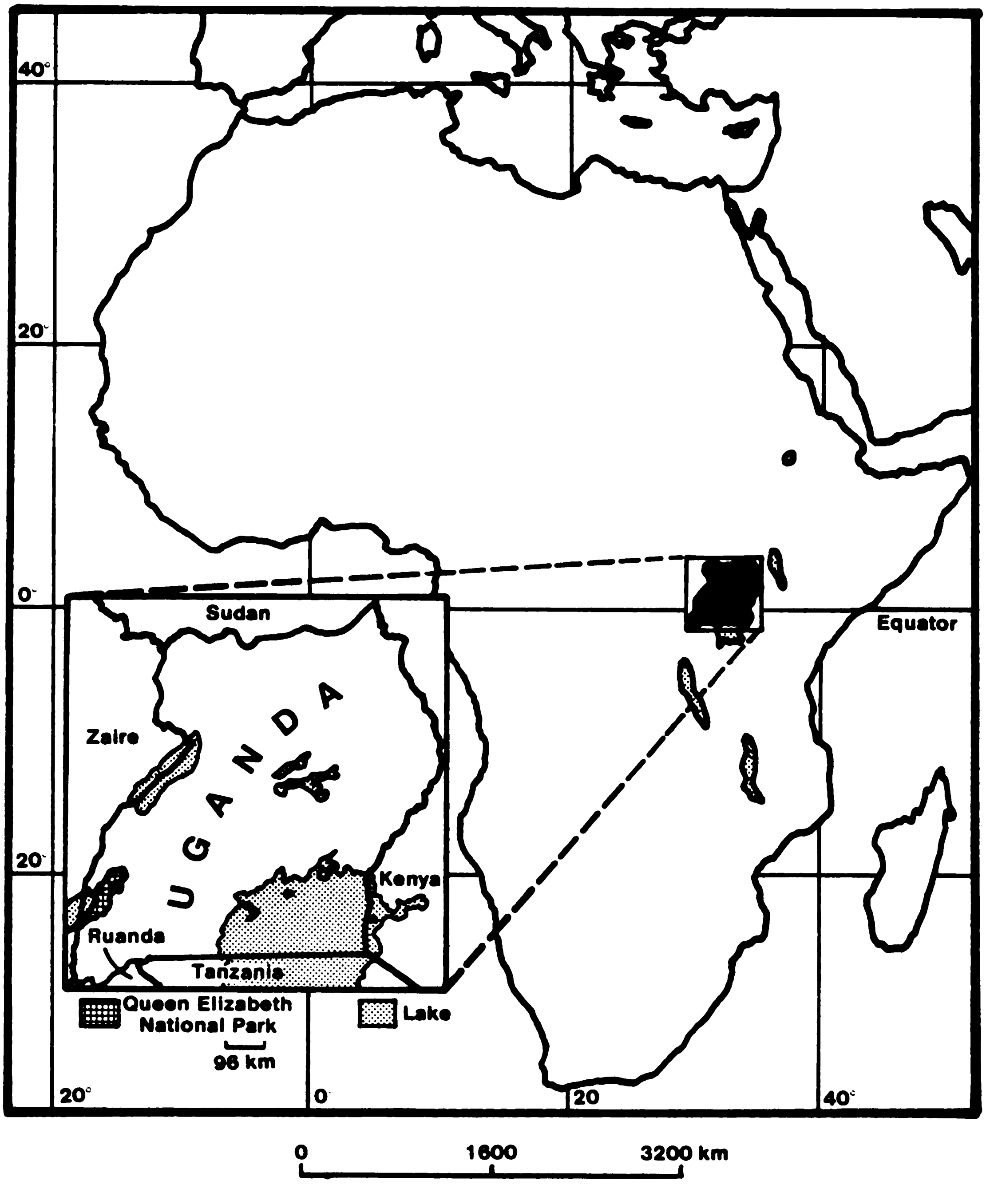


Fig. 2.1. Location of Queen Elizabeth National Park in Africa.

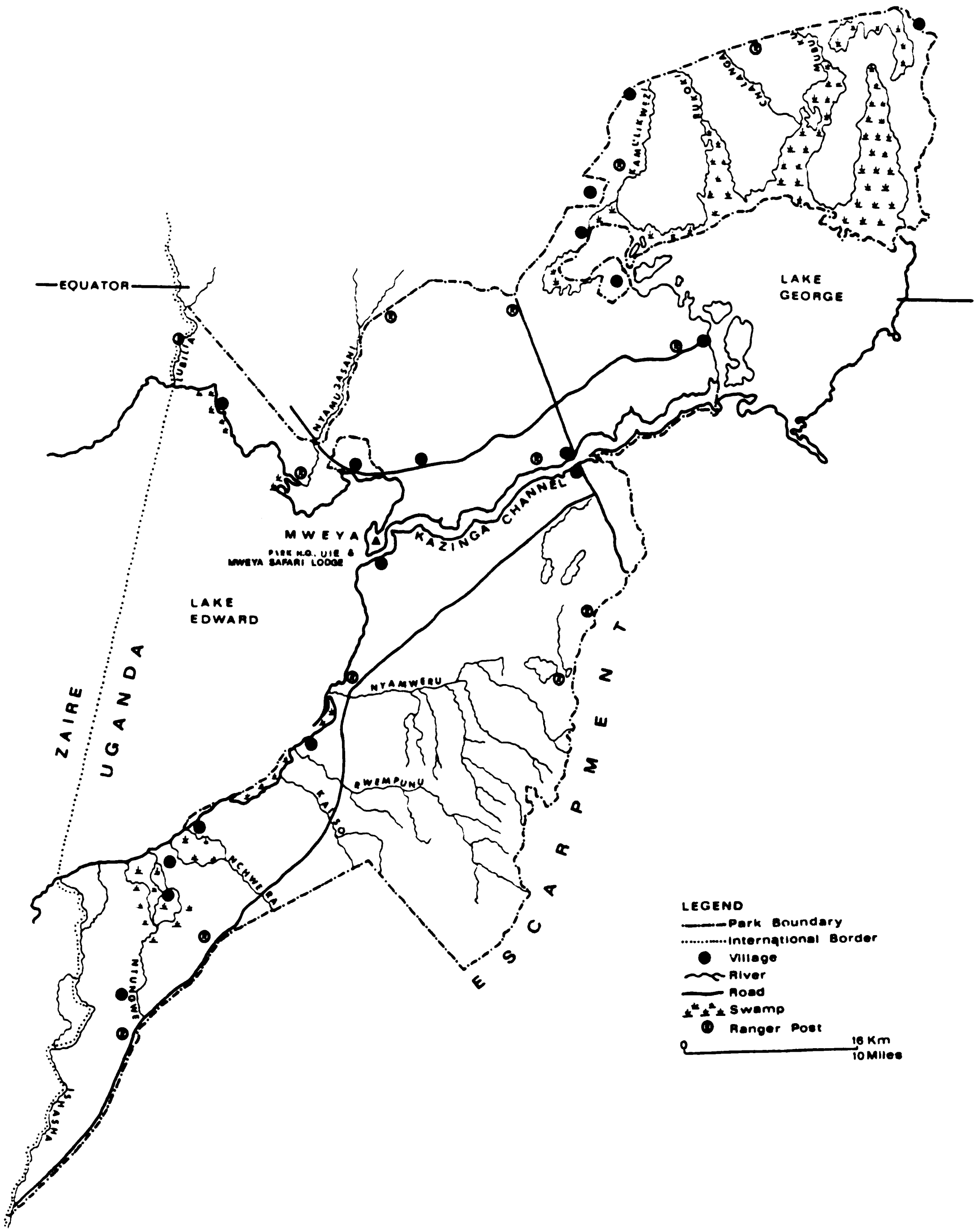


Fig. 2.2. QUEEN ELIZABETH NATIONAL PARK, Uganda.

flourishing salt industry.

Lake George (389 sq km) and Lake Edward (2150 sq km) lie in the northeast and southwest of the park, respectively. Nearly half of Lake Edward is situated in neighboring Zaire where it reaches a depth of over 115 m. In comparison, Lake George is a large but shallow pond, only 3m deep. The 32-km long Kazinga Channel, which connects the two lakes, bisects the park into approximately equal halves. Water flow from Lake George to Lake Edward along the Channel is sluggish because the two lakes are almost at the same elevation. Several streams flowing from the mountains and the eastern escarpment traverse the park and drain into the lakes.

2.1.2. Climate

Considering the park's position astride the equator, temperatures are surprisingly cool with mean maxima near 28 °C and mean minima around 18 °C in all months. Mean hours of sunshine vary from 5.1 in October to 6.5 in July. There are two rainy seasons each year, from March to May and September to November. Amounts of annual rainfall increase towards the eastern escarpment from a mean of about 660 mm on the floor of the rift valley at Mweya to 1250 mm a year in the Maramagambo Forest (Fig. 2.3). Although the seasons are usually well-marked, appreciable quantities of rain also may fall as showers during the dry months. The prevailing winds are mostly northwesterly and westerly. Winds are calm during the dry seasons but often strong and gusty during the rains. The high temperatures, long hours of sunshine and low humidity result in high rates of evapotranspiration, especially during the dry season. In

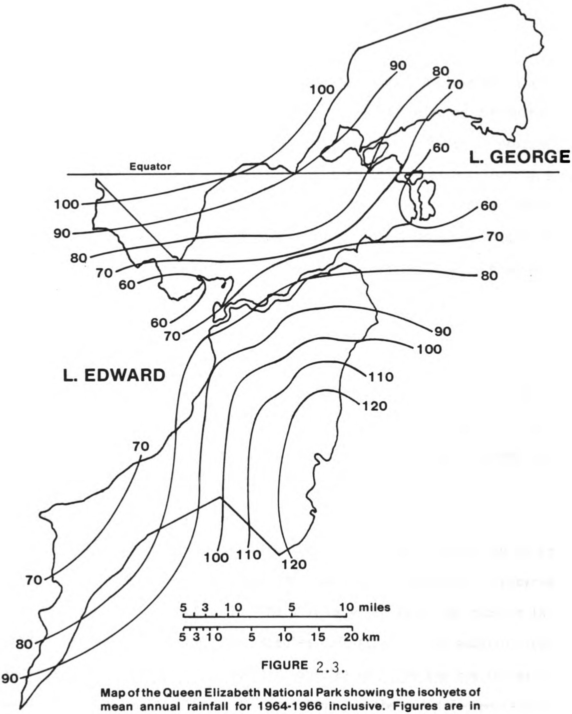


FIGURE 2.3.

Map of the Queen Elizabeth National Park showing the isohyets of mean annual rainfall for 1964-1966 inclusive. Figures are in centimetres.

heavily-grazed areas with little vegetative cover, large quantities of rainwater during thunderstorms are also rapidly lost as run-off.

2.1.3. Soils

The area is underlain by Pleistocene silts, sands and clays which are usually covered by a thick layer of volcanic ash ejected during the formation of the craters (Bishop 1970). The ash has weathered to produce eutrophic soils that are generally loamy, rich in mineral nutrients and with a high reserve of phosphorus and calcium. Because of the youthful state of the profiles and of the rich original ash, the potential fertility of the soils is high (Harrop 1960). The dry climate, however, limits their agricultural potential.

2.1.4. Vegetation

The vegetation of the park has been described by Langdale-Brown (1960), Osmaston (1965), Lock (1967, 1977) and Field (1968). It is varied and includes open grassland, grassland with thickets, woodland, forest and swamp.

Swamps

The most extensive swamp in the park occupies an area of about 250 sq km north and northeast of Lake George. The community is dominated by papyrus (*Cyperus papyrus*). Growing in the shallow water among the papyrus is woody vegetation dominated by species of *Acacia*, the ambatch tree (*Aechynomene elaphroxylon*), aquatic species of *Ficus* and the borassus palm (*Borassus aethiopium*). A population of the cycad *Encephalartos hildebrandtii* occurs in the swamp near the mouth of the Mpanga River.

The makindu palm (Phoenix reclinata) is found in inland swamps in Ankole and on the banks of the Kazinga Channel. The Nile cabbage (Pistia stratiotes) flourishes in Lake George and a few large inland hippo wallows. In the lake, it is carried by the current and blown about by the wind. Occasionally large numbers may be seen floating down the Kazinga Channel after a storm. Swamps are also found along the shore of Lake Edward, especially at the mouths of major rivers.

Open grassland

For the most part, open grassland communities in the park are dominated by the coarse, tufted, fire-encouraged species such as Themeda triandra, Heteropogon contortus and Hyparrhenia filipendula. Sporobolus pyramidalis is also widespread in most areas and S. stapfianus and Microchloa kunthii are common in the less productive grasslands. In areas of low rainfall the grasses tend to be short. In higher rainfall areas, such as the Crater Highlands, they are much taller. In these areas, large patches of tussock grass Cymbopogon afronardus and Indian sword grass (Imperata cylindrica) commonly occur. Some authors (Osmaston 1965; Spinage 1982) have suggested that their occurrence is evidence of former agricultural land use. The grasslands to the north of the park are characterised by trees of Euphorbia candelabrum, which dot the landscape. In the southern extremity of the park their place is taken by the gnarled, large wild fig trees Ficus gnaphalacarpa, whose branches form a favorite resting place for lions. Usually the grasslands are also dotted with thickets.

Grassland with thickets

Areas of very short grass with dense bushes dominated by the thorny scramblers Capparis tomentosa and Azima tetracantha occur near the shores of the lakes and the Channel that are heavily grazed by hippopotamus. This short grassland is rich in species, with 23 grasses recorded. Chrysochloa orientalis and Sporobolus pyramidalis are dominant, but Tragus berteronianus, Sporobolus stapfianus, Eragrostis cilianensis, and Cenchrus ciliaris are common. Increase in density and size of thickets in recent years, particularly along the shoreline, is a major concern among park authorities and bush clearance has been attempted on a limited basis.

Woodland

The most extensive stand of Acacia woodland north of the Kazinga Channel occurs in the Craters region. It is dominated by A. gerrardii but A. sieberiana and A. hockii are also common. Some slopes contain a largely unexplored xerophyllous woodland of Olea chrysophylla, Cordia ovalis and Euphorbia candelabrum. Southeast of Kasese, patches of Balanites aegyptiaca form a wooded grassland which also contains trees of Acacia sieberiana and of A. gerrardii.

Field (1971) reported that between 1954 and 1968 the Craters woodland declined by about 89% under the combined effects of elephant and fire. Mature trees were pushed over by the animals and regeneration was either browsed or destroyed by fire. At present, few mature trees remain in the southern portion of the area but a stand persists near the main road in the extreme north. Since the recent decline in elephant numbers, profuse regeneration of Acacia, particularly gerrardii but also sieberiana and hockii, is rapidly restoring the area to woodland. Along the eastern escarpment north of the Maramagambo Forest, are scattered mature trees of

Ficus gnaphalocarpa and Acacia sieberiana. Ground reconnaissance surveys indicate that A. sieberiana and A. hockii are regenerating rapidly, particularly in the area east and south of Katunguru village. Ficus, on the other hand, has not demonstrated the same vigor as its Acacia counterparts and is not regenerating actively.

In Ishasha, in the southern tip of the park, regeneration by A. sieberiana is brisk. Yoaciel & van Orsdol (1981) have estimated that between 1974 and 1978, woodland there increased by 130%.

2.1.5. Forest

The Maramagambo Forest is a large forest reserve within the park. It covers approximately 450 sq km and is contiguous with the Kalinzu Forest Reserve outside the park to the east. Although this mahogany-rich forest is largely unexplored floristically, it is dominated by mature stands of the Uganda ironwood Cynometra alexandri. In the past it harbored large numbers of elephant during the dry season. Numerous buffalo (Syncerus caffer) also live in the forest. Smaller forests occur along and at the mouths of most of the major rivers flowing through the park.

2.1.5. Fauna

The mammalian fauna of the park is characterised by large numbers of several species, particularly hippopotamus, elephant and buffalo. The area is, however, surprisingly poor in ungulate species. There are no black rhinoceros (Diceros bicornis), zebra (Equus burchellis), giraffe (Giraffa camelopardalis), hartebeest (Alcelaphus buselaphus), eland (Taurotragus oryx), oribi (Ourebia oerebi) or impala (Aepyceros melampus), although all of these species occur within 160 km to the east. Some authors (e.g. Eltringham 1973) have suggested that the intensive, late Pleistocene volcanic activity that gave rise to the craters could have caused widespread mortality and extinction of some animal species, and that subsequent recolonization was prevented by the surrounding forest which acted as a barrier to plains game. Others (e.g. Spinage 1982) believe that the paucity of species is, at least in part, the result of extermination by man due to excessive hunting during previous settlement of the area. It is also possible that the severe rinderpest epidemic which swept through western Uganda earlier in this century eliminated much of the wildlife and cattle (Lugard 1893) and contributed to the absence of some species. At present, numerous settlements and extensive cultivation around the park form an equally effective barrier. Immigration of these species by natural processes is most unlikely.

Along the Lubilia River in the northwest and the Ishasha River in the southwest are vegetative corridors of unsettled land which are continuous with the Kivu National Park in Zaire. Movements of animals, especially elephant and buffalo, across the border occur frequently.

A West African influence is apparent in the composition of both the fauna and flora, and in animals it is most marked in the invertebrates and birds. Traces may be seen, however, among the large mammals. Buffalo are rather smaller than elsewhere in East Africa, averaging 659 kg in weight for the adult male and 475 kg for the female (Grimsdell 1969). There is also a marked brownish coloration, a feature reminiscent of the reddish color of the small West African bush cow. The adult male bushbuck

(<u>Tragelaphus</u> <u>scriptus</u>) are also red as in West Africa and quite unlike the almost black males seen, for example, in Kenya. The bush pig (<u>Potamochoerus</u> <u>porcus</u>) is also red like the West African hog and not black as in the southern and eastern races. The elephants, however, belong to the race <u>L</u>. <u>africana</u> and show no interbreeding as is often asserted. They are, however, polymorphic in size with some being smaller at the shoulder and with lighter tusks than the others (Laws 1966). A West African flavor is also found in the primates with a larger range of species than is normal in East African parks. The long-haired chimpanzee (<u>Pan</u> <u>troglodytes</u>), a West African species, occurs in the Maramagambo Forest in considerable numbers.

Elephant and hippopotamus are without doubt the most important species in the park as far as their effect on the habitat is concerned (Laws 1968, 1970). Estimates of elephant numbers have fluctuated considerably. The mean of 22 counts conducted between 1963 and 1972 is 2375 (SD ± 870; Malpas 1978). Numbers have fallen precipitously, however, in recent years due to poaching.

The hippopotamus is one of the most numerous large mammals in the park. It occurs along most of the shorelines of the lakes and Channel as well as in inland wallows, particularly during the wet season when these are numerous. Hippos retreat to the waters of the Channel and the lakes, however, when the wallows dry up.

The hippo is a significant species in the management of the park. Between 1958 and 1967 about 7000 were shot in a management program. This program was initiated to halt the overgrazing and trampling which had severely reduced grass cover for several kilometers inland and exposed large areas of bare earth to soil erosion (Bere 1959). Vegetative observations under conditions which simulated heavy grazing by hippo showed that stoloniferous species were encouraged at the expense of erect species (Lock 1967, 1972; Field 1970). The decline of the erect species was attributed to their inability to colonize bare ground and to their vulnerability to trampling. During the management cropping program, hippo were completely eliminated from the Mweya Peninsula. Following their removal the grassland showed a spectacular increase in foliar cover and erect species, while prostrate and mat-forming species declined (Laws 1968; Thornton 1971). Other effects of the removal of hippopotamus included increased numbers and biomass of other members of the large mammal community and a greater species diversity (Eltringham, 1974). After the culling ended, however, hippo quickly recolonized the Peninsula and steadily increased in numbers. At present, the composition of the large mammal community is once again similar to that found in 1956 with a preponderance of hippo.

The buffalo is widespread throughout the park and seems to be equally at home in the grassland as in the forest. Two aerial counts by Eltringham & Woodford (1973) in 1968 and 1969 averaged 17938 buffalo. Buffalo were heavily poached during the 1970s, however, and their present number is estimated to be only around 5000.

Topi (<u>Damaliscus lunatus</u>) are restricted to the portion of the park south of the Maramagambo Forest. In recent years, the topi population has fallen by nearly 50% from approximately 5500 in 1975 to about 2970 in 1978 (Yoaciel & van Orsdol 1981). It is estimated that the present population is probably not much more than 1000. Their decline is attributed both to poaching and changes in habitat.

Spinage (1967) gave a figure of 3000 for the waterbuck (Kobus defassa) but the present population is probably closer to 2000. The Uganda kob (Adenota kob) is the most numerous antelope in the park. Its numbers is estimated at 28000 (Malpas 1980). The kob is the only large mammal species which has increased in numbers in recent years.

No figures are available for warthog (Phacochoerus aethiopicus) but they are numerous. Bushbuck (Tragelaphus scriptus) and reedbuck (Redunca redunca) are quite common but are less often seen due to their secretive nature.

Apart from the common animals there are some rare species found within the park. They include the giant forest hog (Hylochoerus meinertzhageni) and bush pig (Potamochoerus porcus). The giant forest hog occurs primarily in the Maramagambo Forest but has relict populations in forested areas throughout the park. The bush pig is only found deep within the Maramagambo Forest. The sitatunga (Tragelaphus spekei) is known to occur in swamps within the park but its status is unknown. Forest duikers, including the red (Cephalophus harveyi) and the blue (C. monticola) are probably more abundant than is commonly realized. The yellow-backed bush duiker (Sylvicapra grimmia) is occasionally found within bushes in the grassland.

Several species of primates inhabit the park. The olive baboon (Papio anubis) is common and frequents open grassland and forest edge. The vervet (Cercopithecus aethiops) is also numerous. Less common and restricted to the Maramagambo and riparian forests are the black and white colobus (Colobus polykomos), the red colobus (C. badius), the redtail (Cercopithecus nictitans), the Uganda blue monkey (C. mitis stuhlmanni) and the chimpanzee (Pan troglodytes).

Among the large carnivores, the spotted hyena (Crocuta crocuta) is probably the most numerous. Others include the lion (Panthera leo) and leopard (P. pardus). Though no figures are available, it is estimated that there are about 200 lions and maybe 100 leopards in the park. The African hunting dog (Lycaon pictus) was found in the park until about 1955. It was exterminated by game and park authorities because of its method of predation (Uganda Game Department Annual Report 1948-1952; Uganda National Parks Annual Report 1953-1955). Small cats include the African wild cat (Felis lybica), and the serval (F. serval). The side-striped jackal (Canis adustus) is found only in the southern part of the park. The ratel or honey badger (Mellivora capensis) occurs in the park but is rare. Other small carnivores include the civet (Civettictis civetta), genet (Genetta tigrina) and five species of mongoose: the greater grey mongoose (Herpestes ichneumon), slender or black-tipped mongoose (H. sanguineus), banded mongoose (Mungos mungo), white-tailed mongoose (Ichneumia albicauda) and marsh mongoosc (Atilax paludinosus).

The ant bear (Orycteropus afer) and the pangolin (Manis temminckii) are two species of large insectivores that are present but not common in the park.

Because of varied park habitats, the avifauna is extremely rich.

Reptilian fauna includes the python (Python sebae) and many species of venomous and non-poisonous snakes and lizards (among the latter, the Nile monitor Varanus niloticus is the largest). No crocodiles occur in the park, although fossilized remains recovered in Pleistocene sediments and show that Crocodylus niloticus once existed in the area.

The fish fauna of Lake George and Lake Edward is varied and supports a flourishing local industry. Rhodes (1965) has described the fish fauna in detail. The smaller size of fish caught by fishermen today compared to a decade ago and the persistent demand by fishermen for smaller-sized nets are circumstantial evidence that the lake system is being overfished.

2.1.6. Human and wildlife history

The region which is now the Queen Elizabeth National Park was once densely settled. Abundant archaeological remains of stone tools of Acheulin culture at Mweya and Katwe indicate that the region has been inhabited for over 50000 years (Posnansky 1971). Later settlements of late Pleistocene are represented by widespread remains of pottery and metallic tools. The presence of hippo harpoons and lance heads suggests that hunting was the predominant way of life. By the end of the 13th century hunting had been replaced by a pastoral economy supplemented by fishing and trading in salt from Lake Katwe. The first European explorers to reach the region were impressed with the material wealth of the people, particularly their large herds of cattle (Stanley 1890; Elliott 1896).

The park owes its existence to three catastrophic epidemics. These were of smallpox, rinderpest and sleeping sickness. The smallpox epidemic occurred in 1889 and affected the local people. It was followed shortly afterwards by an epizootic of rinderpest which decimated 95% of the cattle. The impact of the disease on wildlife was undoubtedly equally substantial and Lugard (1893) observed that "in some districts, almost all the game including the small antelopes seem to have perished". The high cattle mortality precipitated a famine among the pastoralists. In 1920, the human population was stricken with sleeping sickness (trypanosomiasis). To combat the latter, the colonial authorities evacuated the human population from the area in 1924, leaving behind only a few inhabitants to maintain the salt and fish industries. The large-mammal populations benefited from the removal of hunting pressure and increased rapidly. The area was declared a game reserve in 1934 and a national park in 1952.

Rinderpest ceased to be a problem soon after 1920 and since then the only epidemic reported in the park was an outbreak of blue-tongue disease (malarial catarrhal fever) among the topi in Ishasha in 1961. In this case population losses were minimal. Bovine tuberculosis is common especially among the buffalo (Woodford 1972). The disease was probably contracted from domestic stock earlier this century. It is endemic north of the Maramagambo Forest where contact between domestic lifestock and wild bovids was probably common in the mid-nineteenth century and remains frequent to this day.

In the last decade, the large-mammal community has suffered a tremendous decline at the hands of man. This was first documented in 1974 by Eltringham & Malpas (1976, 1980) with respect to the elephant population. Another onslaught followed during and in the aftermath of the 1979 war when roving bands of men with automatic rifles killed large numbers of elephant, hippopotamus, buffalo and topi. The magnitude of their destruction has been estimated by van Orsdol (1979) and Malpas (1980).

Regardless of other influences, the greatest threat to the long-term survival of the park is the continued existence of numerous settlements within and along its borders. When the park was created, some existing villages in the area were either excised from it or were allowed too remain within specified boundaries. Over the past three decades, however, other villages have been established so that there are now 22 such communities in the park. The population of these settlements has also grown so that there are at least 70,000 people living in the park. This is expected to rise even more sharply when the salt factory currently being built in Katwe by a German company becomes operational.

The presence of a large human population within the park has intensified the demand for space and firewood. All of the original villages have expanded beyond their legal limits and the collection of firewood and the grazing of lifestock both accelerate the destruction of habitat within the park (Field 1968; Musoke 1980). The villages serve as centers for poachers and markets for their illegal trade (Edroma 1973). The distribution of elephant carcasses mapped by Eltringham & Malpas (1980) strongly implicated the villages as havens for poachers. Domestic stock may also act as a reservoir for disease (Woodford 1972).

2.2. Census areas

The study was conducted in the central sector of the park bounded by the equator and the Kazinga Channel. Ground counts of large mammals were made at monthly intervals in five selected areas (Fig. 2.4).

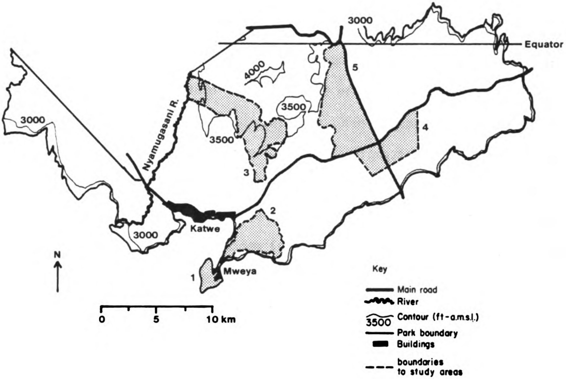


Fig. 2.4. Map of the sector between Kazinga Channel and the equator, Queen Elizabeth National Park, Uganda, showing game census areas.

Area 1 (4.4 sq km) was the Mweya Peninsula. The peninsula lies at two levels, with a steep fault running north and south dividing the area into approximately two equal parts. The area is heavily grazed by hippopotamus. The vegetation is a mosaic of short grass with bush thickets. and is one of the areas where the spread of thickets has been most rapid. On higher ground there is more grass and less thicket, but the lower portion of the peninsula and the steep slopes are densely covered with bush. Because of the absence of any significant quantity of grasses, fire is absent. In the late 1950s the peninsula experienced serious habitat deterioration due to overgrazing. To reverse the situation, 128 hippopotamus were eliminated in 1958 (Bere 1959) and until 1967 recolonization was prevented by shooting. A number of transects were established in 1958 and changes in vegetation recorded until 1965 (Laws 1968; Thornton 1971). Animal counts were made by Petrides & Swank (1965), Field & Laws (1970), Eltringham (1974, 1980) and Yoaciel (1981). This is the `seriously overgrazed' study area of Petrides & Swank (1965) and Area 4 of Field & Laws (1970).

Area 2 (13.0 sq km) was part of the mainland adjoining Mweya Peninsula. It is a series of relatively open grassy ridges separated by valleys with dense bush thickets and strings of small wallows. At the southern end, the vegetation is a mosaic of short grass and thicket similar to that found on the Peninsula. The grass increases in height to the north. Beyond the short grass area is a zone of taller grassland dominated by Sporobolus pyramidalis, with Bothriochloa spp. and Tephrosia nana creeping between the tussocks of Sporobolus. Grazing is heavy but less intensive than further south closer to the shoreline. A medium-height, lightly-grazed Themeda-Hyparrhenia grassland with patches of Imperata cylindrica dominating the northern portion. Fire is frequent in the northern part, but absent in the heavily-grazed southern portion. This is the `over-grazed' study area of Petrides & Swank (1965) and Area 6 of Field & Laws (1970).

Area 3 (26.2 sq km) was an area of volcanic craters north of Kabatoro. The vegetation is tall grassland with scattered mature trees of Acacia sieberiana and A. gerrardii and bush thickets. The dominant grass species are Hyparrhenia filipendula and Themeda triandra. Large patches of Cymbopogon afronardus and I. cylindrica occur on the floors of many craters. Profuse regeneration of trees, particularly of A. gerrardii, is turning large sections of the northern portion of the area into woodland. Fire is frequent during the dry season. This is Area 2 of Field & Laws (1970) and overlaps the `long-grass' area of Petrides & Swank (1965).

Area 4 (17.1 sq km) was located at the junction of the Katwe-Kasenyi Road and the main Mbarara-Kabarole (Fort Portal) Road. It has a series of parallel ridges and wet bushed valleys with strings of small wallows. In the west, the vegetation is a moderately grazed open fire-climax grassland with small patches of thicket. The grassland is dominated by Heteropogon contortus. Other common grass species include Sporobolus stapfianus, Microchloa kunthii, Hyparrhenia filipendula and Sporobolus pyramidalis. Thickets of Capparis and clumps of regenerating Acacia sieberiana tree occur mostly along the valleys. Trees of Euphorbia candelabrum are common on ridge tops. Between 1958 and 1962 the eastern half of the area was the location of an experimental 50% reduction of hippopotamus by eliminating some animals occupying wallows in the area

(Bere 1959). This is the `moderately overgrazed' study area of Petrides & Swank (1965) and Area 8 of Field & Laws (1970).

Area 5 (26.2 sq km) was a slightly undulating, tall to medium height fire-climax savanna grassland dotted with thickets. The Mbarara-Kabarole and Katwe-Kasenyi roads mark its eastern and southern boundaries, respectively. Kikorongo Crater is included in the study area and forms its northern boundary. The western boundary is demarcated by a neglected fire-break along the foothills of the Craters highlands. Its southeast corner is contiguous with Area 4. Trees of Euphorbia candelabrum are common in thickets. Hyparrhenia filipendula and Themeda triandra are the dominant grasses. Their associates include Heteropogon contortus, Bothriochloa spp., Sporobolus pyramidalis, S. stapfianus, Microchloa kunthii and Digitaria diagonalis. The southwestern portion is dominated by extensive patches of Imperata. Patches of Imperata also occur on the western border along the foothills of the Craters highlands and inside Kikorongo Crater. Dense woodlands infested with the tsetse fly Glossina palpalis occur on the fringes of Lakes Nyamunuka and Murumuli southwest of the area. A territorial ground of the Uganda kob has persisted in the area since the study of Buechner & Schloeth (1965) and probably long before then. This is Area 7 of Field & Laws (1970).

The five game census areas represented three habitat types. Areas 1 and 2 comprised a habitat of short grass with dense thicket close to water. Areas 4 and 5 were a habitat of open, medium-height grassland somewhat distant from water. Area 3 was a habitat of tall grass distant from water.

CHAPTER 3

THE UNGULATE COMMUNITY

3.1. Introduction

During the 1950s and 1960s, QENP supported one of the highest biomass of wild ungulates in the world (Petrides & Swank 1965; Field & Laws 1970; Leuthold & Leuthold 1976). Political unrest in the country during the 1970s, however, resulted in large scale poaching and a massive decline in the populations of many species (Eltringham & Malpas 1976, 1980; van Orsdol 1979; Malpas 1980) including elephant (Table 3.1).

Table 3.1. Elephant abundance in Queen Elizabeth National Park, Uganda, illustrating the recent decline in game numbers.

Year	Number
1963	1574
1964	1759
1966	2888
1967	3448
1968	2267
1969	3265
1970	2042
1971	2222
1972	2209
1973	2264
1974	1450
1975	1047
1976	968
1980	153
1982	300*

Sources: Annual Report of the Nuffield Unit of Tropical Animal Ecology 1963-1971; Buss & Savidge (1966); Field (1971); Eltringham & Malpas (1976, 1980); Eltringham (1977); Malpas (1980). *An estimate from several sightings within the park.

To restore the integrity and security of the national parks the Government of Uganda with the co-operation of the United Nations Development Programme (UNDP), European Economic Community (EEC) and Frankfurt Zoological Society (FZS) launched a major drive in 1980 to stamp out poaching. The decline in poaching activity in QENP (Table 3.2) indicates that, in the short term, the program was successful in reducing the level of poaching.

Table 3.2. The number of poaching incidents recorded by author in QENP, Uganda, between 1980 and 1983.

Year	Observed
1980	26
1981	7
1982	1
1983 (1st 6 months)	1

df=3, X^2=48.08, P<<.01***

A park-wide aerial survey made in March 1980 (Malpas 1980) showed that elephant numbers had fallen dramatically. To look further into the matter, five areas (see Fig. 2.4) where ground counts had been made in the past were re-surveyed. All five had been studied by Field & Laws (1970) and four were studied by Petrides & Swank (1965).

3.2. Methods

3.2.1. Counts

The census method used was similar to that of Petrides & Swank (1965) and

Field & Laws (1970). It involved two observers counting from the roof of a hard-top Land Rover driven over a series of approximately-parallel transects about 800 m apart. Each observer counted a strip 400 m wide on one side of the vehicle. The observers instructed the driver to stop from time to time to enable them to enumerate large herds or to make closer inspection with binoculars. During periods of heavy smoke haze in the dry season or in areas where visibility was poor due to dense vegetation, transects were closer together. Each area was covered as completely as possible.

In contrast to procedures in the other areas and because of difficult terrain, counts in Area 3 (the Craters highlands) were made largely from a track. In the south, the route provided good observation points overlooking relatively open country and permitted effective area counts. In the north, visibility was often poor due to tall grass and dense regeneration of acacia trees. There, transect were about 400 m apart except after fires when improved visibility allowed more normal procedures.

Counts were made once a month at about the same time each month. All animals seen were recorded on outline maps along with information on their sex, age, and group size. Familiarity with the areas contributed to considerable accuracy in locating the position of animals. Animals which were intolerant of approach had their numbers estimated first and counted later, if closer observation was possible. With experience, the estimates proved to be close approximations of subsequent counts and are believed to have introduced no large errors. The chance of recording the same animals twice was slight since herds could easily be identified by size, composition and the presence of recognizable individuals.

The assumptions of the census method were (1) that all animals present in an area were visible to observers and (2) that they could be counted accurately. In practice, smaller animals (e.g. warthog) and those with retiring habits (e.g. bushbuck and reedbuck) were more likely than others to be missed. Warthog are also sensitive to temperature fluctuations (Sowls & Phelps 1965) and probably sought shelter underground during cool periods.

Even large and readily-seen ungulates may be difficult to count accurately. Kob, in particular, occurred in large herds which were constantly in a state of flux and very difficult to record. Some buffalo herds were intolerant of approach and would stampede before observers were close enough to count accurately. The method is inappropriate for nocturnal animals. These were mostly either carnivores or omnivores with little impact on the vegetation. The abundance and distribution of rats, mice and other small mammals not assessed in this investigation have been studied in detail by Neal (1967).

In spite of its limitations, the ground census method was an invaluable tool for estimating animal abundance, particularly those of the large and most important members of the ungulate community.

Hippopotamus on land or in wallows were recorded during counts. These represented only a small fraction of those using the area at night, however, especially in Areas 1 and 2. To obtain the numbers that regularly used these areas, counts of hippopotamus along the adjacent shoreline were made using a boat and outboard motor. During the count, two observers with binoculars scanned the water ahead of the boat. The behavior of hippopotamus in this area is such that initially, as a school is approached, few are seen. Then at about 50-100 m, they evidently sense the approach of the boat and surface for a short period before they submerge and take evasive action. During this brief time, the school is counted repeatedly. The maximum number obtained is assumed to be the number present and was recorded. Counts were made on a monthly basis in Area 1 but could be conducted only occasionally in Area 2 due to limited availability of supplies, equipment and man-power.

3.2.2. Variability in numbers

The question of whether the monthly counts were representative samples of ungulate populations was raised during a series of ground counts similar to those made in this study (Field & Laws 1970). Eltringham (1973) made an assessment of the variability in those counts and concluded that they were adequate. The variability of counts in this study was assessed using one-way analysis of variance.

3.2.3. Distribution with respect to habitat

The five census areas represented three types of habitat. Area 3 was an area of long grass distant from water. Areas 4 and 5 were relatively-open medium-height grasslands with scattered thickets somewhat distant from water. Areas 1 and 2 were a habitat of short grass with dense thickets close to water.

The abundance of each ungulate species in the three habitats was compared. A 3-way analysis of variance (ANOVA) show the relative importance of various populations in different habitats. The density of a species in one habitat relative to another was assumed to be evidence of preference.

3.2.4. Seasonal fluctuations in animal numbers

A 1-way ANOVA was used to test the hypothesis that the wet and dry season means were the same for each species in each study area.

3.2.5. Population structure

Due to the low numbers of animals in census areas, data on group size, age structure and sex ratio were collected for the whole sector between the Kazinga Channel and the equator. This was necessary to increase sample size as well as to make the results more representative of the sector. Trips were made regularly to various parts of the sector to collect data.

<u>Group sizes:</u> A group was defined as the number of individuals found within 100 m of each other. A single animal was treated as a group of one. Whenever a group was found partly within and partly outside a census area during a count, the number outside the area was included in the group size data but excluded from the census data.

<u>Age structure and sex ratios:</u> The sex and relative age (such as adult, sub-adult, etc.) of each animal in a group were recorded during counts and other sightings. Relative age was based primarily on body size and horn development. An animal classified as adult was a fully grown individual. Sub-adults and juveniles were about three-quarters and one-half adult size, respectively. Calves were recent offspring.

In many instances it was not possible to determine the sex of buffalo with certainty because the herds were wary and fled when approached. Routine sexing of hippopotamus immersed in water was also not possible.

3.2.6. Long-term trends

The large-herbivore community of Mweya Peninsula (Area 1) has been studied almost continuously between 1956 and 1983 (Petrides & Swank 1965; Field & Laws 1970; Eltringham 1974, 1980; Yoaciel 1981; this study). Abundance of the major species over the 27-year period was analyzed to reveal trends in population.

3.3. Results

3.3.1. Counts

Sixty nine counts were made in Area 1 and 19 each in Areas 2, 3, 4 and 5. The average number of animals ranged from a low of 185.0 (11.7% of total) in Area 1 to a high of 528.9 (33.4%) in Area 5 (Table 3.3). Kob,

Table 3.3. Average large herbivore numbers in the study areas, Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

	Study areas						
Species	1	2	3	4	5	Total	%
Elephant	13.9	11.1	0.5	0.0	0.1	25.6	1.6
Warthog	7.1	14.0	2.5	8.2	3.5	35.3	2.2
Hippopotamus	149.4	148.5	0.0	0.1	0.0	298.0	18.8
Reedbuck	0.0	0.0	1.3	1.7	0.8	3.8	0.2
Waterbuck	0.0	14.4	17.8	4.3	1.5	38.0	2.4
Kob	0.1	31.7	215.8	271.2	499.3	1018.1	64.3
Bushbuck	5.6	10.9	0.5	1.5	1.1	19.6	1.2
Buffalo	8.9	40.7	24.6	48.9	22.6	145.7	9.2
Total	185.0	271.3	263.0	335.9	528.9	1584.1	
Percentage	11.7	17.1	16.6	21.2	33.4		100.0

hippopotamus and buffalo were the most numerous species. They constituted 64.3, 18.8 and 9.2% of total numbers, respectively. All the other species combined accounted for less than 8% of the total numbers recorded.

Hippopotamus were abundant in Areas 1 and 2 with densities of 34.0 and 11.5/sq km, respectively (Table 3.4). Their abundance was associated with the proximity of these areas to water. They were virtually absent from the study areas distant from water.

Large concentrations of kob occurred in Areas 4 and 5 where densities of 15.9 and 19.9/sq km, respectively, were recorded (Table 3.4). Their densities in other areas were much lower. In Area 1, they were virtually absent. No other species had a density higher than 3.2/sq km in any study area.

Table 3.4. Average large mammal densities/sq km in study areas, Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

Study area	1	2	3	4	5
Area (sq km)	4.4	12.9	26.2	17.1	26.2
No. of counts	69	19	19	19	19
Elephant	3.1	0.9	0.0	0.0	0.0
Warthog	1.6	1.1	0.1	0.5	0.1
Hippo	34.0	11.5	0.0	0.0	0.0
Reedbuck	0.0	0.0	0.0	0.1	0.0
Waterbuck	0.0	1.1	0.7	0.2	0.1
Kob	0.0	2.5	8.2	15.9	19.1
Bushbuck	1.3	0.8	0.0	0.1	0.0
Buffalo	2.0	3.2	0.9	2.9	0.9
Total	42.0	21.1	9.9	19.7	20.2

When the average densities obtained in this study are compared with those of 1956/57 and 1963/67, it is apparent that the abundance of large mammals have changed considerably (Tables 3.5). It is also evident that for most species and in most study areas, the changes have been reductions. Elephant and buffalo show the largest decline. For elephant, the magnitude of the reduction has amounted to percentage changes of -47.9 and -74.3 from average densities in 1956/57 and 1963/67, respectively. Corresponding figures for buffalo are -60.9 and -86.2. The decline of large mammals generally, and of big game specifically, has been due to intensive poaching in the park between 1973 and 1980 (Edroma 1973; Eltringham & Malpas 1976, 1980; van Orsdol 1979; Malpas 1980).

Table 3.5. Percentage changes in densities of large herbivores in 1981/83 from 1956/57 and 1963/67 levels in Queen Elizabeth National Park, Uganda.

	Compared with 1956/57*				Compared with 1963/67**				
	Study areas								
Species	1	2	3	4	1	2	3	4	5
ELE	+81.6	-74.4	-98.7	-100.0	+2.9	-75.5	-99.0	-100.0	-100.0
WHG	-78.8	-59.2	+138.5	-43.6	-78.8	-62.6	+377.1	-56.8	-74.8
HIP	-	-	-	-	+3631.3	-43.9	0.0	-99.9	-100.0
RBK	0.0	0.0	+24.0	-17.2	0.0	0.0	+65.4	-33.7	-82.0
WBK	-100.0	-66.8	+195.5	-59.4	-100.0	-68.3	+83.6	-79.4	-96.9
KOB	0.0	+434.2	+6763.9	-14.1	+13.6	+667.9	+715.5	+58.8	-56.6
BBK	-57.7	-56.5	+INFIN	+119.3	-53.7	+14.2	+90.8	-53.8	+39.9
BUF	-45.5	-21.5	-92.4	-84.3	-91.8	-82.1	-80.1	-83.7	-93.3

*Petrides & Swank (1965); **Field & Laws (1970).

Despite the general decline in abundance, there has been an increase in game in Area 3 (the Craters highlands) (Table 3.5). The largest increases were for kob, with percentage changes of +6763.9 and +715.5

from 1956/57 and 1963/67 levels, respectively. Warthog, too, show a large percentage increase in this study area. The numbers of warthog were initially extremely low, however, so that even a modest increase resulted in a large percentage change.

Kob increased in most study areas and decreased significantly only in Area 5 (Table 3.5). The decrease in this study area represented a major change in kob distribution. Large concentrations of kob associated with communal territorial grounds have been a feature of this area for a long time (Buechner 1961; Buechner & Schloeth 1965; Modha 1972).

The decline in kob abundance in Area 5 is believed to have been due to poaching. The study area is bounded by heavily-travelled roads that provide poachers with easy access. From January 1980 to June 1983, the author recorded more incidents of poaching in this study area than in the others combined. It is believed that harrassment by poachers forced some animals to move to less accessible areas. The large increase in the number of kob in Area 3 supports this view.

There were also examples of local exceptions to the general decline. The most dramatic involved the increase in hippopotamus in Area 1 where a percentage increase of +3631.3 occurred relative to their 1963/67 density (Table 3.5). The large increase was due, in part, to the fact that counts in 1963/67 were made during a period of hippopotamus cropping which virtually eliminated the species from the area (Field & Laws 1970). It also emphasizes the remarkable recovery that the hippopotamus population has made since the cropping program ended. Hippopotamus density during this study was higher than the 1956/57 and 1963/67 levels and occurred at the expense of all other species.

Area 1, the Mweya Peninsula (see Section 2.2), is the only study area in which elephant showed a modest increase (Table 3.5). This study area is, however, only 4.4 sq km in size. Given the propensity of elephant to range over wide areas, such a small study area could not be expected to have nor did it have a resident elephant herd. Elephant were, however, found there more frequently than in any other study area. The reason for the restricted movement was probably security. Area 1 was the site of the park headquarters. For this reason, the area and its surroundings (including Area 2) were avoided by poachers despite the breakdown of law and order in the rest of the park. As the most secure site in the entire park, it is suggested that it was used more frequently and intensively than it would otherwise have been.

Table 3.6. Average standing-crop biomass (kg/ha) in the study areas, Queen Elizabeth National Park, Uganda. November 1981-June 1983.

Species	Unit weight (kg)	Study areas 1	2	3	4	5
Elephant	1700	53.53	14.52	0.31	0.00	0.03
Warthog	50	0.80	0.54	0.05	0.24	0.07
Hippo	1000	339.59	114.23	0.00	0.02	0.00
Reedbuck	50	0.00	0.00	0.02	0.05	0.02
Waterbuck	160	0.00	1.77	1.09	0.40	0.09
Kob	65	0.01	1.58	5.35	10.31	12.39
Bubshbuck	50	0.64	0.42	0.01	0.04	0.02
Buffalo	395	7.98	12.36	3.71	11.29	3.41
Total		402.55	145.42	10.54	22.36	16.03

The species of ungulates involved in the study vary greatly in size and weight, and consequently in their energy demands on the environment.

Due to these differences, comparisons of biomass rather than numbers may be a more valid measure of the relative importance of a species in the environment (Table 3.6). The unit weights used in calculation were taken from Field & Laws (1970) and were derived from studies of animal populations in the park. The age structure of the populations was taken into consideration in estimating average individual weights. These weights are substantially lower than those used by some authors (e.g. Petrides & Swank 1965).

Since these weights were determined, many populations have suffered high mortality as a result of the intensive poaching of the 1970s. There is a possibility, therefore, that the age structures and unit weights of the populations studied were quite different. Until new average weights are determined, however, these remain the best estimates available.

From the data (Table 3.6), it is evident that elephant, hippopotamus and buffalo dominated the standing-crop biomass of ungulates in the study areas. Although hippopotamus accounted for only 18.8% of animal numbers (Table 3.3), they constituted 76.0% of the biomass. Similarly elephant constituted only 1.6% of the numbers but 11.5% of the biomass. Kob, on the other hand, contributed 64.3% of the numbers but only 5.0% of the biomass. The ungulate biomass in the study areas evidently was dominated by the few large species.

3.3.2. Variability in numbers

Overall variability in numbers of most species was high (Table 3.7). Hippopotamus numbers along the shoreline showed little variability in contrast to large fluctuations in numbers seen on land. This is not

Table 3.7. Summary of counts of large mammals in the study areas in Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

		Study areas 1	2	3	4	5
No. of counts		69	19	19	19	19
Elephant						
	Mean	13.86	11.11	0.47	-	0.05
	SD	32.37	34.60	2.06	-	0.23
	Range	0-143	0-150	0-9	-	0-1
Warthog						
	Mean	7.07	13.95	2.47	8.21	3.47
	SD	2.33	7.60	3.99	6.16	6.23
	Range	1-12	3-28	0-14	0-20	0-28
Hippopotamus (on land)						
	Mean	17.07	0.37	-	0.05	-
	SD	16.55	0.60	-	0.23	-
	Range	0-75	0-2	-	0-1	-
Reedbuck						
	Mean	-	-	1.26	1.68	0.84
	SD	-	-	2.98	2.69	1.77
	Range	-	-	0-12	0-12	0-6
Waterbuck						
	Mean	-	14.42	17.84	4.26	1.47
	SD	-	9.20	19.67	8.93	3.44
	Range	-	0-39	0-76	0-33	0-14
Kob						
	Mean	0.06	31.68	215.79	271.16	499.32
	SD	0.34	59.88	185.73	239.91	361.76
	Range	0-2	0-260	7-629	27-1122	37-1417
Bushbuck						
	Mean	5.62	10.89	0.47	1.47	1.11
	SD	3.59	6.45	0.96	1.54	1.76
	Range	0-16	2-27	0-3	0-4	0-6
Buffalo						
	Mean	8.88	40.68	24.58	48.89	22.63
	SD	11.91	36.94	39.33	39.01	70.64
	Range	0-42	0-125	0-124	0-98	0-305
Hippopotamus (along shoreline)						
	Mean	149.42	148.50	-	-	-
	SD	23.44	17.03	-	-	-
	Range	111-198	122-169	-	-	-

surprising as hippopotamus habitually return to the water by day. The numbers of warthog, too, were relatively stable. The warthog is largely a sedentary animal and individuals in an area were probably resident. A major cause of variability in warthog was the tendency of individuals to go underground during cool weather (Sowls & Phelps 1965; Clough & Hassam 1970). They also lay under thickets during the heat of the day and could have been overlooked.

Numbers of kob were less variable than those of waterbuck. This was probably because kob tend to aggregate in large herds which remain in one area for considerable periods. Waterbuck, on the other hand, were less common and could be more easily overlooked. They also wander over a larger home range (Spinage 1967, 1982). The numbers of bushbuck were more variable than would be expected from their restricted home range (Waser 1975; Allsopps 1978; Okiria 1980). Variability of this species is, at least in part, due to the low numbers recorded. Areas with particularly low numbers (3, 4 and 5) showed the greatest variability. Bushbuck are retiring in habit and are easily overlooked. Their numbers were estimated to be up to 2.6 times higher than those normally recorded (Waser 1975). Reedbuck occurred in only a few areas and in such low numbers that few conclusions can be drawn from the results.

Counts of buffalo were quite variable. The large variability was due to periodic movement of herds into and out of study areas. Irregular arrivals or departures of herds of various sizes affected the variability of counts.

Variability in counts of elephant was probably due to their ability to range over large areas. This result was not expected in view of their apparent confinement to Areas 1 and 2. None of the census areas was, however, large enough to support a resident population of elephant.

The preceding discussion suggests that variability was influenced by several factors. In the case of small animals or those with retiring habits, variability was partly due to observers failing to see all the individuals present. Species in this category included bushbuck, reedbuck and warthog. For other species, variability was due to movement which took animals out of an area in which they were counted or, conversely, into an area from which they were previously absent. Examples of such species are elephant and buffalo. There were species, such as kob, which were conspicuous and relatively sedentary but were difficult to count accurately. Kob frequently occurred in large herds which were constantly in a state of flux and difficult to enumerate.

3.3.3. Distribution according to habitat

The various species of large herbivores were not uniformly distributed in the study areas. Each species was relatively abundant in some areas and uncommon in others (Tables 3.4 & 3.6). Of the three habitat types studied, the site closest to water (Areas 1 and 2) supported the highest and the tall grassland (Area 3) the lowest biomass (Table 3.8).

Elephant and hippopotamus occurred almost exclusively in the habitat of short grass with dense thicket close to water (Table 3.8). There, hippopotamus and elephant accounted for 82.9 and 12.4%, respectively, of total biomass. Neither contributed significantly to biomass in the habitats away from water.

The composition of standing-crop biomass in the habitats distant from water show a remarkable similarity (Table 3.8; Fig. 3.1). In both habitats, kob constituted over one-half and buffalo more than one-third

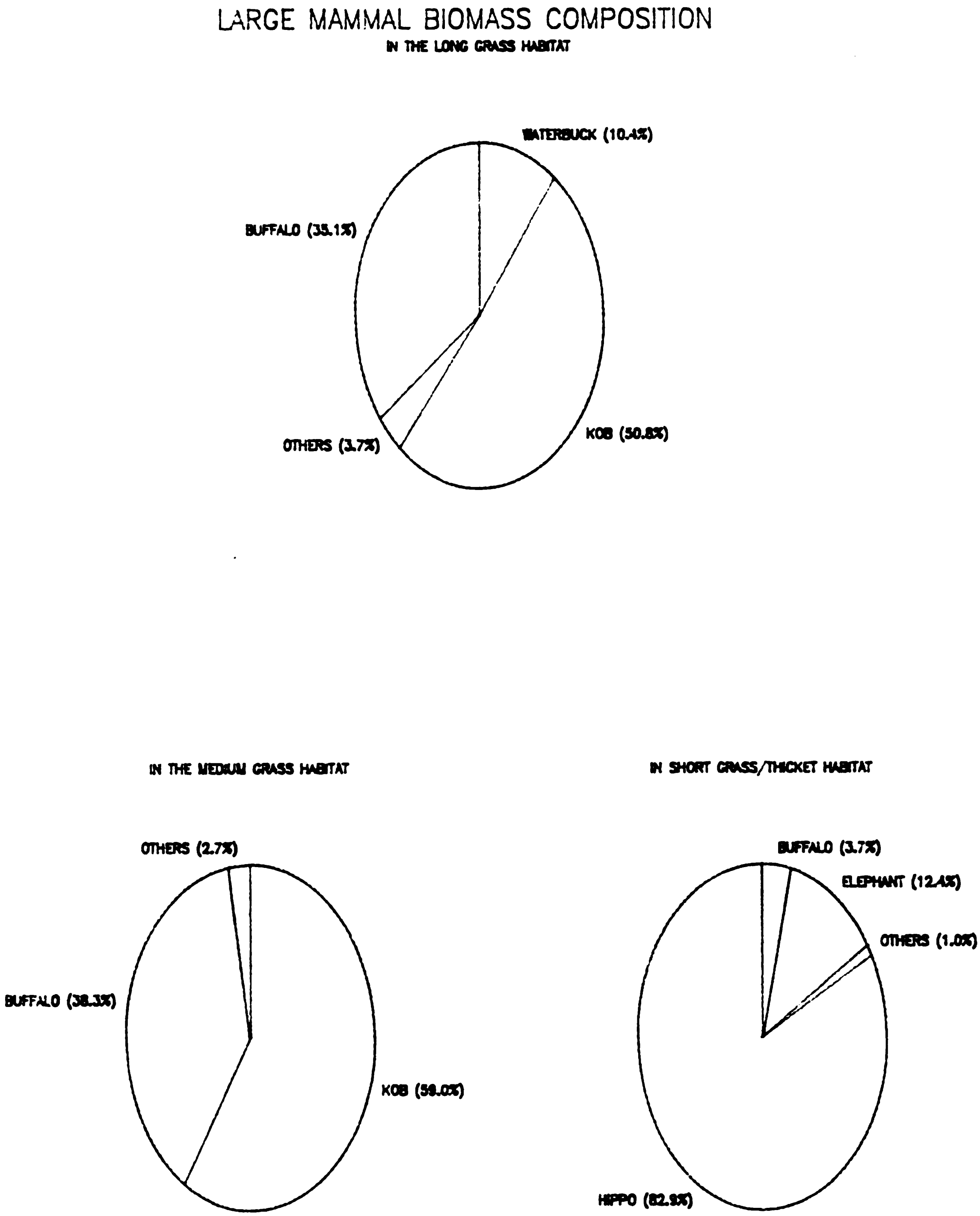

LARGE MAMMAL BIOMASS COMPOSITION
IN THE LONG GRASS HABITAT
WATERBUCK (10.4%)
BUFFALO (35.1%)
OTHERS (3.7%)
KOB (50.8%)
IN THE MEDIUM GRASS HABITAT
OTHERS (2.7%)
BUFFALO (38.3%)
KOB (59.0%)
IN SHORT GRASS/THICKET HABITAT
BUFFALO (3.7%)
ELEPHANT (12.4%)
OTHERS (1.0%)
HIPPO (82.9%)

Fig. 3.1.

Table 3.8. Average standing crop biomass (kg/ha) according to habitat type Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

Species	Habitat type: Tall grass, distant from water (1)		Medium-height grass, somewhat distant from water (2)		Short grass and thicket bushes, close to water (3)	
	Biomass	%	Biomass	%	Biomass	%
Elephant	0.31	2.9	0.02	0.1	34.00	12.4
Warthog	0.05	0.5	0.16	0.8	0.65	0.2
Hippopotamus	0.00	0.0	0.02	0.1	227.52	82.9
Kob	5.35	50.8	11.34	59.0	0.80	0.3
Buffalo	3.70	35.1	7.36	38.3	10.25	3.7
Others	1.12	10.6	0.32	1.7	1.39	0.5
Total	10.53		19.22		274.61	

the biomass. In contrast, kob contributed only 0.3% of the biomass in the habitat close to water and buffalo accounted for only 3.7%.

The results of a 3-way ANOVA to test for the impacts of replication, area and seasonality on species density and total biomass (excluding hippopotamus) show that most of the variability in species densities and total biomass were explained by differences between areas (Table 3.9) supporting the general impression of habitat preferences among ungulate populations.

3.3.4. Seasonal fluctuations in numbers

While the 3-factor ANOVA (Table 3.9) revealed no significant differences in species density between the dry and wet seasons (except for reedbuck, df = 1, F = 6.28, P =1.37), one-way ANOVAs showed significantly different values for bushbuck in Area 1 (df=1, F=2.84, P=9.29), warthog in Area 4 (df=1, F=5.49, P=2.99) and reedbuck in Areas 4 (df=1, F=3.16, P=9.01) and 5 (df=1, F=4.40, P=4.87). Error terms within seasons were generally large, however, indicating that the simple designation of dry versus wet was probably too crude a measure. Testing for each month of the dry and wet seasons as a sub-season, mean densities for sub-seasons were calculated from weekly counts made in Area 1. The results (Table 3.10) revealed significant differences for elephant (df=5, F=7.10, P=0.01), hippopotamus on land (df=5, F=2.52, P=3.77) and warthog (df=5, F=1.97, P=9.39).

The results of the one-way ANOVA confirmed that considerable variability occurred within seasons. Differences in results of the seasonal and sub-seasonal ANOVAs indicate that animal movement associated with moisture levels were hidden by the large variability within both dry or wet seasons. The results provide empirical evidence that large herbivores in the park were sensitive to and responded to changing conditions within seasons.

Despite the results of the 3-factor ANOVA (Table 3.9) which showed no significant differences in animal densities between seasons, field observations indicated that some species undertook local migrations of 10 to 15 km in response to environmental conditions. Kob and buffalo, for example, showed a tendency to move closer to permanent sources of water during the dry season. As a consequence, their dry season densities in habitats further from water were lower than wet season densities (Fig. 3.2), although the differences were not statistically significant.

Fig 3.2 Comparison of season densities

in habitats near and far from water.

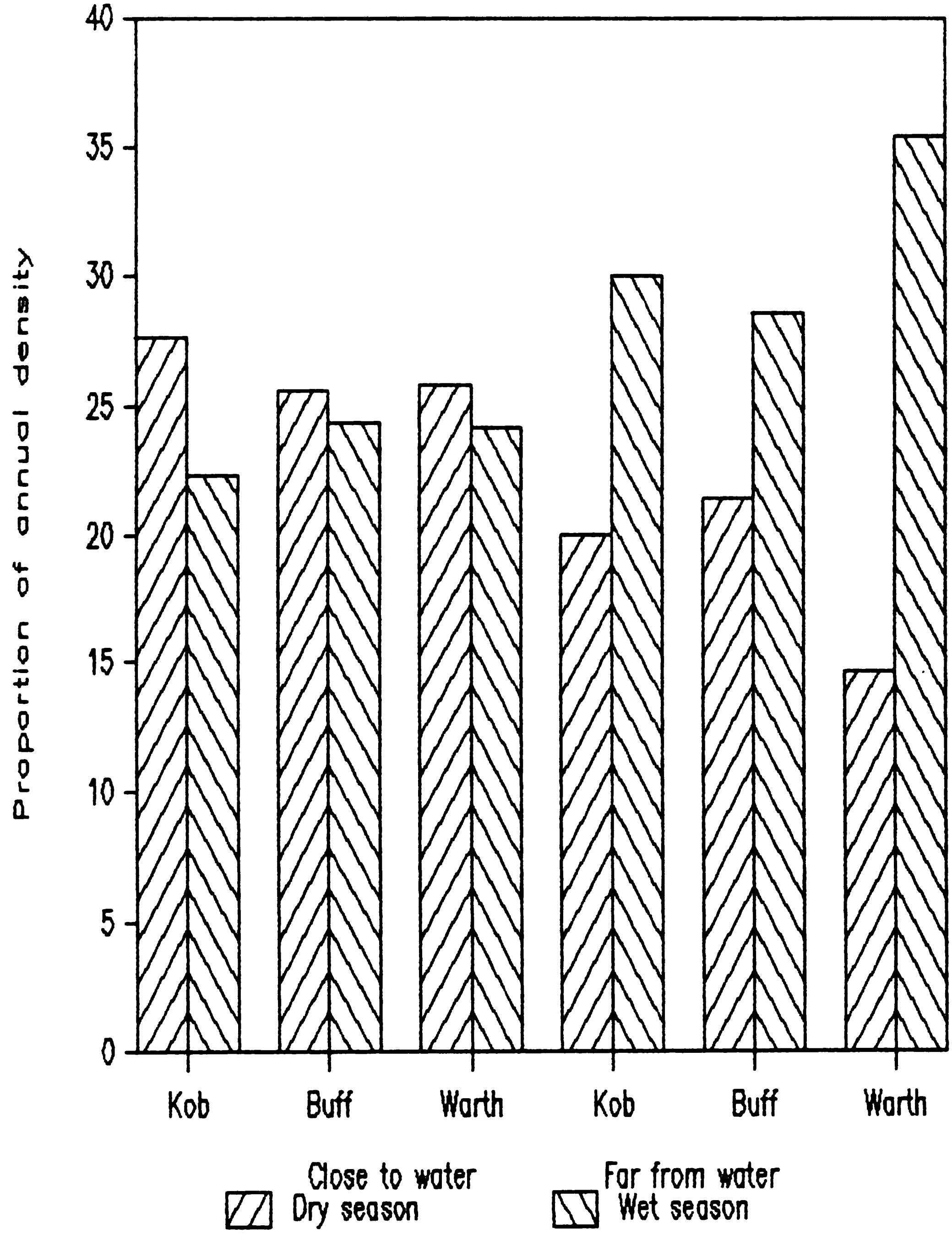


Table 3.9. Results of a 3-factor ANOVA to determine the impacts of season, area and replication on species density in the study areas, Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

		Elephant		Warthog		Hippopotamus	
	df	F	p%	F	p%	F	p%
Replication	9	0.91		1.81	7.88*	0.96	
Area	4	4.54	0.27***	74.04	0.0***	36.45	0.0***
Season	1	0.36		1.58	21.01	0.35	
Area x Season	4	0.13		1.86	12.48	0.35	
Residual error	77						
		Reedbuck		Waterbuck		Kob	
	df	F	p%	F	p%	F	p%
Replication	9	1.19	31.45	1.00	44.69	0.30	
Area	4	4.64	0.24***	16.49	0.0***	13.48	0.0***
Season	1	6.28	1.37**	2.60	10.73	0.21	
Area x Season	4	1.67	16.46	0.70		0.55	
Residual error	77						
		Bushbuck		Buffalo		Total biomass	
	df	F	p%	F	p%	F	p%
Replication	9	1.29	25.67	0.80		0.77	
Area	4	36.04	0.0***	3.77	0.77***	3.60	0.97***
Season	1	0.60		0.21		0.11	
Area x Season	4	0.32		0.50		0.23	
Residual error	77						

*Significant at 90% level; **significant at 95% level; ***significant at 99% level.

When weekly-count data in Area 1 were organized according to monthly sub-seasons (Table 3.11), the average numbers for warthog, bushbuck and hippopotamus along the shore were fairly constant, indicating negligible seasonal movement. These populations were, therefore, largely resident. A large influx of elephant occurred at the end of the dry season and was sustained into the beginning of the wet. Averages for hippopotamus on land were higher during the second and third months of the dry season, indicating an increased tendency to stay on land when forage was reduced in quantity. Buffalo increased at the end of the wet and the beginning of the dry season, the reverse of the pattern shown by elephant.

Table 3.10. Results of 1-way ANOVAs on sub-season data from study Area 1, Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

		Elephant		Warthog		Hippopotamus	
	df	F	p%	F	p%	F	p%
Total	68						
Between	5	7.10	0.01***	1.97	9.39*	2.52	3.77**
Within	63						

		Kob		Bushbuck		Buffalo	
	df	F	p%	F	p%	F	p%
Total	68						
Between	5	1.80	12.5	1.67	15.3	0.20	
Within	63						

	Hippo along shore		
	df	F	p%
Total	18		
Between	5	1.60	22.86
Within	13		

*Significant at 90% level; **significant at 95% level.

Table 3.11. Averagè numbers of animals in study Area 1 according to sub-seasons, Queen Elizabeth National Park, November 1981 to June 1983.

Sub-seasons*	Elephant	Warthog	Hippo**	Hippo***	Bushbuck	Buffalo
1	6.47	6.07	9.80	171.50	5.00	10.07
2	2.92	7.00	27.67	138.33	5.00	7.17
3	64.50	8.75	26.13	143.00	4.63	6.38
4	21.10	6.30	15.90	131.00	4.40	9.80
5	1.63	7.88	12.00	146.33	6.13	8.00
6	5.25	7.31	14.69	159.00	7.69	10.19

*1, 2 and 3 are respectively the 1st, 2nd and 3rd months of the dry, and 4, 5 and 6 are the 1st, 2nd and 3rd months of the wet season. Hippo** and Hippo*** are respectively counts of hippopotamus on land and along the shoreline.

3.3.5. Population structure

Group sizes:

Elephant: Fifty nine elephant groups were recorded. Their sizes ranged from 1 to 201 (Fig. 3.3a), with a mean of 39.6. Solitary animals comprised over 13% of the groups. More than half (53%) the groups were between 2 and 50. About 12% of the groups were larger than 100. The large groups probably represented multiples of family units which had banded together for safety and leadership (Laws et al. 1975).

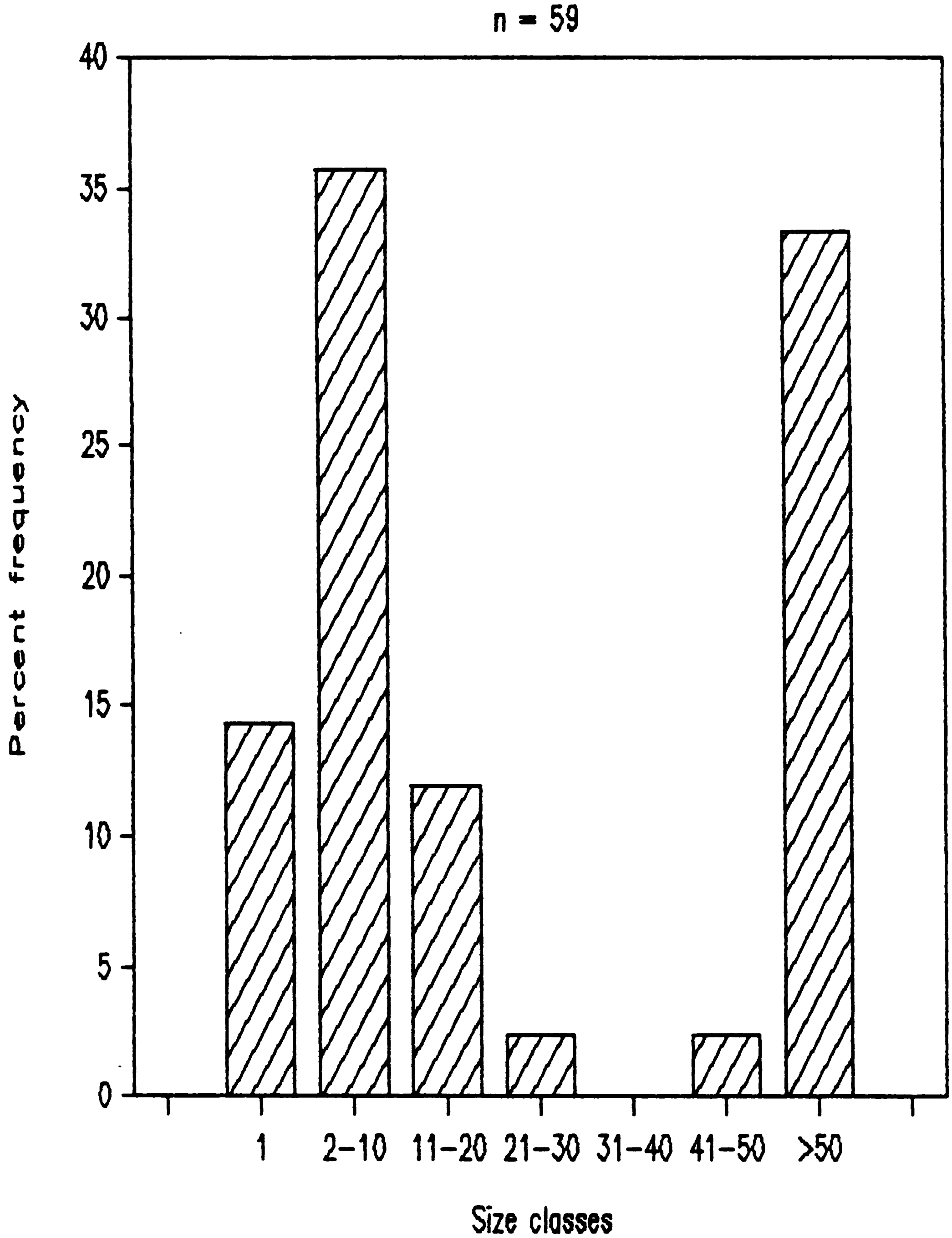
Warthog: Some 449 groups ranging in size from 1 to 13 were recorded (Fig. 3.3b). Fewer than 15% of the groups involved more than 4 individuals. Average group size was 2.5. Groups of one to 4 were common, with nearly 37% of the groups composed of solitary animals.

Hippopotamus: Of 385 groups of hippopotamus recorded along the shore, 20% were solitary animals and nearly 45% included 2-10 individuals (Fig. 3.3c). Those between 11 and 20 made up 15% and groups >20 comprised only 20% of total.

Reedbuck: Data on reedbuck were limited but indicated that individuals are predominantly solitary. The mean size for 67 groups was 1.4, with group sizes one and two comprising 66 and 32%, respectively, of the total observed. Groups larger than 2 comprised less than 2% of the total recorded (Fig. 3.3d). Reedbuck numbers and group size were influenced considerably by the occurrence of fire when then, temporary concentrations developed in relatively open areas. In the open, too, these cryptic antelopes were easier to see. The larger groups recorded in counts, including one of 12, were seen after fires.

Waterbuck: Some 178 groups, ranging in size from one to 38, were

Fig. 3.3a. Elephant groups



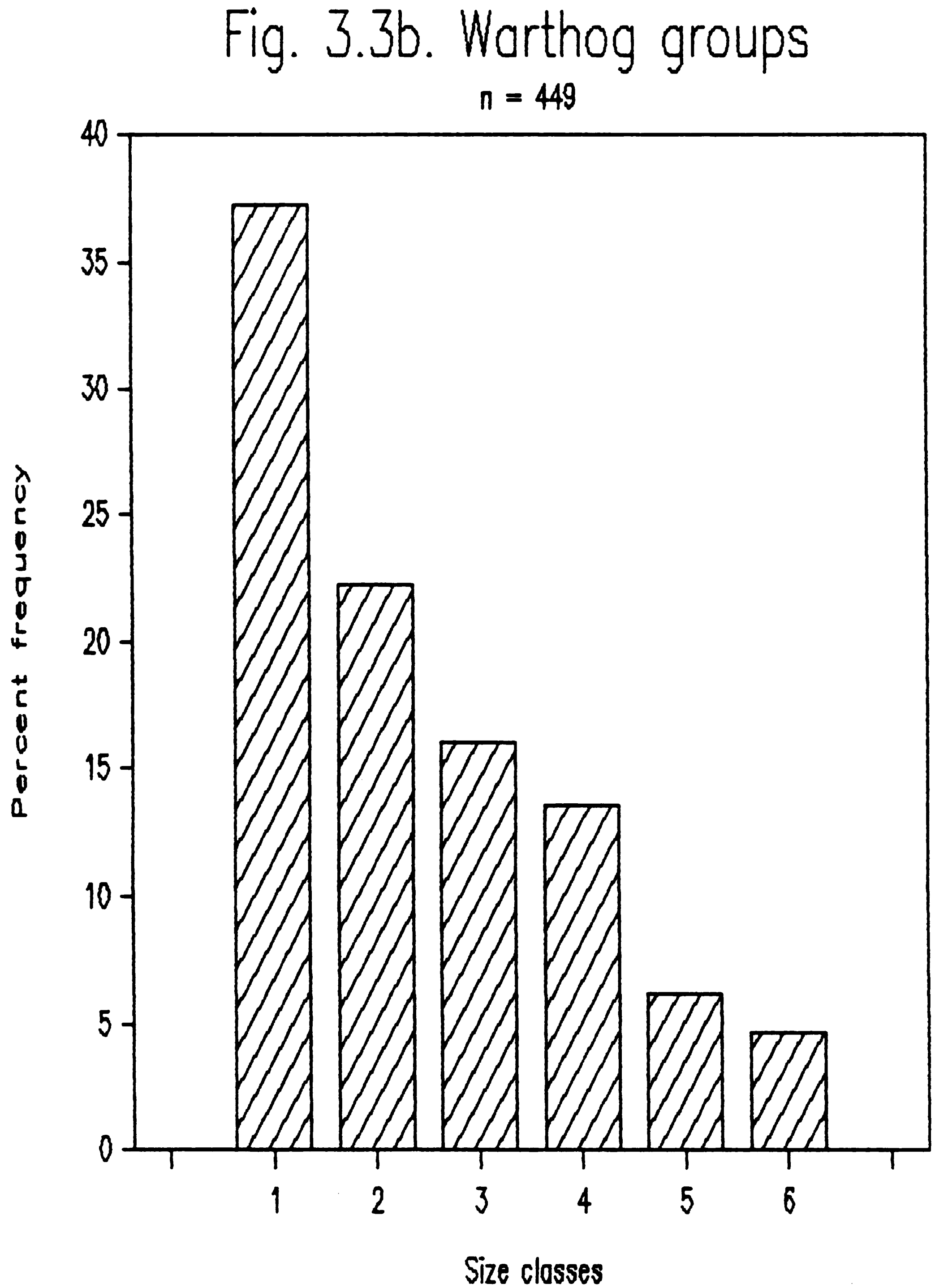
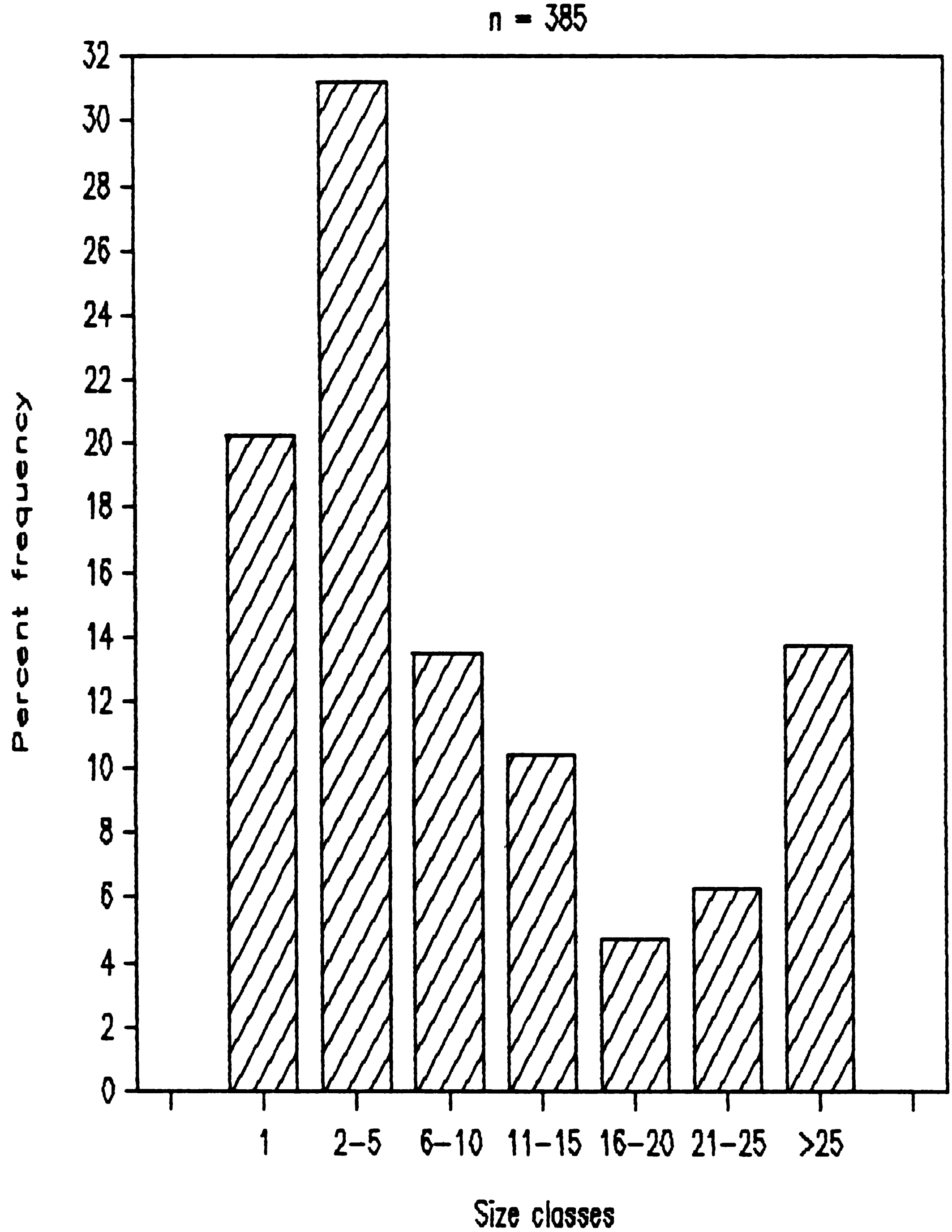


Fig. 3.3b. Warthog groups
n = 449
Percent frequency
0
5
10
15
20
25
30
35
40
1
2
3
4
5
6
Size classes

Fig.3.3c. Hippopotamus schools



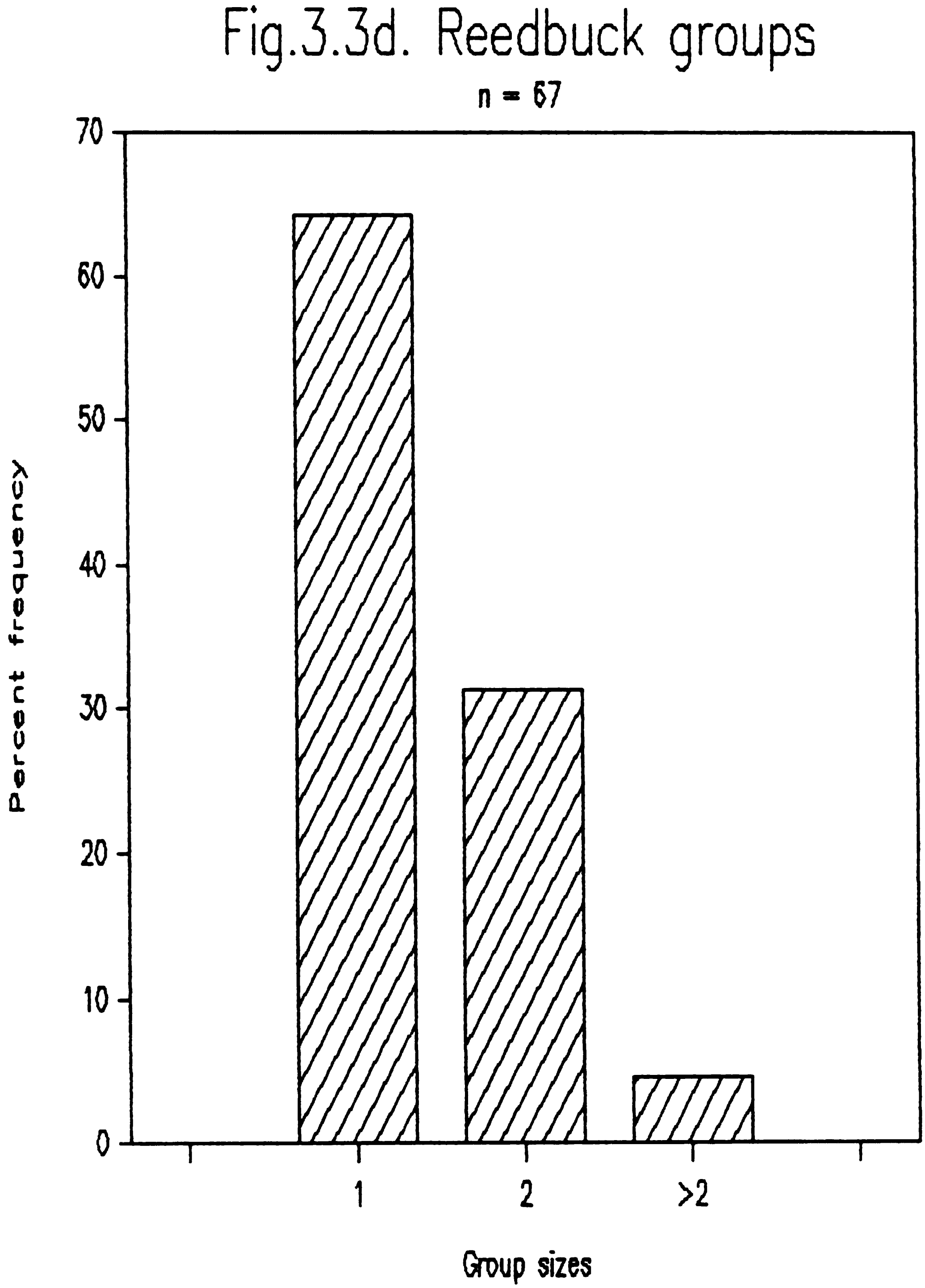
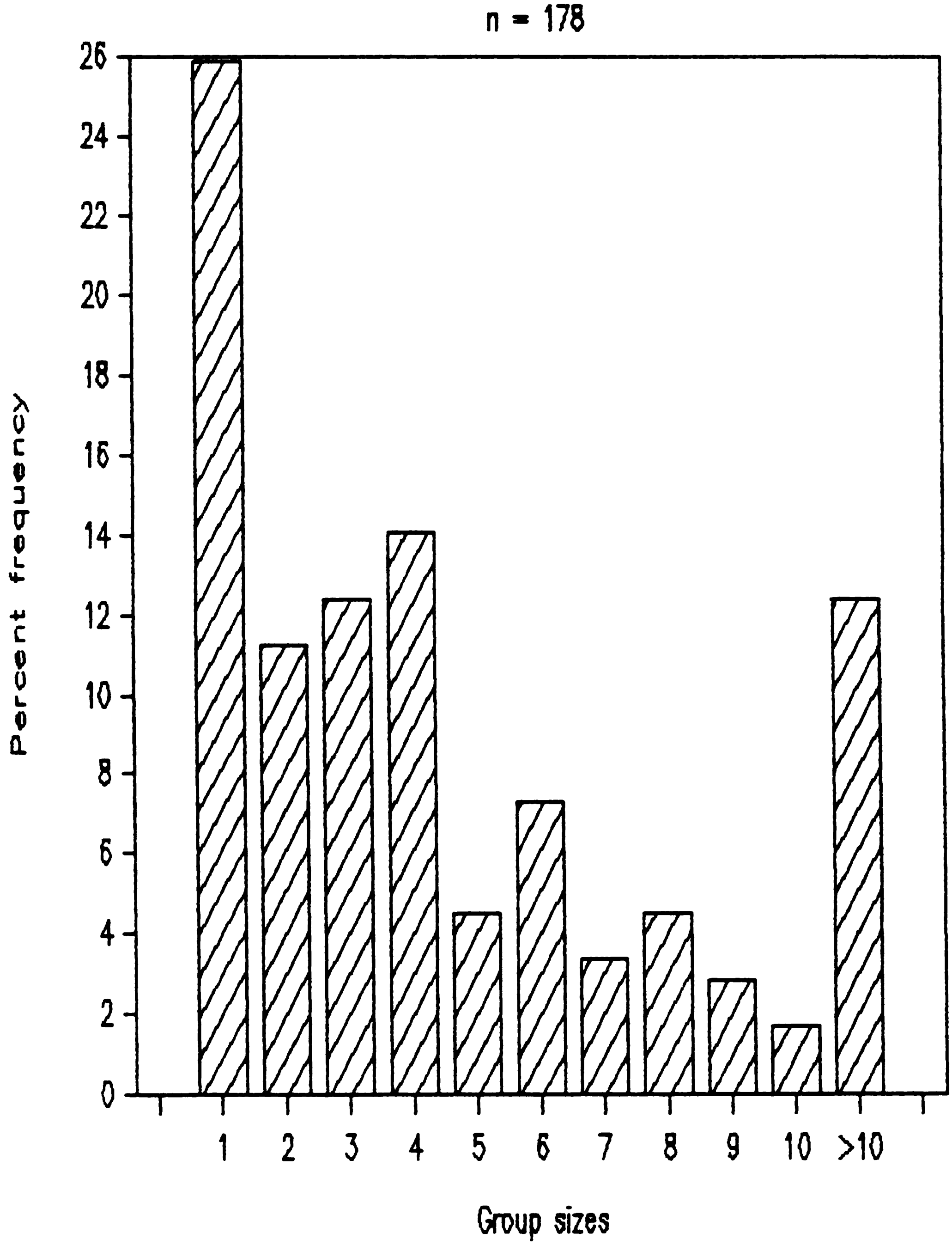


Fig.3.3d. Reedbuck groups
n = 67
70
60
50
40
30
20
10
0
Percent frequency
1
2
>2
Group sizes

Fig. 3.3e. Waterbuck groups



recorded (Fig. 3.3e). Solitary animals were the most common, accounting for nearly 26% of the groups recorded. Groups of 2 to 4 individuals were also frequent. Groups larger than 4 were increasingly less common. The average group size was 6.0. The preponderance of solitary animals was due to relatively large numbers of solitary adult males in the sample.

Kob: For most species, deciding what constituted a group presented little problem because groups tended to be quite distinct. In dealing with kob, however, it was not always easy, especially when confronted with large numbers of animals spread out over a large area. The social organization of these antelopes involves communual breeding territories (Buechner 1961). There were large numbers of animals associated with each territorial ground and large numbers of females and young circulated among territorial grounds located several km apart. These large congregations accounted for some very large groups recorded. Large groups also occurred in areas of tender green grass flushes.

Group sizes ranged from 1 to 1152 (Fig. 3.3f). In spite of the tremendous variability, average group size was surprisingly small (81.8). This was due to the presence of a large number of relatively small groups as well as to a large number of solitary males holding single territories.

Bushbuck: A total of 493 bushbuck groups was recorded (Fig. 3.3g). Groups ranged in size from 1 to 7, with a mean 1.2. Eighty three percent of the sightings were of solitary animals. The most frequent association was that of a female with calf, although mature animals of the same or opposite sex were also recorded. Groups larger than two were relatively rare. The largest group comprised 4 adult males and three adult females.

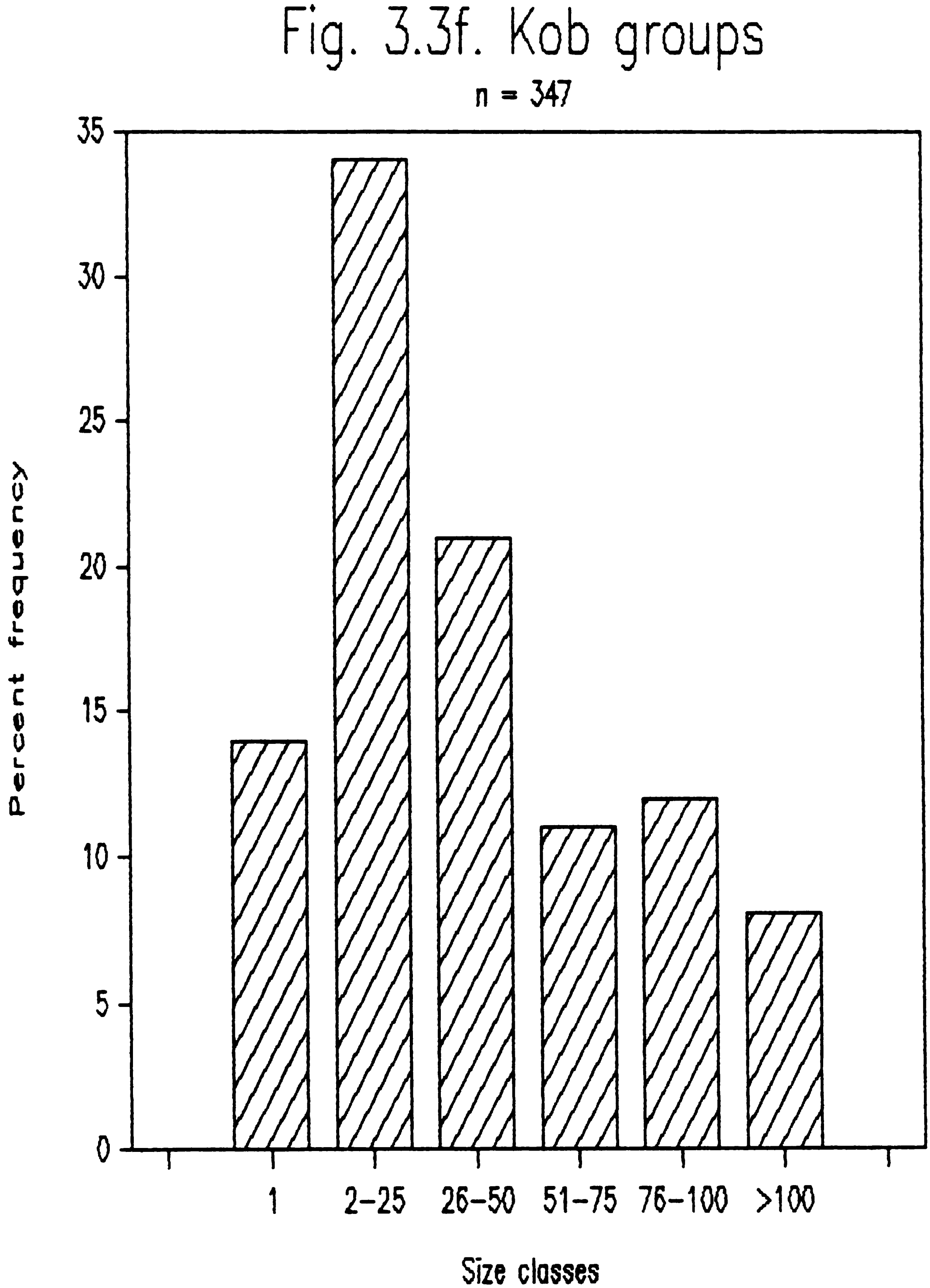


Fig. 3.3f. Kob groups
n = 347
Percent frequency
0
5
10
15
20
25
30
35
1
2-25
26-50
51-75
76-100
>100
Size classes

Fig. 3.3g. Bushbuck groups

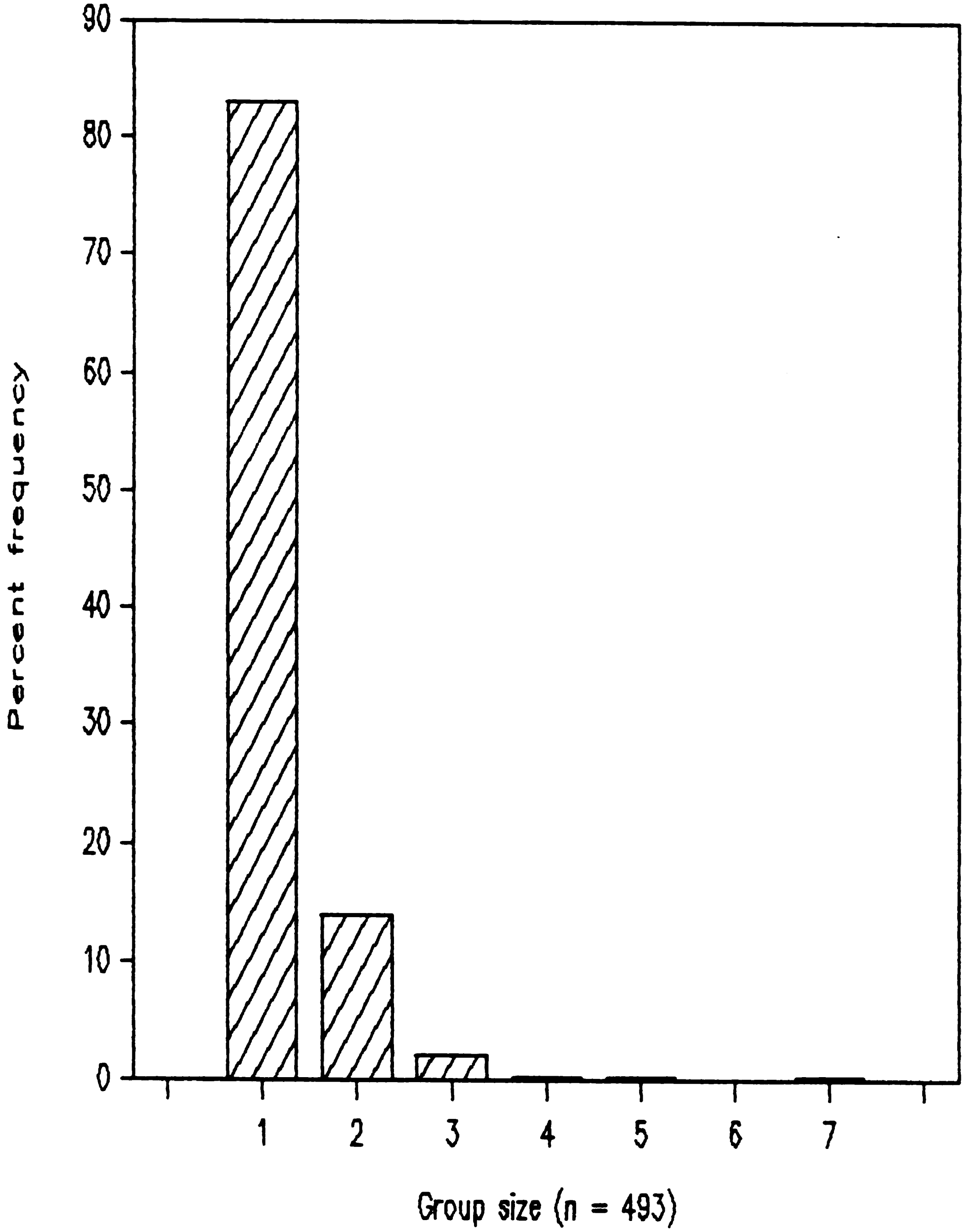


Fig. 3.3h. Buffalo: bachelor groups

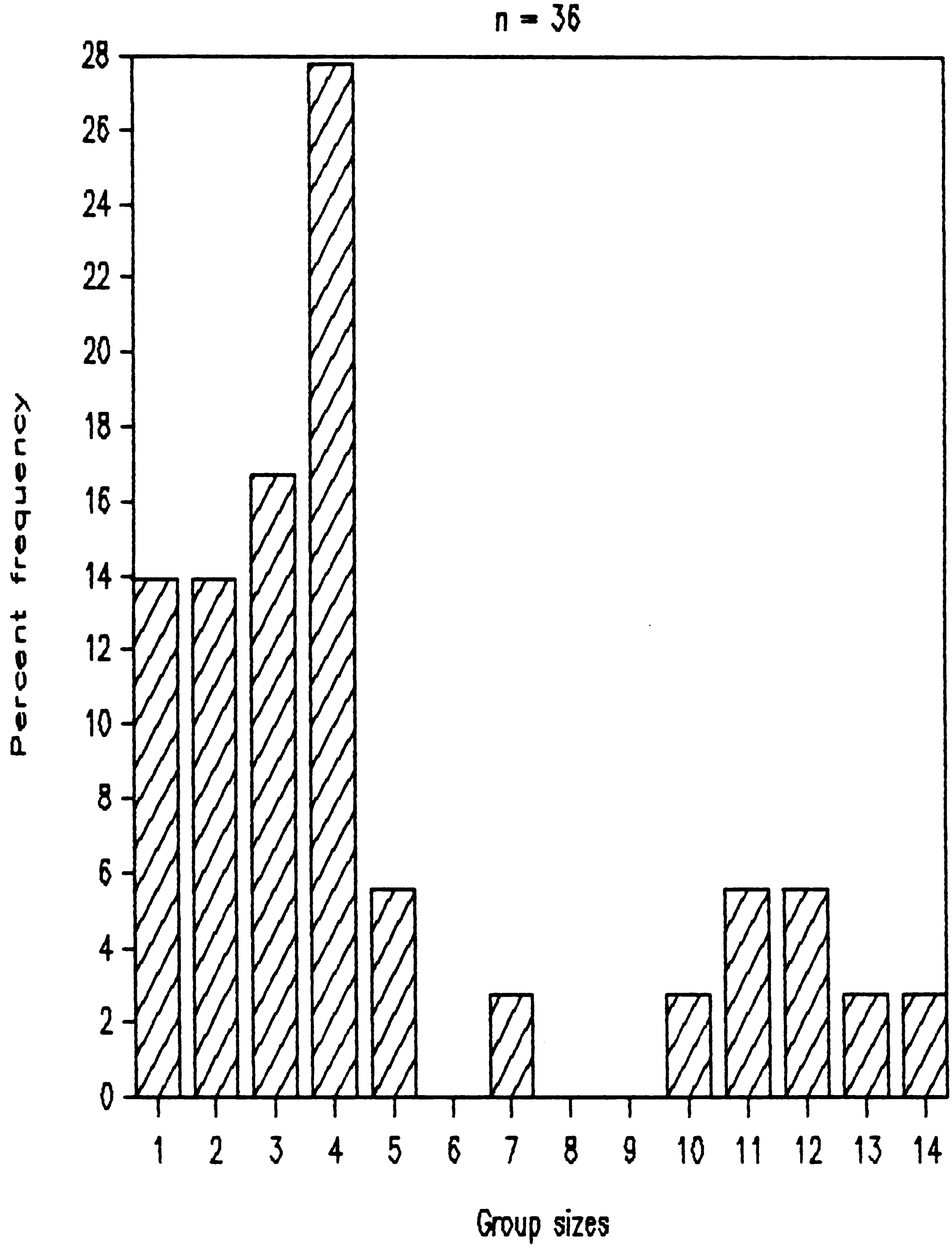


Fig. 3.3i. Buffalo: herds

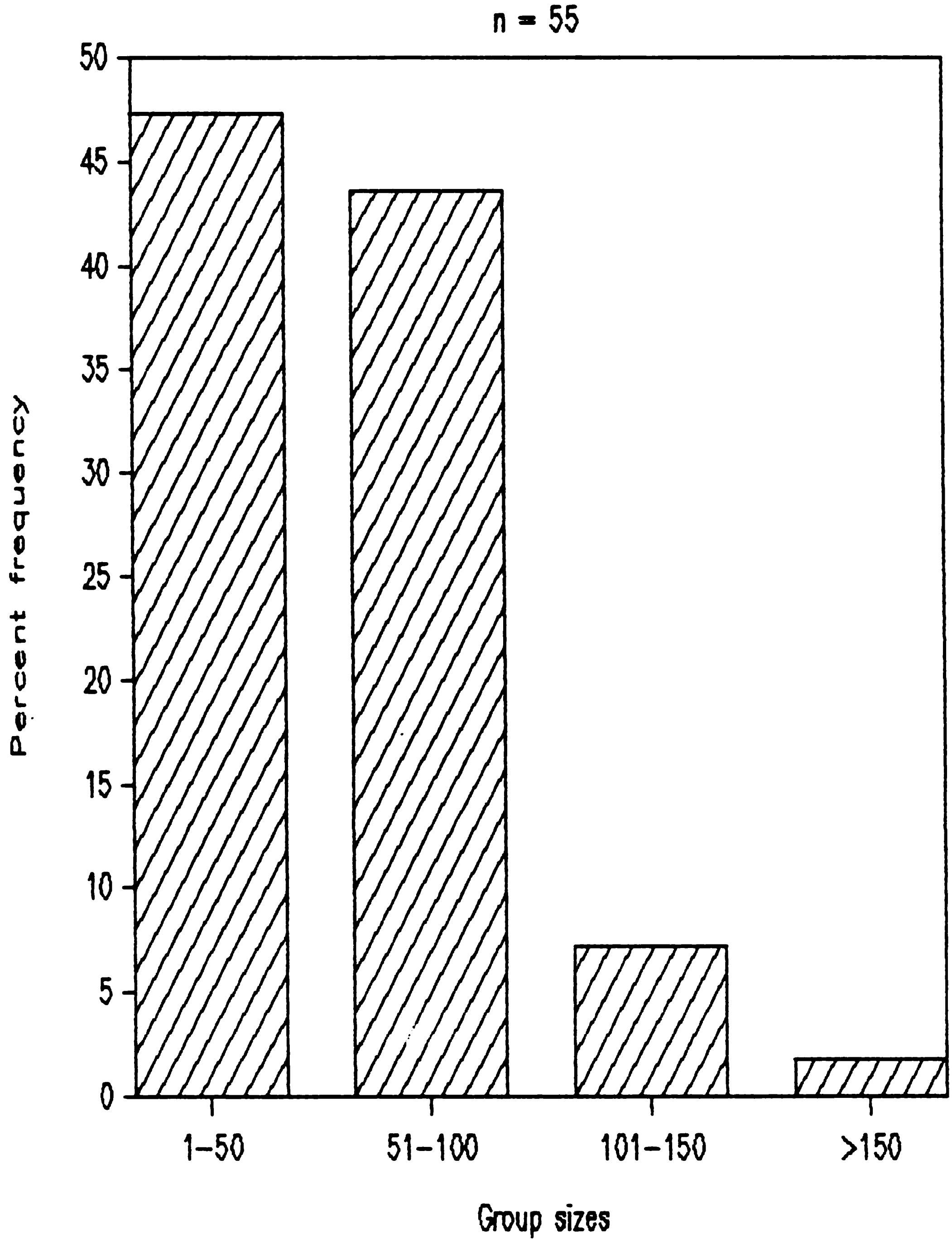


Table 3.12. Size distribution of buffalo bachelor groups, Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

Herd size	Frequency	Percentage
1	5	13.9
2	5	13.9
3	6	16.7
4	10	27.8
5	2	5.6
6	-	-
7	1	2.8
8	-	-
9	-	-
10	1	2.8
11	2	5.6
12	2	5.6
13	1	2.8
14	1	2.8

$n = 36, \quad \bar{X} = 4.8$

Table 3.13. The size distribution of buffalo herds in Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

Herd size	Frequency	Percentage
1 - 50	26	47.3
51 - 100	24	43.6
101 - 150	4	7.3
>150	1	1.8

$n = 55, \quad \bar{X} = 55.3$

Buffalo: Buffalo occur in two kinds of social units. One contains members of both sexes and are classified as `herds,' while the other is comprised of males only and are called `bachelor groups' (Eltringham &

Woodford 1971). Of 91 buffalo groups recorded, 36 (39.6%) were bachelor groups (Table 3.12; Fig. 3.3h) and 55 (60.4%) were herds (Table 3.13; Fig. 3.3i). Among bachelors, group sizes ranged from one to 14. Four was the most common group size and was recorded 27.8% of the time. The data show a slight increase in frequency with size up to 4. Few bachelor groups were larger than 4. The average size of bachelor groups was 4.8.

Among herd groups, sizes ranged from 2 to 305, with a mean of 55.3. Groups between 2-50 and 51-100 were about equally common. Only 5 of the 55 herds recorded were larger than 100.

Large herbivores typically exhibited three broad categories of groupings: (1) species such as elephant, buffalo, waterbuck, kob and hippopotamus occurred primarily in large groups; 2) others (e.g. warthog) commonly occurred in smaller groups or family units and 3) a few, such as bushbuck and reedbuck were predominantly solitary. These observations probably indicate that ungulate species large enough to see one another above the top of the grass tended to form herds, while those which are small in stature live solitarily or in small family groups.

Age structure and sex ratios:

In all six species for which sex ratios were determined, the proportion of females was higher than that of males (Table 3.14). Bushbuck showed the greatest disparity with a male-to-female ratio of 1 to 3.2. The ratio was closest to parity in reedbuck. The sex ratio in this species was 1:1.6.

The percentage of calves in the population ranged from a low of 0.2 for bushbuck to a high of 19.3 for warthog. Warthog was the only species among those studied which produced more than one offspring in a litter. The high proportion of early juveniles in its population relative to those of the other species was, at least in part, a reflection of this capacity.

Elephant, hippopotamus and buffalo had surprisingly high proportions of calves compared with the smaller species, except for warthog. This was unexpected given the greater longevity and lower reproductive rates of the larger mammals.

Sixty six percent of bushbuck recorded were adult females. The preponderance of adult females appears to be a feature of small to medium-sized antelopes. Reedbuck, kob and waterbuck also exhibited the phenomenon, with adult females constituting 52.1, 62.7 and 50.7% of the population, respectively.

Table 3.14. Age and sex classes of eight species of herbivores* in Queen Elizabeth National Park, Uganda, November 1981 to June 1983.

Species	Number in sample	Percentage of age/sex classes in population: Adult male	Adult female	Sub-adult male	Sub-adult female	Juvenile male	Juvenile female	Calves	Sex ratio m:f
Elephant	1856	12.7	33.4	11.3	21.5	6.6	5.9	8.6	1:2.3
Warthog	1106	30.4	37.4	3.4	5.2	1.5	2.8	19.3	1:1.8
Hippo	4458	-63.9-		-17.3-		-8.9-		9.9	-
Reedbuck	94	36.1	52.1	2.8	4.9	0.0	2.1	2.1	1:1.6
Waterbuck	1068	17.9	50.7	5.4	10.3	5.6	4.2	5.8	1:2.5
Kob	28397	14.8	62.7	7.8	4.7	4.3	1.1	4.6	1:2.7
Bushbuck	505	18.1	66.0	4.6	6.8	1.3	3.1	0.2	1:3.2
Buffalo	3218	-73.4-		-11.3-		-4.5-		10.8	-

*Some age/sex criteria used were adopted from Grimsdell (1969) for buffalo, Modha & Eltringham (1976) for kob, Child, Sowls & Mitchell (1965) and Bradley (1972) for warthog and Spinage (1967, 1968) for waterbuck.

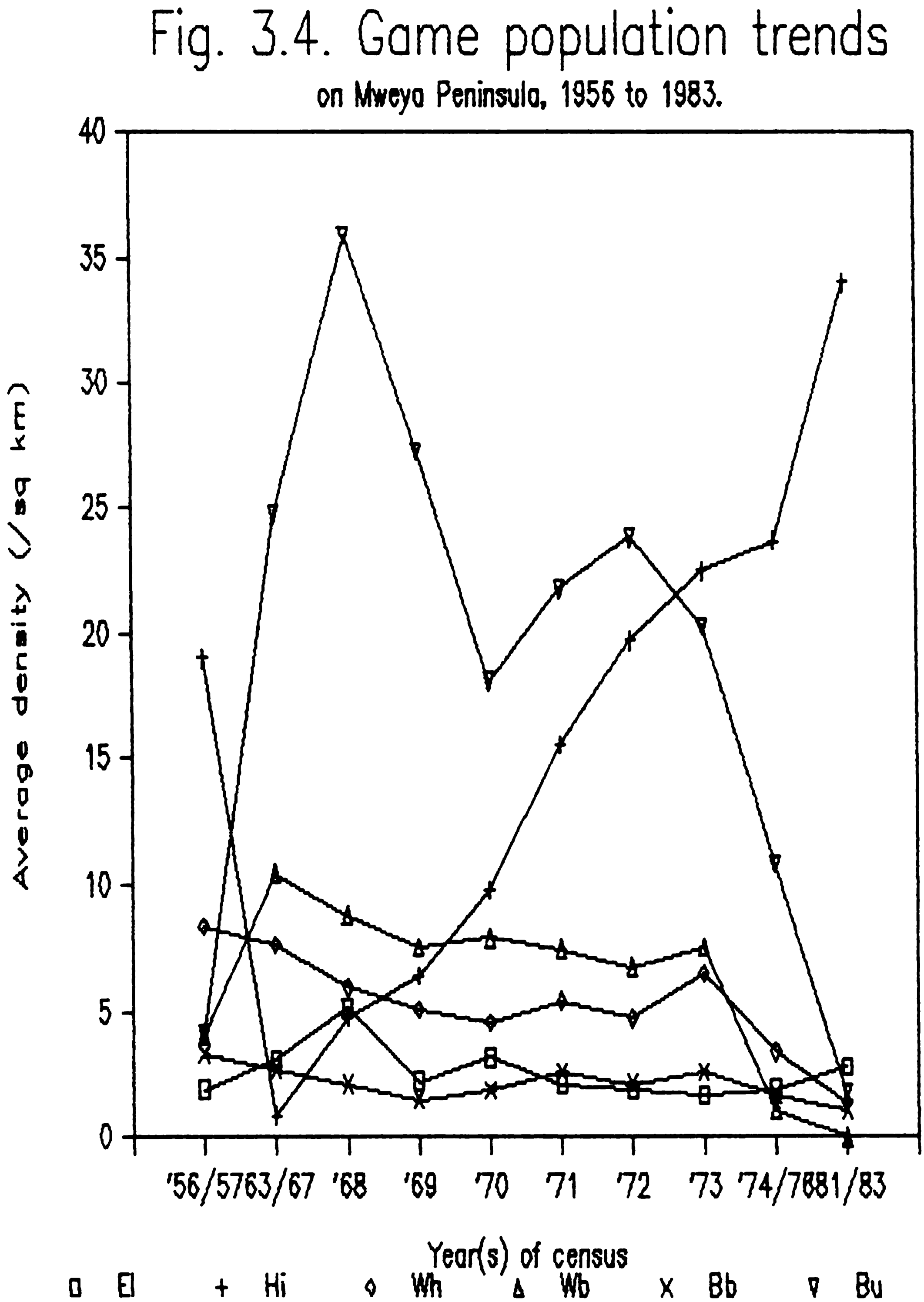


Fig. 3.4. Game population trends
on Mweya Peninsula, 1956 to 1983.
Average density (/sq km)
40
35
30
25
20
15
10
5
0
'56/57
63/67
'68
'69
'70
'71
'72
'73
'74/76
81/83
Year(s) of census
El
Hi
Wh
Wb
Bb
Bu

3.3.6. Population trends on Mweya Peninsula

Populations of large herbivores on Mweya Peninsula have been monitored almost continuously from 1956 to 1983 (Petrides & Swank 1965; Field & Laws 1970; Eltringham 1974, 1980; Yoaciel 1981 and this study). Elephant, buffalo and waterbuck increased between 1956/7 and 1963/7 (Table 3.15) at a time when hippopotamus were virtually eliminated as part of a management program (Bere 1959). The gain was sustained and densities of the various species remained more or less stable until 1973. Counts since 1974 showed a dramatic decline in all species except hippopotamus. The hippopotamus population recovered quickly after the cropping program ended in 1967 and by 1972 had exceeded the 1956/57 level (Table 3.15; Fig. 3.4). Losses by buffalo and waterbuck accounted for most of the

Table 3.15. Average densities/sq km of six herbivore species between 1956 and 1983 on Mweya Peninsula, Queen Elizabeth National Park, Uganda.

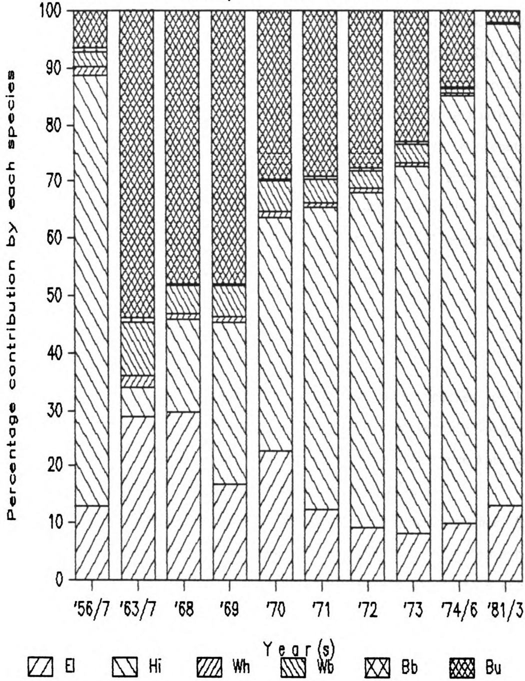
	1956/7*	'63/7	'68	'69	'70	'71	'72	'73	'74/6	'81/3
Elephant	1.92	3.07	5.16	2.22	3.20	2.13	1.87	1.69	1.9	3.1
Hippo	19.01	0.91	4.80	6.40	9.78	15.56	19.73	22.49	23.7	34.0
Warthog	8.36	7.62	5.96	5.07	4.53	5.42	4.71	6.49	3.4	1.6
Waterbuck	4.04	10.46	8.80	7.56	7.91	7.47	6.76	7.56	1.1	0.0
Bushbuck	3.31	2.75	2.13	1.51	1.87	2.58	2.13	2.58	1.7	1.3
Buffalo	4.08	24.75	35.91	27.29	18.04	21.78	23.82	20.27	10.8	2.0

*Authorities: Petrides & Swank (1965) for 1956-57; Field & Laws (1970) for 1963-67; Eltringham (1980) for 1968, 1969, 1970, 1971, 1972 and 1973; Yoaciel (1981) for 1974-76; this study for 1981-83.

recent decline of large mammals other than hippopotamus from the Peninsula. The dramatic increase of buffalo and waterbuck during the period of hippopotamus cropping and their recent decline following

Fig. 3.5. Trends in biomass composition

on Mweya Peninsula, 1956 to 1983.



hippopotamus recovery indicates that hippopotamus compete directly with these species.

It is apparent from the changes in biomass composition between 1956 and 1983 (Fig. 3.5) that there has been a rapid and steady rise in hippopotamus biomass since the end of the cropping program. During the period of cropping, hippopotamus constituted only 5.0% of the biomass. Five years after the program ended they had risen, once again, to a position of prominence accounting for 58.5% of the biomass. Hippopotamus gained dominance at the expense of the other species, accounting for 84.3% of the biomass in 1981/83. The situation observed during the study was, therefore, similar to that of 1956/57 with a virtual monoculture of hippopotamus.

3.4. Discussion

3.4.1. Counts

Counts in this study demonstrated that for most species of large herbivores and in most study areas, numbers were considerably lower than in 1956/57 and 1963/67. The few notable exceptions were kob, which increased in most study areas, and hippopotamus in Area 1.

Poaching was the major cause of the decline in game abundance. Bands of armed men roamed the park between 1973 and 1980 and inflicted a heavy toll on animal populations, particularly elephant and buffalo (Edroma 1973; Eltringham & Malpas 1976, 1980; van Orsdol 1979; Malpas 1980; Yoaciel & van Orsdol 1981). Eltringham & Malpas (1976, 1980) showed that the distribution of elephant carcasses and other animal remains were correlated with the location of villages, providing evidence that game mortality was due to human activities. Edroma (1973) found that the villages in and around the park provided a haven for poachers and a lucrative market for their illegally acquired commodities.

3.4.2. Variability in numbers

Variability of the counts was high. For most species there were no marked trends in the monthly counts so that any one observation was as likely to be representative as any other. Variability was influenced by several factors. In the case of small animals or those with retiring habits, variability was partly due to observers failing to see all animals present. Species in this category included bushbuck, reedbuck and warthog. For other species, variability was due to movement which took animals out of a study area in which they were counted or conversely, into one from which they were previously absent. Examples of such species are elephant and buffalo. There were species, such as kob, which were conspicuous and relatively sedentary but were difficult to count accurately. Kob frequently occurred in large herds which were constantly in movement and difficult to enumerate. The size of the population also contributed to the variability of counts for some species. Reedbuck, for example, occurred in such low numbers that differences between counts by only a few individuals resulted in large percentage change, whereas similar numerical differences in a large population resulted in only negligible variability.

Single monthly counts were judged to be adequate in sampling the population present in an area. Eltringham (1973) reached a similar conclusion in his assessment of variability in the counts made by Field &

Laws (1970). As a technique for detecting long-term trends in animal populations, a monthly ground count is probably adequate provided precautions are taken in drawing the boundary of study areas to minimize movement of animals across borders. It is, however, likely that there is a mutual cancellation of errors over a long period as was found by Matthews (1960) in an analysis of extended counts of wildfowl on a reservoir.

3.4.3. Distribution according to habitat

Elephant, hippopotamus, warthog and bushbuck were most numerous in the areas of short grass with dense thicket close to water. Hippopotamus were dependent on water to keep cool by day and to support their weight as they rested. Elephant, buffalo and warthog, too, used water to cool themselves. They drank regularly but were less dependent on water than hippopotamus.

Elephant are normally extremely mobile and roam over a wide area. Analysis of elephant distribution in this study showed that they were confined almost exclusively to Areas 1 and 2, which together were only about 18 sq km in size. Given the elephant's propensity for movement, these results appeared rather paradoxical. Observations confirmed that the same elephant spent some time elsewhere in the park. Yet they were recorded almost exclusively in Areas 1 and 2 and evidently spent most of their time there.

The restricted distribution of elephant probably reflected the species' instinctive search for security. Poaching had been a serious problem in the park. Despite a breakdown of law and order elsewhere in the reserve, security had been maintained in Area 1 and its vicinity, which included Area 2, because it was the site of the park's headquarters. Elephant had evidently retreated to the most secure area they could find.

Warthog were more abundant in the short grass and thicket areas than in other habitats. Warthog preferred this habitat probably because in the short grass they could see their surroundings and avoid surprise attack from predators. Furthermore, the dense thickets provided shelter from tropical storms, the heat of the sun, as well as cover and concealment from predators. In Areas 1 and 2, the conditions favored by warthog existed primarily because of intense hippopotamus grazing pressure. Warthog occurred in other habitats throughout the park, but in much lower densities. High densities of warthog seem to be an early indicator of overgrazing (Petrides, pers. comm.) Warthog owed their abundance in the short grass and thicket areas to hippopotamus.

Kob and buffalo were most numerous in medium-height and tall grasslands. The low densities of kob in areas of short grass and thicket suggest that they particularly avoided this habitat. Factors which were likely to be important included availability of adequate quality forage, access to water and avoidance of predation. Proximity to water seemed relatively important since kob were observed to drink frequently. But this would be a factor in favor of using the habitat, not avoiding it. Grass species favored by kob include Heteropogon contortus, Themeda triandra and Hyparrhenia filipendula (Field 1972). Because of heavy hippopotamus grazing in Areas 1 and 2, these species were absent or present only in trace amounts (see Chapter 6). Lack of favored food plants was probably an important factor causing kob to avoid the habitat. Finally, how important could predation have been a factor in denying kob use of the short grass and thicket habitat? Potential predators included lion, leopard, hyena and man. With the exception of the nocturnal hyena, the other predators hunt by sight. Kob, too, rely primarily on sight to detect predators. In areas of dense bush visibility would be seriously compromised and the ability to detect a predator in time to avoid being caught severely impaired. Dense bushes also provide cover and concealment from which a predator can stalk and launch attacks. To kob, the relative usefulness of cover to a potential predator is probably the significant difference between an open and a bushed terrain. Areas of dense bushes would place kob in a situation of double jeopardy with their defences curtailed while the offensive abilities of the predator would be enhanced by the abundant cover. Whether the absence of suitable foods or the danger of predation in a high-risk habitat is the more important factor affecting the spatial distribution of the species is unknown.

Buffalo were fairly evenly distributed throughout the study areas. The key to their wide distribution appeared to be a feeding strategy that allowed them to be relatively selective and to maximize their benefits in a wide range of environment. In the wet season when seasonal inland pools and wallows were available, buffalo seemed to prefer to graze the new growth in grasslands distant from permanent water. When the inland wallows dried up during the dry season and drying upland grass made poor grazing, they moved closer to permanent sources of water and increased their intake of browse which at this time of the year contained a higher percentage of protein than did hay (Field 1972). Even normally coarse grasses such as Cymbopogon afronardus and Imperata cylindrica, which were avoided when growing rank, were grazed when tender new shoots sprouted following a burn.

Bushbuck were most numerous in areas of short grass and dense thicket. Bushbuck affinity for areas of dense bush indicated that shrubs were an important resource to the species. Possible benefits included food, shade, concealment and proximity to water. Bushbuck were often observed to browse the thickets. According to Waser (1975) and Okiria (1980) the thickets provide a rich variety of grasses, herbs and woody plants, many confined to this habitat. It is likely, therefore, that bushbuck depended on the bushes for a diversity of food plants not otherwise available.

Since bushbuck were not observed to drink, proximity to water seemed relatively unimportant. Shade, on the other hand, could have been a factor given the intensity of equatorial solar radiation. But shade could be obtained in the other habitats also and was unlikely to be an important factor in bushbuck distribution.

Concealment from predators appeared to be an important potential benefit to bushbuck in the densely bushed habitat. While predators could also be concealed in bush, the ability of bushbuck to hide themselves and the effectiveness of the strategy were demonstrated repeatedly during the 20 months of game counts. When motionless, bushbuck blended in so well with the surroundings of bushes that they were difficult to detect. On one occasion a leopard was seen to pass a pair of bushbuck at a distance of less than 10 m without apparently detecting them. Yet the pair was only partially concealed by bushes. The bushbuck had detected the predator and frozen in their tracks but remained alert. As the predator passed by it gave no indication of having detected the bushbuck which were closer to it than to the census crew of whose presence the cat was certainly aware. Concealment, too, was therefore probably an important factor in bushbuck preference for a habitat with dense bushes.

While association with thickets may be of advantage in avoiding diurnal predators relying on sight, this advantage is lost at night since association with thickets at night greatly limits the area in which a nocturnal potential predator needs to hunt. Waser (1975b) found that bushbuck on Mweya Peninsula showed a pattern of movement away from areas of dense thicket to areas of open grassland at night. Such subtle shifts demonstrate that predation is a major factor in distribution at a macro as well as a micro level.

The distribution of some herbivores was also influenced by seasonal changes involving fire and rainfall. Fire acted indirectly through its effects on the vegetation. By removing mature unpalatable vegetation of low food value and replacing it with nutritious tender growth, fire affected not only the quantity and quality of forage available, but also the distribution of animals attracted to the new growth. From January to March 1982, a large concentration of kob hop-scotched a succession of burned areas in the Craters highlands as each sprouted with new growth following a series of fires earlier in the dry season. Less spectacular concentrations were observed elsewhere in the park. Some isolated burned areas were grazed so intensively that they had not recovered two growing seasons after the fire. Similarly intensively-grazed areas in Kenya took two years to recover (Pratt 1967).

Fire removes vegetation cover. While a mosaic of burned and unburned areas results in habitat diversity and is potentially beneficial to a spectrum of animals, extensive fires leave large areas without cover. To small mammals and the young of many large ungulates that depend on cover to avoid predation, extensive fires may pose a threat to survival. Wide-ranging fires occurred frequently in such areas as the Craters highlands. Such fires appeared to affect temporarily the social organization and distribution of some species, particularly reedbuck.

Areas which were ordinarily devoid of permanent fresh water were inhabited during the wet season by large numbers of animals when temporary pools were created after rains. When the pools dried up during the dry season, animals dependent on water left for areas closer to permanent water. Buffalo, waterbuck, kob and to a lesser extent, hippopotamus were involved in such seasonal movements.

It is concluded that the distribution of various ungulate species in different habitats was not random.

3.4.4. Seasonal fluctuations in numbers

In general, large mammals were little affected by changes in seasons. Elephant, hippopotamus along the shoreline, waterbuck, kob and buffalo all showed no significant seasonal differences in density. Statistically significant differences were demonstrated in one or two study areas for warthog, bushbuck and reedbuck but there was no pattern of seasonal differences for any species.

In the case of bushbuck, observations during game counts in Area 1 indicated that larger numbers tended to be recorded during rainfalls. As most of rain in the park occurred in convectional rainstorms in the wet season, many more counts were carried out during or immediately after rainfall in the wet season than in the dry. The seasonal differences indicated by the data were probably due more to the behavioral response of bushbuck to rainfall than to seasonal differences in abundance.

Reedbuck are adept at hiding, especially in tall brown grass. Their rufuous coat provides a cryptic blend which makes them difficult to spot. In the park, the grass was tall and brown primarily in the dry season. During the rains, especially early in the season when the grass was still short and green, it was harder for reedbuck to hide against a contrasting landscape. The seasonal differences demonstrated for the species in Areas 4 and 5 probably reflected differences in observer ability to see all the animals present rather than seasonal differences in abundance. Seasonal differences in visibility were maintained by frequent fires which also resulted in tender, nutritious new growth to which reedbuck were attracted.

Warthog are short and easily hidden by tall and medium-height grass. Their dark skin also made them difficult to see against a burned landscape. During the wet season when new growth turned the landscape green, they too, were easier to see. They were also attracted to the new growth and consequently were in the open and easier to enumerate. The seasonal differences indicated for the species in Area 4 were again probably due more to inability of observers to see all the animals present during the dry season counts and to improved conditions for counting during the wet season rather than to seasonal differences in abundance.

Analyses of the sub-seasonal data for Area 1 showed that the numbers of hippopotamus on land during the day increased as the dry season progressed. Grass usually ceased to grow, dried up and turned brown by the end of the first month of the dry season. Heavy grazing, principally by hippopotamus, quickly removed much of the standing forage creating a food shortage. The grass was reduced to a uniformly cropped stubble close to the soil surface. Further and further into the dry season, an increasing number of hippopotamus probably failed to meet their daily dietary requirements during the usual nightly feeding. Because of the shortage of forage an animal had to search over a wider area to collect sufficient bulk to fill its stomach. By the second and third months of the dry season apparently an increasing proportion of the hippopotamus population reach a threshold at which the usual nightly feeding was no longer adequate. The increased number of hippopotamus on land during the day is considered to be due to the extension of feeding time in order to obtain enough stomach fill.

Although the average number of hippopotamus along the shore did not change significantly between sub-seasons, it was interesting to note that the averages varied inversely with those of hippopotamus on land, as would be expected.

Prior to the recent escalation of poaching, many elephant would move into forested areas during the dry season or even leave the park altogether so that dry season counts were generally about half of those recorded in the wet (NUTAE 1963-1971; Eltringham 1973). The influx of elephant in the third month of the dry season was unexpected and indicated that poaching and harrassment had probably also denied elephant access to the forests.

When grazing is poor, browse becomes the elephant's primary source of sustenance (Field 1971). Area 1 had dense Capparis tomentosa and Azima tetracantha bushes, both of which were relished by elephant. The availability of these foods and of water probably provided an acceptable alternative to forest resources during this period. Elephant were not resident in study Area 1. This is indicated by their low numbers early in the dry season and later in the wet. During game counts, elephant were found almost exclusively in this area and in the adjacent Area 2. If they were not resident in Areas 1 and 2 and yet were rarely found in the other study areas as the counts showed, then it was logical to assume that they frequently used areas other than those in which counts were made.

Sightings of elephant in the sector between the Kazinga Channel and the equator placed most groups within a triangular area with apices at Mweya Peninsula, Katunguru and Kabatoro. The greatest concentration of sightings was along the Kazinga Channel. Areas 1 and 2 comprised the southern apex of the triangle with borders on the Channel. These areas with permanent water had higher elephant densities relative to the other study areas which were distant from the Channel.

In Area 1, the average numbers of warthog remained more or less the same between sub-seasons (Table 3.11). A one-way ANOVA of the data indicated, however, that there were marginally significant differences between sub-season means (Table 3.10). Though statistically significant, these differences were numerically unimportant. Statistical significance was possible with such small differences between means only because variability between counts were so small.

Despite large variability in numbers between counts, this study has demostrated that the abundance of large mammals in QENP were little affected by seasons. Apparent seasonal differences in the abundance of smaller species such as warthog, reedbuck and bushbuck were shown to be the result of improved visibility during the wet season due to the removal of dense vegetation by fire late in the dry season and inability of observers to see animals in dense vegetation during much of the dry season. Because fire is primarily a seasonal phenomenon, its effects tended to be seasonal.

3.4.5. Population structure

Group sizes:

Elephant: The increase in average group size observed in this study indicates that banding-together has occurred in recent years. Laws (1974) has postulated that group size is a measure of the ecological health of an elephant population. He suggested that banding is a symptom of stress. The stress could be the result of nutritional deficiency due to habitat degradation (Laws *et al*. 1970; Malpas 1978) or of the breakdown of social structure through excessive disturbance (Eltringham 1977). QENP has been found to be a good habitat for elephant on a year-round basis (Malpas 1977, 1978). The stress leading to aggregation was, therefore, likely to be of social rather than physiological origin.

Given the recent history of the park, it is concluded that the increase in elephant group size reflected the high level of poaching in the park in recent years. Eltringham (1977) observed similar banding in the neighboring Chambura Game Reserve, a hunting area that was visited frequently by professional safaris and animal capture units as well as by gangs of poachers. The average group size in that reserve was 28.8.

Bushbuck: The observation that bushbuck were predominantly solitary confirms the conclusion reached in other studies (Waser 1975, Allsopp 1978). Although commonly found alone, bushbuck associate with other conspecifics. The most-frequent association was that of a female and her calf. Adult animals of the same or opposite sex also frequently occur together. Waser (1975) found that encounters between individuals were more frequent than would be expected by chance. Allsopp (1978) observed that an area was utilized by a group, members of which were mutually tolerant of each other. Females even engaged in mutual grooming. Similar observation suggested that when adult males met, they tended to stay together. Serious aggression was shown only in the presence of females and probably only if the females were in estrus (Allsopp 1978). These observations indicate that the bushbuck is a social species whose members choose to live separately.

The significance of solitary life in bushbuck society may be related to predation. As a browser in dense bush habitat the bushbuck would derive little benefit from associating in large herds, and dispersal probably offers a better insurance against predation.

Buffalo: The average size of buffalo herds observed in this study was 55.3. This was considerably lower than the 101.5 and 105.8 estimated by Eltringham & Woodford (1973) in park-wide aerial surveys in 1968 and 1969, respectively. The mean herd size for the sector was 86.3 in 1968 and 88.0 in 1969. Because of recent poaching in the park, the decline in herd size was unexpected. As with elephant, disturbance by poachers was thought to result in herd amalgamation for protection. That would result in fewer but larger herds. While fewer herds were found than in the past, they were smaller not larger. Smaller herd size could have resulted from fragmentation of larger herds, but fragmentation would also have resulted in a larger number of herds. It was concluded that the decline in the number and size of herds was probably the result of the high mortality due to poaching in recent years.

Galton (1871) first proposed the theory that gregarious behavior in animals is a response to predation. This idea has since received widespread attention with regard to avian flocking (Wynne-Edwards 1962; Lock 1968; Lazarus 1972; Diamond & Lazarus 1974; Bertram 1980), fish schooling (Brock & Riffenburgh 1960; Cushing & Harden-Jones 1968) and ungulate herding (Estes 1974; Jarman 1974; Leuthold 1977). Hamilton (1971) argued that by aggregating, animals lower their probability of being captured during an attack by a predator. His `selfish herd' model was based on the concept of a `domain of danger', defined as the area around each animal from which a concealed predator might spring. The domain of danger is the area enclosed by a set of points equidistant between the animal and its surrounding neighbors. As animals form larger groups, this domain, and the probability of a specific individual being captured, decreases. Thus, scattered animals would benefit by forming groups.

The Hamilton model was based on a hypothetical situation in which a predator attacks from within a group. Pulliam (1973) argued that the Hamilton model cannot explain herding behavior because predators usually attack from the periphery of a prey group. Pulliam pointed out that the benefits accruing to individuals within a herd are unequal because animals on the periphery are more vulnerable than those in the center, and suggested that such animals would reduce their risk by abandoning the group. As each successive layer of animals become peripheral, they in turn would disperse until the group disintegrated. This argument assumes, however, that the risk of predation to peripheral animals in a herd is greater than that for dispersed ones. This assumption would be valid only if the same individuals are on the periphery of the group during successive predator attacks (Rubenstein 1978).

Vine (1971) and Treisman (1975a, b) evaluated the probability of a predator detecting prey, and demonstrated mathematically that the probability is lower when prey are aggregated than when scattered. Treisman (1975a, b) further showed that if crypsis is the only means of avoiding predation (that is, once prey is detected its chances of escaping are low) solitary living is favored. If animals are able to detect and escape from a predator, however, grouping is advantageous to the individual regardless of prey density or cover characteristics. The reason is that the increased collective vigilance by a group of prey against predators outweighs any tendency of predators to detect prey groups more easily than solitary animals. If the habitual predator becomes satiated before consuming the entire group or must pause for digestion before further attacks, grouping would also reduce an individual's risk (Robertson 1973; Treisman 1975a; Taylor 1976).

Gregarious behavior may reduce the probability of an individual being caught in a number of ways. These have been reviewed by Bertram (1978) and may be summarized as (1) increased predator detection due to collective vigilance against predators, even though individual investment in vigilant behavior may be lower; (2) communal defence due, in some species, to the greater ability of a group to defend itself by attacking the predator, as do buffalo (Schaller 1972; Sinclair 1977) and musk ox (Ovibos noschatus) (Mech 1970); (3) lowered probability of being caught since, as in the mobbing of predators by birds, the probability of anyone animal being captured is inversely proportional to group size; and (4) predator confusion, since a predator usually selects a single individual to chase, the confusing effects of large numbers of fleeing animals may distract the predator, thus allowing all prey to escape.

Age structure and sex ratios:

Adult sex ratios for kob, waterbuck and bushbuck all show a paucity of males in their respective populations. The reported foetal sex ratio for populations in the park and elsewhere have been shown to be 1:1 (Modha 1972 for kob; Spinage 1968, 1973 for waterbuck; Allsopp 1978 for bushbuck). The large disparity in foetal and adult sex ratios indicates that survival and mortality rates are different in the sexes, with higher survival for females and greater mortality for males.

It has been suggested that the differences in survival rates is largely due to greater predation on males (Buechner 1961; Spinage 1968; Modha 1972). The preponderance of bucks as compared to does, which are killed by predators, may be partly because does are more alert since solitary animals present mostly less-aware targets, but it may also be partly attributable to greater boldness on the part of the buck.

3.4.6. Population trends on Mweya Peninsula

The spectacular increase in the numbers of buffalo and waterbuck on the Mweya Peninsula during the period of hippopotamus cropping and their decline following the recovery of the hippopotamus population indicates that hippopotamus competed with them. The most likely resource for which they would compete would be food. Field (1972) showed that buffalo and waterbuck along the shore grazed the same grasses eaten by hippopotamus. The dynamics of buffalo and waterbuck populations on Mweya Peninsula vis-a-vis that of hippopotamus over the past 27 years confirm that did indeed compete. It seems that when grazing reaches a certain intensity, buffalo and waterbuck are unable to compete with hippopotamus and are forced to seek grazing elsewhere.

During the period of hippopotamus cropping, the relative proportions of a diverse spectrum of large mammal species were more equitable than in previous years when hippopotamus dominated the large mammal community (Eltringham 1974). The diverse community was considered more desirable than the virtual monoculture of hippopotamus because it made better use of available resources without deleterious effects on the habitat.

The relentless expansion of the hippopotamus population following cessation of the cropping program has been the most dramatic feature of the dynamics of the large mammal community on Mweya Peninsula. The expansion has been persistent and at the expense of the forage and the other large mammal species.

Elephant increased slightly between 1956 and 1968 but declined significantly in 1969. Since then, the trend is one of gradual decline until 1974/76 when they increased slightly. Their density in this study was the highest since 1970.

The abundance of warthog and bushbuck have changed little over the years although numbers recorded in recent counts have been low, indicating that both populations have declined recently.

CHAPTER 4

WOODLAND REGENERATION

4.1. Introduction

For nearly 25 years, there has been considerable debate over the relative importance of fire and elephant in controlling woody vegetation. Some authorities (Glover 1963; Lamprey _et al_. 1967; Laws 1969; Vesey-Fitzgerald 1973; Harrington & Ross 1974; Laws _et al_. 1975; Thomson 1975; Caughley 1976) consider elephant to be the principal agents, while others (Harthoorn 1966; Lawton & Gough 1970) are equally convinced that fire is the primary controlling factor.

Fire is a common phenomenon in QENP and until recently elephant were also abundant. Where both occur, however, it is difficult to separate the effects of one from the other. By opening up thickets and allowing grassland to penetrate, elephant encourage the spread of fire. Similarly, trees damaged by elephant are rendered more susceptible to destruction by fire.

The recent elimination of elephant from large areas of the park created a natural experiment. By comparing the current situation with that of a period when elephant were abundant, the relative importance of fire and elephant in controlling the survival and regeneration of woody vegetation could be determined by inference.

The woodland surveyed in the present study was bounded by Equator Road, longitude 29°56'E, Katwe Road and River Nyamugasani. It was similar to and incorporated much of the woodland studied by Field (1971). The dominant grasses were tall, tussocky, fire-resistant species including Cymbopogon, Hyparrhenia, Themeda and Imperata.

The woodland had been virtually free from elephant use for nearly eight years prior to this study. Fire was seasonal but frequent due to abundant grass in the region. It occurred on average at least once every two to three years (Eltringham 1976; this study) and temporarily opened up the area to grazing. Kob, buffalo and waterbuck fed particularly on the tender, young and nutritious grass shoots which sprouted following a burn. Intense fires were reported to occur ocassionally, but none was recorded during this study.

4.2. Methods

4.2.1. Composition and density

The point-centered quarter (PCQ) method developed by Cottam and Curtis (1956) was used to determine species composition of the woodland, as well as density and relative frequency of the principal species. The method was chosen for three reasons: (1) it requires only simple, readily available equipment to apply effectively (an important consideration in a situation where equipment was in short supply); (2) it is easy to perform and can be applied rapidly and accurately, and (3) it provides reliable data which are free from subjective biases (Beasom & Haucke 1975).

The woodland was sampled along four randomly-selected transects running approximately east and west. These were chosen from a set of 17 by drawing two-digit numbers from a table of random digits. Similarly, the first sampling point along a given transect was determined by a three-digit number representing distance in meters from the beginning of the transect. Subsequent sampling points were 30 m apart.

The area around each sampling point was divided into quarters by drawing two imaginary lines through the point, one along the transect and the second at right angles to the first. Within each quarter the nearest tree to the sampling point was recorded by species. Distance from the sampling point to the center of the tree base and girth of the tree at 1.5 m above the ground were also recorded.

Cottam, Curtis & Hale (1953) have demonstrated that for the PCQ method, mean area per tree is derived from the average of distances between trees and sampling points. The average distance is found by summing individually measured distances and dividing by the number of trees (or four times the number of points sampled). The average distance squared is equal to mean area per tree, and density is the reciprocal of the mean area. In terms of trees per hectare, density equals 10,000 (the number of square meters in one hectare) divided by the mean area per tree. These calculations are demonstrated below using data from Table 4.2:

$$\text{Average distance} = \frac{d_1 + d_2 + d_3 + \text{---} + d_n}{4 \times \text{Number of sampling points}}$$

$$= \frac{13,732.51}{4 \times 440} = 7.80 \text{ m;}$$

Mean area = (average distance)^2 = $(7.80)^2$ = 60.88 m^2;

Total density = 1/60.88, which in terms of trees ha^{-1}

= 10,000/60.88 = 164.26.

Total density is used to calculate the absolute density for each species by multiplying by the relative density of the species concerned.

Cottam *et al.* (1953) and Cottam & Curtis (1956) determined that at least 30 points in a sample were necessary for an accurate or reasonable estimate. According to this criterion, the three species of *Acacia* were adequately sampled (Table 4.2). A prohibitively number of sampling points would be required, however, to adequately sample the rarer species. Conversely, it is evident that density estimates for *Acacia gerrardii* and *A. sieberiana* could be obtained with fewer samples.

Importance value index (IVI), a measure of a species' importance within its community (Curtis & McIntosh 1951), was calculated for the major woodland species. IVI is obtained by adding together relative frequency (a measure of spatial dispersion), relative density (a measure of abundance) and relative dominance (a measure of cover). Each sampling point of the PCQ method is treated as a quadrat. Relative frequency is calculated as the percentage of all sampling points at which a species occurred. Relative density is the percentage which a species comprises of all trees in the sample. Similarly, relative dominance of a species is the percentage of basal area contributed by the species to the combined total basal area for all species. The three relative values for each species are added to give the importance value (Table 4.2).

4.2.2. Structure of the woodland

Preliminary observations indicated that the dominant species exhibited two distinct tiers. Girth was assumed to be strongly correlated with height. In a stand of nearly 0.5 ha judged to be representative of the woodland, the girth of *Acacia gerrardii* trees at a height of 1.5 m above ground was measured and plotted to show its distribution.

4.2.3. Regeneration potential

During the application of the PCQ method (Section 4.2.1), every tenth sampling point was used as the center of a circular plot of radius 5 m. Tree seedlings (<0.5 m growing from seed as opposed to rootstock) and saplings (<1.5 m other than seedlings) in each plot were tallied by species. The samples were used to estimate sapling and seedling abundance in the woodland.

4.2.4. Fire, elephant and the woodland

In December 1981, a 0.3 ha plot was established in the woodland after a major fire. Within three days of the fire, damage to trees was recorded by species and height classes (≤1.0, 1.1-3.0, 3.1-5.0 or >5.0 m). Damage to each tree was recorded as one of four categories of increasing severity corresponding to the destruction of <1%, 1 to 25%, 26 to 50%, and >50% of the tree, respectively. The plot was monitored for 18 months to observe the longer term effects of fire. The effects of fire also were observed briefly at several other sites within the woodland.

Sometimes, too, it was possible to obtain indirect evidence of the relative importance of fire and elephant by studying existing vegetation. From an analysis of serial photographic transects, Laws _et al_. (1975) showed that the density of trees in Murchison Falls National Park increased towards the boundaries of the park. This was attributed to game, particularly elephant, avoiding park borders because of attacks and harrassments by people. The result with regard to woody vegetation, is less intensive browsing with greater regeneration along the park borders. Conversely, the more-intensive browsing in the interior results in greater seedling suppression. Thus, where elephant are the principal factor in controlling regeneration, there should be a gradient of decreasing tree density from the park boundaries corresponding to an increasing intensity of use in the interior.

The incidence of fire should not be correlated with tree density in this way. Because grass occurs throughout the woodland, fires are usually extensive and their effects likely to be general. There would be no gradient of tree density as postulated with regard to elephant.

To test the hypothesis that elephant and not fires were the principal factor in controlling woody vegetation, mature Acacia gerrardii and A. sieberiana trees in 1-km-wide consecutive transects between Equator Road and Katwe Road were tallied and converted to average densities (/sq km).

4.3. Results

4.3.1. Composition and density

Qualitatively, species composition of the woodland has remained largely unchanged since 1968 (Table 4.1). Major shifts occurred, however, in the relative abundance of species. The most significant is that of Acacia gerrardii which in 1968 constituted 21.3% of the trees in the woodland, but by 1982 had increased to 82.4%. In comparison, increases by Acacia sieberiana and A. hockii were small numerically but large in terms of percentages. Two other species which were as abundant as A. gerrardii in the earlier survey have declined greatly. Bridelia scleroneuroides and

Table 4.1. Species composition of a regenerating woodland in the Craters region, Queen Elizabeth National Park, Uganda. Nov. 1981 to Feb. 1982.

Tree species	1968* No.	1968* %	1982 No.	1982 %
Acacia gerrardii	109	(21.3)	1451	(82.4)
A. hockii	0	(0.0)	45	(2.6)
A. sieberiana	26	(5.1)	251	(14.3)
Albizia coriaria	5	(1.0)	5	(0.3)
Bridelia scleroneuroides	107	(20.9)	2	(0.1)
Cordia ovalis	8	(1.6)	0	(0.0)
Euphorbia candelabrum	19	(3.7)	1	(0.1)
Ficus gnaphalocarpa	25	(4.9)	3	(0.2)
Maytenus senegalensis	47	(9.2)	0	(0.0)
Olea africana	103	(20.2)	1	(0.1)
Rhus natalensis	18	(3.5)	0	(0.0)
Tarenna graveolens	43	(8.4)	1	(0.1)
Turraea sp.	1	(0.2)	0	(0.0)
Total	511	(100.0)	1760	(100.2)

*From Field (1971).

<u>Olea africana</u> constituted 20.9 and 20.2%, respectively, of the trees in the woodland in 1968 but only 0.1% each in 1982 (Table 4.1).

The average tree density of all species taken together in 1981-82 was 164.3/ha (Table 4.2). The most abundant species were <u>Acacia gerrardii</u>, <u>A. sieberiana</u> and <u>A. hockii</u>; with densities (/ha) of 135.4, 23.4 and 4.2, respectively. The density of all others species combined was only 1.2 (Table 4.2).

4.3.2. Structure of the woodland

The distribution of girth in the sample of <u>Acacia gerrardii</u> trees was bimodal (Fig. 4.1), and demonstrated that two distinct generations were

Fig. 4.1. Girth distribution of Acacia

trees at 1.5 m above ground.

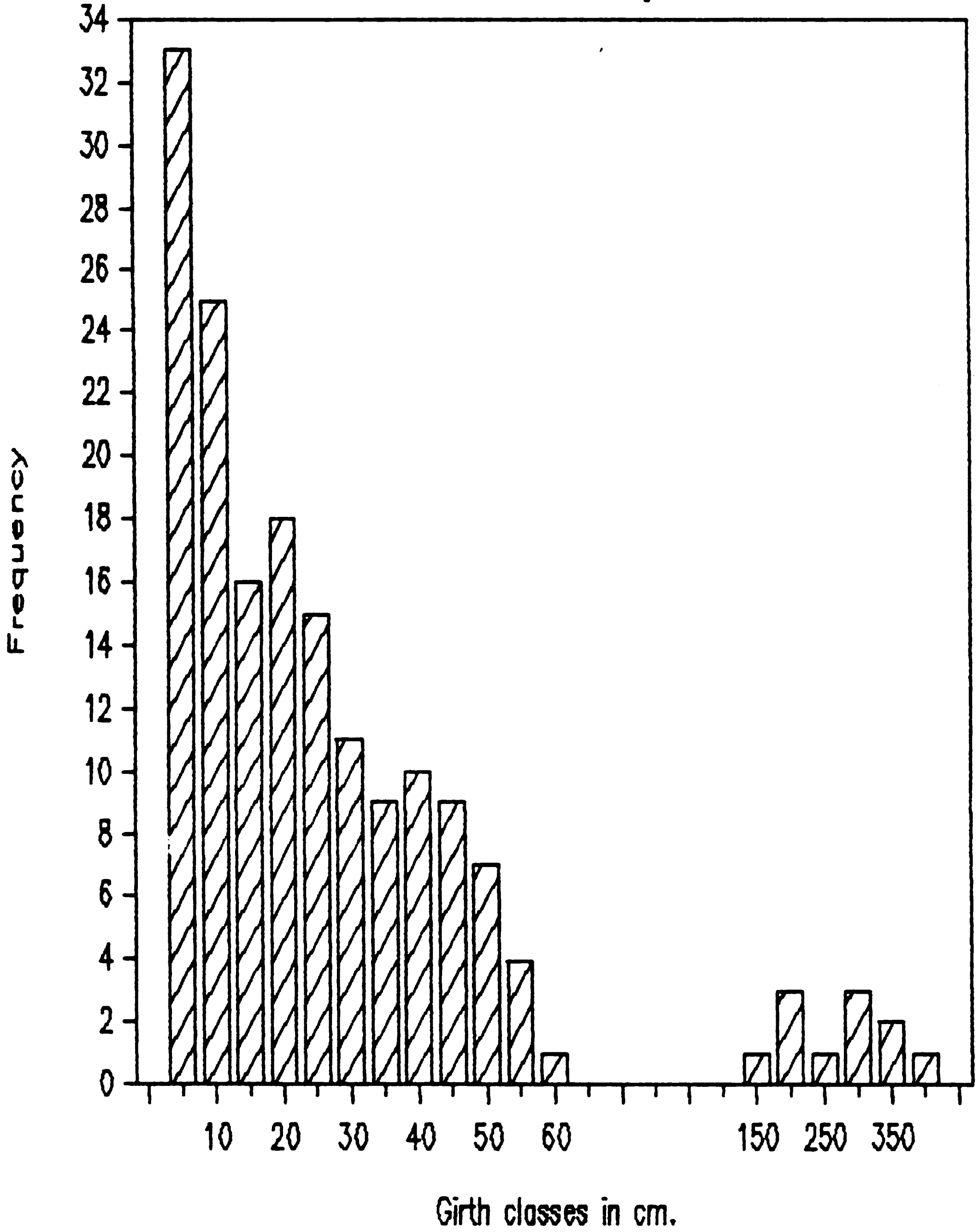


Table 4.2. Species densities and importance values for Acacia woodland in the Craters region, Queen Elizabeth National Park, Uganda. November 1981- February 1982.

Species	No. of sampling points	No. of trees	Σ of distances*	Σ of basal area•
Acacia gerrardii	414	1451	9815.5	6.24
A. sieberiana	129	251	3430.8	4.18
A. hockii	32	45	394.5	0.11
Others	7	13	91.8	0.14
Total	582	1760	13732.5	10.67

*in m

•in m^2

Table 4.2 (cont'd).

Species	Rel. frequency	Rel. density	Rel. dominance	Importance value	Absolute density (trees/ha)
Acacia gerrardii	71.13	82.44	58.48	212.05	135.41
A. sieberiana	22.16	14.26	39.18	75.60	23.42
A. hockii	5.50	2.56	1.03	9.09	4.20
Others	1.20	0.74	1.31	3.25	1.22
Total	99.99	100.00	100.00	299.99	164.26

represented in the population. Visual observations also identified a limited cohort of tall, sparsely-scattered, mature trees and an abundant population of young plants. There were virtually no trees of intermediate height.

The two generations represented discrete periods of tree growth separated by a period of suppression which ended only recently. The paucity of intermediaries, representing recruitment between the two generations, testified to the severity of the suppression. This view substantiates that of Field (1971) who determined that between 1954 and 1968, the same woodland had lost trees at an annual rate of 14.6%, one of the highest reported for any natural woodland.

4.3.3. Regeneration potential

A total of 44 plots with a cumulative area of 3455.75 sq m were sampled. Tallies of 349 rootstocks and 27 seedlings were obtained from 44 plots with a cumulative area of 3455.75 sq m. These are equivalent to densities of 1009.9 and 78.1/ha, respectively (Table 4.3), for a regeneration potential of 1088 young trees/ha.

Table 4.3. Acacia regeneration potential in woodland in the Craters region. Queen Elizabeth National Park, Uganda, November 1981 to February 1982.*

	Seedling	Rootstock
Total number tallied	27	349
Density (ha^{-1})	78.1	1009.9

*n = 44, cumulative area sampled = 3455.75 m^2.

Of the 349 rootstocks, 302 were of Acacia gerrardii, 46 of _A. sieberiana_ and one each of _Ficus gnaphalocarpa_ and _Albizia coriaria_. No attempt was made to tally seedlings by species.

These results show conclusively that the potential for regeneration was extremely high, due overwhelmingly to abundance of rootstocks. The contribution of seedlings was insignificant. Saplings of A. gerrardii from rootstocks were the most abundant and numerically surpassed those of A. sieberiana by a ratio of 6.6:1.

4.3.4. Fire, elephant and woodlands

Fire moves over the landscape as a narrow strip of flames. Observations showed that flames never persisted in one spot long enough to ignite live trees or other woody vegetation. Leaves and tender young shoots, however, were commonly killed. Fire was, therefore, effective in pruning woody vegetation but not killing it.

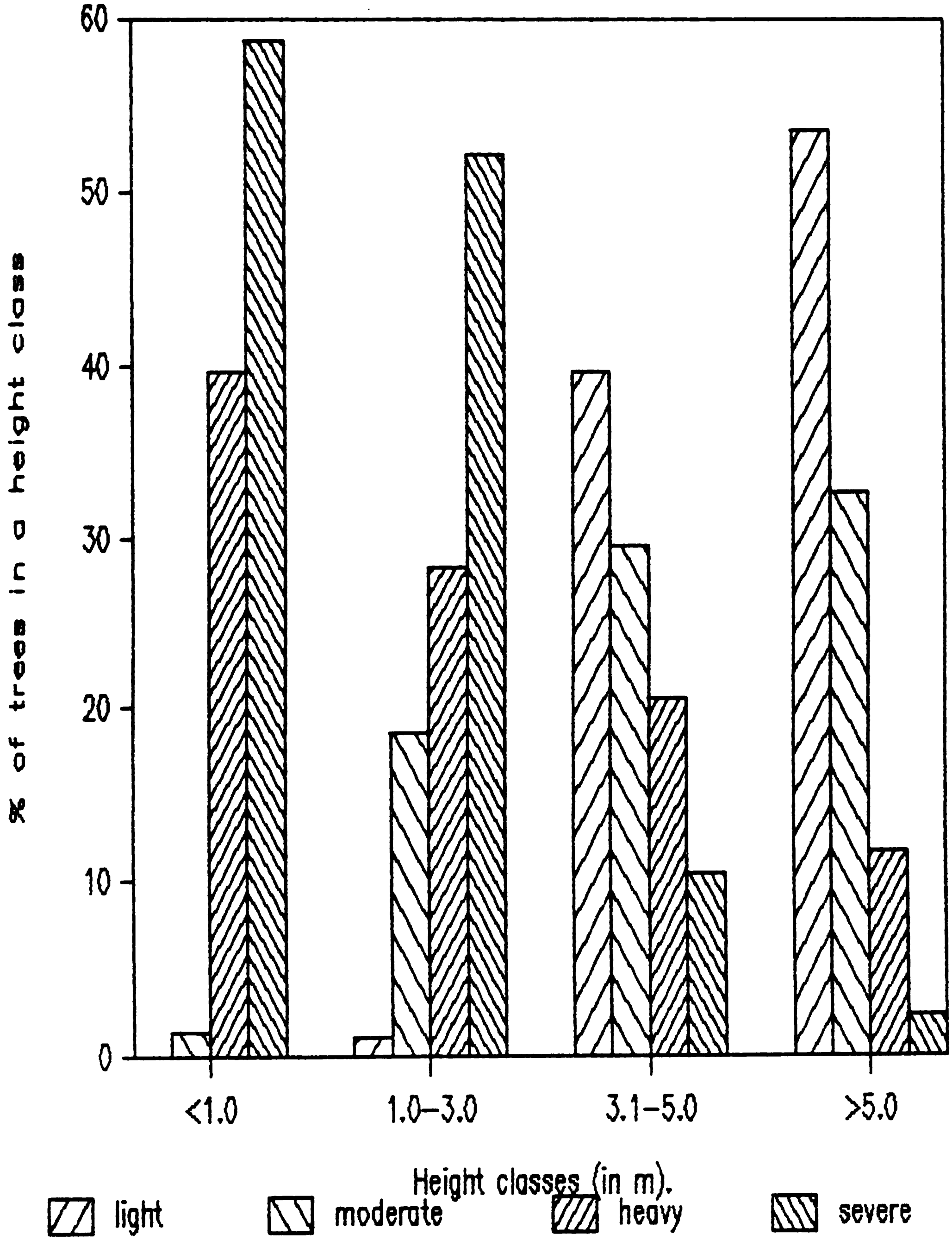
Table 4.4. Severity of fire damage according to tree height.

Extent of damage	Number (percentages) of trees by height class <1.0	1.0-3.0	3.1-5.0	>5.0 (m)
Light	0 (0.0)	1 (1.1)	31 (39.7)	23 (53.5)
Moderate	1 (1.5)	17 (18.5)	23 (29.5)	14 (32.6)
Heavy	27 (39.7)	26 (28.3)	16 (20.5)	5 (11.6)
Severe	40 (58.8)	48 (52.2)	8 (10.2)	1 (2.3)

n=281

Observations indicated that the woody vegetation most severely affected by fire were plants small in size and low in stature. In the woodland, this was principally immature trees. Due to their low height, immature trees were commonly completely engulfed in flames. These same characteristics (small size, low stature and lack of an adequate insulating bark) which rendered immature trees more vulnerable to fire

Fig.4.2. Fire damage to woodland trees



than mature trees, also made some woodland species more vulnerable than others. Among the most susceptible was _Acacia hockii_.

An assessment of the damage inflicted on individual trees showed that fire-damage was not uniform. A strong inverse correlation was found between tree height and severity of damage (Table 4.4, Fig. 4.2). More than 50% of trees in the lower height classes suffered serious losses. Saplings up to 2 m high were killed back to ground level. In tall trees, damage was consistently greatest among the lowest branches. Tall trees rarely had more than 10.2% of their tissues destroyed.

Table 4.5. Average density of mature Acacia trees in consecutive parallel transects between Equator Road and Katwe Road, Queen Elizabeth National Park, Uganda. November 1981.

Distance from Equator Road (km)	Average density (/sq km) of mature _Acacia_ trees
1	45.2
2	21.8
3	21.1
4	5.0
5	4.8
6	2.3
7	0.3
8	0.0
9	0.3
10	0.1
11	0.0
12	0.3
13	0.1
14	0.0
15	0.0
16	0.1
17	0.0

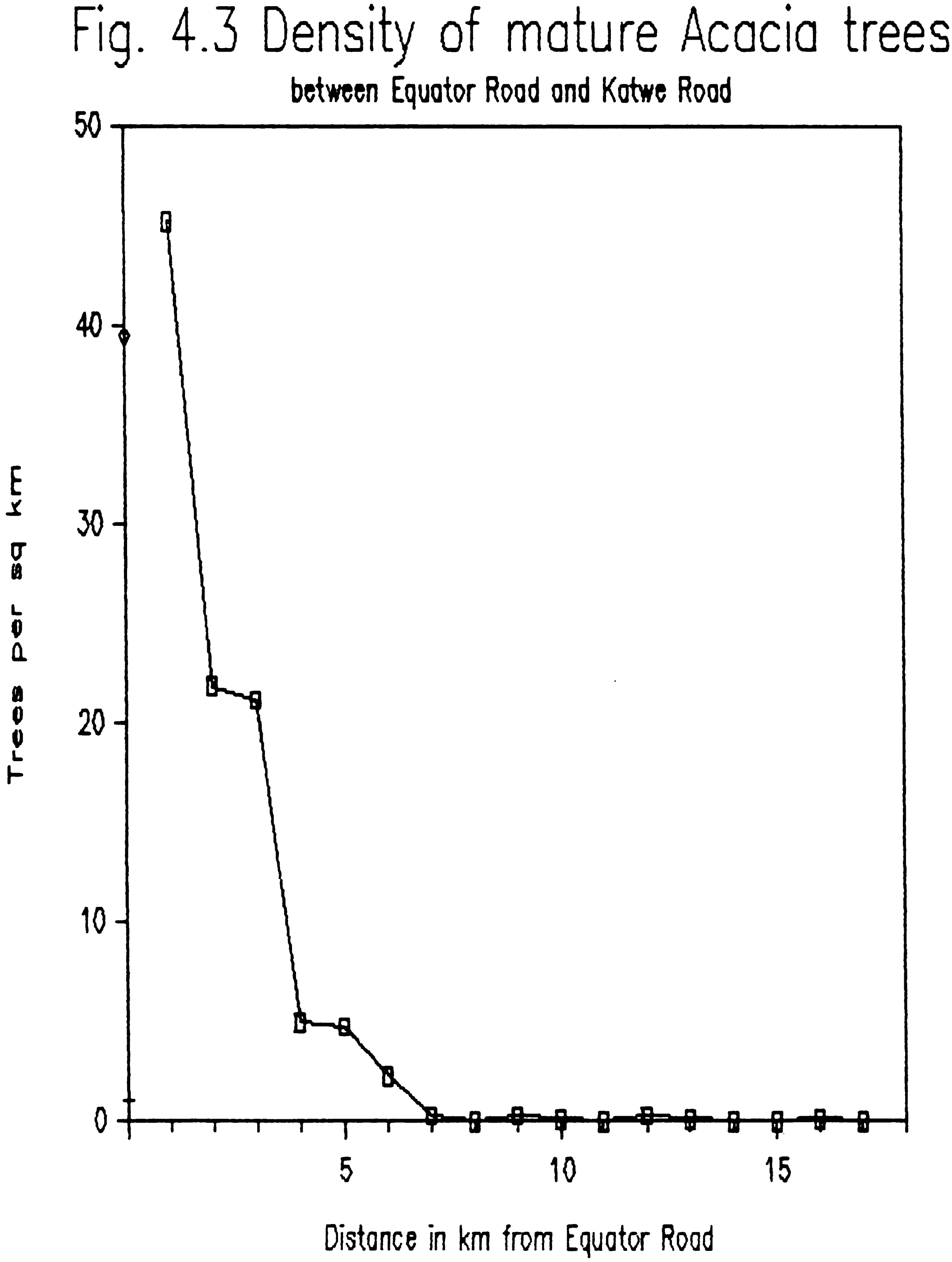


Fig. 4.3 Density of mature Acacia trees
between Equator Road and Katwe Road
50
40
30
20
10
0
Trees per sq km
5
10
15
Distance in km from Equator Road

The average density of mature <u>Acacia</u> within a kilometer of Equator Road was 45 trees/sq km but dropped to 5 at 4 km from Equator Road and were essentially totally destroyed beyond the 7-km point (Table 4.5; Fig. 4.3).

4.4. Discussion

4.4.1. Composition and density

Species composition of the Craters woodland has remained virtually unchanged since the survey by Field (1971) 14 years earlier. Constituent species evidently are well-adapted to frequent fires and persistent browsing, the two most significant ecological factors in the habitat.

Changes in the relative abundance of species probably reflect differences in the rates of regeneration. Species that had increased in the short-term were probably those which possess rootstocks. In the presence of heavy browsing, plants of these species are unable to grow out of the stage at which they are most vulnerable to fire. Though shoots produced from rootstocks may be cut down by animal browsing and destroyed by fire, they are apparently able to produce sufficient food to develop large root systems. When there is a lapse in browsing pressure, the shoots are able to grow rapidly, using the well-established root system. Such adaptation would account for the short-term spectacular increase of <u>Acacia gerrardii</u>.

While the prolific regeneration of <u>A. gerrardii</u> ensures that the species will continue to be an important member of this woodland community, its future status will depend on the intensity of competition with other woodland species.

Species that declined in abundance were regenerating slowly or not at all. Their persistence, however, indicates that the species will probably survive in reduced numbers as the prolific species continue to increase. Their decline in importance is illustrated by what has happened with *Bridelia scleroneuoroides* and *Olea africana*.

If the present densities of trees were maintained, the stand would close and develop into forest. This is unlikely, however, because of frequent fires, inadequate precipitation, animal browsing and competition for resources. Some individuals will be eliminated and tree density will decline from the present high level to a more moderate level. A new equilibrium composition will be established.

4.4.2. Structure of the woodland

The bimodal girth distribution exhibited by *Acacia gerrardii* is evidence that, for a period of time, the woodland was being destroyed at least as fast as it was regenerating. Field (1971) showed conclusively that elephant were responsible for the damage. Using a long-term annual rate of tree destruction for this woodland which he calculated to be 14.6%, the period of regeneration suppression was calculated as approximately 40 years. This would mean that the process began before the area was declared a national park in 1952, possibly while it was depopulated as a sleeping-sickness zone.

In recent years, a number of hypotheses have been advanced to explain why elephant destroy trees, and in the process, wreck their own habitat. Caughley (1976) has suggested that elephant and trees may oscillate in numbers, rather like the lynx and snowshoe hare in the arctic. His evidence was based on the age distribution of trees in the Luangwa Valley, Zambia, where a large number of baobab trees were around 140 years old, suggesting a maximum survival of saplings produced that long ago. On the assumption that the seedlings survived because there were few elephant around to destroy them, a cycle of 280 years (2 x 140) was postulated, since elephant are presently at a maximum.

On the other hand, it could be argued that as the baobab is a grassland tree, woodland and forest were at a minimum 140 years ago. This suggests that elephant were then at a maximum, or rather that they had been so some time before, since their numbers trail those of trees by about a quarter of a period. Hence the cycle would occupy 187 years. Caughley suggests a round figure of 200 years as a compromise.

Wildlife cycles of 4 or 10 years' duration are well-known but they have in common a simple ecosystem with a low input of energy. Such oscillations, or stable-limit cycles, are unlikely in the tropics, or with species that are as long-lived and slow-breeding as elephant and trees. The characteristics of a species that indulges in booms and crashes are rapid reproduction and a short generation time, so that when conditions permit, recovery of numbers is rapid. Elephant have many admirable qualities but profligate breeding is not one of them. It seems unlikely that they could ever become locked into a stable-limit cycle. Indeed, there is no example of an ungulate that cycles in this way. Another objection to this theory is that elephant and trees do not show a simple predator-prey relationship. Trees are certainly destroyed by elephant but elephant do not die in the absence of trees. They can and do turn to other foods. Trees are important to elephant. Elephant health declines when trees are gone, but they survive nevertheless.

Another hypothesis is that of Phillipson (1975), who has observed that, at least in Tsavo National Park, Kenya, elephant numbers have often surged and died down again. He has suggested that numbers follow the pattern of vegetative production, which in turn fluctuates with rainfall. Droughts are certainly periodic in Kenya and every 50 years or so there is a particularly severe one. Phillipson sees this as a mechanism for regulating elephant numbers and has suggested that the cycle should be allowed to run its course, and that human interference in the form of culling to reduce temporary over-abundance is unnecessary.

Phillipson's (1975) estimate of 43-50 years as the interval between severe droughts is far too short a time for an elephant population to complete a cycle. Phillipson supposes that the severe mortality caused by the drought would be followed by a period of 35 years of respite, during which the population would build up to a critical level again, leaving 8 to 15 years of danger from elephant damage. For a species which at best can produce one calf every 4 years, 35 years is a very short time in which to recover. Neither Caughley (1976) nor Phillipson (1975) produces any evidence that elephant undergo a cycle.

The evidence for a climatic cycle upon which Phillipson's hypothesis is based, is slight and tenuous. There are also theoretical objections to the concept of an inherent cyclical rhythm in elephant numbers. MacArthur & Wilson (1967) propose two types of evolutionary strategy in animals which they term r-selection and K-selection. An r-selected population fluctuates widely in size and has the capacity to multiply very rapidly, while the essence of K-selection is that the population is stable (Pianka

1970). The elephant is an extreme K-strategist. It is highly unlikely that cyclical changes in reproductive rates, as assumed by both Phillipson and Caughley, would evolve in such an animal.

Petrides (1974) and Eltringham (1982) have suggested that despite lack of solid evidence that elephant migrate over long distances in modern times, they must have done so before the advent of modern man. According to this hypothesis elephant wandered freely over a wide domain which was probably hundreds of kilometers across. Within this range there would be areas offering better forage and other resources than elsewhere. Eltringham (1982) refers to these as `hot spots', to which elephant would be attracted. Within these hot spots elephant behaved much as they do today, systematically wrecking the habitat. Trees were debarked or pushed over, bushes broken up and grasses uprooted. But the destruction would go only so far. Before the habitat was completely destroyed, the elephant would move on to look for another such hot spot.

The reason for assuming this follows from studies on optimal foraging in birds and other animals. When a rich food source is found, the animal does not remain with it until all the food is consumed but moves away to find another similar food source well before the original food is depleted. This is due mainly to the law of diminishing returns. The less food there is the more difficult it is to find it and the longer it takes to complete a meal. The time would be better spent in seeking out another food source where the original eating rate can be restored. Eltrigham has suggested that this was the case with elephant. But even if they did wreck the area completely, they would then leave and not return for many years, by which time the vegetation would have recovered and could withstand another session of abuse.

Seen in this light, elephant behavior is not unadaptive. It is only when elephant are prevented from moving to new pastures that irreversible damage to vegetation occurs. Eltringham suggested that not only is elephant behavior not unadaptive under the assumed circumstances, it is positively adaptive. For in wrecking trees the elephant convert primary forest to secondary forest, which is a superior habitat for them.

The significance of this hypothesis is that, if it is correct, it would be futile for park authorities to wait for nature to take its course and for elephant in a national park to come into balance with their resources. Under present-day conditions where national parks are "islands" of wild habitats, the more likely outcome would be for the elephant to continue to wreck the area until the whole ecosystem came crashing down, leading to the reduction or extinction not only of elephant but of many other large species as well.

Caution should be exercised in interpreting a phenomenon such as the bimodal structure demonstrated for the Craters woodland. Clearly it provides evidence of wholesale destruction of a cohort of tree sprouts and/or seedlings sometime in the past. It does not, however, provide an answer as to why the failure occurred. Because of recent experiences it is tempting to conjecture that the elephant were responsible. Even if they were, it would not be proof that population cycles exist in elephant. All that can be said is that prior to the current regeneration, tree replacement was prevented for a period estimated to have lasted nearly 40 years. The repression was caused by elephant (Field 1971), a view that is further supported by aerial and ground counts since 1963

(Eltringham 1973; Table 3.1), which show that elephant numbers in the entire park were high. This does not, however, imply that there is necessarily an elephant population cycle and that habitat restoration is likely under modern conditions.

4.4.4. Recruitment potential

The study disclosed that the Craters woodland is regenerating abundantly where earlier a heavy loss of trees due to elephant had been reported (Field 1971). At densities of 1088 saplings/ha, regeneration potential was exceedingly high and almost entirely from rootstock. A great number of seeds were produced but seedlings contributed little towards stand regeneration. The lack of seedlings could have been for a variety of reasons including seed infestation, poor conditions for germination, herbivory and fire but these factors were not investigated.

The current profuse regeneration indicates that the trend towards grassland is not irreversible and that woodland, at least Acacia gerrardii woodland, can be restored by reducing elephant densities (in this case, by poaching). This has important management implications, not only for QENP, but also for many African national parks where too many elephant have led to drastic changes in landscape and habitat. It shows explicitly that to halt further destruction and to restore woodlands and forests, it is necessary to reduce the number of elephant.

The objective of a national park is to maintain a natural landscape. Over-population, no matter what the cause, usually results in overgrazing and degradation of the habitat. Is overgrazing natural? It is imperative, therefore, that it should be recognized as an unnatural situation when it occurs and corrective measures taken to deal with it.

The restoration of woodlands and forests should be an integral part of elephant conservation. Trees are essential to elephant (Laws et al. 1975; Malpas 1978) as well as to other wildlife species and perform many vital ecological functions. Their deep roots are able to tap water sources far below the ground so that they are able to provide succulent browse long after the grass has withered and dried. Nutrients are quickly leached from the surface of many African soils and the deep-rooted vegetation is important to retrieve and recycle them. There is more to conserving trees, therefore, than a pretty landscape and their destruction by elephant should be cause for concern as much for the welfare of elephant themselves as for the rest of the flora and fauna.

4.4.5. Fire, elephant and the woodland

There is substantial evidence that fire can damage or destroy trees (Glover 1963; Lamprey et al. 1967; Lawton & Gough 1970; Vesey-Fitzgerald 1973; Harrington & Ross 1974; Thomson 1975). This study confirmed that this is the case and showed that immature trees were the most severely affected. Observations indicated that this was due, at least in part, to their small size, low stature and lack of thick protective bark. Over-all, fire had the effect of pruning but not killing all woody vegetation.

In spite of fires or because of it, strong regeneration of vegetation has continued. Frequent fires prevented accumulation of large quantities of combustible material which result in intense and devastating fires. Such fires would burn most saplings back to ground level and destroy most of the lower branches of taller trees. Fires of this kind were not recorded during this study. Their absence was attributable to frequent regular grass fires which are generally cooler and less destructive. The conclusion from these data and observations is that although fire could ocassionally have caused serious damage, particularly to immature trees, it could not have been the sole cause of the decline of the woodland or its failure to regenerate in recent times.

More direct evidence that elephant were more important in controlling woody vegetation than was fire is provided by the experimental enclosures set up by Spence & Angus (1971) in Murchison Falls National Park. They excluded fire and elephant in a variety of combinations. They found that, in bushlands, fire did not prevent regeneration of woody vegetation whereas browsing did. In woodlands, on the other hand, either fire or browsing prevented tree regeneration.

Harrington & Ross (1974) carried out a similar series of experiments in Kidepo Valley National Park, Uganda, and found that either factor could prevent tree regeneration. They considered browsing to be the more important factor. Kidepo Valley differs from both Murchison Falls and Queen Elizabeth National Parks. It is much drier and hot fires are more frequent. The growing season is also much shorter. Rootstocks, therefore, may have less food reserves to sustain repeated attempts at regeneration. Precipitation is higher and the growing season longer in the other Uganda national parks. These factors apparently provide additional resilience to withstand fire.

One can conclude from these published data that in most cases tree destruction is due to elephant. Although fire may exacerbate the effects of browsing, it is rarely the sole cause of woodland decline. Evidence to the contrary, such as produced by Lawton & Gough (1970) in Zambia, has come from restricted areas and their conclusions cannot be extrapolated to cover all eventualities. In their case, the study area was not even typical of the Luangwa Valley (Astle 1971).

In fairness to elephant, it should be stated that these animals were not the only browsers in the experimental plots. Some of the damage to trees and woody vegetation could have been caused by other species. Elephant may also be blamed for damage for which they may be innocent. Trees die from a variety of other causes, including old age. In the Akagera National Park, Rwanda, Spinage & Guinness (1971) described tree destruction caused by rainstorm and lightning which might have been attributed to elephant were the species not absent from the park. Western and Van Praet (1973) also revealed the danger of jumping to conclusions by showing that trees supposedly killed by elephant in the Amboseli National Park, Kenya, actually died from an increase in soil salinity.

The present study has demonstrated that active and profuse regeneration has occurred and is continuing in the Craters woodland despite persistent, and occasionally intense, fires. It showed that the current situation was the reverse of that documented by Field (1971) in 1968/69 when elephant were destroying trees and preventing regeneration. The timing of the regeneration, which began after a massive decline in elephant numbers caused by poaching, indicated that elephant were much more important than fire in suppressing regeneration of woody vegetation there. The study has also demonstrated that there were sufficient rootstocks present to enable the re-establishment of the woodland. If fire could also be controlled, re-establishment probably would be even more rapid and more diverse.

The problem with elephant in even the largest of present-day national parks is that they cannot, through self-regulation, adjust their population size rapidly enough to remain within the carrying capacity of the habitat. The rationale of cropping is to help them do so. Whether the resulting equilibrium with the vegetation is natural or not, it is an essential management measure that must be maintained if elephant are to be kept within the confines of a national park and if a totally unnatural landscape is to be avoided. By allowing elephant numbers to increase without control within the park, the elephant is condemned to years of stressful life with an inadequate diet, a disruption of its social life and often serious damage to other large mammals in the community (Petrides & Swank 1974). Cropping has been shown to be efficient and to cause little suffering to elephant populations when carried out by professional biologists (Laws et al. 1975).

CHAPTER 5

THICKET ABUNDANCE AND EXPANSION

5.1. Introduction

Thickets are a prominent component of the vegetation in Queen Elizabeth National Park. Thickets were once much more extensive, particularly along the low-lying lake shores. There were extensively cut between 1912 and 1914, however, to remove the habitat of the tsetse fly (Glossina palpalis) following an outbreak of sleeping sickness (Spinage 1968). Today, isolated clumps occur in the grassland, each bush consisting of a virtually impenetrable tangle of thorny scramblers, particularly Capparis tomentosa and Azima tetracantha.

The concensus among park authorities (G. Okot, personal communication) is that, since about 1973, thickets throughout the park have increased. The increase has coincided with a decline in large herbivores and has fueled speculation that it was caused by a reduction in browsing. This view was enlarged by the Acting Chief Warden in the April 1975 monthly report to the Director of the National Parks. He attributed the increase in thickets to three factors: (1) overgrazing and lack of grass fires, (2) reduction in the number of elephant and (3) higher rainfall, resulting in a more vigorous thicket growth.

The probable causes of thicket proliferation and expansion as well as thicket ecology in general were investigated in the course of this study. The Mweya Peninsula and Kikorongo census area were chosen for intensive study. The two areas differed considerably in the incidence of fire and intensities of browsing and grazing. The peninsula was heavily grazed, the grass was short and thin, and there had been no fire in the area since 1963. Thickets, too, were heavily browsed by elephant and buffalo. Kikorongo, on the other hand, was an area of abundant medium-height to tall grasses where elephant were virtually absent and fires were common.

Comparison of thicket characteristics between the Upper Peninsula (at a higher elevation and generally drier) and Lower Peninsula (generally wetter and closer to the water table) (see Section 2.2 under Area 1) also were made to evaluate the influence of moisture.

5.2. Methods

5.2.1. Clump size, density and cover

A modified version of the point-centered quarter (PCQ) method of Cottam & Curtis (1956) was used to determine clump density. The method was applied in a manner similar to that described for trees in Section 4.2.1. The distance from the sampling point to the margin of the bush was measured at ground level along a line from the sampling point to the perceived center of the bush. The radius of the bush (r) was obtained indirectly by measurement of the clump circumference (c) at ground level, ($r=c/2\pi$). Bush-clump height was measured with a calibrated pole. Assumptions were made that the bushes were circular and that the centers of the clumps were properly located. It is believed, however, that the calculated values for r were approximations of the true values.

5.2.2. Composition of thicket clumps

Plant species present in each bush clump were recorded. The presence or absence of termite mounds was also tallied.

5.2.3. Origin and development of clumps

Termite mounds, Euphorbia candelabrum trees and several species of shrubs were evaluated as possible foci of clump origins. The appraisals included determining the frequency of each component in clump samples, their resilience to browsing, trampling, fire and moisture deficiency, as well as their ability to regenerate quickly when damaged. Some observations were made in experimental enclosures where fire was controlled and browsing, grazing and trampling by large herbivores eliminated.

5.2.4. Thicket expansion

Of 20 thicket clumps on Mweya Peninsula, ten were on the Upper and ten on the Lower Peninsula. The height and circumference of each bush was measured every three months between February 1982 and May 1983. Changes in diameter were averaged to give seasonal and annual rates of expansion. The apparent effects of fire, grazing and browsing were noted.

5.2.5. Thickets as a wildlife resource

Animal use of thickets was noted.

5.3. Results

5.3.1. Clump size, density and cover

The average number of thicket clumps on Mweya Peninsula and in Kikorongo was determined to be 53.6 and 4.4/ha, respectively (Table 5.1).

Thus, thickets were over 12 times more abundant on the Peninsula than in Kikorongo.

Table 5.1. Comparison of thicket parameters in Mweya Peninsula and Kikorongo. Queen Elizabeth National Park, Uganda, May 1983.

	Mweya	Kikorongo
Sample size (n)	428	296
Average height (m)	2.63	3.84
Average basal area (sq m)	51.47	102.75
Mean diameter (m)	8.10	11.44
Mean area/thicket (sq m)	186.59	2291.24
Density (/ha)	53.59	4.36
Cover (%)	27.58	4.45

Thickets in Kikorongo were individually larger than those on the Peninsula. The mean diameter and height for Kikorongo were 11.4 and 3.8 m, respectively, while corresponding figures for the Peninsula were 8.1 and 2.6 m. At 102.8 sq m, the average basal area for thickets in Kikorongo was almost exactly twice as large as the 51.1 sq m for those on the Peninsula. Thicket cover over the study areas was calculated to be 27.6% on the Peninsula and 4.5% in Kikorongo (Table 5.1).

5.3.2. Species composition

A thicket clump commonly contained 20 to 40 plant species (Table 5.2). Bushes on Mweya Peninsula were dominated by the thorny scrambler *Capparis tomentosa* and the even more-thorny *Azima tetracantha*. The two species were commonly co-dominant in the same clump. Even in clumps where one was clearly more abundant, the other was almost always present. Generally, Capparis dominated on higher ground while Azima dominated on lower ground closer to the water table and on saline seepages.

Table 5.2. Common thicket species on Mweya Peninsula, Queen Elizabeth National Park, Uganda, May 1983.

Trees	
Euphorbia candelabrum Trem. ex Kotschy	Euphorbiaceae
Shrubs	
Azima tetracantha Lam.	Salvadoraceae
Capparis tomentosa Lam.	Capparidaceae
Erythrococca bongensis Pax.	Euphorbiaceae
Hoslundia opposita Vahl	Labiateae
Indigofera arrecta A. Rich.	Leguminosae subfam. Papilionoideae
Jasminium eminii Gilg.	Oleaceae
Maerua triphylla A. Rich.	Capparidaceae
Pavetta albertina S. Moore	Rubiaceae
Tarenna graveolens (S. Moore) Brem.	Rubiaceae
Climbers	
Ceropegia sp.	Asclepidiaceae
Cissus adenocaulis Steud. ex A. Rich.	Vitaceae
Cissus quadrangularis L.	Vitaceae
Cyphostemma adenocaule (Steud. ex A. Rich.) Descoings	Vitaceae
Glycine javanica	Leguminosae subfam. Papilionoideae
Momordica sp.	Curcubitaceae
Sarcostemma viminale R. Br.	Asclepidiaceae
Herbs	
Achyranthes aspera L.	Amaranthaceae
Ageratum conyzoides L.	Compositae
Anthericum subpetiolatum Bak.	Liliaceae
Barleria sp.	Acanthaceae
Commelina africana L.	Commelinaceae
Commelina benghalensis L.	Commelinaceae
Cyanotis foecunda DC. ex Hassk.	Commelinaceae
Dyschoriste radicans (Hochst.) Nees	Acanthaceae
Justicia flava (Forsk.) Vahl	Acanthaceae
Ocimum americanum L.	Labiateae
Ocimum suave Willd.	Labiateae
Sansevieria dawei Stapf.	Agavaceae
Sida alba L.	Malvaceae
Sida ovata Forsk.	Malvaceae
Solanum incanum L.	Solanaceae

Table 5.2 (contd.).

Grasses	
Brachiaria eminii (Mez.) Robyns	Paniceae
Cenchrus ciliaris L.	Paniceae
Digitaria velutina (Forsk.) Beauv.	Paniceae
Panicum deustum Thunb.	Paniceae
Panicum maximum Jacq.	Paniceae
Setaria kagerensis Mez.	Paniceae
Setaria sphacelata Stapf. & C.E. Hubb.	Paniceae
Sporobolus pyramidalis P. Beauv.	Sporoboleae

The floristic composition of thickets north of the Kazinga Channel exhibited a remarkable degree of constancy with *Euphorbia candelabrum*, *C. tomentosa*, *A. tetracantha*, *Tarenna graveolens*, *Hoslundia opposita* and *Pavetta albertina* present over wide areas. Differences in dominants, however, were evident. For instance in Mweya Peninsula, *Securinega virosa* was only an occasional member of the thicket community but some 16 km to the north, in Kikorongo, it was frequently the dominant species.

5.3.3. Origin and development

Termite mounds were present in 46.4 and 51.9% of the clumps sampled in Mweya Peninsula and Kikorongo, respectively. If one accepts the theory of clump origin around termite mounds (Osmaston 1961; Jackson & Gartlan 1965), the origin of half of the clumps sampled would still be unaccounted for. Furthermore, if termite mounds were the foci of clump development, a sizable proportion of small clumps in the early stages of development could be expected to be on mounds. In the survey, though, only 4.3% (2 out of 46) of such clumps were associated with mounds.

Since nearly half the number of clumps sampled had mounds in them, it is reasonable to assume that mounds commonly developed in a clump once it was established. In a sub-sample of 200 of the largest clumps, 178 or 89% were found to have mounds. This demonstration that mounds were most common in the largest clumps indicates that thicket clumps are frequently the foci of termite activity and mound formation rather than the reverse.

The frequency of Euphorbia candelabrum within clumps was 89.5 and 96.3% in Mweya and Kikorongo, respectively. Despite the high incidence of the species inside thicket clumps, it was virtually absent from the heavily grazed and trampled grassland between clumps. Furthermore, inside an experimental exclosure devoid of large mammal activity there were 1600 seedlings/ha. Thus the species evidently can, in fact, grow in grasslands but, seedlings did not occur there because they were unable to survive trampling and/or browsing by large herbivores. Examination of a large sample of saplings showed that a young Euphorbia was fleshy, weak and would snap easily should a large mammal even brush against it. Seedlings in the open could not, it seemed, provide nuclei for clump formation.

Observations inside the exclosure showed that several other thicket species, including Securinega virosa, Maerua triphylla and Hoslundia opposita, were capable of establishing themselves in the grassland. Small individuals of these species were also frequent in the heavily-grazed short grass area north of the Kazinga Channel. During the dry seasons, these and most other thicket species commonly wilted and lost their leaves completely depending on the severity of moisture deficiency.

Of the common thicket species, only Capparis tomentosa and Azima tetracantha were capable of vigorous and sustained growth. Their seedlings were firmly rooted, making them resistant to uprooting as a result of browsing or trampling. During the re-construction of vehicle tracks in the park in 1981, numerous thicket clumps were removed. Taking advantage of the opportunity, it was observed that both C. tomentosa and A. tetracantha developed extensive root systems and sprouted readily after damage. Small bushes quickly developed from root sprouts along tracks and in ditches around enclosures. The most remarkable trait in the two species was, however, their ability to remain green and lush and to continue to grow actively even during a severe dry season when all others species essentially ceased to grow.

5.3.4. Expansion

Rainfall data (Table 5.3; Fig. 5.1) show that the period 1965-1978 was wetter than that of 1954-1963. The meteorological data, therefore, tend to support the claim that the increase in thicket abundance and expansion could be due, at least in part, to increased precipitation.

Observations in Kikorongo indicated that frequent fire was a major factor limiting both the abundance and expansion of thickets. During grass fires, young shrub seedlings often were killed and small clumps burned back to ground level.

Some established thicket plants such as Capparis, were extremely resilient to fire. Even when severely damaged, they often put forth new shoots within two to three weeks after a fire. Rarely did fire totally demolish large bush clumps. Usually only the shoots along the margin were burned, arresting growth and horizontal expansion. Fire played an important role in limiting thicket abundance and expansion. The absence of grass fires would eliminate a potent controlling factor.

Table 5.3. Mean monthly rainfall (mm) on the Mweya Peninsula. Queen Elizabeth National Park, Uganda.

	1954-1963	1965-1978
January	26.2	26.7
February	24.6	49.0
March	64.5	74.4
April	75.7	123.2
May	62.2	87.1
June	29.5	42.9
July	25.4	60.6
August	71.1	73.3
September	84.6	76.4
October	82.8	78.8
November	71.1	109.2
December	51.8	39.6
Totals	669.5	841.2

On the Mweya Peninsula, there have been no grass fires since 1963 due to overgrazing by hippopotamus. The area contained one of the highest densities of thickets in the park, with 27.6% of the peninsula estimated to be under thickets. The absence of fire seemed certain to have been a contributing factor to the proliferation of thickets in the area.

On the Mweya Peninsula, the average diameter for 20 thicket clumps increased from 6.2 m in February 1982 to 7.7 m in May 1983, an expansion rate of 9.7 cm per month (Table 5.4). Seasonal monthly growth rates differed significantly. The wet season rate was 12.0 cm/mo. in contrast to the dry season rate of 6.2 cm/mo.

Fig. 5.1. Mean monthly rainfall (mm)

Mweya Peninsula, QENP, Uganda.

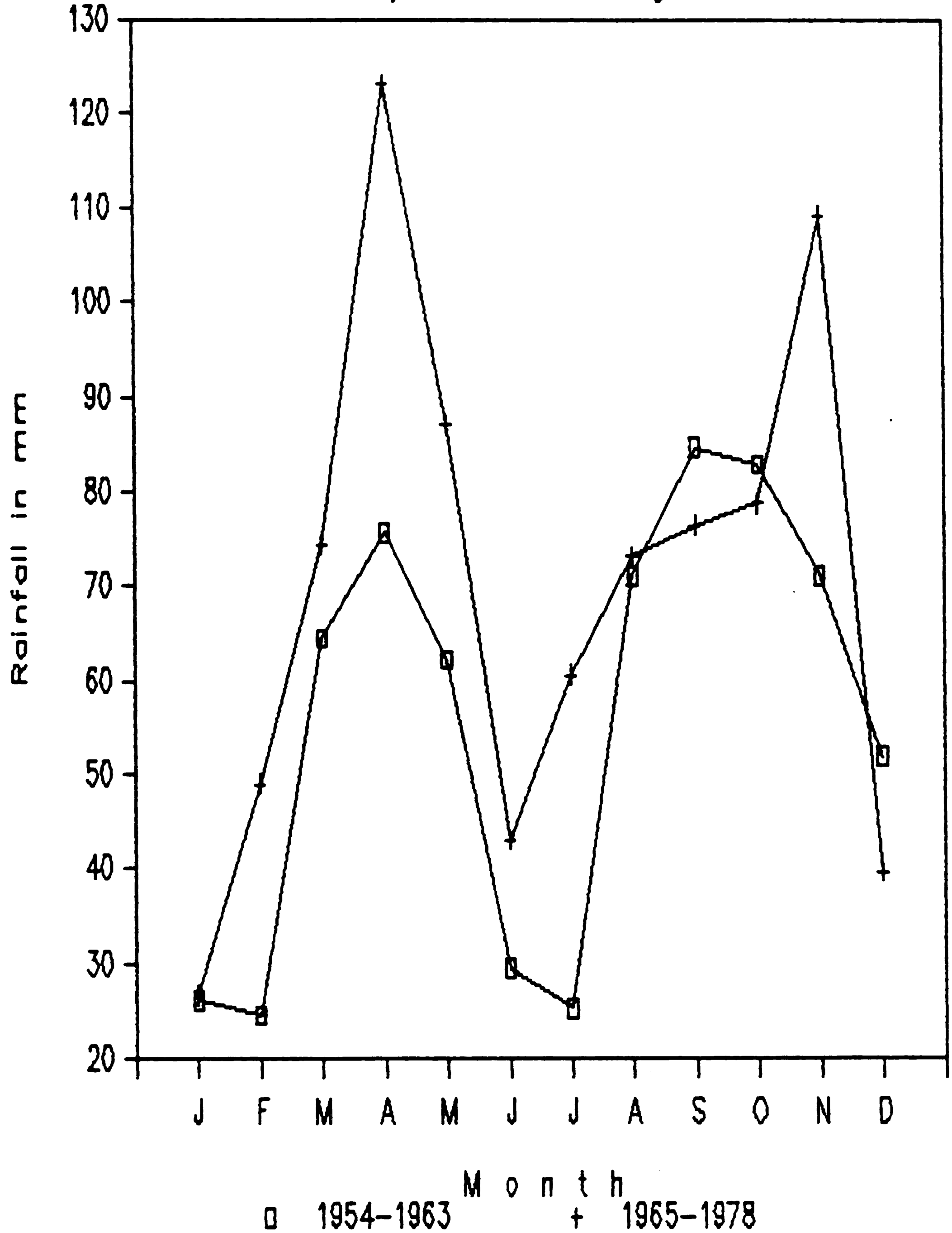


Table 5.4. Changes in diameter (m) of selected thickets on Mweya Peninsula, Uganda, between February 1982 and May 1983.

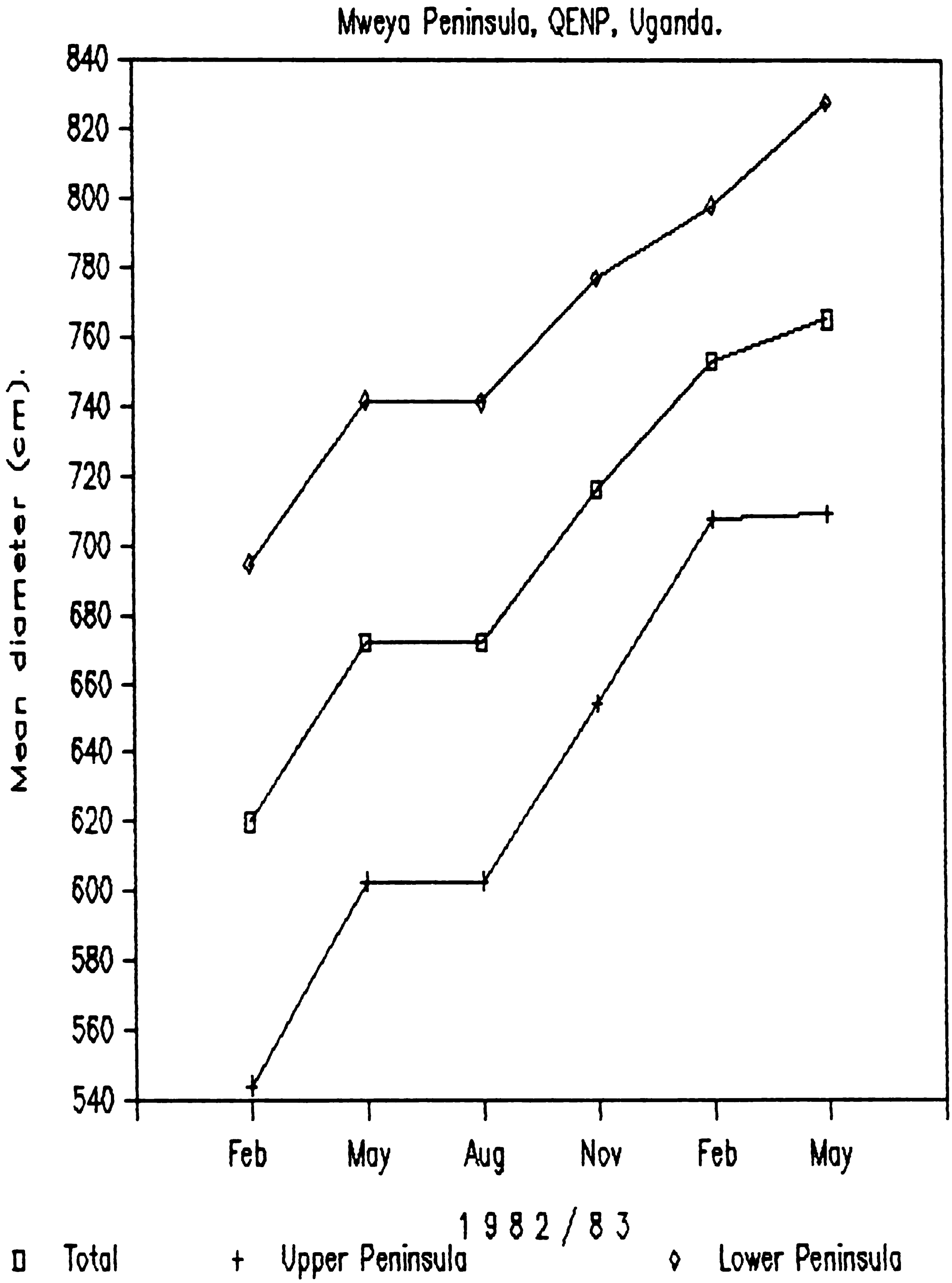
Thicket #	Feb 1982	May 1982	Aug 1982	Nov 1982	Feb 1983	May 1983
1	6.27	6.25	6.13	6.55	7.08	7.17
2	3.16	3.39	3.29	3.32	6.54	6.90
3	3.15	4.12	3.54	3.69	6.75	6.89
4	5.80	6.37	5.82	6.15	4.06	4.29
5	5.05	5.93	5.56	5.73	8.08	8.14
6	5.28	5.78	6.27	6.75	6.64	6.97
7	6.89	7.32	7.56	7.86	8.83	9.21
8	8.06	8.69	8.67	9.08	8.96	8.34
9	5.73	6.74	7.60	7.99	6.89	5.79
10	5.04	5.69	5.87	8.33	6.91	7.21
11	7.50	7.47	7.51	7.66	7.60	7.70
12	7.51	7.62	7.63	8.08	8.26	8.43
13	7.66	8.01	8.04	8.10	8.47	8.66
14	5.15	5.49	5.88	6.08	6.19	6.64
15	5.61	5.90	6.31	6.37	6.44	7.64
16	6.27	6.89	6.75	7.71	7.86	7.92
17	10.91	11.60	11.82	12.66	12.99	12.79
18	4.68	6.11	5.06	5.53	6.03	6.83
19	6.84	7.24	7.33	7.41	7.73	7.75
20	7.35	7.85	7.77	8.08	8.22	8.40
$\bar{X}$	6.20	6.72	6.72	7.16	7.53	7.65
SD	1.77	1.72	1.85	1.98	1.72	1.66

Growth rate: wet and dry season = 12.0 and 6.2 cm/mo., respectively; an annual rate of 9.7 cm/mo.

Despite the steady increase in average diameter (Fig. 5.2), some individual clumps experienced temporary reductions in diameter between measurements (Table 5.4). These losses followed substantial browsing, primarily by elephant, but frequently also by buffalo. Evidently, browsing by ungulate could also exercise considerable control on thicket expansion.

The average diameter of thickets on the Lower Peninsula was much

Fig. 5.2. Growth of bush-clumps



larger than of those on the Upper (Fig. 5.2). This was thought to be due to a higher rate of expansion on account of a presumed higher level of soil moisture on the Lower Peninsula. The data, however, contradict this hypothesis. While the wet season growth rates for the Upper and Lower Peninsula thickets were remarkably similar (12.4 and 12.5 cm per month, respectively), those for dry season were quite different. The rate for the Upper Peninsula was 8.9 cm/mo., while that for the Lower Peninsula was 3.4 cm/mo.

In QENP, the single factor most limiting to plant growth is availability of water. Thickets on the Lower Peninsula are closer to the shoreline and watertable and are better situated to exploit soil moisture on a year-round basis. They were thus expected to have a higher rate of expansion than those on the Upper Peninsula.

The paradox appears to be the result of seasonally intense browsing, particularly by elephant but frequently also by buffalo. During the second dry season of 1982, elephant activity centered on the Lower Peninsula where browse was more abundant and shade trees provided relief from the sun. Water for drinking and bathing was also more readily available than on the Upper Peninsula. On the Upper Peninsula, there were no trees to provide shade and elephant activity was limited to visits during the night, occasionally lingering into the morning. The Upper Peninsula also contained the Headquarters of the park and camps for the staff. As a consequence, there was always some human activity on the Upper Peninsula even at night. Out of a total of 99 hours (h) that elephant groups were on the Peninsula, 62 (62.6%) were spent on the Lower Peninsula. If this is the general pattern during the dry season, the low rate of thicket expansion recorded on the Lower Peninsula during the dry season may have been, at least in part, due to heavy browsing by ungulates.

5.3.5. Thickets as a wildlife resource

A wide range of animals commonly used thickets for food, shelter, shade and concealment (Table 5.5). Thickets were more important to some species than to others. For example, the bushbuck and vervet monkey depended heavily on them for several aspects of their well-being including food,

Table 5.5. Qualitative assessment of large mammal use of the thicket resource in Queen Elizabeth National Park, Uganda, November 1981-June 1983.

	Category of use			
Species	Food	Shelter	Shade	Concealment
Elephant	Common	-	Common	-
Hippo	Occasional	-	-	-
Warthog	Rare	Common?	Common	Common
Reedbuck	-	-	-	-
Waterbuck	Common	-	Common	Occasional?
Kob	Occasional	-	Frequent	-
Bushbuck	Common	Common	Common	Common
Buffalo	Frequent	-	Common	-
Baboon	Common	Common?	Common	Common
Vervet monkey	Common	Common	Common	Common
Lion	-	-	Common	Common
Monitor lizard	-	Frequent	Common	Common

shelter and concealment. The reedbuck and kob, on the other hand, hardly used them at all. Warthog and lion used them extensively for shade and concealment, but not for food. In this brief survey, the diversity of the fauna that benefited from thickets indicated that they were an important wildlife resource. In East Africa, this role has generally been overlooked.

5.4. Discussion

5.4.1. Clump size, density and cover

Thicket clumps in Kikorongo were larger than those on Mweya Peninsula. This was attributed to two causes. First, precipitation was higher in Kikorongo than on the Peninsula and Kikorongo was free of elephant activity. Also fires prevented the establishment of thicket seedlings in Kikorongo.

5.4.2. Species composition

Although species composition in thickets north of the Kazinga Channel showed remarkable constancy, this is apparently not characteristic of the entire park. Lock (1977) reported that on the Ishasha River Flats in the extreme south, many of the associates are replaced by species that are absent in the north such as Capparis fascicularis.

The distribution of dominants perhaps emphasizes the enormous variability in precipitation, drainage and topography as well as the influences of fire and herbivory within the park.

5.4.3. Origin and development of clumps

Several theories have been advanced to explain the origin of thicket clumps. Lebrun (1947) suggested that they develop from the shrub layer below isolated trees. Osmaston (1961) suggested that clumps develop around termite mounds and that the shade of a _Euphorbia_ _candelabrum_ tree, once established, is beneficial to the process on Lolui Island in Lake Victoria, Jackson and Gartlan (1965) found that clumps developed from seeds in monkey droppings around rocks and termite mounds frequently used by the primates. The present study does not support these theories of clump origin around termite mounds or _Euphorbia_ trees.

For a plant to flourish in QENP, it has to be adapted to a large moisture deficit, frequent fires and persistent browsing. The last factor could result in uprooting or breakage. In general, bushes and thickets are better adapted to withstand browsing than are trees. When a tree is broken or uprooted, the physical damage is serious. Thickets are more difficult to destroy. Parts may be severed but regeneration is rapid. No lasting damage is done. When a tree is killed another will not necessarily grow in its place. It seems logical, therefore, that species acting as nuclei for clump formation are shrubs rather than trees.

An alternative theory is that a single bush in the grassland acts as a nucleus from which a clump develops (Lock 1977). Given the persistent browsing and frequent fires, the bush has to be able to grow continually and vigorously in order to survive. Of the common thicket species, only _Capparis_ and _Azima_ had the characteristics necessary to be the nuclei around which thicket clumps could develop.

Termite mounds occur frequently in thicket clumps probably because termites are attracted to the sites by dead stems and accumulation of litter. Similarly, clumps do not develop around _Euphorbia_ trees, but rather the trees are able to establish themselves and to develop within thickets because of the protection provided by thicket clumps. Without the clumps the trees would not survive the trampling and browsing of large herbivores. Rather than being the origin of thicket clumps, termite mounds and _Euphorbia_ trees occur in thickets because the clumps provide a supportive environment.

Once established, a thicket evidently gained species and expanded outward from its origin. Usually the first to establish themselves under the young thicket were some of the common grasses and herbs. They included _Brachiaria eminii_, _Cenchrus ciliaris_, _Sporobolus pyramidalis_, _Achyranthes aspera_, _Phyllanthus_ spp., _Ocimum americanum_, _O. suave_, _Sida alba_, _S. ovata_ and _Solanum indicum_ and the sedge _Kyllinga_. These associates, too, contribute to the changing environment. Gradually woody plants appeared, common among them were _Erythrococca bongensis_, _Euphorbia candelabrum_, _Maerua triphylla_, _Pavetta albertina_ and _Tarenna graveolens_. In time a tree or two, usually a _Euphorbia_, may emerge through the bush. Observations indicated that emergent trees were at greater risk of destruction by elephant than non-emergents, yet some survived to maturity.

Capparis or _Azima_ often remained the major clump constituents. Some very large thickets (30 to 40m in diameter) recorded in this study were thought to have formed by adjacent thickets coalescing. Eventually animals (especially elephant, buffalo and hippopotamus) could break into the thicket and may split it up or even destroy it.

Usually fires scorch only the periphery of the clump and recovery is rapid. Even when all aerial parts were destroyed, bases sprouted vigorously and, in time, probably restored the clump. Under certain circumstances, fire was observed to destroy thickets. Occasionally, the mass of dead wood from a fallen Euphorbia would produce a very hot flame which killed much or all of the thicket.

The continued active growth of many thicket constituents during the dry season may be, at least in part, due to the soil moisture available to them. In West Africa, Okali et al. (1973) have shown that Capparis and other constituents of similar thicket clumps, are able to conserve water because they have deep roots and enjoy restricted water-loss through the stomata.

Certain grass species, including Cenchrus ciliaris, Eragrostis tenuifolia and Sporobolus pyramidalis, were common in both grasslands and thickets. Individuals in the grassland were stunted and feeble, while those within thickets grew taller, stouter, more robust and remained green longer into the dry season, after those in the grassland had wilted and dried. Persistent defoliation of plants in the grassland by hippopotamus was thought to be the reason for the disparity in stature. It would not, however, explain why plants inside thickets remained green longer. This is evidence that clumps are able to retain and conserve moisture much better than is the open grassland. If this is true, the greater amount of moisture available to plants growing inside thickets may also contribute to the noted disparity in stature.

5.4.4. Thicket expansion

The impact of rainfall, fire and browsing pressure were discussed with respect to differences in thicket size and abundance in Mweya Peninsula and Kikorongo. These factors also influence the overall trend towards thicket proliferation and expansion in the park as a whole.

Although higher rainfall in recent years may have resulted in more vigorous thicket growth, it is not considered the likely cause of the trend towards increased thicket density. Rainfall data indicates that the increase in rainfall levels began in 1961. By all accounts, however, the increase in thicket size and density for the park as a whole began about 1973 (E.L. Edroma, personal communication). It is unlikely that it took thickets more than ten years to respond to increased rainfall.

Observations in Kikorongo showed that fire is a major limiting factor in certain areas of the park. In heavily grazed areas, the absence of fire due to lack of fuel, has been a factor in thicket expansion. There is no indication, however, that in recent years the incidence of fires has declined in sectors of the park other than the Mweya Peninsula. For this reason the absence of fire, is also eliminated as the major cause of thicket proliferation.

The only other plausible explanation for the rapid trend towards thicket abundance and expansion is a reduction in the overall level of browsing pressure. This is supported by the fact that the decline in populations of large herbivores in the park was followed shortly by reports of thicket expansion. It is concluded, therefore, that thicket proliferation was a result of the massive decline in large herbivores.

5.4.5. Thickets as a wildlife resource

Thickets clumps were found to be important for the food, shelter, shade and concealment which they provide to a diverse spectrum of animals. The thicket flora is comprised of a rich variety of grasses, herbs and woody plants not otherwise available.

Few ungulates are as dependent on thickets as the bushbuck and bush duiker. These animals live in and feed on thickets and use them effectively to hide or escape from predators (Waser 1975; Allsopp 1978; Okiria 1980). Their entire ecology is dependent on the thicket and its resources.

A number of other large herbivores used thickets primarily as a source of food. They included elephant, buffalo and waterbuck. Field (1971) has shown that the young and tender shoots of Capparis are rich in protein. During the dry season when the coarse, dry hay provided poor grazing, such browse constituted a valuable source of protein. At such times even species such as kob which are primarily grazers, were observed occasionally to browse thickets. Thickets provide grazing and browse to livestock which are kept by inhabitants of the many villages in the park, despite an ordinance forbidding the raising of domestic animals. Goats have been particularly destructive, overbrowsing thickets around a number of the villages (Musoke 1980).

Two common species of grassland primates, the olive baboon and the vervet monkey, obtained a considerable portion of their food from thicket plants, feeding on fruits, berries, seeds and foliage. Baboons on the southern banks of the Kazinga Channel even feed on shoots of Euphorbia candelabrum (Lock 1972). Few animals fed on Euphorbia because they contain a noxious latex, but somehow these baboons have developed a mechanism to detoxify the latex.

Numerous birds and insects also derived sustenance from thickets. All the major woody species in the thickets have edible fruits. These were often eaten by birds which were probably instrumental in dispersing their seeds. From June to August Capparis was frequently completely defoliated by caterpillars of Belenois aurota Fab. (Kenyi 1980).

Lion, waterbuck, warthog, the monitor lizard and guineafowl (Numida meleagris), regularly sought comfort away from the hot equatorial sun in the shade of thickets.

In conclusion, this study has rejected the hypotheses of the possible origins of thicket clumps on termite mounds and around Euphorbia trees in favor of clump development around the nucleus of a single plant in the grassland. That plant had to be a vigorous species to persist in spite of browsing, trampling and burning. The trend in the park towards increased thicket size and abundance was evidenced to be the result of decreased browsing pressure. The increase in rainfall levels in recent years may have resulted in a more vigorous thicket growth but was not directly the cause of the proliferation. Fire was judged to be a major factor in checking thicket abundance and expansion in areas where they were frequent. It is postulated that fire is particularly effective in preventing seedling establishment, resulting in lower thicket density. Differences in thicket size between areas were attributed to varying levels of precipitation as well as to the activities of large herbivores which may break up or destroy thickets.

Although thickets and the grassland have been treated as separate vegetational units, they clearly form parts of a single ecosystem. They are dynamically related since new thickets apparently become established on grassland, while old ones are eventually destroyed and replaced by grassland. Large herbivores not only grazed and browsed the thickets but often took shelter in them, with resulting concentration of fecal material. As a consequence of these relations, the physical and chemical properties of the soil are probably changed during the development of a thicket. These changes, at least temporarily, influence the grassland which subsequently replaces the thicket.

CHAPTER 6

STANDING-CROP BIOMASS, SPECIES COMPOSITION AND GRAZING INTENSITY IN THREE GRASSLAND TYPES

6.1. Introduction

In Queen Elizabeth National Park, grassland types are associated with rainfall (Field 1970) and intensity of grazing (Brooks 1957; Heady 1966; Lock 1972). In the present study, three physiognomic types namely the short, medium-height and tall grasslands were studied to determine species composition, vegetative cover, standing-crop biomass and intensity of grazing. The vegetation inside a 15-year old exclosure on the Mweya Peninsula was compared with that of an adjacent grazed plot. Changes in the vegetation over the past 25 years induced by grazing were reviewed briefly. Present conditions were compared with those reported in earlier studies.

In the late 1950s, excessive grazing by hippopotamus (Bere 1959; Petrides & Swank 1965) resulted in widespread deterioration of habitat. As discussed in Chapter 3, the present hippopotamus population on Mweya Peninsula is substantially higher than that which earlier resulted in habitat deterioration.

Some observers (Yoaciel 1981) have postulated that grazing might not have been responsible for the habitat degradation in the late 1950s. They point to rainfall data which shows that the period 1954 to 1963 was drier than the period since 1963 as evidence that habitat deterioration was probably a climatic episode. This study disagrees, however, and shows that while widespread deterioration similar to that reported for the 1950s has not recurred, hippopotamus are presently overgrazing the range and if allowed to continue could result in range degradation.

6.2. Methods

6.2.1. Species composition and vegetative cover

Species composition was determined by recording plants present within 1-sq-m quadrats taken at 10 m intervals along randomly selected transects.

In the short grassland on Mweya Peninsula, data on vegetative cover and species composition were collected simultaneously. The 1-sq-m quadrat used to determine species composition of the grassland had steel wires stretched between opposite sides at 20-cm intervals. The wires formed a grid with 16 intersections each of which was used as a sampling point to determine vegetative cover. The plant species directly below each sampling point was recorded. Vegetation was not present at every sampling point, of course, in which case litter or the substratum was recorded. Cover for a given species was calculated as the percentage of sampling points at which the species occurred.

6.2.2. Standing-crop biomass and intensity of grazing

The amount of forage available to herbivores in each grassland type was determined monthly by taking samples from a 30-m-square plot established at a site judged to be representative of the grassland. The plot was open to grazing. At about the same time every month, eight 1-sq-m samples were selected by random coordinates and harvested at ground level from within the plot. Live shoots were separated from dead material and further sorted by species. The entire crop was dried and weighed.

In the short and medium-height grasslands, an ungrazed plot protected by barbed-wire fencing 1.5 m high was established adjacent to the grazed plot. Limited resources prohibited construction of a similar exclosure in the tall grassland. Differences between the quantities harvested in the grazed and ungrazed plots at each site were assumed to measure the amounts of forage consumed by large herbivores.

Rainfall data collected at the plot site in the short grassland enabled an evaluation of the relationship between monthly precipitation and live-shoot biomass.

6.2.3. Vegetation within the 15-year old exclosure on the Mweya Peninsula

The experimental exclosure on the Mweya Peninsula was constructed in 1968 and consists of a circular trench around a barbed-wire fencing 80 m in diameter (Strugnell & Pigott 1978). A survey of the vegetation within the exclosure was made to determine the nature of the vegetation the area would carry in the absence of grazing. Species composition, standing-crop biomass and vegetative cover within the exclosure were compared with that of an adjacent grazed plot outside.

The exclosure was also used to appraise the long-term effects of fire on the grassland. Since 1968, one half of the exclosure has been burned annually (except in 1979 and 1980), while the other half has been kept unburned. By excluding animals, the exclosure provided a controlled situation in which fire was the only experimental factor. The species composition of the two halves were compared to determine the long-term effects of fire on the flora.

6.3. Results

6.3.1. Species composition and vegetative cover

The short grassland was found to be the richest in grass species with a total of 23. In comparison, the number recorded in the medium-height and tall grasslands were 14 and 12, respectively.

The main constituents of the short grassland were Chrysochloa orientalis and Sporobolus pyramidalis. Several other species including Tragus berterionianus, Sporobolus stapfianus, Eragrostis cilianensis, E. tenuifolia, Cenchrus ciliaris, Chloris gayana and Dactyloctenium aegyptium were common (Tables 6.1 and 6.2). Cynodon dactylon was abundant locally along the lake shores. The tufted, pyrophilous grasses Themeda triandra and Heteropogon contortus which were common throughout the greater part of the park were conspicuously absent. Common herbs included Alternanthera pungens, Euphorbia spp., Tribulus terrestris and Tephrosia spp.

The short grassland was dominated by stoloniferous and short, mat-forming perennials and prostrate herbs and shrubs. The more common stoloniferous species included C. orientalis, C. ciliaris, C. gayana and C. dactylon. Sward height was 5 to 40 cm, with a mean of 7.2. Mat-forming grasses were represented by Microchloa kunthii, S. stapfianus and S. festivus.

In contrast, the other two grasslands were dominated by taller, tufted grasses such as Hyparrhenia spp., T. triandra, H. contortus and

Table 6.1. The major components of three grassland types in Queen Elizabeth National Park, Uganda. Dry weights are means for 14 months from May 1982 to June 1983.

Plant taxa	g/sq m	%
Short grassland		
Chrysochloa orientalis	12.0	30.1
Sporobolus pyramidalis	10.8	27.1
Sporobolus stapfianus	1.9	4.9
Harpachne schimperi	1.7	4.4
Eragrostis spp.	1.6	4.1
Microchloa kunthii	1.1	2.7
Aristida adoensis	0.7	1.8
Tragus berteronianus	0.6	1.6
Other grasses	0.8	2.0
Forbs	8.5	21.3
Medium-height grassland		
Heteropogon contortus	51.0	29.6
Themeda triandra	42.0	24.4
Sporobolus pyramidalis	28.8	16.7
Bothriochloa spp.	23.9	13.9
Hyparrhenia filipendula	21.0	12.2
Other grasses	1.9	1.1
Forbs	3.6	2.1
Tall grassland		
Hyparrhenia filipendula	219.5	47.8
Themeda triandra	151.5	33.0
Cymbopogon afronardus	46.8	10.2
Imperata cylindrica	22.5	4.9
Other grasses	8.7	1.9
Forbs	10.1	2.2

Cymbopogon afronardus. Despite similarities in flora and structure, the medium-height grassland was of lower stature than the tall. Sward height in the medium-height grassland was 45 to 105 cm with a mean of 89, compared with a range of 80 to 180 cm and a mean of 153 in the tall.

The three grasslands were zoned according to distance from permanent water in which hippopotamus, the dominant herbivores, lived. The intensity of grazing by hippopotamus decreased with distance from the water. It seemed, therefore, that the life-forms of the grasses reflected, at least in part, the intensity of grazing. The stoloniferous and mat-forming grasses being the most tolerant and the tall, tufted species being the least tolerant of heavy grazing.

Several species of annuals were common in the short grassland but not in the other two. They included *Tragus berterionianus*, *Aristida adoensis* and *Chloris pycnothrix*.

Table 6.2. Foliar cover in the short grassland on Mweya Peninsula, Queen Elizabeth National Park, Uganda, at the end of the first growing season, May 1982.

Species*	Percent cover
Chrysochloa orientalis	11.1
Sporobolus pyramidalis	9.2
Alternanthera pungens	8.9
Euphorbia spp.	4.0
Sporobolus homblei	3.5
Chloris gayana	3.0
Herbs (mostly legumes)	2.7
Tribulus terrestris	2.6
Sporobolus stapfianus/festivus	1.9
Eragrostis spp.	1.4
Tragus berterionianus	1.3
Cynodon dactylon	1.0
Litter	3.9
Bare ground	38.4

*Only species accounting for at least 1% cover have been tabulated.

The sward in the short grassland was not only low but also thin. *C. orientalis*, *S. pyramidalis* and the prostrate herb *Alternanthera pungens* provided the most foliar canopy, contributing 11.1, 9.2 and 8.9% of total cover (Table 6.2).

Sward height and vegetative cover reached their maxima at the end of the growing season. At this time the sward in the short grassland varied in height from 5 and 40 cm with a mean of 7.2. Even at this time, however, as much as 38.4% of the ground surface was still exposed (Table 6.2). This proportion increased as the dry season advanced. Due to intense grazing, the sward was reduced to a more or less uniform height <5 cm early in the dry season. Therefore, during much of the dry season the proportion of exposed surface was higher than the 38.4% indicated by this study.

While no quantitative data were obtained for the taller grasslands, observations indicated that their vegetation was sufficiently dense that foliar cover was nearly 100%. The only notable exceptions were localities of kob communal territorial grounds which were kept short by heavy grazing and trampling.

Due to the abundance of grass in the tall and medium-height grasslands, they were always at great risk of fire during the dry season and burned frequently. Much of the short grassland, on the other hand, was never at risk of fire for lack of fuel to support one.

Although mat-forming species were not ordinarily significant components of the medium-height and tall grasslands, it was observed that following fires _Sporobolus stapfianus_ and _Microchloa kunthii_, two mat-forming species, briefly dominated large parts of these grasslands. They accomplished this by growing quickly and flowering gregariously early in the growing season before the taller, tufted species could compete and overshadow them. In full bloom, the inflorescence of _S._

stapfianus gave the sprouting grassland a lavender hue. Gregarious flowering similar to the post-burning phenomenon was not observed in the short grassland.

6.3.2. Standing-crop biomass and intensity of grazing

Standing-crop biomass was highest in the tall and lowest in the short grasslands (Table 6.3; Fig. 6.1). During the period of study, the mean monthly standing-crop biomass was 39.8 g/sq m in the short, 172.3 g/sq m in the medium-height and 459.2 g/sq m in the tall grassland.

In the short grassland, liveshoot biomass in the ungrazed plot was consistently higher than in the grazed, indicating that the intensity of grazing was continuously high. This was true also for the medium-height grassland except for three months in which biomass in the grazed plot marginally exceeded that in the ungrazed (Table 6.3). The larger quantity of live shoots in the ungrazed plots reflected the intensity of grazing pressure on the open range.

When grazing intensities in the short and medium-height grasslands were compared, not only was the quantity grazed in any given month in most cases higher in the short grassland but the percentage of standing-crop biomass consumed was consistently much larger, showing that the short grassland was grazed more intensively. The proportion of standing-crop biomass grazed in the short grassland varied from a low of about 60% in the growing season to a high of over 90% in the dry (Table 6.4; Fig. 6.2), with an average of 75.6%. Variations within season were small. The high proportion of biomass cropped by ungulates explains why

Table 6.3. Mean monthly biomass (g/sq m) harvested in grazed and ungrazed plots in three types of grassland, Queen Elizabeth National Park, Uganda, 1982-1983.

	Exclosure (E)			Grazed (G)		
	Live shoots	Litter	Total	Live shoots	Litter	Total
A. Short grassland						
May	172.0	34.3	206.3	69.8	16.3	86.1
June	322.1	91.5	413.5	68.6	57.9	126.6
July	132.8	227.7	360.5	12.3	43.7	56.0
August	123.7	212.2	335.8	38.5	76.7	115.1
September	94.9	85.9	180.8	27.2	17.6	44.9
October	276.5	180.1	456.7	66.9	53.9	120.8
November	188.3	114.5	302.8	78.1	72.7	150.8
December	325.7	199.5	525.2	43.9	52.9	96.7
January	170.8	309.3	480.1	20.9	23.4	44.3
February	51.0	241.2	292.2	3.5	24.1	27.7
March	15.4	200.9	216.3	2.6	33.8	36.4
April	78.2	184.8	263.0	27.0	21.9	48.8
May	187.1	82.8	269.9	53.7	12.0	65.7
June	136.8	36.8	173.6	43.8	13.5	57.3
Total	2275.3	2201.4	4476.7	556.7	520.3	1077.0
Average	162.5	157.2	319.8	39.8	37.2	76.9
B. Medium-height grassland						
May						
June	561.9	312.4	874.3	183.5	126.8	310.3
July	387.1	306.1	693.1	360.9	326.4	687.3
August	443.6	537.6	981.1	219.3	432.0	651.4
September	228.1	691.3	919.4	231.8	593.9	825.8
October	197.1	314.2	511.3	73.8	314.2	387.9
November	233.9	342.6	576.5	220.1	296.6	516.7
December	277.9	232.9	510.9	164.4	304.9	469.3
January	198.1	699.9	898.0	208.1	352.8	560.8
February	136.2	460.1	596.3	142.7	450.5	593.1
March	123.7	484.2	607.8	69.3	216.6	286.0
April	145.3	426.3	571.6	105.3	120.1	225.3
May	136.8	218.5	355.3	117.8	137.5	255.3
June	223.5	257.8	481.4	142.5	114.2	256.7
Total	3293.0	5283.9	8576.9	2239.5	3786.4	6025.9
Average	253.3	406.5	659.8	172.3	291.3	463.5

Table 6.3. (Contd.).

	Exclosure (E)			Grazed (G)		
	Live shoots	Litter	Total	Live shoots	Litter	Total
C. Tall grassland						
May						
June				869.1	548.9	1418.0
July				650.4	454.2	1104.6
August				513.3	922.8	1436.0
September				472.6	408.3	880.8
October				653.8	446.1	1100.0
November				335.2	796.7	1131.9
December				298.6	466.1	764.7
January				309.3	405.5	714.8
February				274.9	571.4	846.3
March				341.6	371.4	713.0
April				347.9	690.3	1038.2
May				499.2	344.1	843.3
June				403.1	249.2	652.3
Total				5969.0	6674.9	12643.9
Average				459.2	513.5	972.6

the sward was thin and why nearly 40% of the surface was exposed. Such a high level of off-take could not be sustained indefinitely. The question arises whether there is a need for management intervention to prevent the herbivores, predominantly hippopotamus, from altering the habitat from a natural condition.

In the medium-height grassland, the percentages of standing-crop biomass grazed showed large and erratic fluctuations between zero and about 65% (Table 6.4; Fig. 6.2), with an average of 26.5%. In this and the tall grassland, forage production was clearly in excess of what the herbivores were able to consume. They could, therefore, support a higher biomass of ungulates than at present.

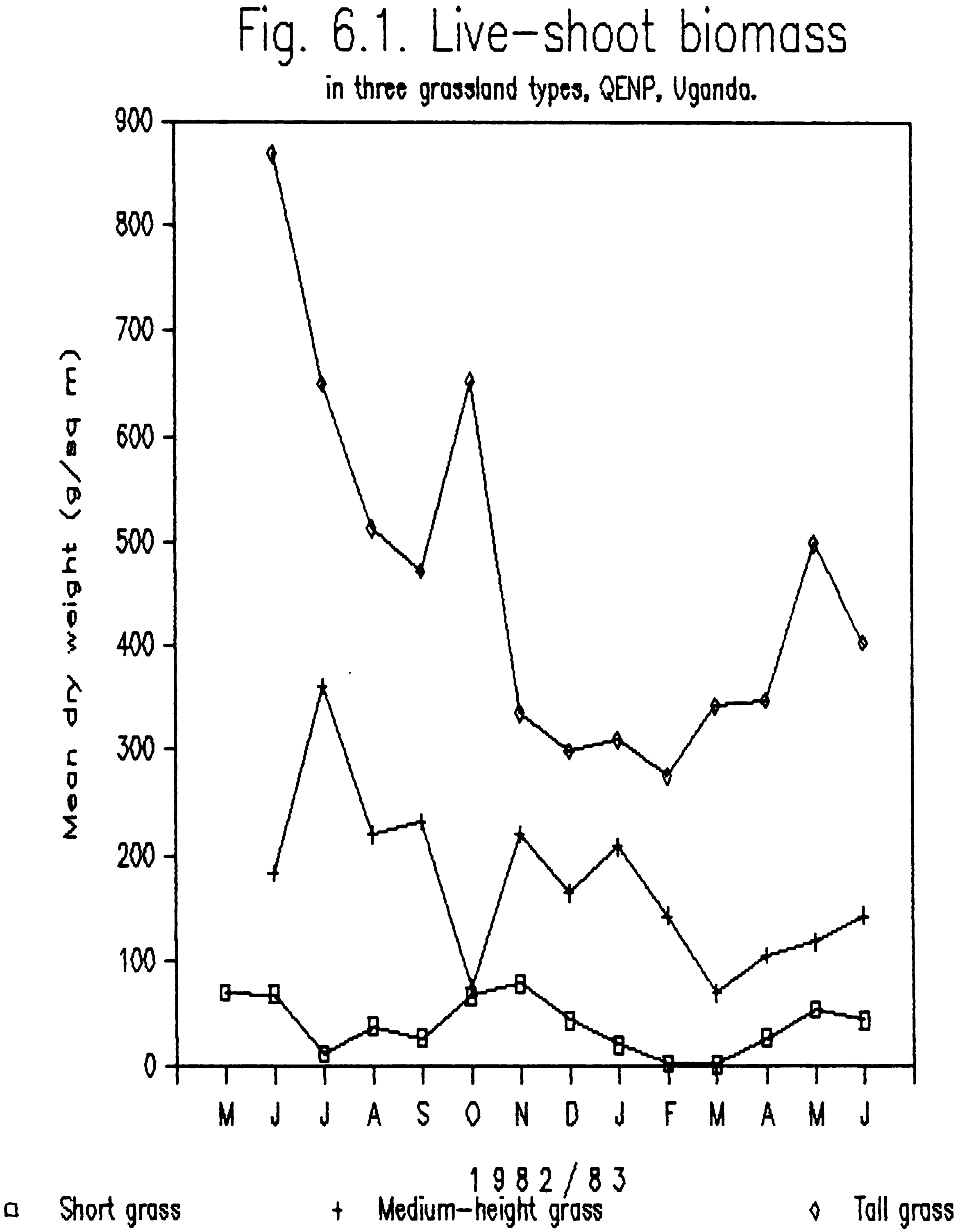


Fig. 6.1. Live-shoot biomass
in three grassland types, QENP, Uganda.
Mean dry weight (g/sq m)
900
800
700
600
500
400
300
200
100
0
M J J A S O N D J F M A M J
1 9 8 2 / 8 3
Short grass
Medium-height grass
Tall grass

Fig. 6.2. Intensity of grazing

Queen Elizabeth Nat'l Park, Uganda.

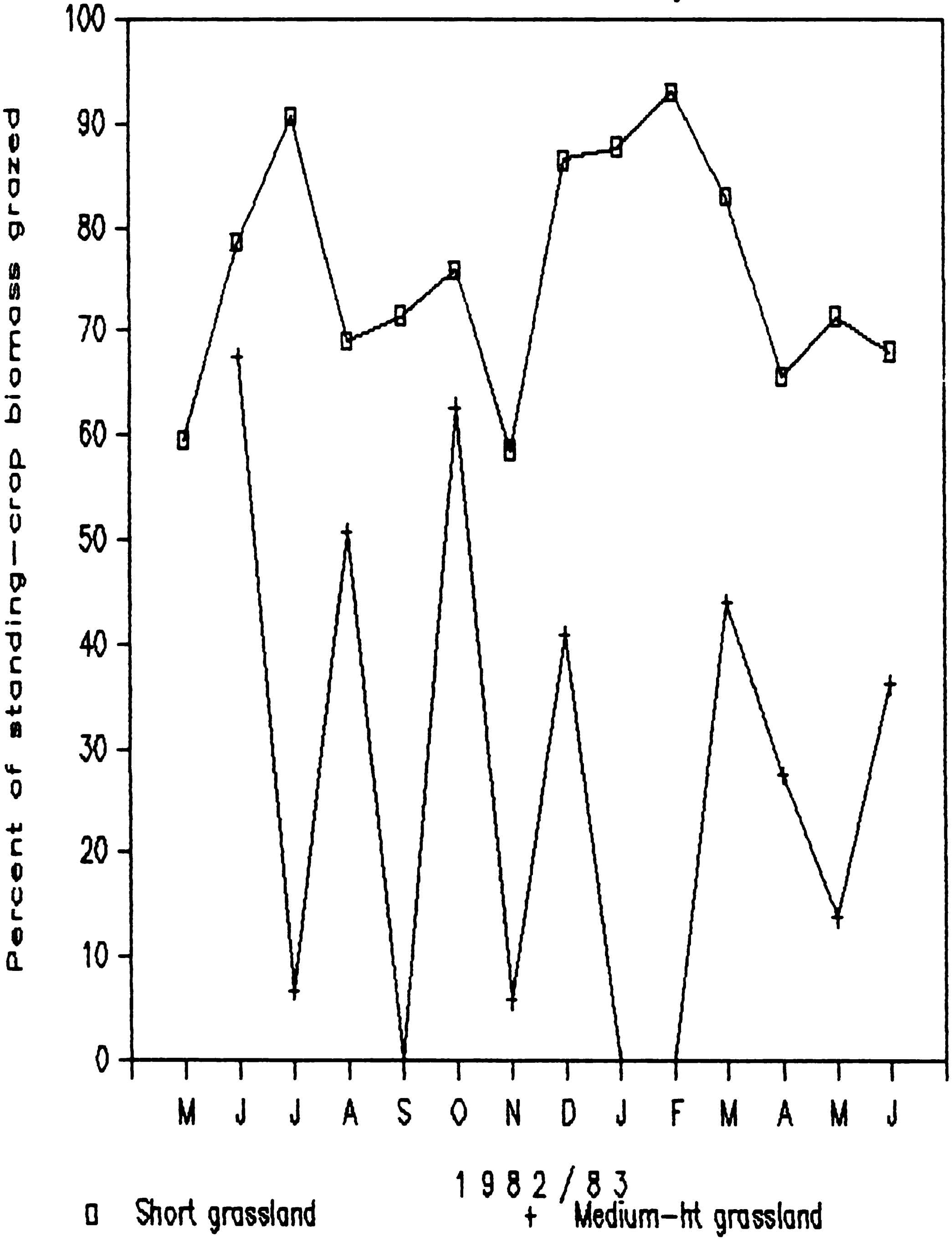


Table 6.4. Estimates (g/sq m) of vegetation removed by ungulates from the short and medium-height grasslands in Queen Elizabeth National Park, Uganda, 1982-1983. (Figures in parenthesis are percentages of standing-crop biomass cropped).

	Grassland type			
	Short		Medium-height	
May	102.2	(59.4)	-	-
June	253.5	(78.7)	378.3	(67.3)
July	120.5	(90.7)	26.2	(6.8)
August	85.2	(68.9)	224.2	(50.5)
September	67.7	(71.3)	-3.7	(-1.6)
October	209.7	(75.8)	123.3	(62.6)
November	110.1	(58.5)	13.8	(5.9)
December	281.8	(86.5)	113.5	(40.8)
January	149.9	(87.8)	-9.9	(-5.0)
February	47.5	(93.1)	-6.5	(-4.8)
March	12.8	(83.1)	54.3	(43.9)
April	51.3	(65.6)	40.0	(27.5)
May	133.4	(71.3)	19.0	(13.9)
June	93.0	(68.0)	81.0	(36.2)
Average	122.8	(75.6)	81.0	(26.5)

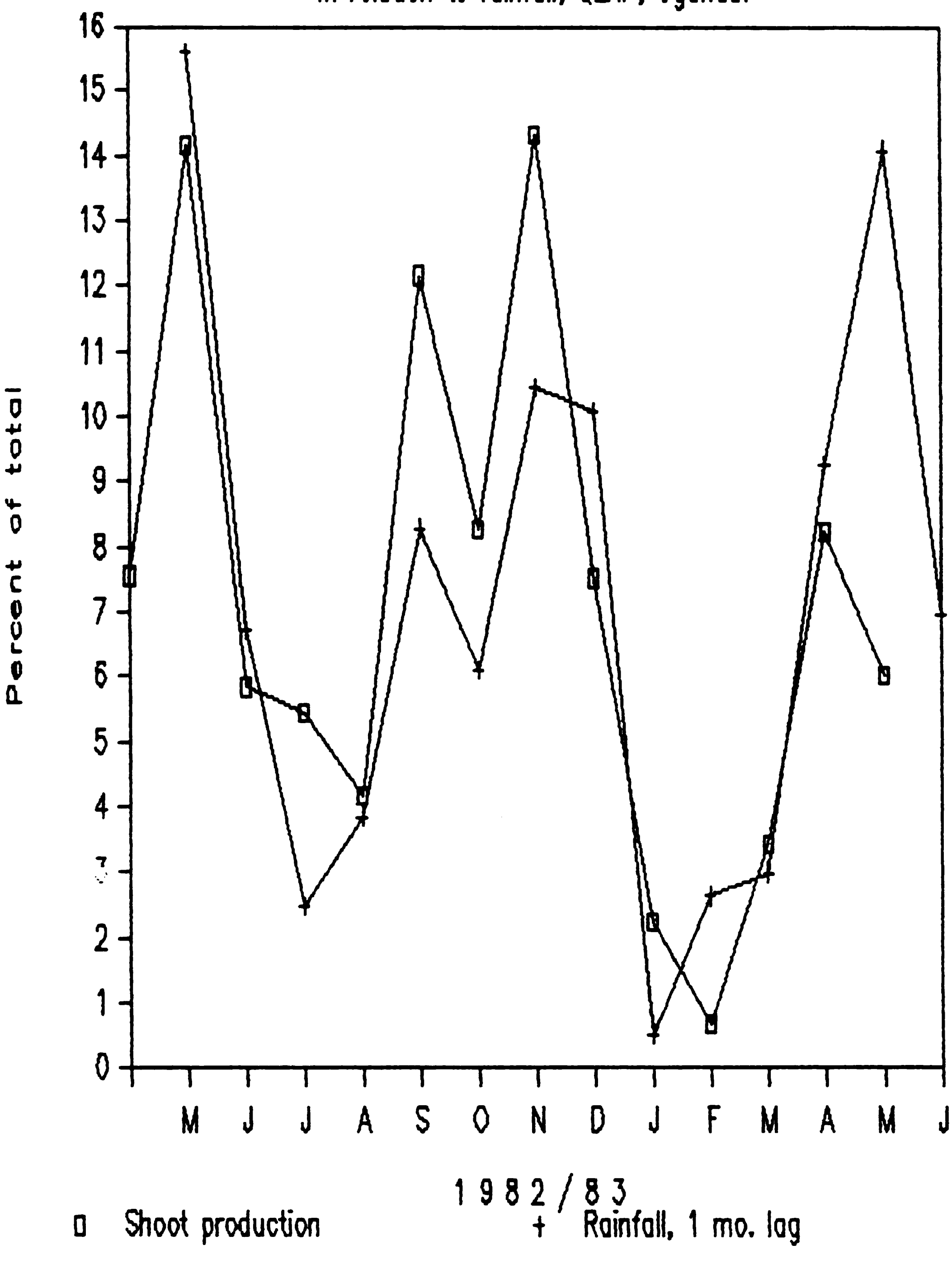
Live-shoot standing-crop biomass fluctuated seasonally, indicating that productivity was a function of rainfall. This relationship was demonstrated (Table 6.5; Fig. 6.3) for the site in the short grassland for which rainfall data was also collected. There was a close relationship between amount of precipitation and vegetative productivity.

6.3.3. Vegetation within the 15-year old exclosure

At the time the exclosure was constructed, it contained a grassland with a mosaic of short (5 cm), closely-cropped and medium-height (40 cm), lightly-grazed patches (Strugnell & Pigott 1978). *Sporobolus pyramidalis* and *Chloris gayana* were the dominant grasses and provided 56 and 30% of

Fig. 6.3. Live-shoot production

in relation to rainfall, QENP, Uganda.



foliar cover, respectively. Associated with them were significant quantities of Bothriochloa insculpta, Cenchrus ciliaris, Heteropogon contortus, Aristida adoensis and Sporobolus festivus.

Table 6.5. Monthly rainfall (mm) at Mweya Peninsula, QENP, Uganda, and mean dry weight (g/sq m) of live shoots harvested in ungrazed plot.

	Rainfall		Live shoots	
	mm	%	g	%
May	139.6	15.6	172.0	7.6
June	60.0	6.7	322.1	14.2
July	22.1	2.5	132.8	5.8
August	34.5	3.9	123.7	5.4
September	74.2	8.3	94.9	4.2
October	54.6	6.1	276.5	12.2
November	93.6	10.5	188.3	8.3
December	90.2	10.1	325.7	14.3
January	4.7	0.5	170.8	7.5
February	23.5	2.6	51.0	2.2
March	26.8	3.0	15.4	0.7
April	82.9	9.3	78.2	3.4
May	126.1	14.1	187.1	8.2
June	62.4	7.0	136.8	6.0

After 15 years, S. pyramidalis and C. gayana have been replaced by C. ciliaris as the dominant grass. Digitaria scalarum was co-dominant with C. ciliaris in the burned sector (Table 6.6). Between them the two species accounted for nearly 65% of live-shoot biomass in the sector which also contained moderate quantities of Hyparrhenia filipendula, C. gayana and Panicum maximum.

In the unburned sector, C. ciliaris accounted for nearly 63% of the biomass. D. scalarum, P. maximum and Brachiaria decumbens were present but in relatively low quantities. Commelina africana and C. benghalensis occurred in moderate quantities in both sectors. The average live-shoot biomass in the burned sector was 370.3 g/sq m compared with 414.0 g/sq m in the unburned. Litter in the unburned sector was considerably higher than that in the burned (Table 6.6). This is not surprising since fire consumes litter and thus prevents it from accumulating.

Table 6.6. Major constituents of the grass sward in the 15-year old exclosure on Mweya Peninsula, Queen Elizabeth National Park, Uganda, May 1982-June 1983.

	Treatment			
	Burned		Unburned	
	g/sq m	%	g/sq m	%
Cenchrus ciliaris	147.6	39.9	260.0	62.8
Digitaria scalarum	91.0	24.6	26.2	6.3
Commelina spp.	43.4	11.7	37.9	9.1
Hyparrhenia filipendula	34.6	9.3	0.4	0.1
Chloris gayana	20.2	5.5	4.3	1.0
Panicum maximum	7.4	2.0	23.0	5.5
Aristida adoensis	4.2	1.1	-	-
Brachiaria decumbens	2.9	0.8	7.1	1.7
Other grasses	7.8	2.1	2.1	0.5
Forbs	11.2	3.0	53.3	12.9
Live-shoot total	370.3	100.0	414.0	100.0
Litter	251.3	-	435.3	-

These results indicate that in the absence of grazing, the species-rich short grassland is replaced by one that is poorer in species but higher in stature and vegetative cover and dominated by C. ciliaris. In the absence of both grazing and fire, the grassland would contain numerous species of woody shrubs. Most of the shubs are susceptible to fire, however, and would be eliminated if fires were frequent. This is evident from their absence in the burned sector of the exclosure.

Frequent fires encourage the growth of a number of pyrophilous species including _H_. _filipendula_ which occurred only in the burned sector. Such species would replace those which would be eliminated by fire. _Themeda triandra_, a common species in the park, which has been reported to be encouraged by frequent fires (Lock & Milburn 1971) did not occur in any appreciable quantity in either the burned or unburned sector of the exclosure.

In the heavily grazed grassland outside the exclosure, plants of _C. ciliaris_ were common as short, stunted and isolated individuals. _C. ciliaris_ was heavily grazed (Brooks 1957; Heady 1966; Field 1972) and was adversely affected by intense grazing. This view was supported by the observation that plants growing within thicket bushes and protected from frequent grazing grew to be taller and more robust, much like those protected within the exclosure.

Forbs and shrubs were more abundant in the unburned sector than the burned. In the burned sector, only 5 species, mostly herbs such as _Achyranthes aspera_ and _Boerhaavia difusa_, were recorded in the grass layer. In comparison, 18 were found in the unburned sector. Most of the latter were woody shrubs, such as _Sida ovata_, _Indigofera erecta_, _Ageratum conyzoides_, _Barleria_ sp., _Grewia_ sp. and _Solanum indicum_. This miscellaneous group made up only 3% of the biomass in the former as opposed to nearly 13% in the latter (Table 6.6).

Euphorbia candelabrum, _Acacia_ sp. and _Capparis tomentosa_ were the major woody species in the exclosure. Chi-squared tests show significant differences between the burned and unburned sectors with respect to the numbers of trees and bushes (Table 6.7).

Table 6.7. Comparison of the numbers of trees of three woody species in burned and unburned sectors of the 15-year old exclosure on Mweya Peninsula, Queen Elizabeth National Park, Uganda. May 1983.

	Treatment			
Species	Burned	Unburned	df	X^2
Euphorbia candelabrum	0	14	1	14.0**
Acacia sp.	13	76	1	44.6**
Capparis tomentosa	1	9	1	6.4*

*Significant at 95% level; **significant at 99% level.

In addition to differences in numbers, there were also significant differences in size and height. The average height of Acacia sp. trees in the burned sector was 82.1 cm (n=13, SD ±45.1) as compared with 190.7 cm (n=76, SD ±76.4) in the unburned. Similarly, C. tomentosa bushes in the unburned sector were larger and consisted of many thicket species including E. candelabrum, Azima tetracantha, Hoslundia opposita, Pavetta albertina and Erythrococcus bongensis. The bush in the burned sector, on the other hand, was small and consisted entirely of Capparis.

These results indicate that fire has adverse impact on woody vegetation, and that frequent fires result in lower species diversity.

6.4. Discussion

6.4.1. Species composition and vegetative cover

In the short grassland, the effect of heavy grazing and trampling has been to eliminate tall, tufted species and to allow a high number of predominantly stoloniferous species and annuals to be established. Some authors (e.g. Edroma 1981) have implied that the mechanism of change involve the selective grazing of tufted species in preference to the non-tufted. The possession of a wide mouth, however, would seem to make the hippopotamus a non-selective grazer. The elimination of tufted species would not be due, therefore, to their being preferentially and selectively grazed. The author postulates that tufted species are eliminated because their life-form puts them at greater risk of being grazed by hippopotamus than the species with prostrate or stoloniferous life-forms that replace them.

Hippopotamus graze by grasping the vegetation between its horny lips and cropping each mouthful with a jerk of the head. This pulling action often uproots whole plants, some of which may be found along the trail of a grazing hippopotamus. Because the hippopotamus is short-legged, it is able to graze extremely close to the ground surface. Plants that grow upright are at greater risk of being grazed or uprooted than those that are prostrate or adhere closely to the ground surface. The mat-forming, prostrate or stoloniferous life-form makes a plant less readily accessible to hippopotamus and as a result is less frequently grazed. Over a period of time, the less-readily accessible plants come to dominate. The creeping and stoloniferous life-form of the many species in the short grassland is the result of this process.

The abundance of Sporobolus pyramidalis, a tufted tussock grass, in the short grassland demonstrated, however, that not all upright-growing species were vulnerable to hippopotamus grazing. To determine what makes this species resistant to grazing, the author attempted to duplicate hippopotamus grazing by plucking leaves of _S. pyramidalis_ by holding the leaves between his thumb and index finger and pulling with a jerk. Not only were the leaves difficult to sever because of the fibers, but they were slippery and easily passed between his gloved fingers. Although the thick lips of the hippopotamus would seem to permit a firm grasp of grass leaves, the leaves of _S. pyramidalis_ may slip also from between the lips of a grazing hippopotamus, thus making the species less vulnerable.

It was noted earlier that the hippopotamus mode of grazing often uproots plants. The advantage bestowed by tough, slippery leaves would be lost if the plants were easily uprooted. While the root system of _S. pyramidalis_ was not thoroughly investigated, attempts by the author to uproot a large sample of these plants showed that they were firmly and securely anchored in the soil. The combination of tough, slippery leaves and firmly-rooted plants evidently has made _S. pyramidalis_ an exception and allowed it to flourish where other upright-growing grasses have been eliminated. Since other tufted grasses are eliminated, the implication is that they have shallow root-systems. This remains to be confirmed.

One of the reasons the short grassland was richer in grass species than the medium-height and tall grasslands was the presence of several annuals in the sward. Many of the annuals are probably normal components of a seral stage and would be replaced in the sequence of plant succession. Under conditions of intensive grazing and trampling, however, the process of sucession is arrested and the seasonal annuals persist in the sward indefinitely, serving as indicators of heavy grazing.

The large proportion of exposed surface also provided strong evidence that the short grassland was overgrazed. This is supported by the fact that many of the constituent species including S. pyramidalis, A. adoensis and T. terrestris are classed plants of disturbed or overgrazed areas (Bews 1917; Rattray 1954; Chipindall 1955; Heady 1966).

Structurally and floristically, the medium-height and tall grasslands were much more similar to each other than either was to the heavily-grazed short grassland.

6.4.2. Standing-crop biomass and intensity of grazing

The close relationship of live-shoot biomass to rainfall in the semi-arid environment of the park emphasizes the importance of moisture to plant growth. It also indicates that moisture may be a factor limiting growth during periods of severe water deficiency such as during parts of the dry season.

Isohytes over the park (see Fig. 2.3) show that the center of the rift valley floor is the driest area in the park. This, in general, was the area of short grassland. The tall grassland, on the other hand, occurred to the west towards the foothills of the Rwenzori range where precipitation is higher. The medium-height grassland was intermediate in location. The gradient in precipitation indicates that even in the absence of grazing, there would probably be differences in standing-crop biomass on account of rainfall.

Live-shoot biomass on a range is not, however, solely a function of moisture levels. As demonstrated by Lock (1967, 1972) and confirmed by this study, grazing also plays an important role. Where grazing is light as in the medium-height and tall grasslands, it has little effect on net production and the natural composition and appearance of the range. Where grazing is intensive as in the short grassland where between 60 and 90% of standing-crop biomass is consumed, grazing may result in changes in botanical composition, production and structure of the range. Excessive defoliation has been shown to exhaust food reserves in plants causing them to lose vigor, deteriorate and eventually die prematurely (Milthorpe & Davidson 1965; Davidson & Milthorpe 1966a, 1966b). Plants that are grazed frequently, whether selectively or otherwise, are eliminated and those that are inaccessible, avoided or grazed less frequently come to dominate.

The changes that result from such a high level of consumption are likely to lead to unnatural conditions such as overgrazing and soil erosion. Since a primary objective of a national park is to maintain natural conditions, there may be a need for management intervention to prevent herbivores from altering the habitat from a normal state.

It is generally accepted that grazing intensity in excess of 50% of standing-crop biomass leads to overgrazing and range deterioration. By this criterion, the short grassland was being overgrazed. The determination that nearly 40% of the grassland was bare ground is further evidence.

6.4.3. Vegetation within the 15-year old exclosure

The striking differences between the vegetation within the 15-year exclosure and the adjacent grazed plot underscores the role that grazing plays in maintaining the short grassland. In the absence of grazing, a taller grassland dominated by <u>Cenchrus</u> <u>ciliaris</u> replaces the short grassland.

In the absence of both grazing and fire, numerous shrubs flourish in the grassland and trees and thicket bushes get established. Fire hinders the establishment of trees and shrubs but encourages a number of pyrophilous perennial grasses such as Hyparrhenia filipendula. Fire also removes vegetative cover and allows some of the short species, presumably intolerant of shade, to maintain vigor and to persist in small quantities. Grazing and fire in moderate frequency and intensity, therefore, tend to maintain species diversity in the grassland.

6.5. The Mweya Peninsula: A case study of vegetation changes induced by grazing

The recent history of game populations in Queen Elizabeth National Park has been one of booms and bursts. Before the turn of the century, an epidemic of rinderpest decimated a large proportion of the game (Lugard 1893). Then a scourge of sleeping-sickness affected the human inhabitants of the area who either left or were evacuated by the colonial government (Hale-Carpenter 1921). Game benefitted from the removal of hunting pressure and increased rapidly. In recognition of their abundance, the area was declared a game reserve in 1934 and a national park in 1952.

Soon after the area became a national park, it became clear that the hippopotamus had exceeded the carrying capacity of the range and were in danger of destroying the habitat (Petrides & Swank 1965). A decision was made to cull the species (Bere 1959) and approximately 7000 animals were cropped between 1958 and 1967 (Field & Laws 1970). The vegetation responded with a spectacular recovery (Laws 1968; Thornton 1971).

On Mweya Peninsula, the cropping scheme resulted not only in improved vegetation cover but also a more diverse and balanced large-mammal community (Eltringham 1974, 1980). After the end of the cropping scheme, hippopotamus increased rapidly at the expense of other ungulates on the Peninsula so that during the study there was once again a virtual monoculture of hippopotamus which threatened habitat degradation. The number of hippopotamus in the park as a whole, however, is estimated to be lower than the pre-cropping level of 14000.

Table 6.8. Changes in frequency* of grass species on the Mweya Peninsula, Queen Elizabeth National Park, Uganda.

Species	3/57	5/58	5/59	5/60	5/62	9/66	1971-4	1974-6	5/82
CO	3.5	37.7	21.1	22.9	6.6	<5.0	3	23	67.8
CD	2.3	9.2	2.1	3.2	11.7	8.9	-	17	6.9
SP	12.9	8.0	25.2	18.9	27.6	31.0	100	68	62.8
CG	0.8	6.4	6.8	7.2	19.4	12.2	92	23	21.2
DA	-	5.2	0.1	2.2	0.5	<5.0	3	3	20.2

Species: CG, Chloris gayana; CO, Chrysochloa orientalis; CD, Cynodon dactylon; DA, Dactyloctenium aegyptium; SP, Sporobolus pyramidalis. *Frequency values between 1958-62 are expressed as % of basal cover. All others are % of occurrence in random quadrats. Authorities: Petrides & Swank (1965) for 1957; Thornton (1971) for 1958-1962; Spinage (1968) for 1966; Edroma (1977) for 1971-1974; Yoaciel (1981) for 1974-1976; This study for 1982.

Since 1957, a series of studies has recorded the frequency of five common grasses (Table 6.8). Of these, one or a combination of three (Chrysochloa orientalis, Sporobolus pyramidalis and Chloris gayana) has always been dominant. At the beginning of the series, C. orientalis was the dominant grass. Its record shows that between 1958 and 1974, it declined in abundance. Much of its decline was coincidental with a period of hippopotamus cropping. But has recovered remarkably since 1974 and in the present study was found to be the most abundant species in the sward.

Sporobolus pyramidalis, on the other hand, increased through out the years of hippopotamus cropping replacing C. orientalis as the most abundant species in 1962 (Table 6.8). It continued to increase in abundance until 1974. Since then, it has declined slightly as C. orientalis increased dramatically to regain dominance as the most abundant species. Its decline has been simultaneous with an increase in hippopotamus density.

The rise of C. orientalis to dominance is a recent event. A survey made in 1976 (Yoaciel 1981), reported that S. pyramidalis was still the dominant grass on the Peninsula. The species has been dominant in the area since 1961 when it replaced C. orientalis following the elimination of hippopotamus (Thornton 1959, 1962, 1971; McKay 1961; Lock 1964; Field & Laws 1970).

C. orientalis is a carpet grass and is encouraged by hippopotamus grazing. The abundance of stoloniferous species and annuals in the sward is indicative of overgrazing. The fluctuations in C. orientalis and S. pyramidalis indicate that the former dominates the grassland when hippopotamus grazing becomes excessive, and the latter dominates when hippopotamus grazing is moderate or relatively low. Conversely, the absence of the tufted perennials T. triandra, H. contortus and H. filipendula is evidence that grazing has been heavy and persistent; and that fire has been absent for lack of fuel for sometime.

CHAPTER 7

CONCLUSION AND RECOMMENDATIONS

7.1. Conclusion

Based on 18 months of field work in Queen Elizabeth National Park, Uganda:

1. Game counts in selected areas of the park showed that the populations of large and medium-sized herbivores in 1981/83 were the lowest recorded since comparable counts were first made in 1956. The magnitude of the decline was particularly large for elephant, buffalo and waterbuck. This reduction is attributed primarily to poaching.

2. Average population densities and standing-crop biomasses have fallen in all except one of four study areas. The only increase occurred on Mweya Peninsula is due entirely to the expansion of hippopotamus. All other species declined.

3. The hippopotamus population on Mweya Peninsula was the highest ever recorded, with a density of 34.0/sq km and a standing-crop biomass of 33,955 kg/sq km. As this example illustrates, there are local exceptions to the general decline in animal numbers. Excessive decreases and increases in wildlife abundance have different but equally-serious management implications.

4. When the first counts were made in the late 1950s, Mweya Peninsula was over-populated with hippopotamus. To arrest habitat deterioration and restore a more balanced community, between 1958 and 1967 a cropping program was implemented. Since the end of the program, hippopotamus have

returned to the peninsula in large numbers. The large-mammal community has degenerated once again to a virtual monoculture of hippopotamus. The abundance, high biomass and great species diversity of large mammals which occurred after the cropping of hippopotamus have been lost.

5. The variability of animal counts from month to month was high but showed no marked trends over the course of the study. Censuses of individual species seemed to be influenced by such factors as body-size, wariness, herding characteristics, mobility, the size of the population, as well as the ability of observers to see all the animals present.

6. Census results showed no significant seasonal differences. This supported the general impression that park animals do not undertake large scale seasonal movements.

7. The distribution of ungulates indicated strong species preferences for certain habitats. Hippopotamus was confined to the short grass and thicket-bush mosaic close to water. Others, such as kob, occurred mostly in open, medium-height grasslands but were present also in the tall grass and in the short grass with bush habitats. Only buffalo, and to a lesser extent warthog, were fairly evenly distributed in all three habitats.

8. A woodland vegetation type in the Craters region in which a heavy loss of trees due to widespread elephant damage was reported when it was first surveyed in 1968 was re-surveyed. The present study disclosed it to be regenerating abundantly. The current profusion of regeneration indicates that the trend towards grassland is not irreversible and that woodland, at least *Acacia gerrardii* woodland, can be restored by reducing elephant densities (in this case by poaching). Regeneration was found to be almost entirely from root stocks. Seedlings contributed

little, if any, towards stand regeneration.

9. Average tree density of all species taken together was 164.3/ha. The most abundant were Acacia gerrardii, A. sieberiana and A. hockii; with densities (/ha) of 135.4, 23.4 and 4.2, respectively.

10. Qualitatively, species composition of the woodland has remained virtually unchanged since 1968. Major shifts have occurred, however, in the relative abundance of species. The most significant is that of Acacia gerrardii which in 1968 constituted 21.3% of the trees in the woodland, but by 1982 had increased to 82.4%. Two other species which were as abundant as A. gerrardii in the earlier survey have declined greatly and are longer important components of the vegetation. Bridelia scleroneuroides and Olea africana constituted 20.9 and 20.2%, respectively, of the trees in the woodland in 1968 but only 0.1% each in 1982.

11. Acacia gerrardii trees in the regenerating woodland exhibited a bimodal girth distribution, confirming the existence of two distinct sub-populations. One consisted of abundant young regeneration and the other of a limited cohort of sparsely-scattered mature trees. In terms of height, the former constituted a lower and the latter an upper tier, with virtually no intermediaries. A period of severe suppression between the two generations is estimated to have lasted two to four decades.

12. Evidence as to the respective roles of fire and elephant in controlling this woodland vegetation and thicket expansion was examined. It was concluded that elephant, not fires, were the primary factor in controlling woody vegetation. This conclusion was based on the observed gradient of decreasing mature-tree density with increasing distance from

the park border. This pattern of tree distribution seemed likely to have developed as a result of differential use of the range by ungulates in response to poaching and harrassment along the border. In Murchison Falls National Park, Uganda, analysis of serial photographic transects showed that similar increases in tree density occurred at the boundaries of elephant ranges. Observations on experimental plots from which elephant, but not fire, have been excluded also support the view that elephant are more important than fire in controlling woody vegetation.

13. The concensus among park authorities is that thickets have increased throughout the park over the last decade. The density of thicket clumps was determined to be 26.4/ha on the heavily-grazed Mweya Peninsula and 2.8 in moderately-grazed and frequently burnt medium-height grassland at Kikorongo. Individual clumps in Kikorongo were generally larger than those on the peninsula.

14. In general, the increase in thickets is probably the result of their release from fires and heavy browsing. In heavily-grazed areas, such as the banks of the Kazinga Channel and the Mweya Peninsula, the absence of fires (due to inadequate fuel to support them) allows thickets to flourish.

15. A thicket clump commonly contained 20 to 40 species of plants. The composition of clumps varied as a result of variations in topography, soil and precipitation within the park. Common clump constituents included Capparis tomentosa, Securinega virosa and Azima tetracantha.

16. It was concluded that thicket clumps originate from the nucleus of a single bush in the grassland. The bush has to be a vigorous species in order to persevere and survive frequent fires and persistent

defoliation by large herbivores.

17. The continued active growth of many thicket species during the dry season when the surrounding grassland is parched and brown is probably because they have deep roots and can restrict water-loss through the stomata.

18. Thicket clumps constitute an important resource to wildlife. They provide food, shelter, shade and concealment for a wide range of animals.

19. Vegetative standing-crop biomass was positively correlated with increasing distance from the hippopotamus-populated waters. Light and moderate grazing enabled the maintenance of good vegetative cover whereas heavy grazing severely reduced grass abundance and resulted in bare soil patches. It is concluded that grazing is responsible for creating and maintaining the mosaic of grasslands in the park. Light grazing results in the accumulation of large quantities of plant litter and the risk of a hot fire. Moderate grazing results in considerably less litter and much reduced risk of fire. Heavy grazing exposes the soil to agents of erosion and is, no doubt, the major factor inducing bush-invasion and habitat deterioration in some areas of the park.

20. In the mixed short grassland on Mweya Peninsula, Chrysochloa orientalis has replaced Sporobolus pyramidalis as the dominant grass species. Chrysochloa is a prostrate species which tends to escape heavy grazing. It was dominant during the late 1950s when the peninsula experienced severe habitat deterioration induced by hippo overgrazing and unusually low rainfall. Subsequent cropping of the hippopotamus resulted in improved cover, a decline in Chrysochloa and a rise to dominance of

Sporobolus. The current return of *Chrysochloa* to dominance is evidence that grazing had once again become excessive.

7.2. Recommendations

1. In the short term, an effort should be made to expand, equip and maintain a disciplined anti-poaching game-ranger force to prevent the further decline of wildlife populations.

2. Reform is necessary to make poaching a more serious crime than it is at present. Stiffer sentencing of offenders could be a deterrence. At present, a poacher needs to succeed only once to make enough money to pay for four to five convictions. Consequently, conviction has not been a deterrence.

3. In the long term, the key to the park's survival as a viable conservation area will be the support of the local citizenry. It is recommended that funds be made available for national conservation education. It is further recommended that schools and communities surrounding national parks be principal targets of the campaign.

4. Immediate action to reduce hippopotamus population density is necessary to halt and reverse the process of habitat degradation in areas such as Mweya Peninsula. Previous experience indicates that a cropping project would result in improved habitat conditions and increased variety of attractive ungulates. Such a program would pay for itself and enable research on the biology of target species. It would also, however, raise questions as to whether poaching can be wrong if culling is correct. A parallel program of conservation education would be critically important to establish a recognition of the objectives and values of national

parks, of national economic benefits through tourism and of modern concepts of resource management.

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