A STUDY OF THE FEEDING HABITS OF THE HIPPOPOTAMUS (*HIPPOPOTAMUS AMPHIBIUS* LINN.) IN THE QUEEN ELIZABETH NATIONAL PARK, UGANDA, WITH SOME MANAGEMENT IMPLICATIONS

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INTRODUCTION

The concept of the ecological separation of species has for long been accepted to be of fundamental biological importance. In Africa many examples can illustrate this principle. Darling (1960) was able to describe very clearly the separation of large mammal species in various habitats in Zambia. However, detailed studies of the feeding habits of a variety of species suggest that in practice ecological niches are not clearcut and considerable overlap in the feeding habits of different species occurs (Lamprey 1963, Bell 1967, Field 1966). In order to determine the degree to which eological separation may occur the author has been carrying out for the past five years a comparative study of the feeding habits of six of the more important species of grazing mammals occurring in the Queen Elizabeth National Park. The feeding habits of the dominant grazing herbivore, the hippopotamus (*Hippopotamus amphibius* Linn.) called for special attention and forms the subject of this paper. Basic data arising from this study may be employed in the more effective use of the land and a more thorough realisation of its biological potential.

DESCRIPTION OF THE STUDY AREA

The Queen Elizabeth National Park is situated in the Western Rift Valley in Uganda and straddles the equator. It lies between longitude 29°45′ and 30°15′ East and latitude 15′ North and 30′ South of the equator. It includes 764 square miles of land surrounding Lake Edward and Lake George which are connected by the Kazinga Channel. Altitude ranges from 2,995 feet to 4,480 feet above sea level.

Rainfall varies from approximately 600 mm. to 1,400 mm. per annum. The highest falls occur along the rift escarpment and the foothills of the Ruwenzori mountains which run parallel in a north-east and south-west direction on either side of the Park. Lowest falls occur along the central region of the rift valley (Figure 1). Rain falls mainly during March to May and September to November. Other months are drier. Incoming solar radiation is high, particularly during the rains when the atmosphere is clear. Smoke haze during the dry season significantly reduces incoming radiation.

The soils consist mainly of porous volcanic ash to the north of the Kazinga Channel and at the eastern end of the escarpment in the region of the volcanic craters. These die out to the north of Lake George and are replaced by alluvial deposits, saline soils and water-logged swamps and to the south of the channel by swamps and sandy sediments.

Volcanic soils, a relatively high rainfall with even distribution during the year, and high solar radiation combine to cause a high primary production of vegetation.

Apart from climatic and edaphic factors the vegetation is also influenced and modified by biotic factors. In general, however, where mammal biomasses are low and soils favourable the vegetation types tend to follow the isohyets. In the highest rainfall areas semi-deciduous forest occurs with Uganda ironwood, *Cynometra alexandri*, dominant. This intergrades through woodland and thicket to savanna grassland. Woodland may include *Celtis africana* or in more open country *Acacia* spp., *Ficus* spp. and *Euphorbia candelabra*. Thicket and bush species include *Capparis tomentosa*, *Teclea nobilis*, *Hoslundia opposita*, *Securinega virosa*, *Erythrococca bongensis* and *Azima tetracantha*. Grassland may occur in combination with each of the other three vegetation types. In general grasslands fall into five categories:

1. Tall grassland in high-rainfall areas with *Cymbopogon afronardus* and *Imperata cylindrica* dominant.
2. Intermediate grassland where *Hyparrhenia filipendula*, *Themeda triandra* and *Bothriochloa* spp. are dominant.
3. Short overgrazed grassland near the shores of Lake Edward and Lake George where *Sporobolus pyramidalis*, *Chloris gayana* and annual grasses are dominant.
4. Flats with *Cynodon dactylon* and *Panicum repens* dominant and *Sporobolus homblei* on saline soils.
5. Swampland with *Cyperus papyrus* dominant.

The high primary productivity leads in turn to a high secondary productivity typifying the Nile basin grasslands and contrasting with the drier regions of East Africa. The very high biomasses are composed of relatively few species and of these the elephant, *Loxodonta africana*, hippopotamus and buffalo *Syncerus caffer* play a dominant role. Thus, based on regular aerial censuses of the Park, eleven to twelve tons per square mile has been estimated for the average biomass of buffalo (Grimsdell 1966) and hippopotamus, and nine tons per square mile for elephant.

THE HIPPOPOTAMUS POPULATION

NUMBERS

In 1958 when the management of the hippopotamus was begun in the Park there were an estimated 14,000 animals. Since then cropping has proceeded at the rate of about 1,000 animals per annum. An aerial count using a Piper Cruiser in 1964 revealed 8,005 animals. A further count in 1966 using a Piper Super Cub revealed 11,029 animals and this is considered to be nearer the true figure. The versatility of the plane enabled a more accurate count to be realised. It seems likely, therefore, that the original estimate of 14,000 and the 1964 count of 8,000 were rather low and that a higher population has been supported in the Park in the past.

DISTRIBUTION

The hippopotamus is diurnally aquatic and nocturnally terrestrial. Luck & Wright (1964) have shown that there is a considerable loss of water directly through the skin of the hippo.

For this reason, hippo are usually to be found within easy reach of water, whilst they also take advantage of it as a refuge and buoyant medium.

In very overgrazed areas however, towards the end of the dry season, tracks of individuals have been followed up to four and a quarter miles from water.

The distribution of the hippo in the Lake Edward and Lake George ecosystem is shown by Clough (1966). Densities of over eighty to the square grazing mile occur in favoured areas and of less than 18 per square mile in less suitable areas. A comparison of the seasonal distribution of hippo from aerial counts shows that the population tends to spread and occupy short-lived inland wallows during the rains and return to the permanent water of the lake-channel-river system during the dry seasons. This occurs despite the poorer quality of the vegetation near the permanent water. Thus, the general distribution of hippo is influenced primarily by the availability of water. Secondary factors influencing population distribution include topography, herd structure, food supply and man. The availability of food will be dealt with in detail later.

(*a*) *Topography*. Hippos prefer gently shelving beaches. This allows them to rest with their weight evenly distributed. In shallow water they kneel partly submerged. Gently shelving beaches permit this at some distance from the shore, thereby affording the animal greater security. Females with calves prefer to suckle in shallow water so that the calf does not have to swim.

Detailed monthly counts of the hippo populations in four areas (Figure 1) were made by boat by R. M. Laws and the author from 1962 to 1966 inclusive. The distribution of hippo was mapped in the following areas:

1. Katwe to Lubilia river.
2. Mweya peninsula.
3. Kazinga channel.
4. Lion bay.

In area 1 the hinterland slopes gradually providing suitable beaches and lagoons which support a high hippo density.

In area 2 hippo prefer the flats which have a gently sloping hinterland and avoid the shore around the plateau and channel, except where there are alluvial fans at the outflow of gullies formed on the steep slopes.

In area 3 hippo concentrate on the alluvial fans and use the broken ground around the gullies to obtain access to the grasslands 200 feet above.

In area 4 the hippo behave similarly to those in the Channel except at the southern end where they form large schools in a particularly suitable lagoon.

(*b*) *Herd structure*. A detailed study of the behaviour of the hippopotamus has yet to be carried out. It is clear from the counts however, that there is an optimum size for a hippo school which is approximately ten. Furthermore, it has been suggested that the current of the water habitat tends to affect school size (Laws R. M. personal communication). Thus, the calm water of the Queen Elizabeth Park might be considered optimal for the species.

There is a tendency for males to prefer wallows, thus of 1,416 hippo (of sex ratio 47% male and 53% female) 59% of wallow hippo and 41% of lake hippo were males. Lactating

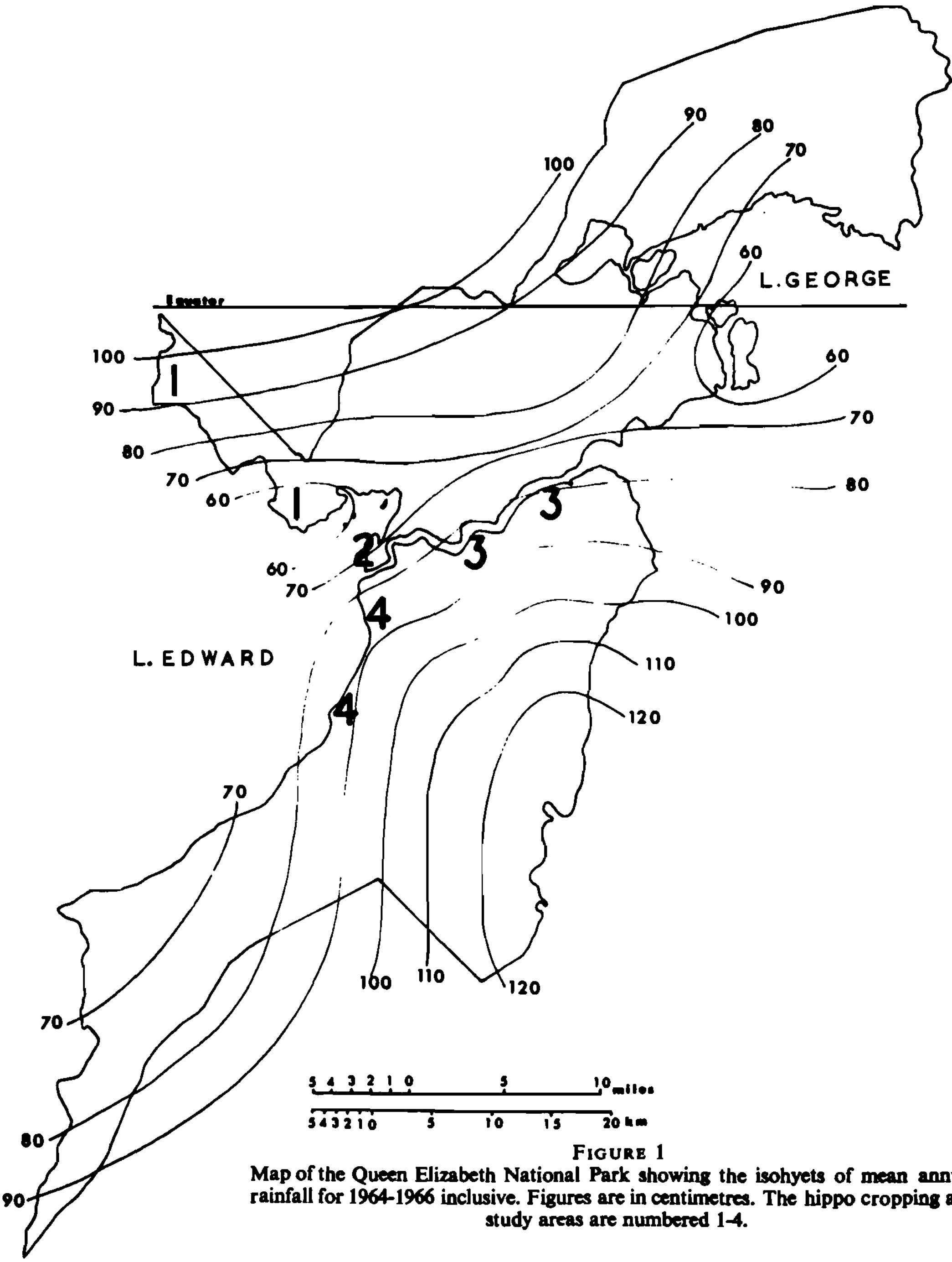


FIGURE 1
Map of the Queen Elizabeth National Park showing the isohyets of mean annual rainfall for 1964-1966 inclusive. Figures are in centimetres. The hippo cropping and study areas are numbered 1-4.

females tend to be segregated and more concentrated in favourable areas than other classes. These are usually high-density areas with preferred shorelines (Laws 1963, Laws and Field 1964).

(*c*) *Man*. It is difficult to assess the influence of man on the distribution of hippo, although it is clear from counts that in the region of villages there are significantly fewer animals. Where hunting or poaching is intense many small schools may join to form a few large schools for mutual protection. This is particularly clear in the Lion Bay cropping scheme where the final 200 individuals congregated in a few large schools in an inaccessible lagoon. Likewise in Kigezi at the south end of the Park, schools of up to 500 animals are to be found within the protection of the riverine swamps.

METHODS OF STUDYING FEEDING HABITS

The cropping of approximately 1,000 animals per annum has provided a considerable amount of both quantitative and qualitative information on hippopotamus feeding.

STOMACH WEIGHTS

From October, 1962, to November, 1963, 928 hippo were shot in the Lion Bay area and all but a few were weighed. Along with the routine collection of other basic data, stomach weights were recorded under varying circumstances.

Preliminary results (Laws and Field 1964) showed that there was no significant seasonal change in adult stomach fill (wet weight). However, the mean dry matter of all stomachs which were weighed declined during the cropping period from 103 to 83 lb in adult females and from 95 to 77 lb in adult males. This may indicate an improvement in bulk of the vegetation as a result of cropping. Stomach fill as a percentage of live weight was fairly constant at 15·2% in females and 12·8% in males (on a wet weight basis). Hippo were usually cropped between 0700 and 0900 hours. Some, however, were taken later in the day to determine the rate of digestion. Results suggest that digestion is not under way until noon and extrapolation indicates that stomach fill is halved by about 1800 hours. This suggests that the morning stomach fill represents two nights feeding. This is supported by the work of Pienaar, Van Wyk & Fairall (1966).

If 83 lb is taken for the mean stomach fill (dry weight) of adult females and 77 lb for adult males and these represent two nights feeding, dry weight intakes are 1·3% and 1·1% of the body weights respectively. A captive hippo weighing 1,250 ±100 lbs., consumed an average of 11·9 lb dry grass per day over a three-month period, without appreciable loss of condition. This represents about 1% of its body weight and is low in comparison with cattle and other ruminants which are nearer 2½%. It may well represent a maintenance level of nutrition when the diet is inadquate for growth or it may be related to reduced energy expenditure in the aquatic medium. Subsequent studie. on another animal have suggested a rather higher intake.

A comparison of stomach fill with reproductive classes (Laws and Field 1964) has shown that the vegetation offtake by adult females is 9·4% higher than offtake by males and that of lactating females 16·8% higher than pregnant females.

TABLE 1

PERCENTAGE OF HIPPO STOMACH SAMPLES CONTAINING DIFFERENT GRASS SPECIES

Plant Species	*Dec.–Feb.*				*Mar.–May*				*June–Aug.*				*Sept.–Nov.*			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Bothriochloa species	66·7	83·3	50·0	100·0	83·3	100·0	83·3	66·7	83·3	50·0	100·0	66·7	83·3	83·3		100·0
Brachiaria decumbens	0·0	66·7	83·3	66·7	66·7	33·3	83·3	83·3	16·7	66·7	100·0	83·3	16·7	83·3		100·0
Cynodon dactylon	33·3	100·0	33·3	33·3	83·3	100·0	50·0	83·3	50·0	83·3	80·0	100·0	50·0	100·0		100·0
Chloris gayana	100·0	83·3	83·3	100·0	66·6	100·0	100·0	100·0	100·0	83·3	100·0	100·0	50·0	100·0		100·0
Heteropogon contortus	100·0	66·7	66·7	83·3	83·3	100·0	83·3	66·7	83·3	50·0	60·0	16·7	100·0	100·0		33·3
Hyparrhenia filipendula	83·3	33·3	66·7	66·7	66·7	66·7	100·0	33·3	83·3	16·7	80·0	33·3	50·0	50·0		83·3
Panicum repens	0·0	50·0	0·0	0·0	16·7	66·7	0·0	50·0	0·0	66·7	0·0	16·7	16·7	66·7		0·0
Sporobolus homblei	0·0	16·7	0·0	0·0	16·7	50·0	0·0	0·0	16·7	50·0	0·0	0·0	16·7	0·0		16·7
Sporobolus pyramidalis	100·0	100·0	100·0	100·0	83·3	100·0	100·0	100·0	83·3	100·0	100·0	100·0	100·0	100·0		100·0
Themeda triandra	100·0	0·0	66·7	100·0	66·7	0·0	100·0	100·0	83·3	16·7	80·0	50·0	83·3	0·0		100·0
Dicotyledons	66·7	16·7	100·0	50·0	50·0	33·3	100·0	66·7	50·0	66·7	80·0	100·0	50·0	50·0		50·0
Unidentified grasses	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0	100·0		100·0

Areas are marked 1-4. Percentages are based on samples from six animals per area per season giving a total of 90 animals altogether.

ANALYSES OF STOMACH CONTENTS

The cropping programme enabled the collection of stomach samples from hippo from the four study areas mentioned above. A minimum of six samples was collected for each of the four seasons of the year in each area, with the exception of the Channel where samples were not available for the last season of the year. Where possible the six samples comprised two adult males, two adult females and two juveniles.

The collection and preparation of the samples is described in Field (1966) and methods of identification based on interspecific variation in characteristics of the leaf cuticle summarised by Stewart (1965).

(*a*) *Qualitative information on species eaten by hippo.* The literature is remarkably poor with respect to the food habits of hippo and in almost all instances refers to qualitative information with little reference to the availability of food. Bere (1959) states that in 122 specimens investigated no aquatic vegetation was observed, the diet being 100% grass. I have occasionally observed hippo eat aquatic vegetation, e.g. *Pistia stratioides*, in wallows shortly before emerging in the evening, but in small quantities only. Herbs are also taken but usually by chance along with grass. One of the tame hippo, however, showed a distinct preference for the spiny creeping herb *Alternanthera pungens*. Analyses of mouth samples of vegetation based on seeds lodged between the teeth of 83 hippo revealed 28 species of grass and five species of herb. Analyses of about 200 stomach samples revealed 31 species of grass whilst sedges and herbs were not further differentiated. Pienaar *et al.* (1966) lists nine species of grass, three species of sedge and four species of dicotyledons eaten by hippo in the Kruger Park. Of these, four species of grass: *Chloris gayana*, *Cynodon dactylon*, *Panicum maximum* and *Themeda triandra*, are known to be important grass species to the Queen Elizabeth Park hippo. M. Modha (personal communication) observed that hippo on Central Island, Lake Rudolph, Kenya, ate *Sporobolus spicatus* and *Cyperus laevigatus*. These are the dominant monocotyledons. K. Curry-Lindahl (personal communication) states that in the Albert Park, Congo, hippo feed mainly on *Panicum repens*. Jackson & Gartlan (1966) state that on Lolui Island, Lake Victoria, Uganda, hippo graze *Andropogon dummeri*, *Hyparrhenia dissoluta*, *Loudetia kagerensis* and *Microchloa kunthii*. *Eragrostis blepharoglumis* was avoided. Ansell (1965) says that in the Luangwa valley, Zambia, *Setaria* aff. *phragmitoides* is believed to be important to hippo but that the fruits of *Kigelia pinnata* occurred in seven out of ten stomachs examined. This is unusual since the hippo is ill-equipped to feed on these fruits.

(*b*) *Frequency of occurrence of species in the diet of the hippo.*

Stomach samples from approximately 200 hippo have been examined to date. Information presented in Table 1 shows the percentage of hippo stomach samples which contain ten different grass species, dicotyledons and unidentified grasses for the four study areas during the four seasons of the year. The data represent 90 samples; the other 110 were collected from one area to determine the degree of variation in the diet between individuals and are not shown here.

The twelve types of plants described are classified according to whether they are consistently eaten, whether abundant or not, in: 1. all areas—*Bothriochloa* spp., *Chloris gayana*, *Heteropogon contortus*, *Sporobolus pyramidalis* and unidentifiable grasses; 2. most areas—*Brachiaria*

TABLE 2

PERCENTAGE OF CUTICLE FRAGMENTS OF GRASS SPECIES PRESENT IN HIPPO STOMACHS

Plant species	Over-all Mean	Dec.–Feb.				Mar.–May				June–Aug.				Sept.–Nov.				Dry Mean	Wet Mean
		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4		
Bothriochloa spp.	5·2	2·7	3·7	2·5	10·0 4·7	4·0	10·8	9·5	3·2 6·9	6·5	2·5	2·6	3·0 3·7	7·2	5·0		5·2 5·8	4·2	6·3
Brachiaria decumbens	13·2	—	12·0	27·2	4·8 11·0	12·0	1·2	20·0	13·3 11·6	0·2	11·2	42·0	33·3 21·7	0·5	16·2		4·7 7·1	16·3	9·4
Cynodon dactylon	10·6	5·3	28·3	0·5	2·7 9·2	6·3	16·7	1·3	20·8 11·3	1·7	11·3	2·4	13·5 7·2	3·0	22·7		22·3 16·0	8·2	13·6
Chloris gayana	7·1	9·5	7·8	4·7	12·7 8·7	6·8	11·8	6·2	7·5 8·1	5·7	4·2	5·4	6·0 5·3	4·8	5·7		8·2 6·2	7·0	7·2
Heteropogon contortus	8·4	22·2	1·3	6·5	4·2 8·5	21·0	2·3	7·8	1·0 8·0	29·7	0·7	1·6	0·2 8·0	24·3	2·5		0·5	8·3	
Hyparrhenia filipendula	3·8	3·5	0·8	4·3	6·0 3·7	3·2	1·3	7·3	1·7 3·4	7·3	0·2	6·0	3·5 4·3	2·7	5·5		3·7 3·9	4·0	
Panicum repens	1·8	—	0·7	—	— 0·2	0·5	2·8	—	9·8 3·3	—	10·3	0·2	0·3 2·7	2·2	0·8		— 1·0	1·4	2·1
Sporobolus homblei	1·7	—	1·8	—	— 0·5	1·7	9·0	—	— 2·7	1·5	8·8	—	— 2·6	2·3	—		0·8 1·1	1·5	1·9
Sporobolus pyramidalis	23·7	25·3	24·7	30·3	18·8 24·8	20·5	32·3	17·7	25·8 24·1	23·3	31·0	20·6	23·3 24·6	23·5	24·0		14·3 20·6	24·7	22·3
Themeda triandra	9·5	19·2	—	7·0	28·3 13·6	10·5	—	11·5	2·8 6·2	14·5	0·2	7·6	2·7 6·2	20·5	—		15·5 12·0	9·9	9·1
Other grass species	3·7	0·5	7·4	2·4	0·7 2·7	3·9	2·2	2·4	4·9 3·3	0·7	8·9	1·0	0·9 2·9	1·7	3·9		13·7 6·4	2·8	4·9
Dicotyledons	2·2	1·5	1·7	7·3	1·7 3·0	1·3	0·7	2·8	1·2 1·5	0·8	2·2	3·0	5·8 3·0	0·5	1·8		0·7 1·0	3·0	1·2
Unidentified grasses	9·2	10·3	9·8	7·3	10·2 9·4	8·3	8·8	13·5	8·0 9·7	8·2	8·7	7·6	7·5 8·0	6·8	12·0		10·5 9·8	8·7	9·7

Figures are means of samples from six animals giving a total of 90 animals altogether. The mean for each season is given beneath the mean for area 4.

decumbens (except in area 1), *Hyparrhenia filipendula* and *Themeda triandra* (except in area 2) and *Cynodon dactylon*; 3. a few areas only—*Panicum repens* and *Sporobolus homblei* (in area 2) and dicotyledons (in areas 3 and 4).

(*c*) *Average number of fragments in the samples.*

Studies by Stewart (1966) have stressed that although faecal analyses can provide accurate qualitative information on the species consumed, owing to the possibility of selective digestion, quantitative data are less reliable. Large differences in the number of fragments in a stomach sample, however, are probably meaningful. They are presented here in Table 2 since they serve to emphasise those species which occur in most samples with an abundance of fragments, in contrast to species which occur frequently but with only a few fragments.

From Table 2 it may be seen that *Bothriochloa* spp. and *Chloris gayana* average less than 10% and nowhere exceed 15% of the cuticle fragments, although they are consistently eaten in all areas. *Heteropogon contortus* also averages less than 10% but in area 1 lies consistently between 20% and 30% of the fragments. *Sporobolus pyramidalis*, however, averages more than 20% and lies between 14% and 32% of the fragments in all areas.

Brachiaria decumbens and *Cynodon dactylon* each constitute more than 10% of the fragments. The former is poorly represented in samples from area 1 and the latter in samples from areas 1 and 3. *Themeda triandra* fragments also constitute about 10% of the total but are rare in area 2. *Hyparrhenia filipendula*, although eaten in most areas, never constitutes a large proportion of the fragments.

Panicum repens and *Sporobolus homblei*, although having a poor average, will in some areas at certain seasons constitute up to 10% of the fragments. Dicotyledons are relatively unimportant except perhaps in area 3.

In Table 2 the mean number of fragments present in samples in the two wet and two dry seasons have also been computed. *Bothriochloa* spp., *Cynodon dactylon*, *Panicum repens* and other grass species, mostly annuals, constitute a greater proportion of the fragments in the wet season whilst *Brachiaria decumbens* and dicotyledons constitute a greater percentage of the dry-season fragments. Other grasses show no appreciable seasonal differences.

Analyses of the available vegetation have been carried out by the author for areas 1 and 4 and by J. M. Lock and D. D. Thornton for area 2. Various methods were employed including line transects in area 2, quadrats along random transects in area 1, and quadrats in restrictively randomised plots in area 4. The frequency of occurrence of grass species in the sward is, however, little affected by these different recording methods and is given in Table 3 for comparison with their frequency of occurrence in hippo stomach samples.

The twelve types of plants may then be further classified as follows:

1. Species consistently present in small quantities in stomachs and abundant in the pasture: *Bothriochloa* spp. and *Chloris gayana*.

2. Species consistently present in large quantities in stomachs and abundant in the pasture: *Heteropogon contortus* and *Sporobolus pyramidalis*.

3. Species present in stomachs in large quantities in most areas and abundant in the pasture: *Cynodon dactylon* (except in area 1) and *Themeda triandra* (except in area 2).

TABLE 3

FREQUENCY OF OCCURRENCE OF GRASS SPECIES IN THREE STUDY AREAS

Species	*Area* 1 (1966) *Nyamagasani to Lubilia R.*	*Area* 2 (1964) *Mweya Peninsula*	*Area* 4 (1963) *Lion Bay*
Bothriochloa species	75	87	28
Brachiaria decumbens	Rare	Rare	8
Cynodon dactylon	6	53	28
Chloris gayana	9	73	36
Heteropogon contortus	63	40	6
Hyparrhenia filipendula	34	Locally common	26
Panicum repens	4	Locally common	Locally common
Sporobolus homblei	Locally common	Locally common	Very rare
Sporobolus pyramidalis	57	93	56
Themeda triandra	17	Very rare	9
Dicotyledons	74	100	Abundant
Other grass species	72	93	Abundant

4. Species present in stomachs in large quantities in most areas but rare in the pasture: *Brachiaria decumbens.*

5. Species present in stomachs in small quantities in most areas but abundant in the pasture: *Hyparrhenia filipendula* (except in area 2).

6. Species present in stomachs in a few areas where they are locally common in the pasture: *Panicum repens* and *Sporobolus homblei.*

7. Dicotyledons are present in stomachs in a few areas but are abundant in all pastures.

OBSERVATIONS ON LIVING ANIMALS

Tame animals were used to provide detailed information on the food preferences of a variety of species of grazing mammals. The advantage of this type of observation is that it provides more detailed information on the food requirements of the individual. Observations may be more precise and on a semi-quantitative basis, i.e. the number of feeding minutes spent on a given plant species. The main disadvantages is that it gives little idea of the variation that might occur within a herd of animals (Field 1966).

In the case of the hippo, which is large and expensive to wean, animals were captured after weaning with the minimum of stress, by immobilisation with anaesthetics. Within three months they were tame enough to handle.

Observations on tame hippo were not so extensive as on other species since it was not possible to visit areas other than the vicinity of their pool at Mweya. However, it has been possible to observe the feeding at night of two tame animals, one of them over a period of eight months. The results are expressed as preference percentages, i.e. number of minutes spent grazing on a species of plant expressed as a percentage of the total number of minutes

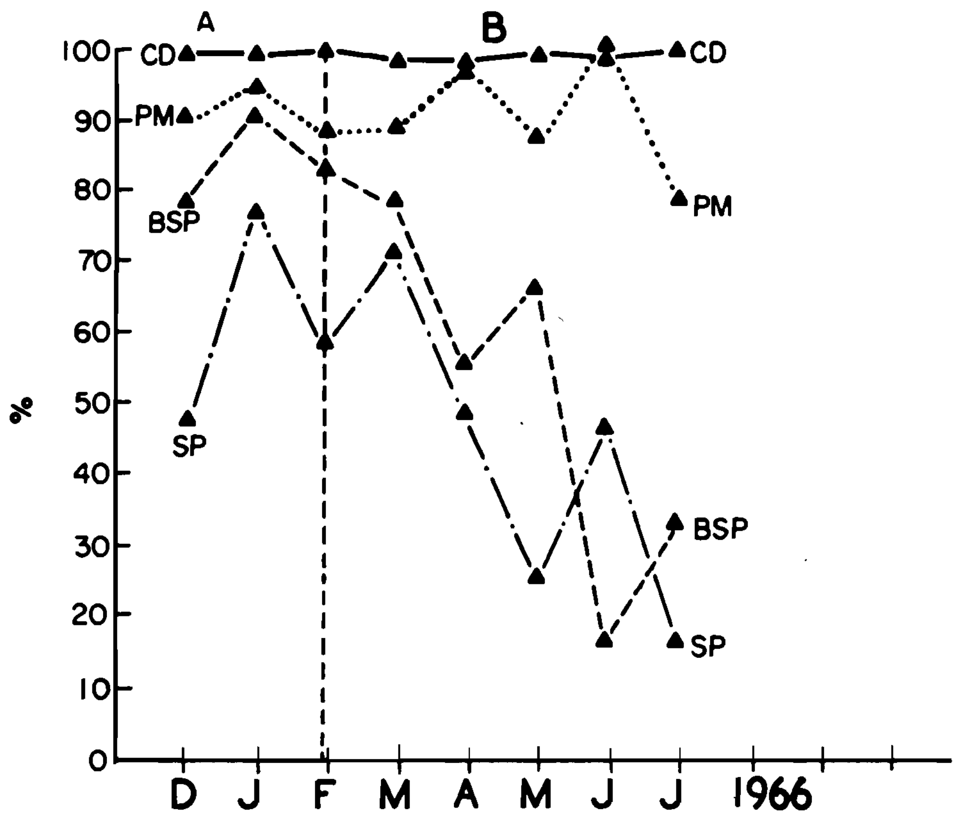


FIGURE 2
Preference % of a tame female hippo. Observations in the first three months, from December February were made in a pen (A) after which the animal was free-ranging (B). Key: BSP: *Bothriochloa* species. CD: *Cynodon dactylon*. PM: *Panicum maximum*. SP: *Sporobolus pyramidalis*.

that the plant was available, and are shown in Figure 2. Results were divided into two periods, the first of three months when the animal was in a small enclosure and the second of five months when it was free-ranging. During the first three months preference for some of the species rose as the area became grazed out and then fell a little with the onset of the dry season. Throughout the observations, however, *Cynodon dactylon* was taken almost 100% and *Panicum maximum* between 80% and 100% of the times that they were available. However, the palatability of *Panicum maximum* began to fall off with the onset of the dry season. *Sporobolus pyramidalis* and *Bothriochloa* spp. were much less preferred.

Cynodon dactylon, being a creeping grass, has a high stem to leaf ratio, but despite this maintains a high average crude protein content (Range 6 to 9%) throughout the year. *Panicum maximum* is a tall tussock grass with a high leaf to stem ratio like *Sporobolus pyramidalis*.

However, it also has a rather lower crude fibre content than *Sporobolus*, which would make it easier to ingest. Analyses at Entebbe of Park samples shows that the whole plant has a relatively high crude protein content.

Penned feeding trials on hippo, using cut grass, helped to confirm the observed preferences for *Panicum maximum*, *Cynodon dactylon* and *Brachiaria decumbens*. *Cynodon dactylon* was used as a standard against which other species were compared.

Observations on the tame animals show that hippo graze with their lips, with a lateral swinging movement. Coarse tussock grasses, like *Sporobolus pyramidalis*, tend to slip between the lips and are not easily broken off. Stoloniferous grasses like *Cynodon dactylon* are lifted from the ground with the lower lip and may be ingested in quantity. Hippo are able to graze almost to ground level.

METHODS OF STUDYING THE EFFECT OF HIPPO ON THE VEGETATION

THE EFFECT OF INTENSIVE GRAZING

Pasture degeneration by hippo has been studied in miniature using captive animals in enclosures.

Results show that stoloniferous plants increased whilst erect species declined. In six months the creeping herb *Evolulus nummularius* increased in frequency by 89%. The preferred grass *Cynodon dactylon* also increased but to a lesser extent, showing how it is able to survive heavy grazing pressures by growing very close to the ground. In contrast *Sporobolus pyramidalis* declined by 10%, *Bothriochloa* species by 62% and *Eragrostis tenuifolia* by 68%. These erect species suffer from the inability to colonise bare patches and respond unfavourably towards trampling. It is of interest to note that at Johannesburg, South Africa, *Cynodon* species have been shown to be the best grasses for stabilising the surfaces of gold mine dumps owing to their exceptional capacity for covering bare ground (James 1966).

THE EFFECT OF THE REMOVAL OF HIPPO GRAZING PRESSURE

Pasture regeneration has been studied in some detail by the Unit in two areas of the Park where hippo have been eliminated and in a series of exclosures where hippo and other animals are not permitted to enter. Vegetation changes in the Lion Bay area, with the removal of approximately 1,000 hippo, have been recorded by the author since 1963, for five consecutive years. Assistance was given by J. M. Lock and D. D. Thornton.

The method involves recording frequency and foliar and basal cover of vegetation at 300 random points within a fixed plot. Frequency is recorded using an oblong metal frame quadrat. Cover is recorded using a rod passing through random holes in a box fitted to a metal stand. This is in effect a point quadrat. Twelve plots are sited in the hinterland behind the bay. One is at the focus of the original hippo population and there are three in each of three one mile wide concentric zones radiating inland from the bay. Two controls are sited in areas unaffected by cropping.

Figure 3 shows the pattern of vegetation changes at plots near the shore.

During the first five years there has been a large initial increase in frequency and foliar cover of nearly all species in plots within one mile of the shore.

Since then, the more erect species of grass have continued to increase at the expense of creeping and mat-forming species. Thus, *Sporobolus pyramidalis* has increased in frequency by 42% and *Bothriochloa* species and *Hyparrhenia filipendula* by 33% and 30%, respectively. *Cynodon dactylon* showed an initial increase with the relief of grazing pressure, but has now declined by 26%. This decline is probably due to the combined effects of competition with erect species and a decrease in available nitrogen in the soil. The mat-forming species, *Sporobolus stapfianus* and *Microchloa kunthii*, showed a decline of 11% and 8% respectively in four years, but increased burning with a corresponding reduction in shade has since enhanced their chances of survival.

As the bare patches caused by hippo overgrazing became stabilised and recolonised, short-lived annuals were replaced by perennials. Thus the annuals *Chloris pycnothrix* and *Eragrostis tenuifolia* have declined by 43% and 33% respectively.

The initial increases have eventually fallen off and the vegetation is subject to small-scale fluctuations as a result of varying climatic conditions and a long-term change resulting from increased burning, now possible with the improved foliar cover. Thus, *Sporobolus pyramidalis* in the one-mile zone increased in frequency by 35% in the first two years and only 7% in the last two years.

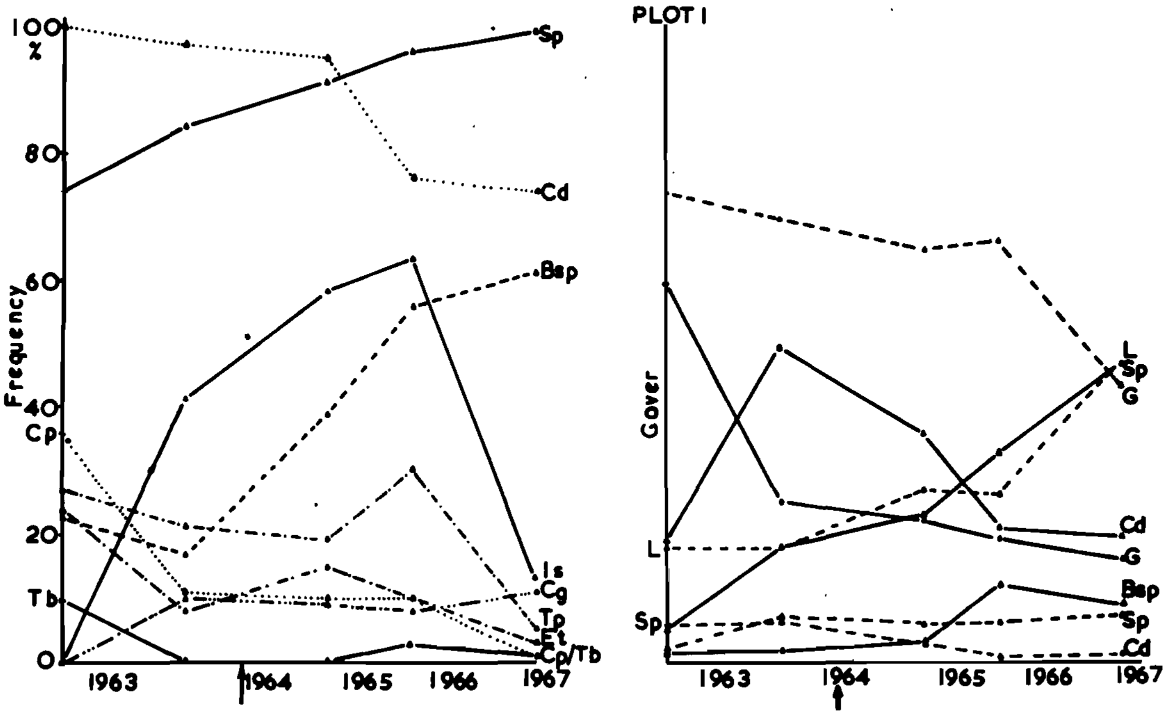
Foliar cover changes parallel frequency changes but are not so marked. Basal cover changes are small but the increase in the amount of litter and subsequent reduction in sheet and gully erosion are evident except where burning has increased.

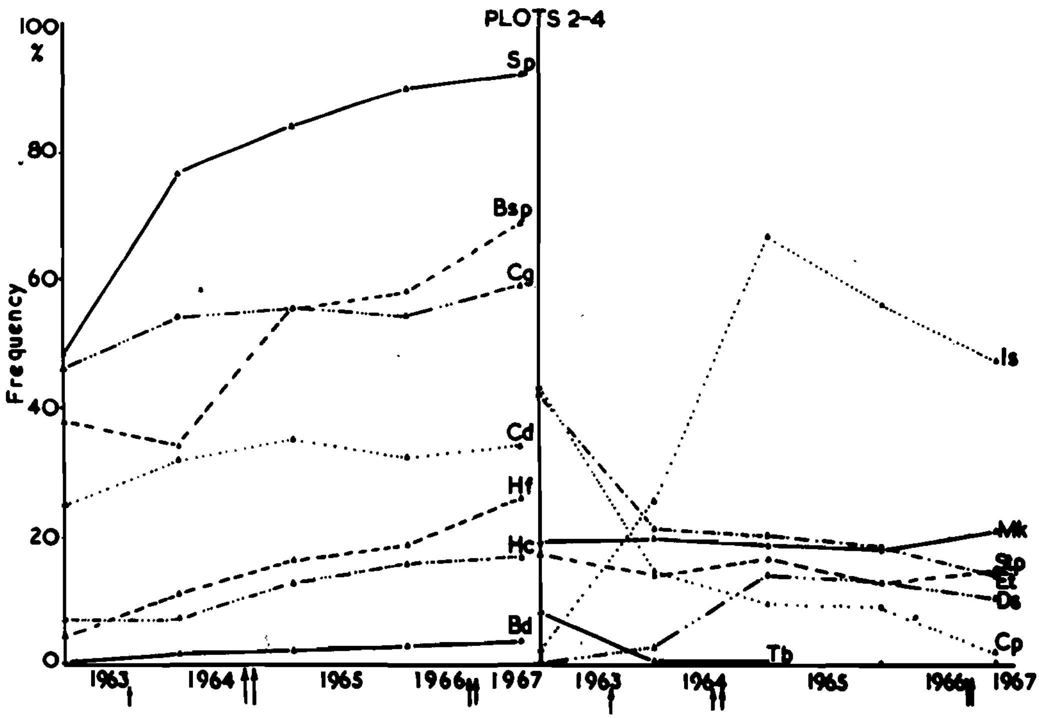
SOME MANAGEMENT IMPLICATIONS

Laws (1963) has shown that on Mweya Peninsula, in the six years 1957 to 1963, there has been a large mammal biomass increase from 215,737 to 264,735 lb per square mile. This represents a 22·7% increase following the elimination of the hippopotamus. The virtual monoculture of hippo has been replaced by a wide spectrum of mammal species using a greater range of the available vegetation. This increase, however, cannot continue indefinitely. It has been seen that the removal of hippo permits an initial improvement of the pasture in both quantity and quality. If the vegetation is allowed to realise its genetic potential under conditions of low grazing pressure and before other species of animal have time to build up, then the full effect of a high stem to leaf ratio, low protein content or the accumulation of unpalatable chemicals in the mature leaf may be experienced by the herbivore.

A moderately grazed pasture will remain actively growing with a high average protein content and an adequate supply of bulk. Palatable species of vegetation such as *Brachiaria decumbens*, though well utilised, will not be eliminated. Annual grasses, which are of little value during dry seasons, will be unable to compete with perennials. A wider range of species of vegetation will be permitted since no one type of vegetation can become dominant. It is generally understood that different species of grass are more similar during their development than they are at maturity. For this reason selection pressures on particular species of grass are not so great in areas of even grazing intensity such as the Serengeti National Park, Tanzania (Bell 1967).

From studies in Lion Bay it has also become apparent that, with the increase in foliar


PLOT 1
100 %
80
60
40
20
0
Frequency
Cover
Sp
Cd
Bsp
Cp
Tb
Is
Cg
Tp
Et
Cp/Tb
L
G
1963
1964
1965
1966
1967


PLOTS 2-4
100 %
80
60
40
20
0
Frequency
Sp
Bsp
Cg
Cd
Hf
Hc
Bd
Is
Mk
Stp
Et
Ds
Cp
Tb
1963
1964
1965
1966
1967

cover, there is a correspondingly greater fire hazard. I do not intend to discuss the question of burning here since it is an immense study on its own. It too may be a useful tool, however, in modifying the vegetation in such a way that it may be made available to the herbivore and thereby constitute a more efficient form of land use. Uncontrolled burning may destroy shade-loving palatable species and favour coarser species of vegetation. Moderate hippo densities would reduce the fire hazard and, by producing a grazing mosaic, prevent its spread in the event of a fire being started accidentally.

It has been stated earlier that hippo occupy inland wallows particularly during the rains. These are used as staging points from which animals may feed over a wider area and thereby constitute a more efficient utilisation of the range. The elimination of hippo from permanent dry-season wallows is usually accompanied by the filling in and drying of these wallows. Hippo clearly maintain open water in these wallows by their movement and so keep them suitable as watering points for other species.

Field (1966) has suggested that the feeding habits of hippo and buffalo tend to be complementary. *Sporobolus pyramidalis* grassland is the result of heavy hippo grazing and is utilised by buffalo. The latter in turn maintain the tussocks short and the grassland open so that creeping grasses may grow between.

For the above reasons an optimum figure has been suggested for the grazing density of the hippopotamus. In the drier regions of the Park which have been the subject of this study, a density of 20 to the square grazing mile neither appears to expose the soil to erosion through overgrazing nor permits vegetation to grow tall and unpalatable. In other areas of the Park, particularly at the northern and southern extremities where there is a higher primary productivity, and in other Parks, different optimum grazing intensities must be calculated.

SUMMARY

1. The hippopotamus is one of the three dominant species which contribute towards the high mammal biomasses typical of the grasslands of the Nile basin.

2. The distribution of the hippopotamus population is influenced by the availability of suitable food, water and resting places, the structure of the herd and the presence of man and other predators.

3. Feeding habits have been studied in detail in several areas of the Queen Elizabeth Park by the analysis of stomach contents. Stomach weights show variation according to age, sex, state of the pasture and time of collection. Microscopic analyses of stomach contents provide qualitative and quantitative data on a frequency basis on the diet of the hippopotamus.

FIGURE 3

Vegetation changes at Lion Bay after the removal of hippopotami in 1963. Plot 1 was on the Lake shore and plots 2-4 in the one-mile zone. Arrows indicate the incidence of fire in the plots. Foliar cover changes in plot 1 are shown by solid lines and basal cover changes by dashed lines. Key: Bd. *Brachiaria decumbens*. Bsp. *Bothriochloa* spp. Cd. *Cynodon dactylon*. Cg. *Chloris gayana*. Cp. *C. pycnothrix*. Ds. *Digitaria scalarum*. Et. *Eragrostis tenuifolia*. G. Bare ground. Hc. *Heteropogon contortus*. Hf. *Hyparrhenia filipendula*. Is. *Indigofera spicata*. L. Litter. Mk. *Microchloa kunthii*. Sp. *Sporobolus pyramidalis*. Stp. *S. stapfianus*. Tb. *Tragus berteronianus*. Tp. *Tephrosia procumbens*.

The species eaten vary according to their availability and the season of the year. The latter may be explained in terms of palatability.

4. Observations on tame animals confirm in detail findings from stomach analyses, and shed light on the mechanism of feeding of the hippo.

5. Grazing studies of pasture degeneration and regeneration emphasise the importance of the hippo in modifying the grassland habitat.

6. Hippo management should be based on a knowledge of the primary production of vegetation in an area and the secondary effect it is likely to have through the vegetation on other large mammals. It should be accompanied by the controlled use of fire as a management tool.

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