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Colloque P. B. I. Lamto Côte-d'Ivoire « Milieux herbacés ».

THE LARGE MAMMAL COMMUNITY OF THE QUEEN ELIZABETH NATIONAL PARK, (UGANDA).

by S. K. ELTRINGHAM.

The Queen Elizabeth National Park is 1978 sq.km in area and is situated astride the equator in the western Rift Valley of south west Uganda. It is a region of varied habitats including open grassland, grassland with thickets, thick bush, forest, swamp and lake shore. Two large lakes, Lake George and Edward, lie on either side of the Park which is bisected by the 34 km long Kazinga Channel connecting the two lakes. The elevation varies from about 910 m at lake level to 1390 m in the area north of Katwe which comprises a series of explosion craters, some containing salt lakes, formed by volcanic activity some 8-10,000 years ago. The climate is cool, considering the latitude, with mean maxima near 28 °C and mean minima around 18 °C in all months. There are two rainy seasons each year, March-May and September-November. Rainfall varies greatly from place to place in the park, with a mean ofabout 750 mm at Mweya where the Kazinga Channel enters Lake Edward. Rainfall increases towards the escarpment and reaches 1250 mm a year in the Maramagambo Forest. Although the seasons are usually well marked, appreciable quantities of rain may fall during the dry months.

The region which is now the Queen Elizabeth Park was once densely settled by pastoralists, who maintained large herds of cattle, and by fishermen. The park owes its existence to three catastrophes which struck the human population. These were small pox towards the end of the nineteenth century, rinderpest in the 1890s and finally sleeping sickness at about the time of the first world war. The only effective way to combat the latter

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scourge was to evacuate the human population. This was done and the large mammals, benefiting from the removal of hunting pressure, came into their own. A game reserve was established in the area in 1934, and in 1952 the national park was declared. Some of the large fishing villages were not evacuated and either existed from the newly created park or were incorporated into it. Over the succeeding twenty years, other villages have been established and the total now stands at sixteen. This is not a satisfactory arrangement as the task of controlling is made that much more

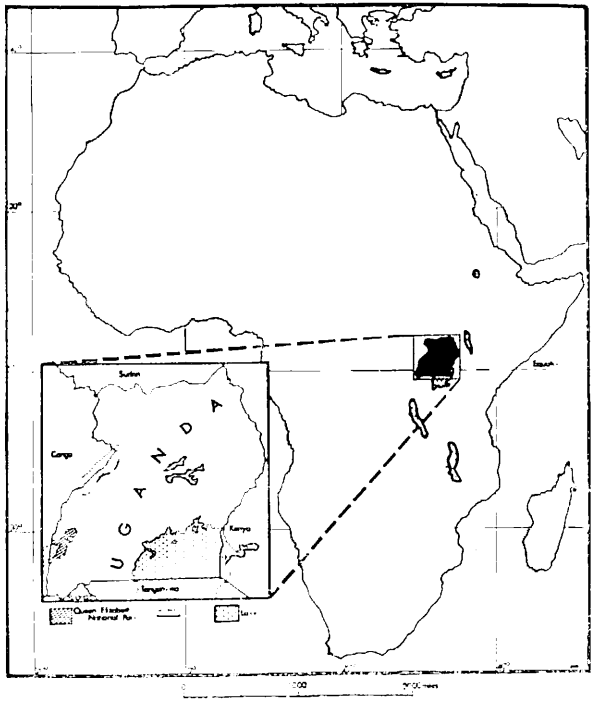

Fig. 1. — Location of Queen Elizabeth Park in Africa.

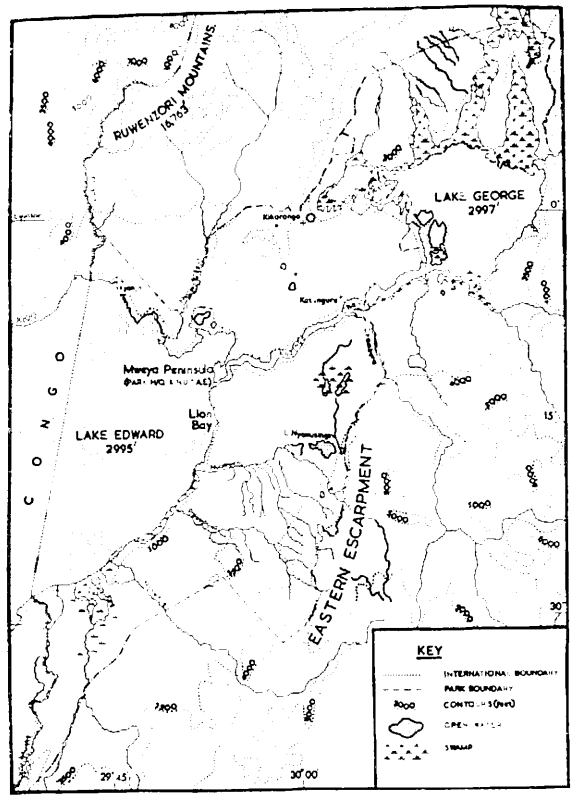

Fig. 2. — Map of Queen Elizabeth Park.

difficult and plans have been mooted to rationalise the fishing activity by removing the smaller villages and concentrating the industry into large units with adequate deep freeze and other facilities. It would be wrong not to exploit the fish of these very productive lakes but the present system gives cause for concern as

far as the long term survival of the large mammals is concerned. Apart from the fishing villages, there are two townships within the park while the town of Katwe supports a small salt industry as well as a large fleet of fishing canoes.

The Queen Elizabeth Park is, therefore, not typical of national parks found elsewhere in East Africa. No other park has such a large human population within it nor, with the exception of Murchison Falls National Park, a history of continuous human settlement over the past few hundred years. Whereas most parks preserve a portion of virgin habitat in its pristine state, the Queen Elizabeth Park is new with probably more animals in it now than ever before. The increase in the large animals has partly been due to immigration but the removal of hunting pressure has certainly been an important factor. Over hundreds of years, man has acted as a predator of the large mammals whose reproductive capacity has evolved to keep pace with the mortality imposed. The sudden removal of the predator has led to a population explosion which in the hippopotamus reached crisis proportions in the late 1950s as will shortly be described.

The large mammals of the Queen Elizabeth Park.

The fauna of the park is typical of the Nile basin in that it is dominated by large numbers of big animals particularly hippopotamus (*Hippopotamus amphibius* L.), elephant (*Loxodonta africana* Blumenbach) and buffalo (*Syncerus caffer* Sparrman). However the area is surprisingly poor in ungulate species. Thus giraffe (*Giraffa camelopardalis* (L.)), Eland (*Taurotragus oryx* (Pallas)), Hartebeest (*Alcelaphus buselaphus* (Pallas)), Impala (*Aepyceros melampus* Lichtenstein), Oribi (*Ourebia ourebi* (Zimmerman)), Zebra (*Equus burchellis* Gray) and black rhinoceros (*Diceros bicornis* (L.)) are amongst those not represented although all these species occur elsewhere in western Uganda. It is thought that the reason for this may lie in the intensive volcanic activity which occurred in the park in comparatively recent times. This would certainly have caused widespread mortality if not complete extinction of the animals and subsequent recolonisation has been hindered by the surrounding forest which is an effective barrier to plains game. At present, the park is almost completely surrounded by forest or cultivation and further immigration of large mammals by natural processes is most unlikely. In the north west and south west, however, the park is continuous with the Parc National Albert in the Zaïre Republic and movements of animals across the border occur freely.

A west African influence is apparent in the composition of both the fauna and flora and in the animals, it is most marked in the invertebrates and birds. However, traces may be seen even in the large mammals. Thus, the buffaloes are rather smaller than those in the rest of East Africa averaging 650 kg in weight for the adult male and 475 kg for the female. There is also a marked brownish coloration, a feature which recalls the reddish colour of the small west African bush cow. The adult male bushbuck (*Tragelaphus scriptus* Pallas) are also red as in West Africa and quite unlike the almost black males seen, for example, in Kenya. The bush pig (*Potamochoerus porcus* (L.)) is also reddish like the west African red river hogand, not black as in the Southern and Eastern races. The elephants, however, belong to the race *africanus*, and show no interbreeding with *Loxodonta africanus cyclotis* as is often asserted. They are, however, polymorphic in size with a type smaller at the shoulder and with lighter tusks than the others (Laws 1966). A west African flavour is also found in the primates with a larger range of species than is normal in East African parks. The long haired chimpanzee, (*Pan troglodytes* Schweinfurthi) is basically a west African species which occurs in the Maramagambo Forest in considerable numbers.

A checklist of the mammals of the Queen Elizabeth Park is in process of being made but it will be some years before all the small mammals in the forests and other inaccessible areas are reliably recorded. However, the large mammals are well known and are sufficiently few for them to be considered individually.

The elephant is without doubt the most important animal in the park as far as its effect on the habitat is concerned (Laws 1970). This is due as much to its large size as to numbers. The elephant is a destructive feeder and its tendency to push over trees is well known. To a certain extent such activity is beneficial in preventing the encroachment of bush and the presence of some elephants is essential in maintaining open patches of grassland. The climax vegetation of much of the Queen Elizabeth Park is probably thick bush and the present vegetation pattern of grassland and thicket is probably the result of elephant and fire. Without elephants to keep back the spread of thickets, there would be no grass to burn. The fire does not destroy the thicket but it does kill the peripheral shoots and prevents the bush from expanding.

Elephants may be found anywhere within the Queen Elizabeth Park but in the dry seasons, they are generally absent from the Craters area and are rare in open grassland elsewhere. At such times, they probably move into the Maramagambo Forest or into riverine forests while some undoubtedly leave the park altogether.

Those north of the Kazinga Channel probably migrate to the Kibale Forest, which lies south east of Fort Portal, although there is as yet no direct evidence of this. In earlier times, the elephants most likely moved up into the montane forest of the Rwenzori range but such movements are no longer possible because of the spread of cultivation.

Although most national parks carrying a high density of elephants have an « elephant problem » this does not seem to have developed yet in the Queen Elizabeth Park which is, in fact, good elephant habitat. The reason for this lies in the vegetation mosaic of grasslands dotted with thickets and trees and with easy access to forest as well as to permanent water. Such a mosaic ensures an adequately balanced diet. Studies on elephant feeding behaviour (LAWS 1970) have shown that elephants can subsist almost entirely on grass if they are forced to, as is the case in the southern part of the Murchison Falls National Park, but under such a regime, the elephants lose condition. Laws considers that a mixed grass/browse diet is desirable with the proportion of grass not exceeding 50 % for the maintenance of good health. Obviously, there will be much seasonal variation and at the beginning of the wet season, when the protein content of grass is at a maximum, a higher proportion of grass in the diet would not be deleterious. In the Queen Elizabeth Park, it has been found that the proportions of grass, browse and herbs in the diet tend to reflect the composition of the vegetation. It was also found that during the dry season, the elephant spend more time in browsing, as might be expected. Because of their size and somewhat inefficient digestive system, elephants spend most of their time in feeding — up to 80% in the Queen Elizabeth Park. The daily quantity of food consumed (in terms of wet weight) varies from 4.8 % of the body weight in males and 5.6 % in females (LAWS 1968) i.e. about 90-280 kg in males and 54 — 280 kg in females. These figures underline the significant role which a large population of elephants plays in the utilization of the primary productivity.

The hippopotamus occurs along most of the shore line of the lakes and Channel as well as in inland wallows particularly during the wet season when these are numerous. When the wallows dry up, the hippopotamus retreat to the Channel and lakes or to large permanent wallows. The overcrowding which follows leads to fighting which may be partly responsible for the notable increase in mortality towards the end of the dry season. The hippopotamus is a significant species in the management of the Queen Elizabeth Park and its numbers were reduced between 1958 and 1962 when about 7.000 were shot. The problem arose because of the over-

grazing and trampling by hippopotamus which reduced the grass cover, in some cases to bare earth, for several miles inland of the lakes and around the large wallows. Severe erosion set in in some places while in others, encroachment of bush followed the reduction of grass presumably because of the absence of fire. Some aspects of the feeding behaviour of hippopotamus which, in conditions of overcrowding, lead to habitat deterioration have been considered by FIELD (1970). Observations on tame hippopotamus in small paddocks, conditions which simulate heavy grazing in the wild, showed that stoloniferous plants increased while erect species declined. Thus, in six months, the creeping herb *Evolulus mummularius* increased in frequency by 89 % while the erect grasses, *Sporobolus pyramidalis*, *Bothriochloa spp* and *Eragrostis tenuifolia* declined by 10 %, 62 % and 68 % respectively. Their decline was attributed to their inability to colonise bare ground and their vulnerability to trampling. On the other hand, *Cynodon dactylon*, the preferred food species of the hippopotamus, is very good at covering bare ground and in the experimental paddock actually increased somewhat despite the heavy grazing. The recovery of grassland following the removal of hippopotamus was followed in the Lion Bay area for five consecutive years from 1963 (FIELD 1970). The most noticeable result has been an overall increase in foliar cover while the detailed changes have tended to be the reverse of those recorded in the experimental paddock. Thus, the erect grass species have tended to increase at the expense of the creeping and mat-forming species. *Sporobolus pyramidalis*, *Bothriochloa spp* and *Hyparrhenia filipendula* increased in frequency by 42 %, 33 % and 30 % respectively while *Cynodon dactylon* decreased by 26 %. The mat-forming species *Sporobolus stapfianus* and *Microchloa kunthii* declined by 11 % and 5 % respectively.

A most beneficial effect of the hippopotamus reduction was the replacement of short lived annuals by the more valuable perennials. However, it is not desirable that hippopotamus should be completely eliminated, or even reduced to a low level, since they have important positive qualities in the maintenance of the rangeland. Moderately grazed pasture is more productive in terms of average protein content than an ungrazed one and the hippopotamus plays an important role in ensuring that the vegetation is adequately grazed. FIELD (1966) has shown that the feeding habits of hippopotamus and buffalo tend to be complementary with the latter species keeping the tussocks of erect grasses such as *Sporobolus pyramidalis* short and the grassland open so that creeping grasses, preferred by the hippopotamus, can grow between. A further beneficial effect of hippopotamus results in their creation of permanent wallows which are utilised by other species of animals

Elimination of hippopotamus usually results in the drying during the dry season of previously permanent wallows.

The effect of the removal of hippopotamus on the other mammalian species has been studied on Mweya Peninsula where counts of the large mammals have been made at intervals since 1956. Counts made by PETRIDES and SWANK (1965) may be compared with a four year series of counts made between 1963 and 1967 by FIELD and LAWS (1970) and counts made by the present author since 1968 (ELTRINGHAM 1972). The first effect of the elimination of hippopotamus on the peninsula in 1957/58 when 270 animals were shot was, not surprisingly, a decline in biomass but an increase in the number of other species. Since then, however, the biomass of all species has increased as well as the number of individuals of other large mammals. There has also been an increase in the energy consumption of the large mammal community. Thus, between 1956 and 1968, numbers of all species increased from an average of nearly 202 to almost 306, the biomass from 122,858 kg to 147,114 kg and the energy consumption from 207,027 Kcals per hour to 252,185 Kcals per hour. This trend has probably been followed in other areas of the Park. The decision to cull the hippopotamus population seems to have been justified although it was not an easy one to take under the climate of opinion concerning national park management obtaining at the time.

The buffalo is widespread throughout the Park and there is no part from which it is altogether absent except for the swamp regions north of lake George. The Buffalo seems to be equally at home in grassland as in forest and it is difficult to be sure of its preferred habitat. In the grassland, it is predominantly a grazer although it often browses in the dry season and to a lesser extent at other times of the year. The forest-dwelling buffalo must certainly browse much more. Such observations as have been made suggest that herds in the Queen Elizabeth Park have a small home range of from 8-10 sq. km. However, fewer herds are present in the grasslands in the dry season and the inference is that they move into the forested regions. A certain proportion of bulls, ranging from 1.9 % to 10.6 % of the total population, is found apart from herds and it is so frequently stated as a fact that these are driven from the herds by the dominant bull that it seems almost eccentric to report that extensive observations made by GRIMSDELL (1969) in the Queen Elizabeth Park give no support to this belief. There is a seasonal movement of bulls to and from the herds with a tendency to leave in the dry season and to rejoin in the wet. Such bulls leave voluntarily and are not driven out. In fact, dominance amongst male buffalo is rarely expressed although [illegible] hierarchy but the dominant bull by no means monopolises all the matings. A certain number of the older bulls spend most of their time away from the herds. Such bulls are vulnerable to predation by lions particularly if they live alone but herd buffalo have little to fear from lions and frequently drive them away. Hyaenas are probably the major predators of the calves although again, the herd affords a very potent protection to the young animals.

Studies of disease in buffalo have shown that bovine tuberculosis occurs in the herds north of the Maramagambo Forest (WOODFORD 1971) with an overall incidence of 9 % diseased animals. It is believed that the tuberculosis was introduced into the area by the domestic cattle which used to be widespread in the north of the Park but not in the south. Bovine tuberculosis, probably transmitted by the buffalo, was found in 9 of 100 warthogs collected in the park and a suspected case was found in an elephant. Thus the disease seems to be well established and may develop into a management problem. A solution suggested by WOODFORD (1971) is that all thin animals should be shot. Buffalo in advanced stages of the disease are invariably thin, but not all thin buffalo are diseased and their poor condition can be due to broken and worn teeth or to other debilitating factors. However, as the proportion of the animals in the population is low, not many buffalo would need to be destroyed. Admittedly, animals in the final stages of the disease have already had ample opportunity of infecting other individuals but it is at the advanced stage that bacteria are most actively excreted and such cases are highly infectious.

Of the antelopes, the Uganda kob *(Adenota kob thomasi)* is the most numerous but its distribution is markedly discontinuous with areas of highest density occurring in the southern region of the park and in the grasslands west of Lake George. The well-known territorial behaviour, first described by BUECHNER (1961) in the Toro Game Reserve south of Lake Albert, has been found in the Park (MOOHA 1972) but the communal territorial grounds are smaller. Although sexual activity is much more intense on the territorial grounds than elsewhere, males holding single territories are responsible for the majority of matings because of their numerical superiority.

The defassa waterbuck (*Kobus defassa* Ruppell) is another very common antelope and its distribution is more even than is the case with the kob although there are areas, such as Mweya Peninsula, where the population density is markedly high. The social structure is similar to that of the kob in that some males are territorial while others congregate in bachelor groups, with

the females and young forming separate herds, but there is no trace of a territorial ground system. The waterbuck is not as dependent on water as its name suggests although it is never far from water and needs to drink every day (TAYLOR and al., 1969). Waterbuck are often seen on the side of the main road as it enters the Maramagambo Forest but they do not penetrate far into the forest. Although primarily a grazer, the waterbuck often browses particularly in the wet season, and for this reason, the species is found in thicker bush, almost bordering on forest, than is the case with kob.

The next most abundant antelope is probably the topi, (Damaliscus korrigum (Ogilby)*)* although in the Queen Elizabeth Park, it is confined to the area south of the Maramagambo Forest. There are two distinct populations although separated by only a few miles and by no more formidable a barrier than a small river. The discreteness of the populations is obvious from their differing breeding seasons with the southern (Ishasha) group dropping their young in August and the northern group calving about a month later. The northern group is much the smaller numbering only about 500 while the Ishasha herds total 4,000-4,500 concentrated in a home range of only 80 sq.km. The curious social structure of the topi has recently been studied at Ishasha by JEWELL (1972). Although the topi is often said to hold territories rather like the waterbuck or kob do, it was found that the territorial system of the Ishasha topi was quite different and could hardly be called territorial at all. JEWELL found that at the time of the rut in January and February, the topi gather together in large herds which move continuously across the grassland. Within this moving mass are master bulls which attempt to gather together a harem of females which defend fiercely against other males. The bulls are moving with the herd but at a slower rate so that eventually they find themselves left at the rear. They then lose their social dominance and join the peripheral males. These males then gradually move to the front of the herd, enter it and revert to their dominant status. There is, therefore, a stream of dominant males passing through the moving herd from front to back, each defending females in its sphere of influence. Such behaviour is clearly territorial in nature but semantic difficulties arise since the spheres of influence are continuously moving and can hardly be termed territories. An interesting feature of the behaviour is that when the adult males have completed the rut and all or most of the females are pregnant, the young males take over and go through precisely the same routine of herding females and defending spheres of influence. While such behaviour may well serve as a safety factor in ensuring that all females are impregnated, it is difficult to avoid the conclusion that the phenomenon has some adaptative value in training the young males for the more serious activities of later life. A similar social organization was noticed by JEWELL (pers. comm.) during the calving period in August with transient dominant males continuing to herd females and subordinate males forming peripheral groups. Detailed studies of the topi are being carried out in the Serengeti National Park, Tanzania, and it will be interesting to see how the behaviour there compares with that at Ishasha.

Small antelope include the bohor reedbuck *(Redunca redunca* Pallas*)* which is distinctly aggregated in its distribution. This species has not received detailed study in the Queen Elizabeth Park and not much is known about their social structure. A group of males with some females is found in one of the territorial grounds of the kob near the equator and quite a dense population exists close to the western shore of Lake George, but elsewhere in the Park, the reedbuck is a rare animal usually seen singly.

The bushbuck *(Tragelaphus scriptus* (Pallas)*)* is widespread throughout the park and is very numerous in places. It is a creature well adapted to the mixed thicket/grassland mosaic which covers much of the Queen Elizabeth Park but it is not found in open grassland nor in thick. It is almost entirely a browser and spends much of the day deep inside thickets. For this reason, sightings of this species are not as frequent as would be expected from the population size. A detailed study of the bushbuck has not yet been made in the Queen Elizabeth Park. The closely related sitatunga *(Tragelaphus spekei* Sclater*)* is included in the park's checklist of mammals but it has not been reliably reported for some years. It used to exist in the swamps north of Lake George and a specimen was seen there in 1966 but the absence of subsequent records suggests that it has been poached to extinction in the park.

At least four species of duiker occur in the Queen Elizabeth Park. The one most commonly seen is the bush duiker *(Sylvicapra grimia* (L.) which lives in the more open bush area. The three forest duikers are the red duiker (*Cephalophus harveyi* Smith) the blue duiker *(C. monticola* (Thunberg)*)* and the yellow backed duiker *(C. sylvicultor* (Afzelius)*)*. The forest duikers are rarely seen and nothing is known of their ecology in the Queen Elizabeth Park.

All three species of tropical African pigs are found in the Queen Elizabeth Park. The best known is the warthog *(Phacochoerus aethiopicus* (Pallas)*)* which is diurnal and very common in the grasslands. It is also found in the forested regions although it is primarily a grazer feeding on short creeping grasses. It shows similar food preferences to those of the hippopotamus and it is possible that the two species are complementary to each other with the hippopotamus feeding at night and the warthog during the day. Warthogs spend the night in burrows which they excavate for themselves often at the base of disused termite nests. The oft-repeated remark that warthog occupy aardvark holes is questionable since the warthog is many times more numerous than the aardvark which would be hard put to dig enough holes to accommodate the large warthog population in the park. Grazing is most intensive in the early morning and late afternoon and evening. During the heat of the day, warthog tend to lie under bushes and during rainy weather, they will often retire to their burrows during the daylight hours (Child, pers. comm.). While feeding, they move about in family groups of several females with their young but adult males are often found alone. Warthog are very fond of wallowing and are rarely seen in areas where permanent water is absent as in the craters region of the park.

The giant forest hog *(Hylochoerus meinertzageni* Thomas) is not uncommon in the Maramagambo Forest but because of the absence of tracks, it is rarely seen by visitors. It also occurs in the riverine forest of the Ishasha river which forms the south west border of the park and in the open bush of the Kamulikwezi Circuit north east of Lake George. Isolated populations occur elsewhere and the gallery forest around Lake Mahiga, one of the crater lakes, contains a family group. No detailed study of this species has been made in the Queen Elizabeth Park, or elsewhere for that matter, and not much is known of its ecology.

The bush pig *(Potamochoerus porcus* (L.)*)* is a rare animal in the Queen Elizabeth park to judge from the paucity of sightings but it is probably quite plentiful in the Maramagambo Forest. A young bush pig found abandoned in the forest was reared in the Mweya laboratories and will be used in feeding experiments but otherwise, no work on this species has been carried out in the Park.

Of the three species of aardvark, *Orycteropus afer* (Pallas) occurs and is sighted a few times each year. The porcupine *(Hystrix galeata)*, which just qualifies as a large mammal, is also present but is very rare. Quills are sometimes picked up in the Ishasha area.

The large carnivores comprise the lion *(Panthera leo* (L.)*)* the leopard *(Panthera pardus* (L.)*)* and the spotted hyaena *(Crocuta crocuta* (Erxleben)*)*. Lions are plentiful in the park and prey on a variety of herbivores. Buffalo are taken regularly as are warthog which are sometimes dug out of their burrows. In the south of the park, the lions feed extensively on topi. Leopards are probably more numerous than lions but because of their secretive and more nocturnal habits are less often seen. The spotted hyaena is also common and appears to be largely a scavenger although many cases of it taking young animals have been reported. In the area west of Lake George, the hyaenas are particularly abundant and spend the day above ground often in in wallows. Elsewhere, they are strictly nocturnal and lie up in erosion gulleys or in burrows during the day.

The numbers of large mammals in the Queen Elizabeth National Park.

[illegible] large mammal [illegible] numbers [illegible] by the staff of the research [illegible] by aerial survey. A total count of elephant is made four times a year, once in each wet and dry season. In recent years, the number of buffalo herds have been counted at the same time and the total population estimated from a knowledge of the mean herd size and the proportion of bachelor males in each area. Hippopotamus have been counted less frequently. Total counts of the antelope are not practicable and estimates of the populations are made from sample counts.

Table 1 summarises the total number of aerial counts made of the elephant, hippopotamus and buffalo in the Queen Elizabeth Park, excluding the forested regions, since 1960. It can be seen that there are considerable differences between some of the totals which could either represent changes in the numbers of animals or reflect differing observer ability. A further complication is that some of the elephant counts were made in dry season and others in the wet. As has been pointed out above, many of the elephants move into the forest during the dry season or even leave the [illegible] so that the dry season totals should be lower than those recorded in the wet. A closer inspection of Table 1 shows that individual observers tend to be consistent in their counts but that some observers see more elephants than do others.

TABLE 1. Results of aerial counts made of the large mammals in the Queen Elizabeth National Park.

Date		Numbers of			Names of	
		Elephant.	Hippo.	Buffalo.	Observers	Pilots
June	1960		12.393		Poppleton	Newton
Jan.	1962		9.252		Laws	»
June	1962		8.810		»	
June	1963		8.117		»	
July	1963 *	1758			Field, Lock	Savidge
Oct.	1963 *	1389			Buss, Field, Lock	»
March	1964 *	1295			»	»
May	1964 *	2222			»	
May	1964		8.005		Laws	
June	1966			16.036	Grimsdell	Onslow
June	1966		11.800		Field	Wheater Onslow
June	1966	1891			Lock	Onslow
Sept.	1966	3884			Field	
Feb.	1967	2757			»	Ross
May	1967	4139			»	Wheater
May	1968	2087			Lock, Woodford	Eltringham
Jul./Aug.	1968	1229			Woodford, Eltringham	Eltringham
Nov.	1968	3410			Field	Woodford
Nov.	1968			17.478	Woodford	Eltringham
March	1969	3581			Field	
Aug.	1969		10.187		Modha	»
Dec.	1969	2948			Woodford, Modha	»
Dec.	1969			18.040	» »	»
Aug.	1970	1671			Wyatt	»
Nov./Dec.	1970	2550			»	»
Nov./Dec.	1970			17.953 *	Woodford, Wyatt	»
Feb.	1971	1683			Wyatt	»
Feb.	1971			13.449 *	»	»
May	1971	2360			»	»
May	1971			11.610 *	»	»
July	1971	1605			»	»
July	1971			14.060 *	»	»
Nov.	1971	3233			Din	»
Nov.	1971			17.180 *	Din	»

* Buss & Savidge 1966 (Other data from the Annual Reports of the Nuffield Unit of Tropical Animal Ecology).

There is also the complication that the technique has probably improved with time and that observers become more experienced with practice. With all these reservations in mind, Table 2 has been constructed to show the average number of elephants recorded each year in the wet and dry seasons. This analysis suggests

TABLE 2. — The average number of elephants recorded in wet and dry seasons since 1963.

Year	Wet seasons		Dry seasons	
	No. of counts	Mean No. of elephant	No. of counts	Mean No. of elephant
1963	1	1389	1	1758
1964	2	1759	0	—
1966	1	3884	1	1891
1967	1	4139	1	2757
1968	2	2749	1	1229
1969	2	3265	0	—
1970	1	2550	1	1671
1971	2	2797	2	1644

that numbers increased by over 100 % between 1963 and 1967 but that there has been a marked decline since. Possibly the early counts were too low while the 1967 count may have been exaggerated but the increase probably represents a genuine trend. There is also reason to think that the decline since 1967 has not been as abrupt as the figures suggest. The dry season totals have remained fairly constant and the wet season fluctuations are probably due to a variable number of elephants entering the park each year and taking up temporary residence. Taking a rough approximation of the counts over the last four years, a period of relative stability, it seems that the population of elephant in the park during the wet season is about 3,000 falling by half to about 1500 in the dry. These are minimal figures since elephants present in the Maramagambo Forest cannot be counted by aerial survey.

The numbers of hippopotamus show a falling trend in the early 1960s which can be correlated with the culling of the population which took place at the time. The sudden jump from 8005 to 11800 between 1964 and 1966 is surprising but the 1969 count suggests that the higher figure has been maintained. It is possible that hippopotamus from outside moved into the park after the shooting ceased in 1965 and took over the space left by the culled animals. Numbers have not, however, risen to the pre-shooting level of the mid 1950s which was certainly more than 12,000 and

probably in excess of 15,000. A close approximation to the present population is probably 11,000.

The buffalo have not been counted directly as frequently as the other species. Three full photographic counts made in 1966, 1968 and 1969 gave a mean of 17,185. The 1966 total was thought to be low and the mean of the 1968 and 1969 counts — 17,759 — is probably a closer estimate. With the buffalo not counted in the Maramagambo Forest, the total park population may be of the order of 19-20,000. Since, 1969, the buffalo totals have been estimated from a count of the herds based on a knowledge of the herd size and the proportion of bachelor bulls in the population. The 1970 estimate was close to the total counts but subsequent estimates have been lower. Some of these may reflect dry season movements into forests but some misinterpretation of herds may well have occurred. It is often difficult to decide whether groups of buffalo close together represent one ore more herds and different observers make different judgements. The count made in November 1971 suggests that the population is still of the order of 17,000.

Estimates of the population size of the antelope are more difficult to make. The only reliable figure is that for the topi which were counted at Ishasha on three occasions in the first quarter of 1970 by Dr. JEWELL when they were grouped into one or two large congregations. A mean of 2,962 adults was recorded. Sample counts showed the proportion of calves to be about 25 % i.e. 750 in number giving a total of 3,712. Allowing for observational errors, a round figure of 4,000 was suggested. The smaller population of topi in the Kikeri area numbers about 550 so that the number of topi in the park is about 4,500.

The others antelopes are much too dispersed to be counted accurately by direct counts and only estimates can be made. Sample flights are currently being flown to estimate the populations by the techniques of stratified random transects (JOLLEY 1969). The work is in its early stages but preliminary results suggest a population of up to 10,000 kob and 3,500 waterbuck. Counts of warthog are also made but the numbers recorded appear to be much too small. This species is difficult to see from the air and individuals are often hidden under bushes or below ground.

An alternative method of obtaining an estimate of numbers is to calculate the densities in study areas and extrapolate the results to the whole park. The method is obviously fraught with [illegible]

[illegible]

series of monthly counts made in ten study areas of the park by FIELD and LAWS (1970) between 1963 and 1967, gave some interesting data on densities but the results cannot be applied to the park as a whole since the study areas were not selected on a statistical basis and most of them were grouped together in the middle of the park north of the Kazinga Channel.

An estimate for the numbers of predators is very much guess work. The lions are perhaps the easiest to deal with because they are relatively few in number and more obvious than the others. The only reliable method of estimating their population size depends on knowing every lion individually within the territory of each pride. This would, of course, involve a tremendous amount of work which would not be justified by the rather trivial nature of the results. However, in certain areas of the Queen Elizabeth Park, the number of lions is known with fair accuracy. Thus, about 20-25 lions occupy about 160 sq.km. around Mweya while in Ishasha, there are two prides ranging from 25-35 in about 110 sq. km. The southern pride moves over the international border and uses an undetermined area of the Parc National Albert. These figures suggest a density of about one lion for every 7 or 8 square km. The area of the park is 1978 sq.km. but about 750 sq.km. of these are forest or swamp and are unsuitable for lions. If the remaining 1230 sq.m. contain similar lion densities, the total for the whole park would be between 150-180. The numbers around Mweya and Ishasha are undoubtedly high and the same density may not obtain all over the Park. However, these figures seem reasonable and are similar to the results obtained if subjective estimates of the number of lions in various areas of the park are totalled.

It would be impossible to hazard a guess for the total number of leopards but they are probably more numerous than lions. Because of their retiring nocturnal habits, they are rarely seen and are thought of as rare but if an area is studied intensively, a surprising number of leopard may be found. Thus in an area of no more than 10 sq.km. around Mweya, no less than six leopards are known individually. If the same density obtains throughout the park, well over a 1,000 leopard are present.

No reliable estimates of the hyaena population have been made but the species is by no means rare. Work currently in train may enable a rough estimate to be made soon but it would be wiser [illegible] guess.

The biomass of the large mammals.

The biomass as a measure of animal densities is more important than the actual numbers. The Queen Elizabeth Park is an area of high biomass and the figures recorded from the park exceed those published for any widlife community anywhere in the world. FIELD and LAWS (1970) give a year-round standing crop biomass for the grasslands of the park of 29,490 kg sq.km. with a range of 5,140 kg/sq.km. in long grass areas to 36,510 kg/sq.km. in a heavily overgrazed region of thicket and short grass where hippopotamus represented 71 % of the estimated biomass. The year round biomass on Mweya Peninsula, which has a more diverse community of large mammals, was 33,430 kg./sq.km. in 1968 (ELTRINGHAM 1972). The only other area in which biomass figures of this order have been recorded is in the neighbouring Parc National Albert in the Zaire Republic where BOURLIÈRE and VERSCHUREN (1966) report a density of 20,170 kg./sq.km. in one region. These data will be seen in proportion if it is mentioned that in the Serengeti National Park, an area noted for its abundant wildlife populations, the standing crop biomass is no more than 6,300 kg./sq.km. (STEWART and TALBOT 1962).

Productivity of the large mammals.

The contribution made by the large mammals to the secondary productivity in the Queen Elizabeth Park has not been properly evaluated although it is hoped that data which have been accumulating over the past ten years will allow this to be done in the near future. Productivity has two facets; the first concerns the natural increment in numbers and the second, the growth rates of individuals. Although there are irregular variations in numbers in certain areas, it is unlikely that the populations of large mammals are now changing in size very much. The elephant population has probably increased in the last ten years but this has been due to immigration rather than to increased production. There was no evidence of significant change in numbers of any species during the four-year series of counts carried out by FIELD and LAWS (1970). Hence, most of the secondary productivity is probably due to individual growth. Again, the data are inadequate to give a precise figure but ELTRINGHAM (1972) has shown that the productivity is about the same as that of domestic stock.

Studies made on large mammals in the Queen Elizabeth Park.

A short account of the research work carried out in the Queen Elizabeth Park has been given by ELTRINGHAM (1969). At the time when the Nuffield Unit of Tropical Animal Ecology was established in 1961, the management cropping of excess hippopotamus in the Queen Elizabeth Park was at its height. The opportunity for examining so many carcasses of a large wild mammal is not one which often presents itself and the study of the population dynamics of the hippopotamus was the obvious choice for the first major research project of the new Unit. The work was

FIG. 3. — The elephant moving away with dart in tail region. (Photo J. Dragesco, Université de Paris)

carried out mainly by Dr. R. M. LAWS, the director, assisted by Mr. C. CLOUET a research student from Cambridge who studied the reproductive ecology. Changes in the vegetation following the elimination of large numbers of hippopotamus were studied by Mr. J. M. LOCK and Mr. C. P. FIELD. Mr. FIELD also investigated the comparative feeding behaviour of the more important her-

vity studies have always been a feature of the Unit's research programme using the technique developed by ROTTISON et al. (1956) for domestic cattle. The method requires the continuous surveillance of the animals during which observations are recorded every 4 minutes. The actual activity in which the animal is occupied at the four minute mark is recorded according to a pre-arranged series of categories such as feeding, wallowing or fighting. The four minute interval was chosen on a statistical

FIG. 4. — Injecting the antidote into an ear vein. (Phot. J. Dupuy, Université de Paris.)

basis as giving an optimal effort/result ratio. The method has been used particularly at the time of the full moon when observations can be carried on into the night. The most extensive series of such observations have been made with the elephant. Altogether about 380 hours of more or less continuous observation have been carried out over periods of up to three days and nights. In addition, a few more hours of observations have been made of

elephants which were lost to view early in the study period. The success of the technique relies to some extent on the movement of the elephants. These are very difficult to follow or observe if they enter thick bush which was the usual cause of a premature termination of the observation.

FIG. 5. — The local immobilization. (Phot. J. Dupuy, Université de Paris.)

Examination of dead animals is a very valuable technique in many studies ranging from feeding behaviour to reproductive biology. However, with large mammals in a national park, there are sampling problems. No difficulties arise if the sample is obtained as a result of management culling although the composition of the sample may not be ideal for scientific purposes. However, the Uganda National Parks authorities have always been

very helpful in allowing the Unit to collect samples of various species for study. Obviously, the size of the sample has to be limited and some of the samples may not be as statistically significant as could be wished but nevertheless, data of great value have been derived from such studies. Because of the valuable nature of the sample, every effort is made to extract the maximum amount of information from the carcases. Hence, a routine form has been drawn up on which many measurements are entered whether or not they are intended to be used by the particular research worker taking the sample. Certain organs and the skull and lower jaw are preserved as a matter of course. As a result of the scientific collections made in the park and the analyses of animals shot for management purposes, the size and weight distribution of the populations are known with fair accuracy. It has been possible, therefore, to draw up unit weights for biomass estimates far more accurately than is usual elsewhere. Similarly, the construction of accurate life tables has been made possible. This technique relies on the ability to age the animal which is usually done on the basis of the sequence of tooth eruption and wear. This gives the relative age of the animal but determination of the absolute age is more difficult. Some progress has been made by a study of the cementum layers in the teeth. Cementum is laid down unevenly with periods of maximum deposition coinciding with the rains. A section of the tooth, therefore, presents a series of lines with each line representing the growth in a single season. The age of the tooth is half the number of lines in a region with two wet seasons. Unfortunately, the dry seasons in the Queen Elizabeth Park are rarely severe enough to give very clear cut lines but nevertheless, some success has been achieved with the method particularly in the case of waterbuck. Another approach is to examine the teeth of known age animals from zoos but there is always the risk that the artificial diet in captivity has affected the rate of tooth wear. Useful data can be obtained by taking successive impressions of the teeth over a number of years from animals captured by drug immobilisation. However, such a procedure requires a long time span.

Drug immobilisation has proved to be a most valuable technique which often circumvents the need to shoot specimens as most measurements can be taken from an immobilised animal while collections of parasites and even biopsies are possible. The method is also invaluable for marking purposes. All the elephants used in the behaviour studies were captured beforehand and painted with large white letters or numbers so that instant recognition

was possible. Many other elephants have been marked in order to follow their movements. Waterbuck is the other species in the Queen Elizabeth Park which has been extensively marked following drug immobilisation while smaller numbers of kob, topi, warthog and even hyaenas and lions have been captured. The drug used on the waterbuck was succinycholine chloride which acts on the neuromuscular junctions to produce paralysis of the skeletal muscles. This class of drug has the disadvantage that

Fig. 6 — Marking completed. (Photo: J. Dasmann, University of Paris)

the dosage is often critical and the weight of the animal needs to be estimated with some accuracy. Also, with one exception there is no antidote. A further objection is on ethical grounds in that the animal is fully conscious and liable to stress on seeing its archenemy bending over it. This problem can be resolved to some extent by keeping the eyes covered or by the use of tranquilizers but it is obviously undesirable to release a tranquilized animal into a dangerous environment when its reactions are

searched for by quartering the ground. This is done by flying the aircraft at a height of 1000 ft. (300 m) along transects one mile (1.6 km) apart (feet and miles are used because these are the units in which the aircraft's instruments are calibrated). Each transect is covered twice so that the observer scans a strip half a mile in width. It has been found that with large animals, the average observer is able to cope with counting an area of this size. However, it is not possible to record the smaller antelopes by this method because the height is too great and the distance too far. Consequently, the populations are sampled by means of a series of transects which are selected randomly. The method has been described by JOLLY (1969). Briefly, it consists in dividing the area to be sampled, in this case the park, into a number of strata each containing ecologically similar habitat relative to the species being sampled. Each stratum is then divided into sampling units and the units to be actually sampled are selected by placing a grid over a map of the area and selecting co-ordinates by means of a table of random numbers. In the present work, the sampling units are transects 500 ft. (152 m) in width and running north to south. Once the selected transects have been marked on a map, the aircraft is flown over them at a height of 500 ft. which is maintained as accurately as possible with the aid of a radar altimeter. The transects are delineated by plastic streamers fixed to the wing strut. The position of these streamers is determined beforehand by flying over a series of ground markers with a graduated scale fixed to the wing strut. Within this restricted area, and from the lower height, waterbuck and kob can be easily counted as can warthog although their gray colour may cause them to be overlooked. The total number of animals in the stratum is estimated from the number in the transect knowing the areas of the transect and of the stratum. JOLLY (1969) describes the method whereby standard errors may be calculated. PENNYCUICK (1969) discusses some errors involved in aerial transect counts and points out that the slight lateral or banking movements inevitable even on calm days introduce a bias towards a large sample. This is because the transect strip approaches the observer and becomes smaller when the aircraft banks towards the ground on the observer's side while the strip becomes larger when the bank is in the opposite direction. As banking in either direction is likely to be random, the net result is a widening of the transect and an over-estimate of the population.

The future of large mammal research in the Queen Elizabeth National Park.

The Nuffield Unit of Tropical Animal Ecology was established in 1961 for a ten year period which has now come to an end. However, this has not meant the end of research since the assets of the Unit have been taken over by a new organisation with the full approval of the Nuffield Foundation and other sponsoring bodies of the old Unit. The new organisation is to be known as the Uganda Institute of Ecology and it is being funded by the Uganda government through subventions made to the Uganda National Parks and Makerere University Kampala. Although the activities of the Institute will at first continue to be mainly confined to the Queen Elizabeth Park, it is anticipated that eventually it will be responsible for the co-ordination of all wildlife research in Uganda, whether in national parks, game reserves or elsewhere. Particular emphasis will be made on the conservation and management of wildlife habitats and on the education of Ugandans for wildlife research. Although this paper has been confined to the large mammals, the work of the Institute is, of course much wider. The large mammals, do not exist in a vacuum and from the beginning, the importance of the vegetation was recognised and a botanist has always worked at NUTAE. In 1969 the Queen Elizabeth National Park was selected by the International Biological Programme as a site for the study of primary productivity. This IBP unit will remain until the end of 1972 but it may be safely assumed that afterwards, botanical work will continue at Mweya. Other sectors of the ecosystem, particularly the small mammal and bird communities, have received detailed attention with particular reference to their interactions with the large mammals.

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SUMMARY

The large mammal fauna of the Queen Elizabeth Park is typical of the Nile Basin but many species which might be expected to be present are absent. This may be due to the extensive volcanic activity which took place in the area within the last few thousand years. Recolonisation would be difficult because of forest barriers and subsequent human settlement. The most important species are the elephant *(Loxodonta africana)*, the hippopotamus *(Hippopotamus amphibius)* and the buffalo *(Syncerus caffer)*. Elephant numbers vary from about 1,500 in the dry season to around 3,000 in the wet. Although this is a high density, there is as yet no evidence that elephants are destroying their habitat as has happened elsewhere in Africa. Hippopotamus number about 11,000 and now appear to be in balance with their environment. Between 1956 and 1966, about 7,000 were shot in a culling operation designed to reduce the severe overgrazing that had developed in the park. The population of buffalo is at least 17,000 and possibly nearer 20,000. Herds north of a large forest, which extends across the park, are affected by bovine tuberculosis. The disease was probably acquired from domestic cattle which used to be present in the area. Estimates of the number of antelope suggest that about 4,500 topi *(Damaliscus korrigum)*, 10,000 kob *(Adenota kob)* and 3,500 waterbuck *(Kobus defassa)* are present. The biomass of the large mammals in the grasslands varies from 5,140 kg to 36,510 kg sq.km, with a year round average of 29,190 kg/sq.km. These figures are higher than those recorded for any other wildlife community. The productivity of the large mammals is due primarily to individual growth and is of the same order as that of domestic stock. An account is given of the work of the Nuffield Unit of Tropical Animal Ecology in the Park and of the techniques used in large mammal research.

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