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The biomass of game animals in Nairobi National Park, 1960-66

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(With 4 figures in the text)

The large animals of Nairobi National Park have been censused intermittently once a month from mid-1960 until the end of 1966. Of the 23 species discussed, the density per kilometre has been determined accurately for the following: Grant's gazelle, Thomson's gazelle, waterbuck, impala, wildebeest, hartebeest, eland, buffalo, warthog, giraffe, zebra and ostrich. From these figures the biomass has been calculated for each species each year. After a peak biomass of 12,775 kg/sq. km during the drought of 1960–61 the population declined to and remained fairly level at about 5690 kg/sq. km from 1962 to 1966. This figure includes about 1050 kg/sq. km of cattle and sheep. The large predators account for only about 1·4% of the total biomass of wild animals while removing about 15·5% from this group annually.

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Introduction

As the human population of the world continues to climb at an ever-increasing rate, determining the most productive use of the land reaches greater urgency. In Africa there has been considerable debate whether the harvest of domestic animals or wild animals is the better form of land use (Darling, 1961; Dasmann & Mossmann, 1961; Dasmann, 1962; Stewart, 1963; Parker, 1964; Riney & Kettlitz, 1964; MacArtney, 1965; Talbot, Payne, Ledger, Verdcourt & Talbot, 1965; Roth, 1966). The debate is not only biological, but economic and political as well. Usually the first exercise in resolving this biological problem is by comparing the biomass of different assemblages of ungulates that can be supported in a given habitat without degrading the ecosystem. This optimum biomass is known as the carrying capacity.

Most biomass estimations for wild game in Africa are derived from approximations of total numbers over a short period; there is generally little indication that the biomass so determined is at the optimum level. The work reported herein is as close as possible to being a total count of all animals made intermittently over six years. Since the total biomass over the last five years has remained fairly constant it is probable that we are dealing with the natural carrying capacity of this habitat under the prevailing climatic conditions.

The census results for the following species are considered to be reasonably accurate: Olive baboon, *Papio anubis* Fischer; zebra, *Equus burchelli* Gray; Grant's gazelle, *Gazella granti* Brooke; Thomson's gazelle, *G. thomsonii* Gunther; impala, *Aepyceros melampus* Lichtenstein; waterbuck, *Kobus ellipsiprymnus* Ogilby; *K. defassa* (Ruppell) and hybrids; buffalo, *Syncerus caffer* Sparrman; eland, *Taurotragus oryx* (Pallas); Coke's hartebeest, *Alcelaphus buselaphus* (Pallas); wildebeest, *Connochaetes taurinus* (Burchell); warthog, *Phacochoerus aethiopicus* (Pallas); giraffe, *Giraffa camelopardalis* (Linnaeus) and Masai ostrich, *Struthio camelus* Linnaeus. The population of 17 buffalo is the result of the warden introducing 11 animals in 1965.

Those aspects of the census not directly associated with biomass such as calving seasons, sex ratios, predation, fluctuation in numbers etc. have been dealt with elsewhere (Foster & Kearney, 1967; Coe & Foster, in press). Special studies which have taken place in the park include population counts (Petrides, 1956) and behavioural–ecological studies of the waterbuck (Kiley-Worthington, 1965), the lion (Schenkel, 1966*a*), impala (Schenkel, 1966*b*) and giraffe (Foster, 1966). Wright (1960) studied predation in the park. L. M. Gosling is presently studying the territorial behaviour of the hartebeest, R. M. Bradley, the ecology of the warthog, and Dr D. R. M. Stewart, feeding habits of plains game by faecal analysis.

Habitat

Nairobi National Park (44·2 sq. miles, 114·8 sq. km, Fig. 1) is the most remarkable park of its size anywhere in the world. A fence separates more than two dozen indigenous big game species which occupy the park from the modern metropolis of Nairobi lying immediately to the north. The southern boundary of the park is open to the vast expanse of the Athi-Kapiti Plains.

In 1947 when the park was first gazetted the game of the Athi-Kapiti Plains used to migrate in the dry season to the permanent water of the park, the Ngong Hills, and the northeast towards Thika. The Nairobi-Mombasa road, and later the park fence bordering this road disturbed the northward path of migrating game. This movement was further confined in 1967, when a fence was constructed running along the eastern side of the Ngong hills and south of the Kiserian River, to join the south-western corner of the park fence. Game is however still free to move in and out of the park along its southern boundary, where the Kitengela Conservation Area of the Athi Plains is, as yet, still comparatively undisturbed. Some species of plains game continue to use the park as a dry season concentration area and disperse to the south in the wet season.

Dams have been built in the park to provide additional water for game in the dry season. One intention in so doing was to increase the carrying capacity of the park in the dry season for the benefit of tourists. Since the Nairobi area was renowned for its perennial water supply, even in droughts, the carrying capacity is more likely to be related to the quantity and quality of forage during the dry season. It therefore seems likely that the new dams have not significantly affected the carrying capacity of the park.

Fire is a natural part of the ecology of most plains habitats in East Africa and parts of the park were burnt every year, with the intention of preserving the plains habitat by burning small woody plants that appear to be part of the natural succession in this area. Fire has been almost entirely excluded from the park in the last three years. Warden Kearney

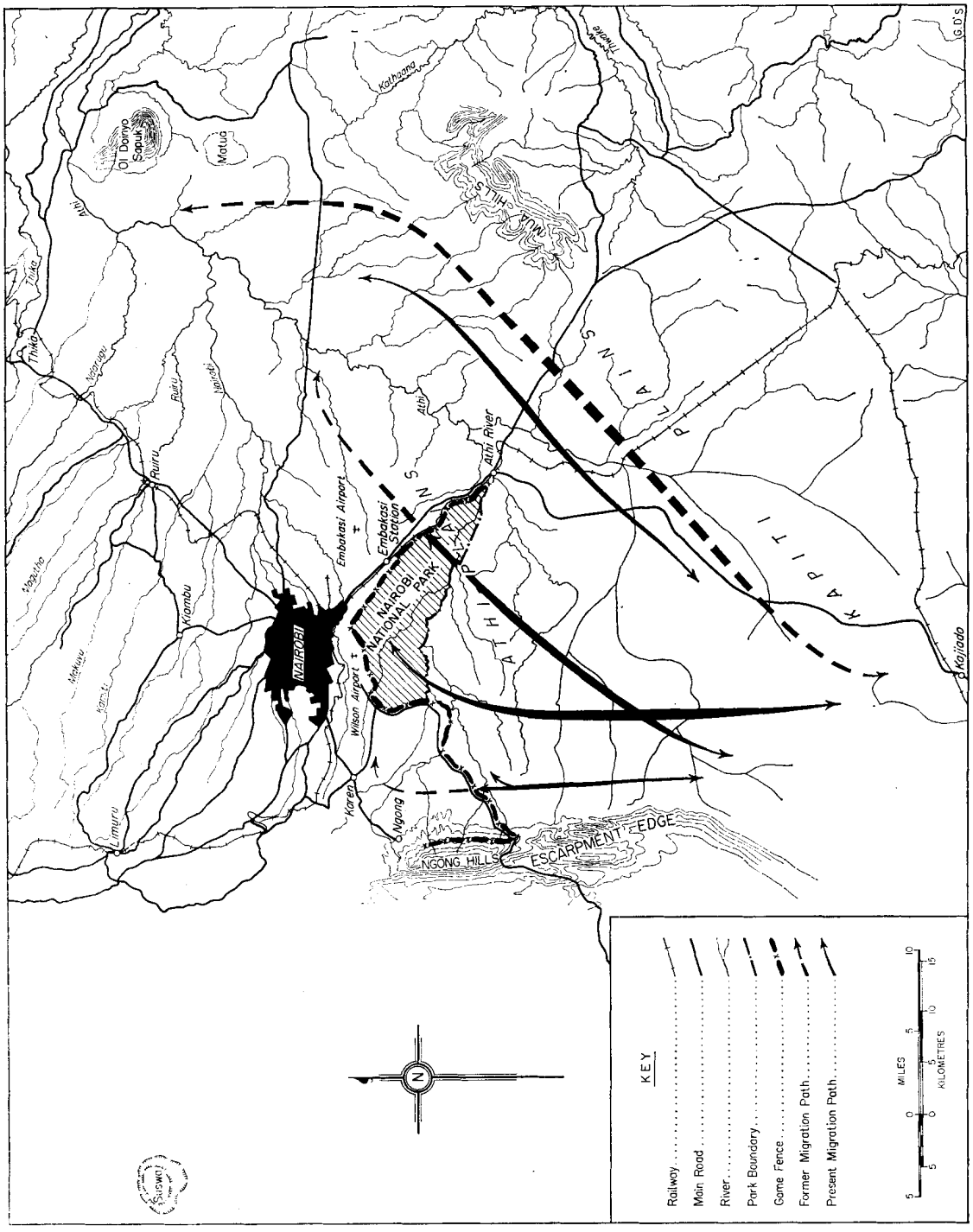

FIG. 1. Nairobi National Park.

mows the grass in a few important tourist areas in order to stimulate the growth of new grass thereby attracting plains game. Grass is kept short in some other areas by heavy grazing pressure. Elsewhere there is evidence that woody vegetation is increasing. This change in burning policy could well affect the area's carrying capacity but its affect is not as yet evident.

It is obvious that the park's fences, dams, and the recent absence of fire have created artificial factors in the habitat and these factors must be borne in mind in any discussion related to the consideration of the carrying capacity over many years. However it is felt that these changes have not been important in the time under consideration though in future years the absence of fire may render much of the habitat less suitable for plains game while the recent exclusion of the domestic stock (see below) could make part of the park more suitable.

The vegetation of Nairobi Park comprises three main types: an elevated western forested portion (1700–1800 m in altitude), open grassland (1520–1700 m) similar to a much larger area to the south of the park, and forested river beds which descend through steepening valleys to join the Athi River on the park's southern boundary.

Nairobi stands at the junction of the highland croton forest and the plains. The forest area (1000 ha) is a remnant of the former region and results from the higher precipitation on this elevated ground. The area is interspersed with open glades so that the actual forest covers only about 350 ha. It rests mainly on friable clay soils. The dominant tree species are *Croton megalocarpus*, *Schrebera alata*, *Brachylaena hutchinsii* and *Olea africana*. Many forest species display a sharp browse line at about 5·7 m as a result of heavy browsing by giraffe.

Almost half the park's total area is covered by grey or black generally neutral alkaline clays which are popularly known as "black cotton" soils. They are characterized by an impeded drainage and a fairly restricted plant community. The most conspicuous floral elements are the small tree *Acacia drepanolobium* or "whistling thorn", and four grass species: *Pennisetum mezianum*, *Bothriochloa insculpta*, *Themeda triandra* and *Digitaria macroblephara*.

Other open areas of the park are covered with reddish brown soils and include the following scattered trees: *Acacia gerrardii*, *A. seyal*, and *Balanites glabra*. The mature grasslands are characterized by *Themeda triandra*, *Bothriochloa insculpta*, *Digitaria macroblephara* and *Pennisetum mezianum*.

The riverine vegetation which bisects the plains is characterized by *Acacia kirkii*, *A. xanthophloea*, *Ficus spp*, and *Markhamia hildebrantii*. For greater detail of the vegetation of the park see Heriz-Smith (1962).

Methods

Members of the East Africa Natural History Society have censused Nairobi Park since July 1960. Weather permitting, this was carried out on the last Sunday of each month. No counts were made from April 1964 to December 1965. The counts were resumed in January 1966 and are still continuing. When the census was started in July 1960 the park was divided into ten areas. Some of the larger sections were later subdivided to produce a total of 15 counting areas. These were censused monthly by one or more observers in a vehicle. Counters started at 8.00 a.m. and usually finished by noon. They attempted to count, sex and age (newborn, subadult and adult) all individuals.

There is a possible source of error in counting a herd twice should it move across an area boundary during the count. It is assumed that over the period of a year the times an animal is counted twice in a census is cancelled out by the times it is not counted at all.

Those species for which the census is reasonably accurate have already been listed. Other game species are more difficult to count and the maximum number seen on a count over a year is probably more representative of the total population present than the average for the year. The following species fall into this category and are so treated in Table I: lion, *Felis leo* (Linnaeus); cheetah, *Acinonyx jubatus* (Schreber); reedbuck *Redunca redunca* (Pallas); *R. fulvorufula chanleri* (W. Rothschild); and bushbuck *Tragelaphus scriptus* (Neumann). The leopard *Felis pardus* Linnaeus population has been set arbitrarily at ten while black rhinoceros *Diceros bicornus* (Linnaeus) and hippopotamus *Hippopotamus amphibius* Linnaeus have been determined with the help of the warden. The numbers of cattle and sheep are fairly accurately known for 1966 but an estimate has been used for earlier years.

Other species, such as the smaller primates and carnivores, are almost impossible to census accurately, and since they contribute little to the total biomass of game animals, they have been omitted.

Results

Table I and Fig. 2 indicate the changes in numbers of game animals for the years 1961, 1962, 1963 and 1966. Data for 1960 and 1964 have been omitted as these years were only censused for three and two months respectively.

In converting numbers of animals estimated to be in the park to biomass of animals per unit area one encounters the problem of finding a suitable average weight for a member of a population of each species. Ideally this figure should take into account the number of young in the population but much work would be needed to determine this variable. Some weights given in the literature clearly refer to trophies (Meinertzhagen, 1938) and are not suitable for determining an average adult weight while others do not seem to adjust sufficiently for the young in the population. Where possible we have employed the figures given by Stewart & Zaphiro (1963) who follow Bourlière (1962) in which he makes the reasonable compromise of using the minimum adult weight for the population in determining biomass. In this way it is hoped that the overestimation involved in including immature animals may be approximately compensated for by the underestimation of older animals. A variety of authorities have been used when the species is not included by Stewart & Zaphiro (1963). Where there is a difference between two authorities we have accepted the lower figure so that our calculation of biomass is probably an underestimation. Should better weight figures become available, the biomass can readily be recalculated from the population figures.

Table I lists the biomass for each important species and the authority for deriving the biomass from the population count. Figure 3 illustrates the change in biomass over the years. By comparing Fig. 3 with Fig. 2, one can readily see how a relatively uncommon but heavy animal like the giraffe changes in apparent importance.

Simon (1962) obtained a peak of 12,775 kg/sq. km in Nairobi Park by considering only the last half of 1960 and the first half of 1961. The population was highest during this period and was the accumulative result of a long drought which began with poor rains before 1961 and the failure of the long rains (March to May) in 1961 (Fig. 4). The three plains species, zebra, wildebeest and hartebeest migrated into the dry season concentration

area of Nairobi Park reaching a peak in 1960. These species died in large numbers during the time up to and including the torrential rains in late 1961. At this time these species were in poor condition and their deaths have been attributed to their drinking large quantities of water without an accompanying increase in high quality forage (Payne, W. J. A., pers. comm.). The coincidence of this rain with the calving of wildebeest accelerated the crash in this species. A sharp decline in biomass continued into 1962 as the rains

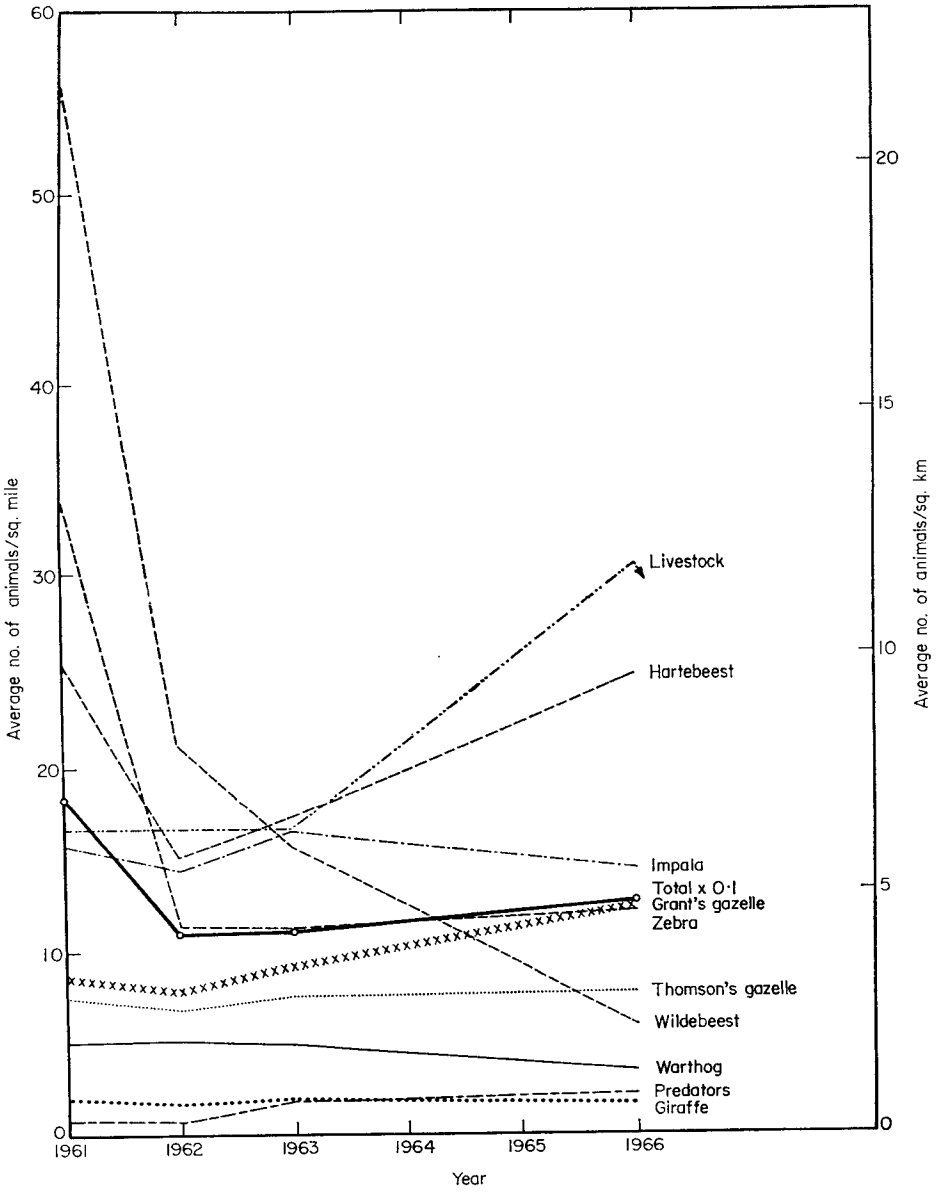

FIG. 2. The average number of large animals/sq. km in Nairobi National Park 1961–66.

TABLE I

The numbers and biomass of animals in Nairobi National Park 1961–66

Species	Adjusted weight (kg)	Reference	Average number of animals/sq. km 1961 10 counts	1962 11 counts	1963 7 counts	1966 10 counts	Mean 1962–66	Average biomass of animals kg/sq. km 1961 10 counts	1962 11 counts	1963 7 counts	1966 10 counts	Mean 1962–66
Baboon	17·3	Simon, 1962	1·54	1·49	1·58	1·44	1·51	26·4	24·5	27·1	24·9	25·9
Hyaena	49·9	Simon, 1962	0·04	0·04	0·13	0·10	0·09					
Lion	149·8	Simon, 1962	0·15	0·11	0·15	0·15	0·14					
Cheetah	49·9	Simon, 1962	0·04	0·03	0·05	0·09	0·05	31·3	26·6	36	36·6	33
Leopard	54·5	Lamprey, 1964	0·09	0·09	0·09	0·09	0·09					
Grant's Gazelle	49·9	Stewart & Zaphiro, 1963	3·32	3·03	3·49	4·36	3·63	163·9	150·9	174·1	217·4	180·8
Thomson's Gazelle	19·5	Simon, 1962	2·90	2·68	2·93	3·02	2·87	56·4	52·2	53	59	54·8
Waterbuck	149·8	Bourlière, 1962	1·15	0·40	0·58	0·79	0·59	172·2	59·5	69·7	117·8	82·3
Impala	45·4	Stewart & Zaphiro, 1963	6·08	5·54	6·40	5·55	5·93	275·6	251·1	290·2	251·7	264·3
Wildebeest	165·7	Stewart & Zaphiro, 1963	21·54	8·22	6·03	2·29	5·51	3552·5	1360·5	997·7	378	912·1
Hartebeest	136·2	Stewart & Zaphiro, 1963	9·90	5·82	6·67	9·58	7·36	1347·5	791·1	906·7	1303·8	1000·5
Eland	363·2	Stewart & Zaphiro, 1963	4·86	0·19	0·19	0·51	0·29	176·4	68·6	63·53	185·9	106·1
Bushbuck	54·5	Simon, 1962	0·25	0·19	0·28	0·22	0·23	13·8	8·6	14·7	11·9	11·7
Reedbucks	40·9	Simon, 1962	0·14	0·09	0·07	0·10	0·09	5·8	3·2	2·8	4·4	3·5
Buffalo	499·4	Lamprey, 1964	0·0	0·0	0·0	0·15	0·05	0	0	0	74·4	24·9
Cattle	277·0	Ledger, pers. comm.	2·93	2·93	2·93	7·88	4·58	639·8	638·8	638·8	1750	100·9
Sheep	15·9	Ledger, pers. comm.	3·50	3·50	3·50	3·93	3·64	55·7	55·7	55·7	62·7	57·9
Hippopotamus	181·6	Simon, 1962	6·054	0·054	0·054	0·056	0·054	94·5	94·5	94·5	94·5	94·5
Warthog	59·0	Lamprey, 1964	1·98	2·01	3·85	1·35	1·76	116·7	118·7	113·8	77·9	104·0
Giraffe	771·8	Lamprey, 1964	0·79	0·68	0·80	0·66	0·71	606·4	527·6	637·5	511·0	558·8
Zebra	238·4	Stewart & Zaphiro, 1963	13·01	4·38	4·27	4·29	4·31	3094	1047·6	929·3	1020·3	999·1
Rhino	998·8	Lamprey, 1964	0·035	0·035	0·035	0·14	0·069	35·0	35·0	35·0	140·0	70·0
Ostrich	113·5	Austin & Singer, 1961	0·87	0·87	0·78	0·81	0·82	99·4	99·4	89·3	92·8	94·0
Grand total			70·81	42·57	42·93	47·55	44·29	10564·2	5415·2	5229·2	6416·2	5686·8
Total excluding cattle and sheep			64·38	35·94	36·50	35·74	36·06	9869·8	4720·8	4534·8	4603·6	4619·7

encouraged some of those still alive to disperse into the Athi-Kapiti plains. Since 1961 the rains have approximated to the norm for the area (90·7 mm) and the biomass has remained constant from year to year at about 4550 kg/sq. km if the cattle and sheep are excluded.

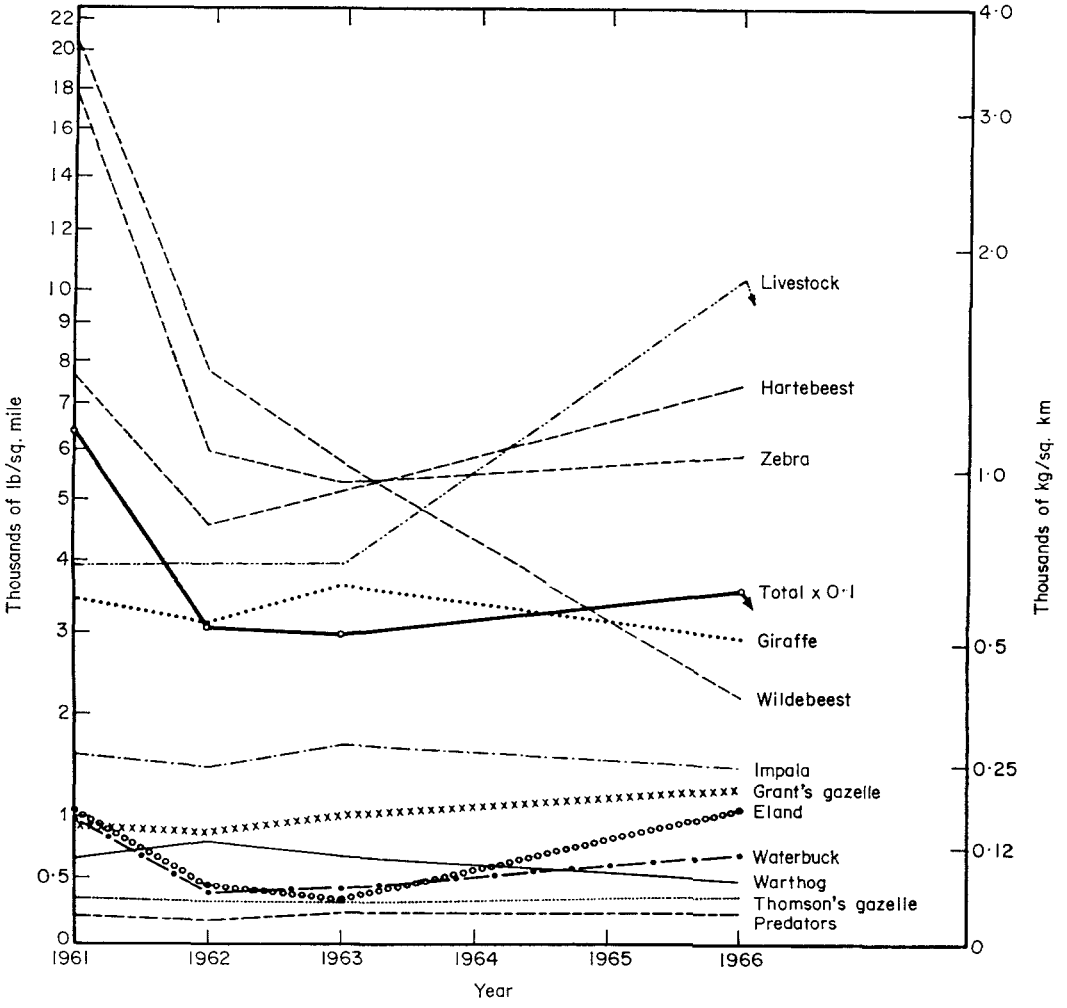

FIG. 3. The biomass of large animals/sq.km in Nairobi National Park 1961–66.

The Somali livestock have been present in the park since it was gazetted but by 1966 they had increased in biomass to where they were the most important species and contributed about 1750 kg/sq. km to the total biomass of 6300 kg/sq. km. However the livestock were confined to the south-west quarter of the park (areas 8 and 9) and their effect of grazing competition was restricted. In May 1967, all domestic livestock was removed from the park. It will be interesting to see if the wild ungulates take advantage of the increase in available food by increasing their own biomass.

The history of the three plains species since the drought is strikingly different. Hartebeest have continued to increase and may well prove to be the first species to take advantage of the removal of cattle. Zebra have remained remarkably constant on a yearly basis but show the greatest monthly fluctuations due to migration in and out of the park. In 1966 there were 154 animals recorded at the end of the rains in May and 1664 in October at the

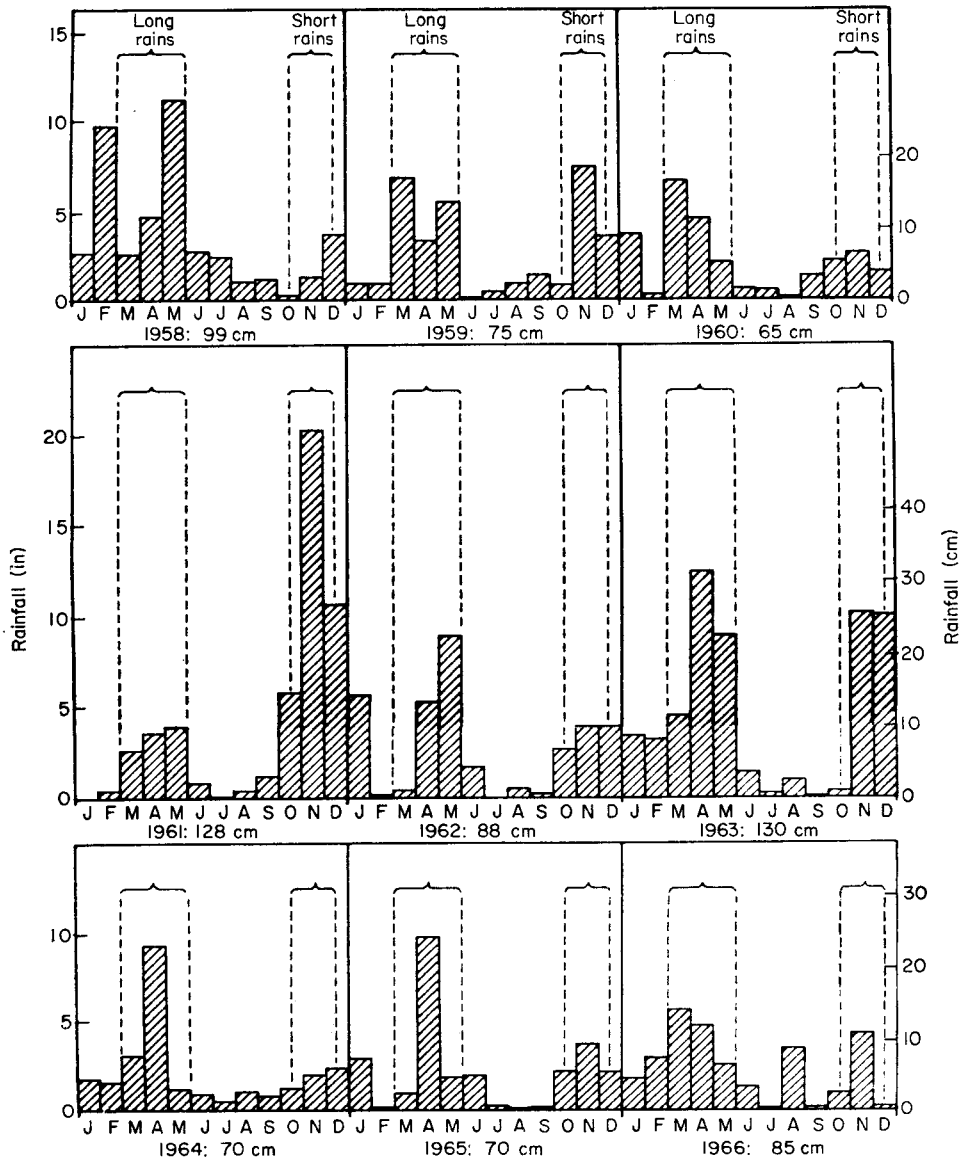

FIG. 4. The rainfall in Nairobi National Park 1958–66. Data are the average of records taken at Wilson and Embakasi airports.

end of the long dry season. Wildebeest have continued to decline. The reasons for this phenomenon have been discussed in detail elsewhere (Foster & Kearney, 1967) and include the possibilities of disturbance along the migrating paths of wildebeest, of fire having been mostly excluded from the park since the drought, of interference by the cattle and of the lion having a distinct prey preference for this species.

Discussion

Table II compares the biomass of various areas with a variety of ungulates. Ideally one is comparing the carrying capacity in each case but often the biomass expressed may be closer to the maximum rather than the optimum. In such cases one would expect to find overgrazing and/or overbrowsing. However, it is not possible to assess this over a short period unless the condition of the habitat is extreme. Without detailed vegetational analysis it is easier to detect that an area is heavily grazed than overgrazed. The woody vegetation of Nairobi Park, for example, shows heavy use by giraffe but it is not easy to show that it is over-utilized. The fact that the biomass of giraffe has remained constant for at least six years suggests that they may be in balance with their food supply. Similarly the grass near the Somali dwellings was heavily grazed by cattle while other short grass areas are heavily grazed by game. The latter areas, however, are not necessarily overgrazed and they may merely represent a vegetation catena formed as a result of the grazing succession of the ungulates.

Thus when comparing the biomass of ungulates on different areas, it is necessary to realize that while some areas may be understocked, others are overstocked. The later tendency is increased by the fact that workers may tend to select areas with a large biomass.

The authors believe that the population of ungulates in Nairobi Park at present is close to the carrying capacity of the habitat under existing climatic conditions; and it was probably double the carrying capacity during the drought.

The removal of domestic stock and the control of fire will possibly raise the carrying capacity of the area in which domestic stock and wild ungulates competed for forage.

Table II indicates that the biomass of Nairobi Park (6300 kg/sq. km) is of the order one would expect in the acacia savanna habitat of East Africa. Some areas (e.g. Bourlière & Verschuren, 1960) have a far greater biomass but these may represent examples of overstocking, though differences in climate, and habitat make comparison difficult.

Domestic stock in Africa and North America rarely approach the biomass for the mixed herds of Nairobi Park and never near the 12,775 kg/sq. km found by Lamprey (1964) in the Tarangire Reserve of Tanzania.

The explanation for the apparent superiority of the indigenous herds is generally thought to be that they have evolved food preferences that to a large degree eliminate competition (Talbot, 1963). Domestic stock, however, have had insufficient time to become adapted to their environment so that their food preferences largely overlap that of game species and one another (Heady, 1960). These assertions have yet to be proved conclusively.

The biomass of large predators is only 1·4% of the total biomass of wild ungulates. Lamprey (1962) calculated that in the Tarangire Game Reserve lions removed 10% of their prey species per annum. Coe & Foster (in press) have attempted to calculate the percentage of the total average biomass of game species removed by lion and cheetah each year in Nairobi Park. They concluded that these two predators remove at least

TABLE II

A comparison of the biomass of large mammals from different areas

Location	Habitat	Area (sq. km)	Species	Biomass (kg/sq. km)	Reference
Nairobi Park	Mostly open plains	114·8	Wild and domestic ungulates	5250–12,600 over 6 years carrying capacity about 6300	This study
Nairobi Park	Mostly open plains	114·8	Wild and domestic ungulates	8225 one census	Petrides (1956)
Tarangire G.R., Tanzania	Open Acacia savanna	1683·5 entire area	Wild ungulates	1050 yearlong	Lamprey (1964)
Tarangire G.R., Tanzania	Open Acacia savanna	31 Dry season concentration	Wild ungulates	12,300 average of 4 years	Lamprey (1964)
Ngorongoro Crater, Tanzania	Grassland	310·8	Wild and domestic ungulates	6125 resident population	Lamprey (1964)
Serengeti Plains	Grassland and acacia savanna	16,835	Wild ungulates	6300	Stewart & Talbot (1962)
East Africa	Savanna, tribal grazing land	—	Domestic stock	1960–2800	Talbot & Talbot (1963)
East Africa	Managed European ranches	—	Cattle	3728–5600	Ledger, Payne & Talbot (1961)
Albert N.P. Congo	"Steppe"	—	Wild ungulates	7574 and 20,469 two areas	Bourlière & Verschuren (1960)
Western U.S.A.	Average of all virgin ranges	2,917,635	Domestic stock	3448	Watts, Stewart, Connaughton, Palmer & Talbot (1963)
Western U.S.A.	Prairie	—	Bison and other wild ungulates	2450–3500	Petrides (1956)

15·5% of the total biomass per annum (13·7% lion, 1·8% cheetah). This amounts to the removal of about 700 kg/sq. km/annum and probably represents what man could take in a cropping programme in the absence of predators.

It is clear that if one excludes practical difficulties, there could be a greater potential in harvesting wild game than domestic stock in semi-arid regions of East Africa.

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