POPULATION DENSITIES AND THE RANGE-CARRYING CAPACITY FOR LARGE MAMMALS IN QUEEN ELIZABETH NATIONAL PARK, UGANDA

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The highest known densities of large terrestrial mammals occur on the grasslands in the western arm of the Rift Valley, in western Uganda (Petrides and Swank 1958, Petrides 1963) and the eastern Congo Republic (Bourlière and Verschuren 1960, Bourlière 1963).

While prehistoric environments no longer exist, the plant and animal assemblages present in parts of East Africa, and in a few other regions of the African continent, provide as close a resemblance to Pleistocene conditions as it is now possible to experience. With increasing human populations and expanding industrialisation, the historical value alone of such areas, as examples of conditions now generally gone, is great. There is an indication here, too, that biological productivity may be far higher here than for most cultivated animal-plant communities and that the possibilities may indeed be great for a high economic return from wildlife husbandry and wild animal-viewing on selected lands in East Africa (Petrides 1955, 1956, Darling 1960, Riney 1960, Huxley 1961, Talbot 1963, Dasmann and Mossman 1960).

During the period October 1956 to June 1957, the authors were engaged in ecological research on big game populations in Queen Elizabeth National Park, Uganda, East Africa, under Fulbright research grants. Dr. William Gaines and Geoffrey Watt, United States Educational Commission in the United Kingdom, London, were most helpful in making the many necessary administrative arrangements. An additional grant toward travel expenses was supplied by the Conservation Foundation and New York Zoological Society through the co-operation of Dr. Fairfield Osborn. Dr. Harold J. Coolidge, National Research Council, was instrumental in the establishment of the project. In Uganda all possible assistance was given especially through the good offices of the Honorable R. L. E. Dreschfield, R. M. Bere, Capt. F. Poppleton, and the trustees of the Uganda National Parks; Major B. G. Kinloch, then Chief Game Warden, Uganda Game and Fisheries Department; Dr. A. J. Haddow of the Virus Research Institute; Prof. L. C. Beadle of Makerere College; and C. Swabey of the Forest Department. George H. Petrides assisted in the collection of field data.

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STUDY AREAS

Queen Elizabeth National Park is a tract of about 750 square miles located in extreme south-western Uganda, at the Congo Republic border. The vegetation tends toward a fire-influenced

Themeda-Acacia community, but over wide districts of the park overgrazing is evident with resultant degraded vegetation (Table 2) and eroded soils (Table 4). Overgrazing is induced primarily by the abundant hippopotamus *Hippopotamus amphibius* population present, as reviewed in an earlier paper (Petrides and Swank 1958). Hippos were abundant during the day in Lakes Edward and George and in the Kazinga Channel which connected the two lakes. These were the major bodies of water in the park. Hippos also occurred in a number of pools and wallows inland from the main bodies of water. Ranging out from their daytime haunts, at night the hippos grazed the surrounding territory. The intensity of grazing decreased gradually, but overgrazed areas occurred up to five miles from the major waters.

Two of the study areas which were selected in the park gave evidences (see beyond) of being severely overgrazed. One of the seriously overgrazed areas was a narrow-necked peninsula of 2·1 square miles. It was almost an island. The other heavily eaten tract adjoined the base of the peninsula and was 9·0 square miles in area. Both these plots were bounded by Lake Edward and the Kazinga Channel.

For comparative purposes, an apparently undergrazed area of dense knee-high grasses and an area which showed an intermediate degree of grazing intensity were chosen. The latter area, after study, was judged to be moderately overgrazed.

The moderately overgrazed study plot was 5·6 square miles in extent. It was located in a central portion of the park, lying mostly over two miles from both the Kazinga Channel and an arm of Lake George. The undergrazed area of 11·8 square miles lay in the crater area of the park, which afforded many panoramic views of the plot.

The most open country was in the undergrazed grassland of the crater area. The density of shrubs and of low candelabra euphorbia trees on the lands under study thickened with increasing overgrazing (Table 2).

CENSUS METHOD

Direct and complete counts of the "game" present were made from a Land Rover vehicle driven over the rangelands. Patterns of coverage were developed so that on the 9·0 square mile area, for example, travel of 65 miles or more was involved during a wildlife census. The authors and an African game scout normally comprised the census crew. Binoculars were used and high grounds were utilised for lookouts. The effort was made to tally all animals by sex, herd size, and location (Petrides and Swank, unpublished). Indications of relative age also were noted by classifying all individuals either as adults or as quarter-, half- or three-quarters-grown.

The upland censuses were begun in early morning and continued from about 6.30 a.m. until about noon. On some occasions, unusually high numbers of wild animals required extension of the survey until 2.00 or 3.00 p.m.

Errors in seeing animals on open grasslands are believed to have been few. The gregarious nature of most species and their usual avoidance of dense brush made most animals reasonably evident upon careful examination of the terrain. Many could be approached rather closely by car. In patches of thick bush, some animals may have been missed, but efforts were made to cover these areas carefully. Unusually difficult places were surveyed on foot.

Most of the ungulate species of this study tended to avoid the bush. The bushbuck *Tragelaphus scriptus* was an exception. Woody vegetation was its chosen habitat. In an experiment, exploding firecrackers were thrown near observed bushbuck and the animals failed to move. It seemed that only when they thought themselves in view did they become startled. Of all species, this was the only one whose total numbers are considered to be possibly subject to any considerable error. Special censuses were conducted at dawn and at dusk on the peninsula and in other areas where observations and signs gave evidence of exceptional bushbuck activity. Any errors due to failure to observe animals, however, would result in underestimates rather than overestimates of abundance so that the population data reported here are at least minimal.

Because of the large areas and long census periods involved, some movements of animals occurred within the areas and across their borders. Movements during census periods, however, were never general and were usually evident from the noted characteristics of the individuals and herds counted. It is believed that census errors due to animal movements were small ones. Rainy periods, incidentally, did not prevent cross-country travel in this locality.

Hippos were concentrated in the waters which surrounded the peninsula area and which bounded the mainland seriously overgrazed area on two of its four sides. Observations indicated that these animals normally went ashore at points near their daytime locations. Main hippo trails mostly led directly inland.

Hippos were counted in the major bodies of water mostly from a motor launch. Moving slowly, the boat would be halted when a herd was sighted ahead. Then, using binoculars, counts would be made repeatedly until a maximum number of individual heads (or eyes) had been tallied. It was assumed that this number represented the size of the total group. Repeated counts of selected herds were undertaken from shore for several hours at a time and tended to confirm the suitability of the method.

It was believed that all hippos along the shore of the peninsula grazed within that study plot. Hippos very rarely were seen in the daytime to move away from the peninsula across the channel to park lands outside the study. But such occasions were very few and probably were balanced by individuals moving in the opposite direction. The extent of nocturnal movements of this type could not be determined, but observations at night yielded no evidence of this type of activity by hippos.

On the mainland seriously overgrazed area, a check on the launch counts was provided by counts of hippo tracks which crossed the primitive motor-vehicle roads encircling the perimeter of the area. On several occasions, heavy afternoon thunderstorms washed out all old animal tracks on these roads. Counts then were made early the next morning. The total number of individuals entering and leaving the area, on the several occasions when conditions were suitable, was in good agreement with the numbers of hippos counted along the nearby shorelines. On each area the inland pools and wallows were located and the hippos therein counted in conjunction with the regular censuses.

Major censuses were undertaken monthly, with additional tallies being made as circumstances dictated. The launch surveys were at longer intervals.

UNGULATE POPULATION DENSITIES AND BIOMASSES

The animal censuses were taken to represent the ungulate populations present on each area during the period nearest that census date. The average number of animals per day was determined for each species and converted to a square-mile basis for each study area (Table I). In compiling estimates of the total average biomasses present on each area (Table I), the data for the numbers and weights of each sex and size class were computed separately and then combined.

RANGE CONDITIONS

Species composition, relative forage production, and erosion characteristics were determined (Tables 2, 3 and 4 respectively) for the range vegetation of each of the several study areas. The relative food preferences of the collective herbivore community for the important forage grasses also were appraised (Table 5). To determine these factors, a survey method was adopted

TABLE 1: AVERAGE POPULATION DENSITIES OF LARGE MAMMALS PER SQUARE MILE IN QUEEN ELIZABETH NATIONAL PARK, UGANDA (based on monthly censuses during November 1956–May 1957)

	Lightly grazed area	Moderately over-grazed area	Heavily over-grazed area		Approximate average weights (pounds)*
Size of area (sq. miles)	(11·8)	(5·6)	(9·0)	(2·1)	
Elephant	3·8	3·7	8·7	4·5	5,000†
Hippopotamus ..	2·9	1·8	38·5	44·8	3,000
Buffalo	32·0	47·2	10·4	9·6	1,000
Waterbuck	0·6	1·6	8·7	9·5	450
Kob	0·3	47·8	1·2	0	150
Bushbuck	0	0·1	1·4	7·8	100
Reedbuck	0·1	0·3	0	0	100
Warthog	0·1	2·2	6·9	19·7	175
Duiker	0	0·1	0·1	0	40
Total Numbers ..	39·8	104·8	75·9	95·9	
Biomass (pounds)‡ ..	56,100	69,200	160,500	182,000	

* Nocturnal use of this area by hippos could not be calculated and is omitted; total biomass supported doubtless was higher than indicated.

† Data of Buss (*in litt.*) are in close agreement with more recent analyses (Petrides and Swank, unpublished) and indicate that this figure is more appropriate than the 7,000 pound weight of Petrides (1963). Biomass totals are reduced correspondingly.

‡ Biomass data were summarised from detailed tallies of animals classed by sex and size classes as well as by species.

which was a modification of the line-point transect technique combined with clip-plots.

The vegetative survey method adopted was patterned basically after one of Osborn (1947). His technique was established for "use by field men who must make quick appraisals of large areas of (both grassland and brush) range . . . within a short season". It involved the representative sampling of vegetation by pacing along parallel routes through the vegetation, "stopping at regular intervals and recording the species and degree of use of one or more plants nearest the toe of the right foot". Because of the large areas to be sampled and the short time available, his system was modified to use a Land Rover and to determine not only the vegetative composition and degree of forage use, but also to appraise the amount of standing forage and the extent to which the soil was exposed to erosion.

Using two persons, one with a stop-watch, the vehicle was driven along straight lines. After every 15 seconds of driving at 15 miles per hour, a stop was made. This placed the stops about 330 feet apart or 16 stops per mile of travel. Where bush was encountered on the line of travel, sample "spot-plots" were located by pacing.

Each observer had a stiff wire several feet long, with one end bent into a circle $\frac{3}{4}$ in. in diameter. This diameter is the same as is used in the three-step method of range survey (Parker 1954). The wires were held against the outside edges of the forward and rear bumpers in a standardised and unbiased manner, with the loop touching the underlying vegetation or substratum. If vegetation was "hit" within the loop, the species was listed and the degree of grazing was recorded as "full", "partial", or "none". Otherwise, the type of exposed ground surface was noted (as in Table 5).

The number of plants grazed was computed (Table 5) as prescribed by Osborn (1947), adding half the number of those partially grazed to the number of those fully grazed. Vegetation was not encountered by the sampling device at each stop, of course. Also, even when vegetation was "hit", it was not always a grass (Table 2). On the severely overgrazed area, therefore, the "nearest plant" was tallied at each fifth stop in order to increase the size of sample for grass species (Table 5).

Supplementing the random spot-plots, every tenth spot was taken as the centre of a circular 0·001 acre plot on which grasses and forbs were clipped to the soil surface. Woody twigs up to a diameter of one-quarter of an inch also were taken to a height of six feet from shrubs in such plots. The collected clippings from each plot were divided into categories of grasses, forbs, and woody plants, placed by plots in marked paper sacks, and air dried until weight losses terminated. From the clip-plots additional data were collected on species composition of the vegetation and especially on the total average biomass of above-ground vegetation on the area (Tables 2 and 3).

Striking qualitative differences in vegetative characteristics also were evident on the study areas as a result of variation in grazing intensity. The major differences in general aspect between study areas have been described. Among obvious signs of intensive use on the several overgrazed study areas, however, were:

1. Excessively high rates of utilisation and evident rapid destruction of the dominant grasses, especially *Themeda triandra*, *Hyparrhenia filipendula*, and *Heteropogon contortus* (Tables 2 and 5).

TABLE 2: PERCENTAGE COMPOSITION OF RANGE VEGETATION FOR AREAS WITH DIFFERENT GRAZING INTENSITIES, QUEEN ELIZABETH NATIONAL PARK, UGANDA, 1957

	Undergrazed Area	Moderately overgrazed area		Seriously overgrazed area
Dates of surveys	June 1–3	May 21–23	Feb. 26–28	March 20–30
Numbers of plots	30*	30*	600†	710†
Grasses:				
Themeda triandra ..	42·3	7·2	10·0	0·4
Hyparrhenia filipendula ..	24·3	13·4	8·9	
Cymbopogon afronardus ..	8·0			
Heteropogon contortus ..	4·7	16·0	14·2	
Hyparrhenia dissoluta ..	4·3			
Imperata cylindrica	3·3	5·8	0·5	
Sporobolus pyramidalis ..	2·8	5·9	7·9	12·9
Bothriochloa insculpta ..	2·3	3·0		1·2
Sporobolus stapfianus.. ..	2·0	18·6	45·9‡	7·8‡
Michrochloa abyssinica ..		72·7		
Hyparrhenia rufa	1·0			
Digitaria gazensis	1·0			
Chloris gayana	0·7	3·9	2·1	0·8
Brachiaria decumbens.. ..	0·5	10·0	2·1	8·2
Panicum maximum	0·3		1·1	
Eragrostis racemosa				4·3
Tragus berteronianus				6·6
Cynodon dactylon				2·3
Axonopus flexuosus				3·5
Chloris sp.				3·1
Bothriochloa radicans.. ..		3·3		1·2
Cenchrus ciliaris				1·2
Chloris virgata				0·4
Setaria sphaceolata		2·5		
Unidentified			1·6	0·8
Total grasses	97·5	92·3	94·3	54·7

Forbs:				
Indigofera spp...	2·5	0·8		0·8
Other non-grass herbs§ ..		2·2	0·5	31·2§
Woody plants:‖				
Capparis tomemtosa		3·9	3·7	6·6
Maytenus buxifolius				2·3
Acacia spp.				1·2
Cissus quadrangulata				1·2
Euphorbia candalabra ..		0·3	0·5	0·8
Grewia similis				0·8
Tarrena viridula				0·4
Flueggea virosa		0·5	0·5	
Craterostigma plantagineum ..			0·5	
Totals	100·0	100·0	100·0	100·0

* Percentages by volume as determined by clip-plot analysis for the two surveys in May–June.

† Percentages by frequency for the two surveys in February–March. On the seriously overgrazed areas the nearest plants also were tallied on every fifth observation whenever bare ground was "hit" (see text). "Nearest-plants" and vegetation "hits" are combined here for that area.

‡ *Microchloa abyssinica* was not identified until it flowered later in the year. Doubtless, it was included with *Sporobolus stapfianus* during the dry-season surveys. Clipping studies on the moderately overgrazed area in May, revealed that *Microchloa* comprised 40 per cent of the combined two species then.

§ The following non-grass herbs were tallied. None showed signs of grazing. Many forbs may have been removed completely by elephants which kick them loose, and by hippos which plucked them with their sharp-edged lips. Other ungulates too may utilise complete plants so that signs of grazing are absent. The species and their relative numbers were: *Alternanthera repens* (23), *A. sessilus* (1), *Boerhaavia coccinea* (8), *B. stillata* (2), *Corbichonia decumbens* (18), *Cyperus obtussifolia* (1), *Eclipta prostrata* (1), *Evolvulus mummularius* (2), *Fortulaca quadrifica* (9), *Ruellia patula* (1), *Sida ovata* (3), *Tephrosis* sp. (3), *Tribulus terrestris* (4), unidentified (4).

‖ Only browse available within six feet from the ground was considered. None of the sampled woody plants showed signs of browsing.

2. The increase of those species typical of eroding ranges, including *Sporobolus pyramidalis*, *Brachiaria decumbens*, and *S. stapfianus* (Table 5).

3. The heavy utilisation of these last species despite their relative unpalatability (Table 5).

4. Invasion of the remnant grasslands by shrubs, and their dominance on many overgrazed lands.

5. The high proportion of bare ground unprotected even by overhanging vegetation (Table 4).

6. The measurable uphill extensions of severe erosion gullies (Petrides and Swank, unpublished).

7. The occurrence of remnant basal clumps of dominant bunch grasses, which showed only a centre of bare ground and a surrounding fringe of closely grazed and dying stubble.

8. The occurrence of considerable areas of grass stubble less than an inch long at the end of dry seasons.

9. The failure of grass fires to penetrate the study tract except in minor locations, because of lack of fuel.

DETERMINING THE CARRYING CAPACITY

The carrying capacity of an area is the maximum number or mass of organisms which can be sustained by the environment for an indefinite period. The carrying capacity varies according to the species supported. While often measured in animal numbers per unit area, a better expression of carrying capacity probably is the total weight, or biomass supported. When grazing animals are not controlled by other factors, the carrying capacity of an area is attained when forage for the animal population is produced and consumed at a rate which is the highest that that environment can sustain for a prolonged period.

In this study it was obvious that the undergrazed study area of 11·8 square miles produced far more forage than its animal inhabitants consumed. The 56,100 pound average living biomass of all grazing animals per square mile* on this area, therefore, was a minimum figure in terms of the total weight of large grazing mammals which could be supported on a stable basis by such a *Themeda-Hyparrhenia* vegetative community. In the opposite direction, it was equally apparent that the two seriously overgrazed study areas could not permanently maintain their high average biomasses, which approached 200,000 pounds per square mile.

The study tract which evidently came closest to maintaining a permanent balance between the vegetation produced and that consumed was the moderately overgrazed area. Its rate of degradation and its condition were considered to be not so serious as prevailed on the more barren and gullied seriously overgrazed areas, but it was decidedly overgrazed as indicated by the symptoms listed above.

The average biomass computed for this area was only 69,200 pounds per square mile. This was not much higher than that computed for the 11·8 square mile area whose thick grassy cover (Table 3) was much undergrazed, but the moderately overgrazed area was several

* Metric conversions: Multiplying by 259 converts square miles to hectares; multiplying by ·00175 converts pounds per square mile to kilograms per hectare.

miles from the Kazinga Channel where numerous hippos spent their days. From their signs on the moderately overgrazed tract and from viewing them at night there with spotlights, however, they obviously grazed in the area to a greater extent than was indicated by daytime tallies. Censuses of the Channel shore, unfortunately, were of little value in this instance because of the uncertain routes of the hippos ashore at a distance from the water. Nocturnal censuses on lands also were tried and discontinued as impractical. Their numbers were not easily determined but it was apparent that a considerably greater hippo biomass utilised the area than was recorded.

The actual average biomass per square mile supported by the moderately overgrazed study area was judged to be certainly over 100,000 pounds per square mile and probably at about the 130,000–140,000 pound level. The biomass carrying capacity of *Themeda-Hyparrhenia* grassland which was properly grazed was estimated to be, then, between the approximate 56,000 and 135,000 pound square-mile biomass figures computed above. It was judged to lie above but close to the 100,000 pound level.

TABLE 3: FORAGE WEIGHTS IN POUNDS PER ACRE AS RELATED TO GRAZING INTENSITY OF BIG GAME, QUEEN ELIZABETH NATIONAL PARK, UGANDA, 1957

Study area*	End of season	Grasses	Forbs	Woody Plants	Totals†	General area characteristics
Undergrazed (30)	Rainy, June 1–3	4,231	47	*Trace*	4,278 ± 389	Dense grasses
Moderately overgrazed (30)	Rainy, May 21–23	1,244	29	73	1,346 ± 520	Fire limited; shrubs invade
Moderately overgrazed (30)	Dry, Feb. 26–28	436	4	‡	513 ± 106	
Severely overgrazed (66)	Dry, Mar. 20–30	382	153	194	729 ± 133	Advanced shrub invasion
Apparent utilisation of vegetation on the moderately overgrazed study area during the grazing season:						
Pounds		808	25	—	833	
Percentages		65	85	—	62	

* Number of clip-plots is indicated.

† The comparable totals as printed in Petrides (1962) are somewhat in error. Variation is shown here as one standard error.

‡ Woody plants were not clipped.

TABLE 4: PERCENTAGE FREQUENCIES OF SOIL SURFACE AND EROSION CHARACTERISTICS, AS RELATED TO THE GRAZING INTENSITY OF LARGE WILD MAMMALS, QUEEN ELIZABETH NATIONAL PARK, UGANDA, 1957*

Study areas	Undergrazed area†	Moderately overgrazed area‡	Severely overgrazed area‡
Total spot-plots	158	600	710
Type of soil surface:			
Erosion pavement	0	6·1	50·8
Bare soil	51·3	45·5	19·6
Termite mounds, game trails, rocks, hippo wallows and pools ..	0	2·1	1·5
Litter	24·6	14·6	10·6
Vegetation	24·1	31·7	17·6
	100·0	100·0	100·0
Protection of soil:			
Plots non-vegetated but protected by litter or overhanging vegetation	72·1	15·7	17·0
Bare ground, neither littered, vegetated, nor overhung by vegetation	3·8	52·6	65·4
Vegetation	24·1	31·7	17·6
	100·0	100·0	100·0

* Sizes of areas and dates of surveys are as given in Tables 1 and 2.

† Early rains prevented cross-country travel in the undergrazed area until the beginning of the following dry period. The long grasses in the undergrazed area, however, provided a thick protective canopy of soil cover at all seasons, despite their bunch-grass growth habits. Considerable bare ground was exposed between grass tussocks there after fires, but no serious erosion was seen which might have been induced by burning.

‡ These areas were studied at the end of a dry season. Most grasses were in a short stubble stage.

§ The peninsula severely eroded area was not sampled in this survey but was contiguous with and similar to the mainland severely overgrazed area surveyed here. It is estimated that the peninsula area (2·1 square miles) showed even more eroded and bare ground.

TABLE 5: CONSUMPTION OF AND RELATIVE PREFERENCES FOR FORAGE GRASSES EATEN BY WILD MAMMALS, QUEEN ELIZABETH NATIONAL PARK, UGANDA, 1957

Grass species	Random frequencies of plants sampled*		Numbers grazed†		Percentages consumed‡	
	(1)	(2)	(1)	(2)	(1)	(2)
Panicum maximum	2	2	2	2	100·0	100·0
Hyparrhenia filipendula	17	17	15·5	15·5	91·2	91·2
Themeda triandra	19	20	17	18	89·5	87·5
Heteropogon contortus	27	27	22·5	22·5	83·3	83·3
Chloris gayana	4	6	4	4	100·0	66·7
Sporobolus pyramidalis	15	48	11·5	23	76·7	47·9
Eragrostis racemosa	0	11	0	4·5	0	40·9
Bothriochloa insculpta	0	3	0	1	0	33·3
Brachiaria decumbens	4	25	2	7	50·0	28·3
Tragus berteronianus	0	17	0	3	0	17·6
Cynodon dactylon	0	6	0	1	0	16·7
Sporobolus stapfianus	87	107	14	15	16·1	11·7
Axonopus flexuosus	0	9	0	1	0	11·1
Unidentified grasses	3	5	1·5	1·5	50·0	30·0
Grasses not grazed§	1	16	0	0	0	0
Totals	179	319	86	118	48·0	37·0

* Numbers of plants sampled by the spot-plot method, see text.

† Numbers of the plants sampled which were fully grazed or equivalent (see text). These data also indicate the relative frequencies of the several plant species in the collective diets of the grazing mammals.

‡ Constituting the relative forage preference values by plant species for the mammal consumers collectively.

§ These species and tallied frequencies were *Imperata cylindrica* (1), *Bothriochloa radicans* (3), *Cenchrus ciliaris* (3), *Chloris* spp. (8), and *Chloris virgata* (1).

(1) Data for the moderately overgrazed area, February 26–28.

(2) Data for the moderately overgrazed and seriously overgrazed areas combined February 26–28 and March 20–30.

TABLE 6: WET WEIGHTS OF SOLID RUMEN CONTENTS, IN POUNDS, FOR INDIVIDUAL ANIMALS, QUEEN ELIZABETH NATIONAL PARK, UGANDA, NOVEMBER 1956–JUNE 1957

Species	Adults		Young animals*	
	Males	Females	Three-quarters grown	Half grown
Hippopotamus	291,311	552		59
Buffalo	234,181	145		56
Waterbuck	50	28, 30, 32	31	19
Kob	19, 21	18		14
Bushbuck	4, 4,		3	
Warthog	5, 3, 2	1	1	1

* No quarter-grown animals were collected.

TABLE 7: ESTIMATED DAILY CONSUMPTION OF FORAGE IN POUNDS OF DRY WEIGHT PER SQUARE MILE, BASED ON STOMACH CONTENTS AND POPULATION DATA, QUEEN ELIZABETH NATIONAL PARK, UGANDA, NOVEMBER 1956–JUNE 1957

Species	Stomach contents wet weight*	Stomach contents dry weight†	Estimated daily dry consumption‡	Average population§	Population consumption
Elephant ..	—	—	50‡	4	200
Hippopotamus	400	80	40	30?	1,200
Buffalo ..	150	26	13	47	611
Waterbuck ..	40	7	3·5	2	10
Kob	15	2	1	48	48
Bushbuck ..	3	1–	0·5	—	—
Reedbuck ..	(3)	1	0·5	—	—
Warthog ..	2	1–	0·5	2	1
Duiker ..	1	¼	—	—	—
Total daily consumption of dry-weight forage, in pounds					2,070

* See Table 6.

† Based on comparisons of wet and dry weights; samples varied by species.

‡ Estimated at 50 per cent of the stomach contents' weight (Annison and Lewis, 1959). For the elephant, this value was determined from measurements of excretions, see text.

§ Per square mile; figures rounded from those of Table I.

TESTING THE VALIDITY OF THE CARRYING CAPACITY ESTIMATE

To appraise the accuracy of the biomass carrying capacity estimate for the *Themeda-Hyparrhenia* grassland, three methods of checking were tested:

Clip-plot Surveys

Data permitting the estimation of forage removed during a grazing season fortunately was more complete for the moderately overgrazed study area than for the other tracts (Table 3). Yet mainly because of the dates of study, it was necessary to undertake the clip-plot measurements in opposite order to that which would have been desirable. The first collections were made February 26–28 when only stubble remained after a two-month dry* grazing period. Full growth of the range grasses then occurred during the subsequent three-month rainy season, and the second survey was made May 21–23.

On the basis that 808 pounds per acre of dry-weight grass forage were cropped during the grazing season (Table 3) and assuming that this removal was due entirely to feeding by large herbivores, 517,120 pounds of grasses were thus consumed per square mile. This comprised 65 per cent of the grown stand of green forage.

It has been computed (Stoddart and Smith 1943: 162) that a 1,000-pound domestic steer requires about 20 pounds of dry forage per day. Whether these figures are applicable to East Africa's large herbivores has not been determined. If it can be assumed that within reasonable limits they do apply, however, then there was forage enough consumed on the moderately overgrazed area to account for 25,856 animal-days per square mile. All the forage eaten was not measured because, in particular, there was unmeasured sprout growth which followed grazing that occurred during the growing season. But even disregarding this factor and assuming that the forage missing represented all that was eaten during the pair of wet and dry seasons, which comprised a half year (182 days), 142 cattle or 142,000 pounds biomass could have been supported on each square mile.

As a general rule in temperate-zone range management (Stoddart and Smith 1943), 50 per cent of forage grasses can be removed annually by grazing without harm to the range. In Uganda, there are normally two dry and two rainy seasons each year. The present study involved range measurements during only one pair of wet and dry seasons. On the moderately overgrazed study tract, it was apparent that removal of 50–60 per cent (see also beyond) of the grass forage was excessive. Yet this must have occurred *twice* each year. The determination that forage was removed to this extent is further evidence that the area was indeed overgrazed and that the carrying capacity must lie below the estimated 130,000–140,000 pound per square mile average biomass present.

Because of weight variation in the forage sampled (Table 3), it could be argued that the 142,000 pound estimate of biomass using the area is subject to equivalently wide confidence limits. The variation in grass weights alone was not computed but was certainly considerably

* Rainfall recorded at park headquarters was 4·74 inches during December-February, in contrast to 9·01 inches for March-May. A 2·45 inch rainfall during January was about twice the usual amount for that month. The area over which it fell is not known, but it could well have been due to a local thunderstorm.

smaller than for the entire sample series, since woody materials were involved in the latter. In any event, the use of the mean forage weight values for the clip-plot surveys provides the most reasonable basis for estimating the biomass which was supported by the vegetation. The estimated biomass supported per square mile is remarkably similar to that calculated from animal censuses and perhaps lends strength to the estimate of the size of the unmeasured hippo population.

Spot-plot Survey

It was calculated by the spot-plot method (Table 5) that 48 per cent of the grasses present had been consumed on the moderately overgrazed area during the grazing season preceding the February 1957 survey. While not identical to the 65 per cent figure for forage removal determined by the clip-plot method, it is within reasonably close range. Using the 48 per cent figure and the data of Table 3, 382,157 pounds of grasses per square mile apparently were consumed during the half-year. Applying the earlier assumption that 20 pounds of forage are required per day by a 1,000-pound ungulate, the biomass standing crop can be computed to have been 105,000 pounds per square mile.

Stomach Content Surveys

The amount of forage consumed by the large mammals conceivably also may be determined through the examination of their digestive tracts. In order to do so, one must know (1) the average daily population of the ungulate species, (2) the amount of food in the rumen or other suitable portion of the digestive tract, and (3) the relation of this amount to the daily consumption of food.

The population composition and size are available (Table 1). The weights of the stomach contents of a limited number of specimens also were obtained (Table 6). These weights for buffalo and hippo stomachs are within the range of some listed by Longhurst (*in litt.*). Data on the relation between the average rumen weight and the daily food intake, however, apparently have not been determined for many species.

For domestic cattle, Annison and Lewis (1959) conclude that "roughly half of a meal of hay leaves the rumen in the following twenty-four hour period". This would indicate that the materials in the rumen weigh about twice as much as the food consumed daily. How widely this relationship between the weights of the rumen contents and the amount of daily food consumption prevails among the ruminants is unknown. For trial purposes with the present data, it is assumed that the relation is applicable to the large ungulates of Queen Elizabeth National Park. The daily dry weight of forage consumed by those species is computed (Table 7) on this basis to be 2,070 pounds per square mile. Included in this figure are data for the elephant, which species we were not authorised to collect on our study areas. The work of Benedict (1936), however, permitted the conversion of faeces weights to weights of foods consumed. Benedict reported that adult male Indian elephants consume between 110 and 150 pounds of dry hay per day. He also determined through feeding experiments that 413 kilograms of dry hay resulted in the excretion of 232 kilograms of faeces. Thus, each pound of dry droppings was equivalent to 1·78 pounds of forage consumed.

Still further, he tabulated the number of faecal boluses passed by an elephant hour by hour over an eight-day period. During that time, 399 boluses were excreted during the hours between 7 a.m. and 7 p.m. and 411 during the night-time hours, with only slight differences in the numbers produced daily. These data, and the co-operation of the park staff, enabled two game scouts to follow an adult male elephant on 1 May for a 12-hour period during daylight. During this time, which Benedict's data had indicated was an unbiased portion of the day, they collected 108 pounds of elephant droppings. After drying, their weight was reduced to 26·4 pounds. The loss in weight in the droppings of our wild African elephant was 78·0 per cent as compared with a 76·3 per cent reduction in Benedict's tame Indian elephants.

Setting the dry weight value of 26·4 pounds against the 1·78 ratio determined by Benedict and allowing an equal amount of defaecation as above during the complimentary twelve-hour period, the rather average size adult African elephant was computed to consume 94 pounds of dry weight forage per day. Since it is estimated that the average elephant weighed about 5,000 pounds as opposed to 9,500 for adults (Buss *in litt.*, Petrides and Swank, unpublished), the food consumption of the average elephant also should be reduced in proportion; this yielding a figure of about 50 pounds of dry forage per day per average elephant.

The total dry-weight of forage consumed per square mile by the entire population of large mammals on the study area may be converted to herbivore biomass if again it can be assumed that 1,000 pounds live-weight of large herbivore requires 20 pounds of dry-weight forage per day. On this basis, the average large-mammal biomass present per square mile on the moderately overgrazed study area must have been about 103,500 pounds.

It is not certain whether this close approximation to the earlier estimates of the biomass present is meaningful. A number of assumptions have been made which cannot easily be tested for the several animal species involved. At least, however, there is no decided evidence here which is in opposition to the estimates of biomass present which were derived in other ways.

CONCLUSION

The moderately overgrazed study area evidently was subjected during the period of study to a large-herbivore grazing pressure of about 135,000 pounds biomass per square mile. The deteriorating condition of the range indicated that a lower total population biomass is necessary if the area's ability to support the large-mammal population on a permanent basis is to be saved.

It is estimated that the proper average biomass carrying capacity for the several herbivore species inhabiting the study plots is about 100,000 pounds per square mile. This is about four times as high as the biomass carrying capacity determined for the "plains game" ungulates of Nairobi National Park and for the best natural livestock ranges in the western United States (Petrides 1956).

Both the hippopotamus and elephant are large and long-lived species. Their nutritional requirements per unit weight on a population maintenance basis are doubtless lower than for a corresponding biomass of smaller and shorter-lived species. A somewhat lower carrying capacity presumably would prevail if only species of the latter sort were present.

It is also likely that hippos in transferring plant nutrients from land to water cause an accelerated rate of depletion of the habitat. This probably is a more serious loss than might be true for a population of entirely terrestrial species whose defaecations would be more completely retained within the soil structure. On this basis, the calculated carrying capacity biomass of 100,000 pounds per square mile may be a minimal figure.

SUMMARY

Regular censuses were made of wild hoofed animals in *Themeda-Acacia* grasslands near Lake Edward in extreme western Uganda. Regular counts of large herbivores were made in conjunction with tabulated vegetative and erosion investigations. These latter indicated that the study areas variously were severely overgrazed, moderately overgrazed, and undergrazed. Mammal populations and biomasses were determined per square mile on each of four census areas, and the probable maximum population biomass which could be supported permanently was calculated for the area nearest in balance with its animal inhabitants. This estimate was tested against three alternative methods of computation. The computed carrying capacity of the *Themeda* grasslands and its nine species of ungulates was 100,000 pounds biomass per square mile. The carrying capacity biomass densities of this study far exceed those of the best livestock ranges and may be the highest on record for terrestrial areas.

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