THE INFLUENCE OF THE AFRICAN ELEPHANT ON THE VEGETATION OF THE KRUGER NATIONAL PARK

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INTRODUCTION

The biomass of herbivores in the Kruger Park is relatively low, viz. 10,500 lbs./sq. mile, as compared to other game sanctuaries e.g. 25,000 to 47,000 lbs. in Nairobi National Park (Petrides 1956); 21,000 to 100,000 lbs. in Serengeti (Grzimek and Grzimek 1960) and 200,000 in Queen Elizabeth Park (Swank and Petrides 1958). Despite this fact, a recent severe drought period revealed a number of very vulnerable areas. As may be expected, the first areas to show signs of overutilisation were those near watering points. This is a normal phenomenon in the dry season, but a total or partial lack of water in temporary waterholes and water courses during the wet season resulted in an abnormal prolongation of concentrated grazing pressure. Range degradation therefore increased enormously and the grazing suffered both qualitatively and quantitatively. In certain areas steps have already been taken to reduce the populations of dominant species such as impala, zebra and wildebeest.

Although less numerous than the dominant ungulates, elephants exerted a marked effect on the vegetation. They were compelled by prevailing conditions to browse more than usual and considerable numbers of trees were uprooted or pushed over. The cumulative effect over a period of years, particularly in the absence of fires which would normally destroy such dead woody material, is one of havoc and devastation. This phenomenon naturally led to speculation among both laymen and wildlife administrators as to the extent of the destructive influence of elephants on their habitat in the Kruger National Park. The situation inspired a comprehensive survey of the numbers and physical condition of trees and shrubs in the area concerned, the results of which are submitted in this paper.

A. *GENERAL*

The Kruger National Park is the last sanctuary of any consequence for the African elephant in the Republic of South Africa, and is situated in the Transvaal Lowveld. It covers an area of approximately 7,340 sq. miles and is bordered by the Crocodile River in the south and, at present, by the Levuvhu River in the north, along both of which barbed wire fences

have been erected. Since 1961, the western boundary also consists of an unnatural barrier of wire fences running more or less parallel with the eastern boundary, which is the Lebombo Range — the national boundary between the Republic and Portuguese East Africa. Only parts of this boundary are fenced.

The mean annual precipitation is about 20 inches; most of it concentrated in the rainy season (October to March). At this time the Park is also subjected to high temperatures rising to ± 110°F. Winters are nearly frost-free.

Topographically the area may be subdivided into an undulating western half and a more or less flat, low-lying eastern part separated by a mostly subterranean sandstone reef. Apart from the Lebombos and the scattered, smaller outcrops dispersed throughout the entire Park, the only mountainous areas are those in the southwestern sector between Malelane and Pretoriuskop restcamps, and the portion north of Punda Milia. The altitude varies between ± 600 ft. in the east to about 2,700 ft. in the south-west. It follows that the five permanent rivers and larger seasonal water courses run across the area and pass into Portuguese East Africa though the Lebombos.

B. *VEGETATION AND ELEPHANT POPULATION*

Evaluation of the present situation is not possible without a basic knowledge of the vegetation and of the population history of the elephant in the area under consideration.

1. *Vegetation*

According to current geobotanical conceptions the vegetation can be classified as tropical bushveld with three distinct strata, viz.

(i) the upper stratum consisting mainly of deciduous trees of 15-35 ft., which constitutes the major component of about 70% of the area;

(ii) a substratum of shrubs or stunted trees of 3 to 10 ft., dispersed throughout the entire area and dominating the other 30% thereof;

(iii) the lowest stratum consisting of some 200 grass species, together with a great variety of herbs which are normally of lesser significance but thrive in denuded areas.

Although climatological conditions vary only slightly, a number of definite vegetation types, which may be linked with soil types, have developed.

The following major associations have been distinguished:

(1) *Mixed* Combretum *veld*

With the exception of the immediate vicinity of Pretoriuskop this covers the sandy granitic soils of the western part as well as the skeletal soils of riolitic origin of the Lebombo ridge from the Crocodile River in the

south to Punda Milia in the north. From a point just south of the Olifants River northwards the common dominant, *Combretum apiculatum*, is closely associated with *Colophospermum mopane*, while south of this point, species like *Terminalia sericea* and several *Combretum* species occur as sub-dominants.

(2) *Large-leafed, deciduous woodland with tall grass (Pretoriuskop tall grass veld)*

This covers a relatively small area around Pretoriuskop rest camp. Dominant tree species are *Terminalia sericea* and *Parinari curatellifolia*.

(3) *Acacia nigrescens/Sclerocarya caffra association*

On the deep, poorly drained, basaltic soils of the eastern half of the Park, along the Lebombo ridge and from the Crocodile River in the south to the Olifants River in the north, the vegetation is dominated by *Acacia nigrescens* with *Sclerocarya caffra* as sub-dominant.

(4) *Colophospermum mopane veld*

With minor exceptions the area north of the Olifants River up to Punda Milia, between the Lebombo ridge in the east and the Combretum/Mopane associations in the west, is dominated by *Colophospermum mopane*. On the deep basaltic soils of the Lebombo flats it rearly outgrows the shrub stage, but in the area between Shingwidzi and Punda Milia rest camps, it occurs as very large trees, constituting typical forest conditions.

(5) *Communities of Punda Milia, Nwambya and Pumbe sandveld*

These are relatively small areas, the latter two of which border Portuguese East Africa just south of the Levuvhu and Olifants Rivers respectively. The former area contains the mountainous region north of Punda Milia rest camp. Their contribution to the subsistence of the herbivores is relatively small, but their very rich floristic compositions render them important.

The interested reader is referred to Brynard (1964) and Pienaar et al. (1963) for detailed descriptions on the vegetation of the Park.

2. *The population history of the elephant in the Kruger National Park since 1905*

It is known that elephants existed in the Transvaal Lowveld and were pursued by hunters, but no information on their numbers is available prior to 1905. Since then regular reports have been submitted on the development of the population. These data are fully dealt with by Pienaar *et al.* (1966), the main points being:

1905 — Col. Stevenson-Hamilton mentions the existence of a few elephants (10) in the isolated country between the Letaba and Olifants Rivers.

1912 — Estimated at 25.

1926 — Proclamation of the Park in its present form.

1931 — Estimated at about 131.

1946 — Estimated at about 480.

1947 — Estimated at about 560.

1954 — The late and last warden of the Park submitted a figure of 740.

Since 1958 the biological section of the Park staff has been responsible for enumerating the population. Ground counts and, subsequently, aerial counts have showed consistent increases. In 1964 a complete census by helicopter revealed the total number to be 2,474.

Part of the increase is undoubtedly apparent and due merely to improved census methods. However, there was also a considerable influx of animals from the adjoining territories of Portuguese East Africa and Rhodesia whence the animals came to escape persecution.

During this period in the history of recolonisation small groups, preceded by solitary bulls, slowly began infiltrating the whole Park. It was an insiduous process and the first elephant in almost a century again set foot south of the Sabi River only in 1941. In 1952 the last elephant-free zone, i.e. Pretoriuskop, was re-entered.

The present distribution pattern as revealed by the latest census is as follows: The majority of elephants (1,994) were encountered north of the Olifants River, 319 between the Olifants and Sabi Rivers and 61 south of the latter. Of the group in the north, 1,139 were found in or near the original habitat i.e. in area C (Fig. 1).

During the time of the most recent census (August — dry season), all the larger herds were concentrated near permanent watering points, i.e. in the vicinity of the larger watercourses with permanent waterholes or along the perennial rivers (areas B to F), whereas only bachelor bulls, solitary or in small herds, were encountered in those areas with meagre water supplies (areas 1-10).

The water supplies in areas A and I to III are sufficient to sustain large breeding herds, but for some unknown reason they are not popular dry season resorts of elephant. Water supplies in the remainder of the Park (areas a to j) consist, with the exception of a few windmills, of rain water stored in waterholes or hollows. Utilization of these areas is therefore restricted to the summer months.

It is against the background provided above that the results of the present survey must be evaluated.

C. *METHODS AND TECHNIQUES*

To ensure that this initial and fundamental survey would cover every aspect of the relationship between the elephant and its present habitat, it

was decided to distribute as many sampling areas as possible throughout the entire Park.

The position of each of these areas was determined as follows:

A large-scale map of the Park was covered by a transparent 2 inch grid (1" = 4 miles) and points of intersection (150) on the grid were marked on the underlying map. For practical reasons all sampling-points had to be easily accessible. All points were therefore moved, along either the x or y axes of the grid, to the nearest road.

Apart from the sampling areas localised in this way, a further 15 special transects were located in the four seriously abused areas, viz. the Pafuri area (area A); along the Shingwidzi River west of the rest camp (in area B); near Letaba rest camp (in area C) and immediately east of Tshokwane (in area E) as well as along the Sabi River.

Exact distances of sampling points from landmarks — mostly road junctions — were determined on the map for later use in the veld.

Sampling areas were laid down as transects of 6 x 999 yards to obviate the possible influence of very localised, abnormal under- or over-utilisation.

Each transect was subdivided into 3 equal parts of 333 yards, and the data separately recorded.

Lots decided the side of the road to be used for sampling.

The centre lines of transects were as far as possible at right angles to the road and originally determined by means of a compass. This method was too time-consuming and was superseded by a quicker method whereby an assistant was aligned with a predetermined compass reading. Two or three other assistants then aligned themselves with the first and leap-frogged each other as the survey progressed.

The exact width of the sampling area was determined by the surveyor by means of a stick, the length of which, when added to that of the surveyor's outstretched arm, totalled 9 feet.

For the purposes of this survey, trees and shrubs were divided into the following three categories:

I. A. *Undamaged*

B. *Browsed*

(a) by elephant,

(b) by other animals,

(including all plants that had been browsed but not seriously damaged).

C. *Destroyed*

(a) by elephants, including

(i) plants obviously uprooted and killed by elephants,

(ii) trees pushed over but still growing, and

(iii) specimens badly damaged;

(b) by other causes, such as old age, disease, fire and lightning.

II. Woody plants were also classified according to size as follows:

A. *Trees:* This category includes all acknowledged tree species (except *Colophospermum mopane* and *Pterocarpus rotundifolius).* Both of these are tree species but, as a result of fire damage, a very large percentage of plants occurs as many-stemmed shrubs of 2-6 ft. high. These are potentially able to develop into trees but, for all practical purposes, must be classified as shrubs. Typical trees of the two species were classified in their particular categories. For possible future reference all plants of both species were, however, recorded separately.

(a) *Small:* All individuals with a crown height lower than 6 ft.

(b) *Young:* All specimens with a crown height exceeding 6 ft. but, judged on the local ability of the particular species, not yet full-grown. Boles were usually up to about 9 inches in diameter.

(c) *Large:* Fully-grown specimens. Boles were normally more than 9 inches in diameter.

(d) *Outstanding:* Exceptionally large specimens.

B. *Shrubs:*

(a) *Small* and

(b) *Large* specimens of typical shrub species or trees in shrub form (such as *C. mopane* and *P. rotundifolius*), classified according to available knowledge of growth form for the particular species.

With this classification it is possible that a young tree of a particular species might surpass an outstanding specimen of another in size and height. In general, it was a practical classification in view of the fact that the most important species in the Park are *Combretum apiculatum, Terminalia sericea, Acacia nigrescens, Sclerocarya caffra* and *Colophosperum mopane,* which together constitute about 80% or more of the total tree population and, with the exception of *C. apiculatum,* normally attain roughly the same size.

In some instances it was difficult to decide whether two or more boles close together represented one or more individuals. Therefore all adult trees — young to outstanding — in which division of stems took place underground, were recorded according to number of boles present. This was fortunately a difficulty which was not commonly encountered.

In the small-tree group, a large proportion is many-stemmed, but the above procedure was not applied to them as they could mostly be separated easily. The relatively few cases which presented difficulty did not merit the application of this very time-consuming procedure.

Accurate records were kept for every transect in respect of quality and quantity of the grazing, species composition of the upper strata, as well as particularly heavy utilisation of specific trees and shrubs by elephant.

RESULTS

While working out the results of the survey, it became apparent that the numbers of small trees and shrubs surpass those of the larger categories to such an extent that their inclusion in the final analysis would obscure the facts (see Table 1 a and b). Discussions are, therefore, confined to the data for "adult" trees, including young, large and outstanding, and large shrubs only, and unless stated otherwise, the terms "trees" and "shrubs" refer to this classification.

CONDITION OF THE HABITAT IN AREAS SEASONALLY UTILISED BY ELEPHANT

This survey represents part of a wider elephant study conducted in the Park, of which the census of 1964 and discussion thereof by Pienaar *et al.* (1966) forms the basis. Attention is therefore firstly focused on the seasonal grazing areas as presented in that paper (Fig. 1).

(a) *Areas utilised by high concentrations of elephant during the dry season (Areas A to F).*

Total elephant population (census 1964)	2,179
Total area in sq. miles	3,505
Elephant density per sq. mile	0.62

These areas are, with the exceptinon of area B which is traversed by a seasonal river with permanent waterholes, and area E where a few permanent dams as well as relatively permanent waterholes in a large watercourse constitute the water supply, all centred around the perennial rivers. Areas C and D also include seasonal rivers with permanent waterholes.

As yet the Crocodile River, along the southern boundary of the Park, plays an insignificant role in the distribution pattern of elephant in view of the fact that the recolonization process has not reached this area. This also applies to the Sabi River, west of Skukuza. Whether the timid breeding herds will ever penetrate these winter grazing areas, which lie close to civilization, remains to be seen.

These areas inevitably support, in addition to elephant, heavy concentrations of other game. The estimated biomass of both groups for these particular areas is presented in Table 2. From these data it would appear that undesirable reactions in respect of the flora must arise in one of the winter-grazed zones.

TABLE 1(a)

AVERAGE NUMBER OF TREES/TRANSECT IN THE DIFFERENT SEASONAL GRAZING RANGES OF ELEPHANT IN THE KRUGER NATIONAL PARK, CLASSIFIED ACCORDING TO SIZE AND PHYSICAL CONDITION

Area		Small					Young					Large					Outstanding				
		Alive			Dead		Alive			Dead		Alive			Dead		Alive			Dead	
		Undamaged	Browsed		Elephant	Others	Undamaged	Browsed		Elephant	Others	Undamaged	Browsed		Elephant	Others	Undamaged	Browsed		Elephant	Others
			Elephant	Others				Elephant	Others				Elephant	Others				Elephant	Others		
A	*	51.0	12.6	17.3	—	0.8	21.3	127.3	1.6	13.8	7.8	2.9	7.3	0.3	15.1	5.5	2.1	1.9	—	0.3	0.8
	%	62.4	15.4	21.1	—	1.0	12.4	74.1	0.9	8.0	4.5	9.3	23.5	1.0	48.6	17.7	41.2	37.3	—	5.9	15.7
B	*	99.5	6.1	4.0	0.8	0.5	49.9	13.1	0.1	16.6	14.1	12.6	1.3	—	8.8	5.4	1.4	0.1	—	—	0.1
	%	89.7	5.5	3.6	0.7	0.5	52.9	13.9	0.7	17.6	14.4	44.8	4.6	—	31.3	19.2	87.5	6.3	—	—	6.3
C	*	152.3	11.1	1.5	1.3	1.3	90.6	24.6	0.2	23.3	19.5	10.5	1.2	—	8.9	3.6	0.6	—	—	0.2	—
	%	90.9	6.6	0.9	0.8	0.8	57.3	15.6	0.1	14.7	12.3	43.4	5.0	—	36.8	14.9	75.0	—	—	25.0	—
D	*	203.5	28.8	0.4	0.3	8.0	121.2	38.5	0.1	12.4	14.0	18.7	4.6	—	5.5	6.2	1.5	0.2	—	0.3	0.3
	%	84.4	12.0	0.2	0.1	3.3	65.1	20.7	0.1	6.7	7.5	53.4	13.1	—	15.7	17.7	65.2	8.7	—	13.0	13.0
E	*	105.1	10.3	4.0	—	2.6	57.4	17.3	1.7	3.3	22.4	8.0	6.1	—	6.7	6.9	1.3	0.6	—	0.3	0.3
	%	86.2	8.4	3.3	—	2.1	56.2	16.9	1.7	3.2	21.9	29.1	22.2	—	24.4	25.1	52.0	24.0	—	12.0	12.0
F	*	281.8	14.5	3.4	3.5	1.9	59.4	16.5	0.1	17.1	10.5	13.6	1.4	—	4.0	3.0	1.3	0.1	—	—	0.2
	%	92.4	4.8	1.1	1.2	0.6	57.3	15.9	0.1	16.5	10.1	61.8	6.4	—	18.2	13.6	81.3	6.3	—	—	12.5
Average	*	159.4	13.8	2.9	1.2	2.6	73.1	23.4	0.4	17.3	15.3	12.6	2.3	—	7.1	4.6	1.2	0.2	—	0.1	0.2
	%	88.6	7.7	1.6	0.7	1.5	56.5	18.1	0.3	13.4	11.8	47.4	8.7	—	26.7	17.3	70.6	11.8	—	5.9	11.7
1-10	*	114.0	6.3	3.0	0.8	2.8	91.7	14.7	2.6	7.9	16.3	14.1	1.2	—	4.5	7.3	1.6	0.1	—	0.2	0.2
	%	89.8	5.0	2.4	0.6	2.2	68.8	11.0	2.0	5.9	12.2	52.0	4.4	—	16.6	26.9	76.2	4.8	—	9.5	9.5
a-j	*	230.7	15.4	5.4	0.5	2.8	118.4	13.9	1.4	6.1	17.4	17.5	2.2	—	3.6	5.5	1.7	0.1	—	0.2	0.5
	%	90.5	6.0	2.1	0.2	1.1	75.3	8.8	0.9	3.9	11.1	60.8	7.6	—	12.5	19.1	68.3	2.4	—	9.2	20.1
I-III	*	142.5	1.6	1.5	0.6	0.7	69.1	10.5	1.7	5.1	17.8	8.1	1.4	0.2	1.1	6.0	1.8	0.2	—	—	0.2
	%	97.0	1.1	1.0	0.4	0.5	66.3	10.1	1.6	5.0	17.1	48.2	8.3	1.2	6.5	35.7	81.8	9.1	—	—	9.1
K.N.P. Average	*	164.3	10.9	3.5	0.9	2.5	91.1	18.4	1.2	11.5	16.3	14.0	2.0	—	5.7	5.6	1.4	0.1	—	0.2	0.2
	%	90.2	6.0	1.9	0.5	1.4	65.8	13.3	0.9	8.3	11.8	51.3	7.3	—	20.9	20.5	73.7	5.3	—	10.5	10.5
		98.1%			1.9%		80.0%			20.1%		58.3%			41.4%		79.0%			21.0%	

* Number.

TABLE 1(b)

AVERAGE NUMBER OF SHRUBS/TRANSECT IN THE DIFFERENT GRAZING RANGES OF ELEPHANT IN THE KRUGER NATIONAL PARK CLASSIFIED ACCORDING TO SIZE AND PHYSICAL CONDITION

		Small					Large				
		Alive			Dead		Alive			Dead	
		Un-damaged	Browsed		Elephant	Others	Un-damaged	Browsed		Elephant	Others
			Elephant	Others				Elephant	Others		
A	*	6.8	6.4	341.1	—	1.1	10.8	83.8	317.6	2.3	5.3
	%	1.9	1.8	96.0	—	0.3	2.6	20.0	75.7	0.6	1.3
B	*	301.7	31.5	4.2	3.7	1.4	154.2	98.6	1.7	12.8	3.6
	%	88.1	9.2	1.2	1.1	0.4	56.9	36.4	0.6	4.7	1.3
C	*	290.4	37.7	1.5	2.1	0.7	148.7	144.1	0.4	9.5	4.4
	%	87.4	11.3	0.5	0.6	0.1	48.4	46.9	0.1	3.1	1.4
D	*	286.7	24.5	0.4	0.4	2.8	74.9	74.7	0.3	3.0	2.7
	%	91.1	7.8	0.1	0.1	0.9	48.1	48.0	0.2	1.9	1.7
E	*	176.7	3.0	1.6	—	2.7	22.7	6.0	1.0	1.0	15.7
	%	96.0	1.6	0.9	—	1.5	48.9	12.9	2.2	2.2	33.8
F	*	531.3	22.9	7.6	0.5	1.5	153.5	57.4	0.2	15.7	16.0
	%	94.2	4.1	1.4	0.1	0.3	63.2	23.6	0.1	6.5	6.6
Average	*	307.4	28.4	9.7	1.8	1.5	119.4	98.2	4.5	9.3	6.1
	%	88.1	8.1	2.8	0.5	0.4	50.3	41.4	1.9	3.9	2.6
1-10	*	258.0	12.4	4.5	1.4	2.2	190.9	44.5	2.8	5.1	9.4
	%	92.6	4.5	1.6	0.5	0.8	75.5	17.6	1.1	2.0	3.7
a-j	*	258.7	13.4	3.1	0.6	4.4	152.6	35.3	1.5	4.5	10.2
	%	92.3	4.8	1.1	0.2	1.6	74.8	17.3	0.7	2.2	5.0
I-III	*	247.8	0.6	1.2	0.2	2.2	216.4	11.1	1.6	3.5	16.1
	%	98.3	0.2	0.5	0.1	0.9	87.0	4.5	0.6	1.4	6.5
K.N.P.	*	280.0	19.6	9.9	1.4	2.4	150.7	65.7	8.8	6.8	8.8
	%	89.4	6.3	3.2	0.5	0.8	62.6	27.3	3.7	2.8	3.7
		98.9%			1.3%		93.6%			6.5%	

* Number.

TABLE 2

PERCENTAGES OF ADULT TREES AND SHRUBS UTILISED BY ELEPHANT AND DEAD FROM OTHER CAUSES IN THE DIFFERENT SEASONAL GRAZING AREAS IN THE KRUGER NATIONAL PARK

AREA	BIOMASS/SQ. MILE		TREES				SHRUBS			
			Elephant			Other causes	Elephant			Other causes
	Elephant	Other herbivores	Browsed (a)	Destroyed (b)	a + b	Dead	Browsed (c)	Destroyed (d)	c + d	Dead
A	24.080	23,100	65.6	14.1	79.7	6.8	43.6	0.8	44.4	1.7
B	4,358	4,765	11.7	20.5	32.1	15.8	36.4	4.7	41.1	1.3
C	7.740	6,661	14.1	17.7	31.8	12.6	46.9	3.1	50.0	1.4
D	1,223	10,918	19.4	8.1	27.5	9.2	48.0	1.9	49.9	1.7
E	1,887	16,230	16.3	10.7	27.0	26.2	21.4	6.0	27.4	22.8
F	2,683	28,532	14.1	16.6	30.7	10.8	23.6	6.5	30.1	6.6
Average	4,352	10,582	16.4	15.5	31.9	13.0	41.4	3.9	45.3	2.6
1-6	1,716	2,973	12.0	9.6	21.6	18.6	21.8	2.1	23.9	2.6
7-8	174	10,929	14.4	11.9	26.3	17.1	20.7	4.3	25.0	2.0
9-10	645	19,752	5.6	4.1	9.7	9.3	8.9	1.4	10.3	6.1
Average	993	9,789	9.9	7.8	17.7	14.7	17.6	2.0	19.6	3.7
a-e	—	734	8.7	9.7	18.4	12.7	28.4	3.5	31.9	1.8
f-h	—	2,577	14.3	4.7	19.0	12.4	18.0	3.0	21.0	14.0
i-j	—	5,113	3.9	3.5	7.4	12.2	3.9	0.4	4.3	6.2
Average	—	2,120	8.6	5.3	13.9	12.4	17.3	2.2	19.5	5.0
I-III	—	16,944	9.8	5.1	14.9	19.5	4.5	1.4	5.9	6.5

Total biomass* in lbs./sq. mile ranged from 9,127 (Area B) to 47,180 (Area A); for elephants alone from 1,223 (Area D) to 24,080 (Area A); and for other herbivores from 4,700 (Area B) to 29,000 (Area F) and 23,100 (Area A).

At the moment area A (Pafuri) supports the highest total *and* elephant biomass. It is a relatively small, secluded area (± 25 sq. miles). In the north the Levuvhu River, with a fence on its northern bank, separates it from civilization while in the east, only a barbed-wire fence (Portuguese East African border) serves this purpose. A continuous line of waterless ridges in the south and west completes the seclusion of the territory. Because of the isolation, it lends itself excellently to the determination of the relation between elephant biomass and utilisation of the woody strata under the very worst of conditions. However, only about 14% of the trees in the area had been killed by elephants, as compared to 20% in area C, while 66% were browsed, 19% being the highest in the other areas. Together with the negligible number browsed by other animals and killed by other causes, this leaves only 14% of the trees untouched.

An explanation of the small percentage of trees killed is probably to be found in the floristic composition of the area. A typical gallery forest — 50 to 300 yards wide — including colossal, indestructible specimens of several tree species such as *Ficus sycomorus, Xanthocercis zambesiaca, Lonchocarpus capassa, Acacia albida, Acacia robusta,* etc. borders the Levuvhu River. This is followed by a silt-covered flood plain with *Acacia tortilis* ssp. *heteracantha,* as absolute dominant, but also including a dense belt of *Acacia xantophloea* and thickets of undergrowth consisting of *Macrorungia formosissima, Hyphaene crinita* and *Azima tetracantha.* The *A. xantophloea* forest was severely thinned out by elephants until a few years ago, but at present the damage is negligible. *A. tortilis* and *A. nilotica* ssp. *kraussiana* are mostly browsed — sometimes severely — but not often uprooted or killed outright. The outer zone encompasses the higher-lying ground nearer to and including the ridges surrounding the valley. *Colophospermum mopane,* which is found exclusively in the scrub form on the lower-lying areas, is the dominant tree species here. Associated tree species include *Boscia albitrunca, Adansonia digitata, Gyrocarpus americana, Commiphora* spp. and *Terminalia prunioides.*

For the past 10 years the grass stratum in this area, and particularly on the flood plain itself, was about non-existent. This condition originated in the flooding of the valley and deposition of heavy silt during the summer of 1957, which subsequently led to tremendous overgrazing, increased termite activities and total destruction of the stratum. Under these conditions the heavy utilisation of the upper strata is quite logical.

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* See Pienaar et al. (1966) for detailed information on biomass.

The whole situation becomes much more disquieting when it is kept in mind that this destructive browsing takes place during a period of some six months every year.

The elephant population here consists of bulls only, which come from adjoining territories inside and outside the Park's boundaries. With the onset of the rainy season, they leave the area completely.

The situation in the other areas is briefly as follows:

Areas B, C and D are mainly situated in the C. *mopane*/C. *apiculatum* veld, both components occasionally forming nearly homogeneous stands. Grass cover varies from mixed to completely sweet and, during normal years, may be relatively poor on the granitic rises, but is usually very lush in the lower regions. Generally speaking, area D has the poorest grazing as it includes the low-grade pasture on the ridges along both banks of the Olifants River. All three areas display roughly the same high shrub population with C. *mopane* dominant, total shrub numbers per transect being: Area B — 613; Area C — 645 and Area D — 470.

Areas E and F lie partly in *Acacia nigrescens*/*Sclerocarya caffra* veld and for the rest in *Combretum* veld. Grazing conditions normally vary from fair to extremely good. Shrub concentration in the two areas differs tremendously, with that in area E the most sparse of all areas (140/transect) and that in area F the most dense (807/transect).

During the dry season, severe overgrazing occurs in the close vicinity of water. Most of these areas recover, often remarkably rapidly, during the summer months, under normal rainfall conditions. Adequate temporary water is then available in the customary summer ranges of the game to entice them away from the trampled areas.

Fig. 2 contains the figures for the trees browsed and killed by elephant in these areas. The markedly higher intensity of utilisation in area A than in the other areas is quite evident and needs no further explanation.

Total utilisation of trees (both browsed and destroyed) is more or less on the same level in areas B to F, i.e. 27% (E) to 32% (B), but the data for the two components separately show marked differences. The percentage destroyed varies between 8.1% (D) and 20.5% (B), and precentage browsed from 11.7% (B) to 19.4% (D) (Table 2).

The results, when presented in this manner, bring to light two hitherto unsuspected phenomena.

Firstly, it would appear that an increase in elephant biomass, at least up to 7,000 lbs./sq. mile (= 1 elephant/sq. mile), has little effect on the rate of utilisation of the areas generally.

Secondly, the competing biomass of other animals also seems to have no influence on elephant browsing in the areas in general. At first this

appeared difficult to believe as it was assumed, even before commencing the survey, that the results would show a positive correlation on the supposition that overgrazing would force the elephant to the upper strata. When it is borne in mind, however, that the grazing in all areas is commonly fair to good, it is apparent that only a small proportion of the transects would be in overgrazed areas. The influence of other herbivores will be overshadowed when comparing large areas including all types of browsing. This point will be discussed in greater detail below.

In the shrub stratum complete destruction by elephant is negligible — the highest being the 6.5% of large shrubs in area F and the lowest in area A (0.8%). Furthermore these figures, in most instances, only represent severely damaged plants able to recover again (Table 2).

Browsing of shrubs in areas A to D is severe (36-48%), but drops down to 23% and 13% in areas F and E respectively. This can be due to lower biomass, but is more probably coupled with botanical composition. The first four areas contain the highly palatable mopane shrub, while the plants in areas E and F are, with the exception of *Grewia* spp., not preferred items of diet. This is probably also the reason why *Grewia* spp. receive such marked attention from the elephant in areas E and F.

Even during normal rotational burning most shrubs, particularly those like *C. mopane* and *P. rotundifolius,* are burned back to ground level from whence they resume coppice growth. Browsing of shrubs is normally much less detrimental. It usually involves only the breaking off of small branches or stripping of leaves and is, therefore, of no real conseqeunce.

(b) *Areas mainly utilised by low concentrations of elephant during the dry season (Areas 1 to 10)*

Total area in sq. miles	1,375
Total elephant population (census 1964)	195
Elephant density per sq. mile	0.14

Insufficient water supplies render these areas unsuitable for the larger breeding herds. Areas 9 and 10 are the exceptions to this rule. The reasons for the low concentration here have been expounded above.

During the census, no elephants were encountered in area 2, but that was only a temporary situation caused by the drying-up of Malonga spring, situated in the centre of the area.

Elephant concentration, as reflected by the results of the survey, is on the whole very low. As the areas (2 to 7 and 9) are relatively small, they naturally covered only a few transects. This shortage of replications makes the results somewhat unreliable. Comparison between individual areas was also hampered by this fact, therefore the figures for different areas were pooled as shown in Table 2.

The dominant woody plant in area 1 is mopane shrub, and it is only ousted in the extreme north of the region by the tree form and in the north-

western part by the sandveld vegetation of Punda Milia. Grazing here is the best in the Park, qualitatively and quantitatively.

Area 2 embodies the entire Nwambiya sandveld.

Areas 3 and 5 contain predominantly shrub mopane and the large tree group is a rarity. Grazing is excellent.

Areas 4 and 6 lie in the granite belt, with *C. apiculatum* and *C. mopane* the dominants. Grazing varies from fair to good.

The Pumbe sandveld and a portion of the *A. nigrescens/S. caffra* veld are included in area 7. Grazing varies from fair to outstandingly good.

The biggest area of the group (8) is situated entirely in *A. nigrescens/S. caffra* veld and includes some of the poorest grazing (mainly due to the dominance of the unpalatable *Bothriochloa insculpta* stinkgrass) and some of the most heavily grazed areas in the Park.

The largest portion of the area south of the Sabi River is utilised mainly by bull elephants which concentrate along the two rivers (areas 9 and 10) during the dry season. These areas resemble each other floristically and include dense riverine forest, thornbush thickets, *Acacia nigrescens* and *Combretum* veld. Generally the grazing is of good quality, but high concentrations of other game cause the riverbanks to become trampled.

Apart from the areas specifically mentioned, overgrazing very seldom occurs and, if so, only in the close vicinity of watering points.

When interpreting the results a possible error in the biomass allocations must be taken into account, especially in areas 7 and 8. Utilisation of 26% of adult trees (Table 2) for these areas appears to be abnormally high for the relative elephant biomass. More regular counts at all times of the year, for a few years running, may clarify the picture. On the other hand, the position may be exactly the same as in the adjoining area E, where grazing conditions and the low number of palatable shrubs were held responsible.

Tree utilisation (browsed and destroyed) amounts to only 17.7% (vide 31.9% for areas A to F). Only 7.8% were completely destroyed. The highest destruction was encountered in areas 7 and 8 (11.9%) and the lowest in 9 and 10 (4.1%). Browsing follows the same pattern, being highest in areas 7 and 8 (14.4%) and lowest in 9 and 10 (5.6%).

Total shrub utilisation for the three groups of areas is relatively low: 24% for the north (1 to 6) and negligible in the south (areas 9 and 10) at 10%. Larger shrubs are much more extensively browsed in areas 1 to 8 (± 21%) than in areas 9 and 10 (9%).

On casual inspection, none of these areas would appear to have suffered severely from elephant action, particularly the southern region, which has only recently been recolonized. Actually the converse is true,

and it is evident that most of the wooded areas suffer from progressive bush encroachment rather than from denuding of woody growth.

Cursory observation led to the belief that lone bull elephants are more destructive than the breeding herds, but the present results offer no conclusive proof that this is really so. This is one aspect however, that merits further investigation.

(c) *Areas utilised by elephants only during the summer months*

Total area (I to III)	350 sq. miles.
Total area (a to j)	2,130 sq. miles.
Total	2,480 sq. miles.

Insufficient or no permanent water renders areas a to j unsuitable as winter range for elephants. The other three areas have ample permanent water to provide even for large herds, but are usually shunned by all elephants probably in view of unsuitable topographical or floristic composition of the habitats.

It must be pointed out that the total elephant population does not move into these areas during the rainy season. They also inhabit, during this period, the outer perimeter of the regions discussed above and, particularly in the north of the Park, a considerable efflux into Portuguese East Africa takes place. During this season the overall elephant concentration will, therefore, be much lower than during winter.

With the exception of area II, a close similarity exists between all these areas and those surrounding or adjoining them as regards floristic composition.

Area (a) Partly shrub, and for the rest *Colophospermum mopane* in the tree form.

(b) Mixed *C. mopane/Combretum apiculatum* woodland.

(c) *Combretum/C. mopane* in the west, with shrub mopane dominant on the Lebombo flats in the east.

(d) Lebombo milieu with mopane and *C. apiculatum* trees as dominants.

(e) *Combretum*/mopane trees.

(f) Mainly *Acacia nigrescens/Sclerocarya caffra,* but also includes a portion of the Lebombo vegetation on the Portuguese East African border.

(g) *Combretum* and mopane trees in alternating strips.

(h) Surrounds area E, extending from the eastern to the western boundary, including a variety of veld types such as *Combretum, A. nigrescens/S. caffra, Acacia delagoensis/Albizia evansii* on the sandstone reef, and Lebombo vegetation.

(i) Almost entirely *Combretum* veld.

(j) Includes the Lebombo range between the Crocodile and Sabi Rivers.

I. A mountainous area in which dense pure stands of *Androstachys johnsonii* on the summits are very prominent. It also harbours a riverine forest, the Punda Milia sandveld vegetation and *C. mopane* veld (trees).

II. Pretoriuskop tall grassveld.

III. The Lebombo flats between the Sabi and Crocodile Rivers — thus *A. nigrescens/S. caffra* veld. It includes fairly open parkland interspersed with large areas of dense *Dichrostachys cinerea* spp. *africana var. africana* thickets. Some of the best, if not the very best, grazing in the Park is encountered in this region including species such as *Themeda triandra, Panicum coloratum* and several *Digitaria* species. This area carries the highest ungulate biomass in the Park.

As a general principle, it may be accepted that mopane veld provides dense stands of good quality grass, while in pure *Combretum* veld, particularly on the water-sheds with the bedrock near the surface, a relatively poor grass cover, comprising species of lower quality, is generally found. *Combretum apiculatum* trees, in extreme cases of the latter, are usually stunted and inclined to be many-stemmed. *Acacia nigrescens/S. caffra* veld has a very high grazing potential, normally consisting of palatable and good-quality grazing.

As is the case in the dry-season ranges, the worst overgrazing in this summer-grazed group is found in the central district of the Park (including areas f, g, and h). Drought conditions, coupled with high grazing intensity and dominance of *Bothriochloa inscupta* in large areas, are responsible for this condition. The grass stratum in all these ranges is, however, generally in excellent condition. When this, and the fact that the areas are only used by elephant in summer, are accepted, then it may be expected that damage in die woody growth will be the lowest in the Park. This surmise is indeed confirmed by the results of the survey (Table 2).

Utiliisation intensity differs markedly from that in areas A to F, and amounts to roughly 9% for browsed and 10% for destroyed trees.

The same applies to utilisation of the larger shrubs. In this category a marked difference also exists between the two area-groups themselves.

Total utilisation for areas a to j amounts to 19.5%, compared to only 5.9% in I to III, which indicates that even during the summer months the latter group of areas is very seldom visited.

On the other hand, very little difference exists between areas a to j and 1 to 10, which emphasizes the fact that under prevailing conditions

the Kruger Park woody plants constitute a very important part of the diet of the elephant.

In conclusion, it may be remarked that in spite of actual under-utilization of 80-90% of the Park, action will have to be taken — as has been decided already — in order to counteract abnormal destructive activity in winter-grazed areas with high biomass, and particularly in the regions surrounding permanent water (vide Figs. 4 and 5).

INFLUENCE OF ELEPHANT BIOMASS ON UTILISATION OF THE UPPER STRATA

Demarcation of a park or nature reserve into small areas and allotment of specific biomass figures to each must, to a certain extent, be subject to conjecture. The more detailed such a demarcation, the bigger will the margin of error be. In the case of elephant, which can cover great distances in a short time, the chances of wandering from one area into an adjoining one are much greater, and so too the error in allotments of biomass.

To be able to present a more satisfactory picture of the relationship between utilisation of woody growth and elephant biomass, it was decided to divide the Park into three areas only, viz.

(i) northern district, i.e. north of the Olifants River,

(ii) central district, between the Olifants and Sabi Rivers, and

(iii) southern district, bordered by the Sabi and Crocodile Rivers.

As has been pointed out in the historical review, the majority of the elephants (i.e. 1,994) are still to be found in the vicinity of the area where the original nucleus resided. 319 were found in the central and 61 in the southern district.

The animals often wander from the northern to the central region across the Olifants River, as well as from the central to the southern region over the Sabi River and back. The same applies to the Portuguese East African border. The extent of interchange in the population between the various districts is very difficult to determine, but it would appear that, according to census figures and field observations, the movement is rather limited during the winter months.

Judging from the data presented in Table 3 and Fig. 3, it is abundantly obvious that a positive correlation exists between elephant biomass and utilisation of trees and shrubs.

As was expected, utilisation in the southern district is very low, so much so that many more trees died from causes other than elephant action (12.2% compared with 3.9% destroyed by elephant). Natural mortality is even higher than total elephant utilisation which amounts to only 8.9%. The position in the shrub stratum is exactly the same. Total destruction amounts to only 0.8% and browsing to 6.2%, which together only just

TABLE 3

PERCENTAGES OF ADULT TREES AND SHRUBS UTILISED BY ELEPHANT AND DEAD FROM OTHER CAUSES IN THE NORTHERN, CENTRAL AND SOUTHERN REGIONS OF THE KRUGER NATIOAL PARK

	AREA	BIOMASS IBS./SQ. MILE		ELEPHANT			OTHER CAUSES
		Elephant	Other herbivores	Browsed (a)	Destroyed (b)	a + b	Dead
TREES	North	3,726	4,939	14.9	14.3	29.2	14.1
	Central	887	10,924	14.2	8.1	22.3	12.4
	South	436	12,947	5.0	3.9	8.9	12.2
	Average	2,258	8,282	12.2	10.4	22.6	13.2
SHRUBS	North	3,726	4,939	34.9	3.0	37.9	1.6
	Central	887	10,924	23.8	5.9	29.7	7.9
	South	436	12,947	6.2	0.8	7.0	6.9
	Average	2,258	8,282	27.3	2.8	30.1	3.7

surpass the natural mortality rate. Not only the obviously very low elephant biomass (436 lbs./sq. mile), but also the very excellent condition of the grass-cover, as well as the variety and concentration of edible shrubs, must be held responsible for this condition.

In contrast to this the central region, as in so many other instances, gives cause for concern. With an elephant biomass of only 887 lbs./sq. mile, total tree utilisation amounts to 22.3% and that of the larger shrubs to 29.7%. Admittedly biomass may be higher with periodic infiltration from the north, and to a lesser extent from the south, but only after a theoretical increase of ± 1,000 lbs./sq. mile, i.e. some 300 animals, does the relation between total utilisation and elephant biomass attain a position where it compares favourably with that of the two other districts (Fig. 3).

As mentioned before, the situation in this region must be attributed to the poor pasture position, as well as to the absence of favourite shrubs. This state of affairs is particularly true of the *A. nigrescens/S. caffra* veld north of Tshokwane up to the Olifants River and also, more recently, of the area immediately north-east of Orpen rest camp.

Under prevailing conditions (elephant biomass ± 3,700 lbs./sq. mile), a stage has been reached in the northern district where the number of trees destroyed by elephant just exceeds the tally ascribed to other causes (14.9 and 14.3%). Total utilisation of trees reaches 30% and of shrubs 38%. With the exception of the Pafuri region (A) and a few other smaller areas near water, the state of the vegetation in general appears to be fundamentally sound.

The gradient of the graph (Fig. 3) would suggest that when the point is reached where elephant biomass for the entire Park reaches the generally accepted carrying capacity for elephant (1 elephant, i.e. 7,000 lbs./sq. mile), the utilisation rate will have reached dangerous proportions.

INFLUENCE OF GRAZING CONDITION AND DISTANCE FROM WATER ON UTILISATION OF THE WOODY GROWTH

Before commencing this survey, it had been observed that destruction or utilisation of the woody strata was closely linked with distance from watering points, particularly in the dry season ranges.

In such situations two factors play a significant part, viz. local concentrations of game (biomass) and condition of the pasture. The highest game concentrations and grazing intensities, with consequent severe trampling, are always encountered in the immediate vicinity of water. When moving away in all directions the same number of animals utilise a larger area, with the result that biomass and grazing intensity drop very rapidly.

Transects were classified into three categories, i.e. poor, fair and good grazing, according to the observed state of the grazing at the time of the survey. The average results of utilisation of these categories throughout

TABLE 4

PERSENTAGES OF ADULT TREES AND SHRUBS UTILISED BY ELEPHANT AND DEAD FROM OTHER CAUSES UNDER DIFFERENT GRAZING CONDITIONS AND AT VARIOUS DISTANCES FROM WATER SUPPLIES IN THE KRUGER NATIONAL PARK

AREA	TREES				SHRUBS				Total number of living shrubs/ transect	Total number of living trees/ transect
	Elephant			Other causes	Elephant			Other causes		
	Browsed (a)	Killed (b)	a + b	Killed	Browsed (c)	Killed (d)	c + d	Killed		
Nearer than one mile	16.5	12.3	28.8	12.7	33.1	3.7	36.8	3.1	602.3	281.0
From 1-5 miles	11.3	10.4	21.7	13.2	27.1	2.5	29.6	3.9	521.1	289.9
Further than 5 miles	8.5	5.4	13.9	14.3	16.4	2.1	18.5	4.6	473.3	371.6
Special points	50.5	26.7	77.2	16.5	42.5	1.0	43.5	3.0	591.3	159.9
Poor grazing	21.6	14.7	36.3	11.8	39.8	2.8	42.6	3.0	609.7	283.4
Fair grazing	11.6	10.8	21.4	13.7	28.2	2.8	31.0	3.8	550.0	323.1
Good grazing	8.3	6.7	15.0	14.5	18.0	1.8	19.8	4.1	456.6	269.2