AN AERIAL CENSUS OF ELEPHANT AND BUFFALO IN THE KRUGER NATIONAL PARK, AND THE IMPLICATIONS THEREOF ON INTENDED MANAGEMENT SCHEMES

By

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INTRODUCTION

An analysis of the available historical data relating to the population growth of elephants in the Kruger National Park reveals not only considerable defects and gaps in the official estimating of numbers throughout the years, but it also becomes ever more evident, particularly during recent times, that observers are unsure of their methods and are searching for more exact census techniques.

The population history of elephants in this protected area of the Lowveld dates back to the early years of its existence — i.e. 1905, when the late Warden, Col. J. Stevenson-Hamilton, divulged that a small number of elephant (perhaps 10) had escaped the relentless pursuit by ivory hunters, before the proclamation of the Sabi Game Reserve in 1898 and the Shingwidzi Reserve some few years later, and found sanctuary in the wild and inaccessible country between the Letaba and Olifants Rivers.

By 1912 their numbers had grown naturally and as a result of possible immigration from adjoining Portuguese East Africa, to 25. The proclamation of the Kruger National Park in 1926 guaranteed their strict and continued protection and during 1931 it was suggested that there might be as many as 135 of these pachyderms in the whole Park.

Prior to his retirement in 1946, Col. Stevenson-Hamilton stated the number of elephant in this area, which had been administered by him for so many years, to be at least 450, but his successor, Col. Sandenbergh, favoured a figure of 560 during the following year (1947).

The official estimation of elephant numbers by Mr. L. B. Steyn, the third Warden of the Park, was 740 in 1954.

During 1958 the recently established Biological section calculated that there may be 995 elephant in the Park, but pointed out at the same time that this figure was based more on guess-work than fact, and could very well be much higher.

The need for a more reliable method of counting had by then become imperative.

Reports were received of successful aerial censuses of elephant (by means of a light plane) in the Murchison Falls National Park in Uganda by Buechner, Buss, Longhurst and Brooks during the period 1957-1959, and subsequently also by Glover, Sheldrick and Parker and others in the Tsavo Park in Kenya. This method of counting elephant as well as other wild animals, has decided advantages over any other census technique and has in time become standard practice amongst particularly the Fulbright scholars and other scientists in East Africa. (Vide Talbot, Zaphiro, Fraser-Darling a.o.), as also with the Grzimeks, M. and B. on the Serengeti plains of Tanganyika.

During March, 1960, the Biological section of the Kruger Park had their first opportunity to test the efficiency of the aerial census technique in practice. This was made possible through goodwill of the Quelea Research Unit of the Plant Protection Institute of the Department of Agricultural Technical Services, who undertook an aerial survey in search of Quelea breeding colonies in the Park.

For the purpose of this particular survey a twin-engined, five-seater Piper Apache plane was employed and a total of 986 elephant was eventually counted along the various flight-routes. An estimated 200 elephant were not encountered during the census, and for the first time it was believed that the elephant population in the Kruger Park had exceeded the 1,000 mark.

In the subsequent report to the Board the merits of this type of survey were expounded at length and a similar but more complete census in the near future was advocated.

A subsequent aerial search for Quelea breeding colonies and possible anthrax carcasses during April, 1961, yielded, in passing, a total of 597 elephants, particularly in the northern districts.

During the period 9-12 April, 1962, the Quelea Research Unit once again visited the Kruger Park and during the subsequent aerial survey the whole area was covered more or less adequately for the first time by the flight plan. The surprising number of 1,601 elephant was recorded and another estimated 150 were not encountered along the flight routes. It was thus established that the total number of elephant in the Park was not less than 1,750.

Conditions were particularly favourable for this type of survey in view of the prevailing drought, and it was the first systematic and relatively comprehensive aerial census to be completed in the Kruger Park. It was nevertheless felt that the survey was by nature not as complete as one would have wished, and that even better results would be achieved if a similar census was conducted during a more suitable time (i.e. during the winter months), when one could concentrate on the counting of elephants alone, and not be encumbered with the search for Quelea colonies or other distracting requisites.

In reports to the Board it was repeatedly stressed that an exhaustive aerial census of elephants in the Park had now become an urgent necessity for obtaining more reliable population data, from which the reproductive potential of the population could be calculated.

This long-awaited aerial census became a reality during the first week of August, 1964.

TECHNIQUE EMPLOYED

After due consideration, it was decided to conduct the aerial survey during the dry winter season. In the first instance, the prevailing drought severely limited the water supply available for game, and consequently, large concentrations of elephant converged on these watering points. Secondly, most of the deciduous trees had lost their leaves on account of an intense cold spell experienced, and therefore, visibility from the air was at a premium.

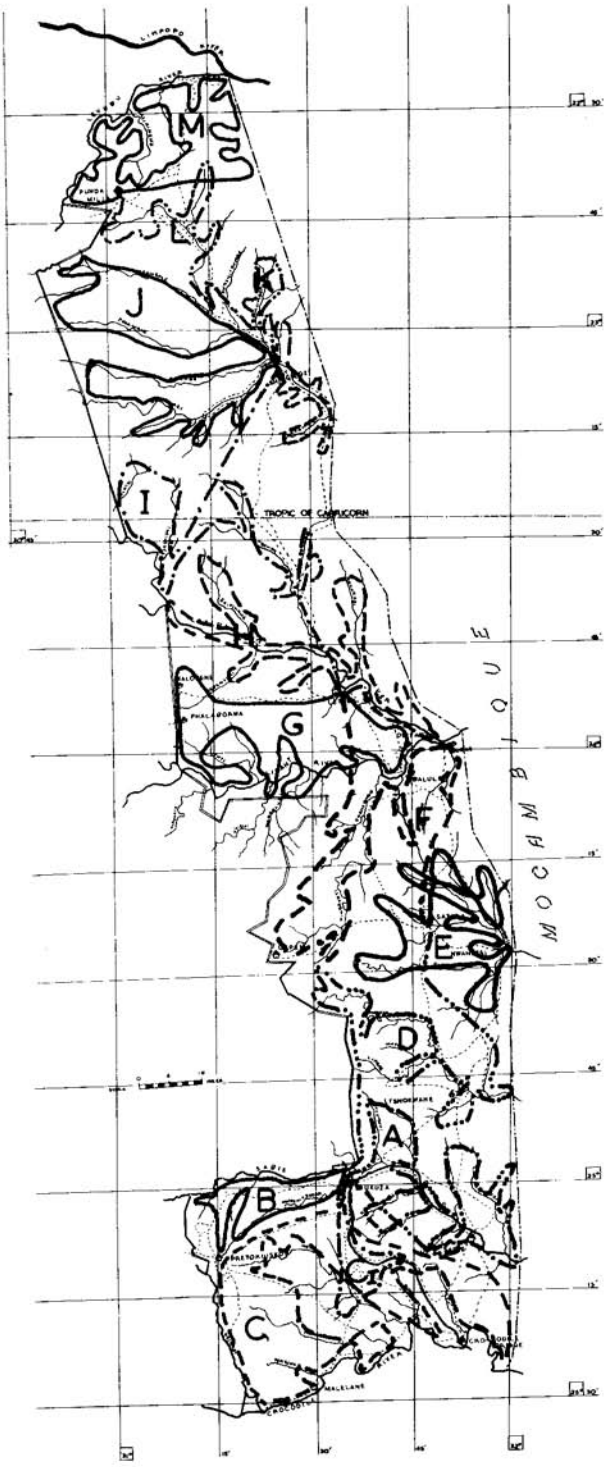
A three-seater Bell helicopter was used and was rented at considerable expenditure from Messrs. Autair. The survey lasted a week. Flights were executed by the pilot, Capt. C. Gill and he was accompanied by the Biologist of the Kruger National Park and the Board's official photokgrapher, Mr. R. Tibbs, who was responsible for photographing all elephant and buffalo, single or in herds, that were observed along the routes.

To obviate overlapping of herds and double counts, flight routes were so planned as to cover the water complex of an area in its entirety (cf. Map No. 1). The distances of the flight routes varied from 80-260 miles and daily flights were executed with military precision. All in all, the total distance covered was approximately 2,300 miles. An altitude of some 1,000 feet above ground level was maintained, providing an unobstructed field of vision of about $1\frac{1}{2}$ miles on either side. When considering that the Park covers a total area of 7,340 square miles, then a 3 mile wide transect along the 2,300 mile course made for a very comprehensive aerial survey.

Two cameras were used — a 35 mm. Nikon, fitted with 135 mm. telephoto lens, and a $2\frac{1}{4}$" x $2\frac{1}{4}$" Hasselblatt. One door of the helicopter was removed to facilitate unhampered photography.

Good photographic records of virtually all the elephant and buffalo herds were obtained, as manoeuvrability of the helicopter was such that the photographer could be placed in the correct position. Most of the photographs were taken from a height of 100-200 feet above ground level, but for the large elephant and buffalo herds it was necessary to rise to a height of about 500 feet.

From a safety point of view, and because animals could be herded into the open, the helicopter was infinitely better than a light 'plane', and for this type of aerial survey even better than the Piper Cub Special P.A. 11 or Cesna, recommended by Zaphiro, Longhurst and others.



Map 1.—Flight plan of routes covered by helicopter during aerial census of elephant and buffalo. 27.7.64-3.8.64.

The extra expenditure involved in the case of the helicopter was doubly justified by the fact that herds could be recounted and even analysed for herd composition and age structure without undue strain on the animals, or overtaxing the aircraft or the observers. This is a feature which cannot be overemphasised, and places the helicopter in a class of its own. Despite the high cost, the Board should be strongly advised to utilise a helicopter for all future game censuses of this nature.

About 600 negatives were later developed and enlarged to a constant size of 10" x 12" and 12" x 15" prints. From these it was possible to make a complete analysis of the age structure of elephant breeding herds, as well as an accurate check of aerial counts. A special Perspex grid was used to make accurate counts of the buffalo herds from the enlarged prints.

RESULTS

The final tally of elephant counted amounted to 2,374, but there remains some doubt as to whether all the elephant breeding herds in the Central District were counted. This total should therefore, be regarded as an absolute minimum and another 100 can safely be added to this.

The total estimate after a previous and less complete aerial surrvey in April, 1962, was 1,750. In the light of the present data, it is clear that this was a very conservative estimate and should have been quite a bit higher. The apparent increase of 624 is therefore not a natural one, but rather the result of improved census methods.

Temporary or permanent immigration from Portuguese East Africa and even Southern Rhodesia, could likewise have added to the increase.

Two elephant herds of 42 and 34 respectively, were seen during March, to enter the Kruger Park from Portuguese East Africa at Kalabyene spruit in the Lebombo Mountains.

The possibility is not excluded that in consequence of the severe drought, a considerable number of immigrant elephant entered the Park from the adjoining sandveld, leaving again after sufficient rain had fallen (cf. i.a. the 86 elephant bulls counted at Pafuri during the census).

To arrive at a figure of the residential elephant of the Park with any degree of certainty, it is desirable to conduct another census during the wet season. This, together with a marking operation, identifying a sufficient number of elephant in our border areas, would disclose the tempo and magnitude of seasonal or periodic influx.

Assistance could be solicited from the Portuguese authorities to report on marked elephant crossing the border. This matter is urgent, and should be carried into effect in the very near future, as it has a definite bearing on computations of the reproductive potential and carrying capacities for the different seasonal feeding ranges of our elephant population.

It is in any event important to recognise and eliminate all possible sources of misapprehension which might confuse the real issues determining this apparent significant increase in numbers.

Despite the fact that over the past few years, a few hundred bulls have been destroyed during control operations along the fence, or have died in fights, or from other injuries, there is still a slightly higher sex ratio (see below) of bulls compared to cows. There remains little doubt that this is a result of migrant bulls entering the Park from Portuguese East Africa particularly.

An analysis of the distribution of elephant in the different districts and sections of the Kruger Park is provided in Table 1 below. Definite localities recorded for breeding herds, smaller groups or solitary elephant are presented in Map No. 2 appended. It is significant that the distribution pattern shows a definite tendency for breeding herds to mass in the western half of the Park, north of the Olifants River and at Kingfisherspruit (with Makadze, Bangu and Olifants Gorge areas as exceptions). Unisexual (all-male) herds and solitary animals give preference to the Lebombo flats of particularly the Punda Milia, Shingwidzi (especially Dzombo) and Satara sections, and to Pafuri.

South of Tshokwane we have a mirror image of the above situation, and the breeding herds are found in the eastern sector of this area, viz. on the Lebombo flats and in the Mlondozi block, along the Sabi river east of Skukuza, the Nwatimhiri bush and at Gomondwane. The nomadic bulls, solitary or in herds, are found mostly near Malelane and westwards along the Sabi towards the tall grassland of the Pretoriuskop section.

This distribution of elephants follows a constant pattern which has developed through the years during the recolonisation process, and has been confirmed time and again by previous aerial surveys.

The western boundary — Tsende river — Groot Letaba river triangle, as well as the 5-mile wide strip on the south bank of the Letaba river, is the area most densely populated by elephant in the Kruger National Park, and also harbours the heaviest concentrations throughout the year. This is the area marked C on the accompanying Map, No. 4 (see below). The some 1,030 square miles of this area amounts to only one seventh of the total area of the Park, but affords sanctuary to nearly half of the Park's total elephant population.

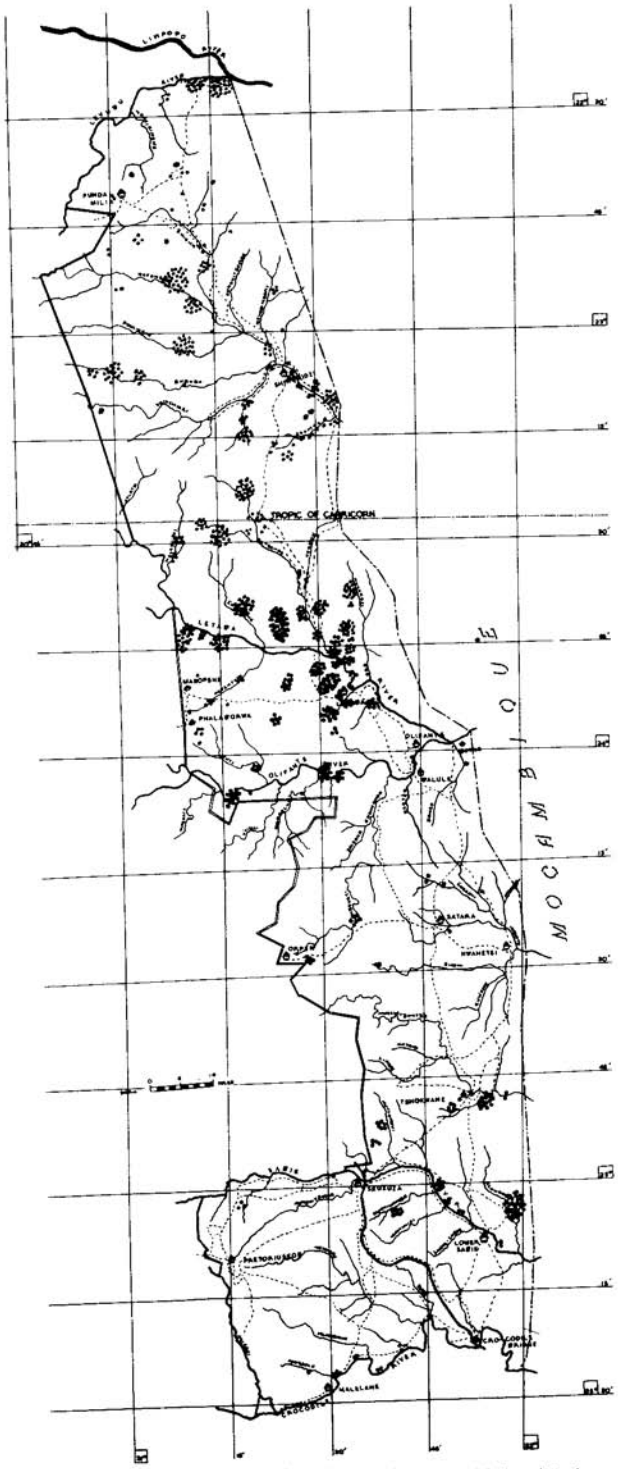
With the exception of the Skukuza-Lower Sabi river area, breeding herds, significantly, avoid areas which have been developed for tourism. In respect of the Skukuza-Lower Sabi area it needs to be noted that elephant have no other recourse, as both sides of the river are bounded by tourist roads. It is also significant that it is in this area where in later years the only four attacks on tourist cars by elephant have occurred—fortunately with no harm to the passengers.

This definite behavioural pattern in the distribution of elephant breeding herds, is of the utmost importance when considering further tourist development. The tourist, either directly or indirectly, becomes a definite biological factor in determining the destiny of the elephant population in such areas.

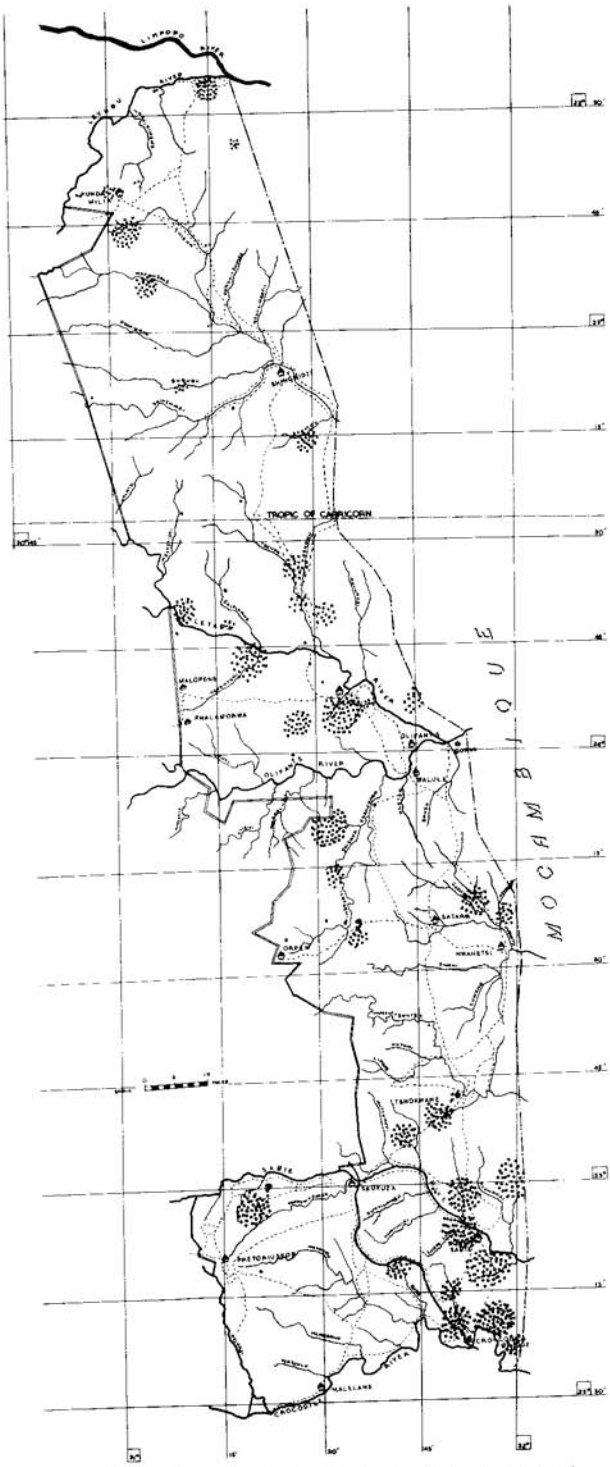
TABLE No. 1

DISTRIBUTION OF ELEPHANT IN THE VARIOUS DISTRICTS AND SECTIONS OF THE KRUGER NATIONAL PARK DURING THE AERIAL CENSUS IN AUGUST, 1964

	Calves less than one year	Juveniles and Sub-adults 1-11 years	Adult cows and bulls in breeding herds	Solitary bulls	TOTAL
1. Pretoriuskop section	—	—	—	9	9
% of number in breeding herds	—	—	—		
% of total	—	—	—	100%	100%
2. Malelane section	—	—	—	22	22
% of number in breeding herds	—	—	—		
% of total	—	—	—	100%	100%
3. Crocodile Bridge section	2	8	16	4	30
% of number in breeding herds	7.7%	30.8%	61.5%		100%
% of total	6.6%	26.7%	53.4%	13.3%	100%
A. SOUTHERN DISTRICT	2	8	16	35	61
% of number in breeding herds	7.7%	30.8%	61.5%		100%
% of total	3.3%	13.1%	26.2%	57.4%	100%
4. Tshokwane section	15	46	119	14	194
% of number in breeding herds	8.3%	25.6%	66.1%		100%
% of total	7.7%	23.7%	61.3%	7.2%	100%
5. Satara section	0	3	6	9	18
% of number in breeding herds	0.0%	33.3%	66.7%		100%
% of total	0.0%	16.7%	33.3%	50.0%	100%
6. Kingfisherspruit section	9	32	64	2	107
% of number in breeding herds	8.6%	30.5%	60.9%		100%
% of total	8.4%	29.9%	59.8%	1.9%	100%
B. CENTRAL DISTRICT	24	81	189	25	319
% of number in breeding herds	8.2%	27.6%	64.2%		100%
% of total	7.5%	25.4%	59.2%	7.8%	99.9%
7. Letaba section	51	194	291	90	626
% of number in breeding herds	9.5%	36.2%	54.3%		100%
% of total	8.1%	31.0%	46.5%	14.4%	100%
8. Mahlangene section	53	205	312	27	597
% of number in breeding herds	9.3%	35.9%	54.7%		99.9%
% of total	8.9%	34.3%	52.3%	4.5%	100%
9. Shingwidzi section	38	141	195	125	499
% of number in breeding herds	10.2%	37.7%	52.1%		100%
% of total	7.6%	28.3%	39.1%	25.1%	100.1%
10. Shangoni section	5	31	38	23	97
% of number in breeding herds	6.8%	41.9%	51.3%		100%
% of total	5.2%	31.9%	39.1%	23.7%	99.9%
11. Punda Milia section	3	7	16	149	175
% of number in breeding herds	11.5%	26.9%	61.5%		99.9%
% of total	1.7%	4.0%	9.1%	85.1%	99.9%
C. NORTHERN DISTRICT	150	578	852	414	1994
% of number in breeding herds	9.5%	36.6%	53.9%		100%
% of total	7.5%	29.0%	42.7%	20.8%	100%
TOTAL NUMBER IN KRUGER PARK	176	667	1057	474	2374
% of number in breeding herds	9.3%	35.1%	55.6%		100%
% of total	7.4%	28.1%	44.5%	20.0%	100%



Map 2.—Distribution of elephant in the Kruger National Park during aerial census, July, 1964.
● — 1 to 3 elephants.



Map 3.—Distribution of buffalo herds in the Kruger National Park during aerial census, July, 1964.
• — 1 to 10 buffalo.

The encroachment on the habitats of the shy and unsociable breeding herds are urgently warned against, as this can only spell disaster for both man and beast.

During the census a total of 9,664 buffalo was counted, and although three herds were not encountered along the flight routes, their numbers were well known. This brings the total buffalo population in the Kruger National Park to a minimum figure of 10,514.

A synopsis of the distribution of the different herds is provided in Table No. 2, and Map No. 3 pinpoints the localities where buffalo herds were recorded during the census.

The figure of 10,514 arrived at, correlates remarkably with our previous estimates of buffalo numbers, namely 9,600-10,550. (Pienaar, 1963).

It is apparent that in the past, observers were inclined to over-estimate buffalo concentrations. The largest single herd encountered, was one along the Crocodile river, east of the Ranger's quarters, which numbered 691. This represents only a portion of the well known 'large herd' of the Lebombo Flats. Presumably as a result of grazing pressure and overcrowded watering points, it would appear that this herd has now almost permanently split up. Four other herds were also seen in this area. They are as follows: Mabian-zau valley, south of Lower Sabi — 576; along the Orami spruit near Gomondwane, two herds of 224 and 385 respectively, and at Nkongoma —148, making a total of 2,024 for the section as a whole.

The aerial photographs of these herds were of such excellent quality and were so thoroughly checked, that these figures can be regarded as an absolute minimum. (Vide Fig. No. 1 and 2.)

The buffalo population of each district is in direct proportion to the total area of the district and consequently with that of the grazing potential of the area. Buffalo, unlike many other ungulates, are not limited in their range or otherwise adversely affected by the composition of the grazing. This can be clearly demonstrated by the distribution of the herds. This species cannot be classified as a selective grazer, and apparently does not mind utilising coarse grazing or old veld. This is in direct contrast to other species which are attracted to fresh burns.

The tall grassland around Pretoriuskop is the only area which does not harbour at least one resident herd of buffalo, but the indications are that this sour veld will also shortly be colonised by buffalo.

Twenty-three herds, totalling 100 or more were identified, of which 7 were recorded in the Southern District, 10 in the Central District and 16 in the Northern District.

Saliji mouth with 522 and Zwartkops with 516 yielded the largest single herds between the Sabi and Olifants rivers. In the Northern District the largest herds were 602 east of the Bulweni firebreak in the Letaba section, 479 along the Sokulungu firebreak near the Ngwenyene mouth and 419 near Mananganane in the Punda Milia section.

TABLE No. 2

DISTRIBUTION OF BUFFALO HERDS IN THE VARIOUS DISTRICTS AND SECTIONS OF THE KRUGER NATIONAL PARK DURING THE AERIAL CENSUS IN AUGUST, 1964

PRETORIUSKOP SECTION:			
Mbyamiti-Nwashitsaka-Mklari-herd	—	±450	(Not counted)
Samarôla spruit	—	10	
Total	—	460	
MALELANE SECTION:			
Bumi headwaters (Mpondo spruit) Including also Mbyamiti-Matimashewu-Mlambane-Mtomene-Randspruit	—	210	
Total	—	210	
CROCODILE BRIDGE SECTION:			
Nkongoma-Crocodile river	—	148	
Orami near Mkohlolo junction (Gomondwane)	—	224	
Orami at Nsosweni	—	385	
West of Nhlowe road in Mabianzau valley	—	576	
Dzueni on the Crocodile river	—	691	
Total	—	2024	
TOTAL FOR SOUTHERN DISTRICT	—	2694	
TSHOKWANE SECTION:			
Munweni, eastern boundary	—	336	
Saliji mouth	—	522	
Saliji immediately south of Gaben	—	446	
Lion pan	—	356	
Nwatindlopfu windmill	—	270	
Nwaswitsontso immediately west of Kumane	—	11	
Northern bank of Sabi river, immediately east of Nwatiwambu mouth	—	32	
Silolweni, south-west of Tshokwane	—	38	
Total	—	2011	
SATARA SECTION:			
Lower reaches of Mavumbye, south-east of Mananga	—	316	
Gudzane dam — Gudzane windmill — Mbadzane herd	—	±200	(Not counted)
Solitary bulls	—	±50	(Not counted)
Total	—	566	

KINGFISHERSPRUIT SECTION:

Shisakashangondzo, south of Houtboschrandt	—	178	
Zwartkops	—	516	
Pelwane mouth, Msala hill herd	—	±150	(Not counted)
Timbavati, (Mshatu firebreak drift)	—	10	
Timbavati, Pelwane mouth	—	10	
Timbavati, Msala hill	—	4	
Timbavati near western boundary	—	7	
Total	—	875	
TOTAL FOR CENTRAL DISTRICT		3452	

LETABA SECTION:

Mfuleni spruit, Letaba area	—	53
Headwaters Shinobyeni spruit, Lebombos	—	160
Malopanyane valley	—	168
Sokulungu firebreak near Ngwenyene mouth	—	479
Hlanganine spruit near dam site	—	289
East of Bulweni firebreak, south of Letaba rest camp	—	602
Misumane mouth, Olifants river	—	3
Nwanetzi drift, Letaba section	—	2
Mahudzi spruit, Letaba section	—	7
Total	—	1763

MAHLANGENE SECTION:

Baobab tree camp, Letaba river	—	49
Ngombasis mouth, Letaba river	—	330
Immediately west of Nshawu	—	245
West of Tsende river, south of Kaleka firebreak	—	108
Tsale windmill	—	3
Mhlopene mouth, Letaba river	—	4
Hlaruene mouth, Letaba river	—	9
Tsende-Nwambu confluence	—	4
Pambi, Mbyashishe	—	4
Total	—	756

SHANGONI SECTION:

Bububе middle firebreak junction	—	82
Mphongolo at Mbomene	—	256
Shingwedzi near Shangoni	—	6
Along Pukwane west of Dhili	—	7
Total	—	351

SHINGWIDZI SECTION:

Mahlati region	—	230	(It is possible
Tsange headwaters	—	186	that a herd
Shingwidzi west of Kokodzi mouth	—	3	along the
Mafayeni spring	—	19	Mphongolo was
		— .	not counted)
Total	—	438	
		— .	

PUNDA MILIA SECTION:

South-west of Jan's pan near Mananganane	—	419
Hape area, Pafuri	—	356
On the way to Matŭkwane, Punda Milia	—	120
Malonga spring	—	92
Levubu river west of Kowa-kulu mouth	—	20
Shisha, north of Muwawi	—	20
Shipudze spruit	—	18
Gumbandevu	—	15
		— .
Total	—	1060
		— .
TOTAL FOR NORTHERN DISTRICT	—	4368
TOTAL FOR KRUGER PARK	—	10,514

It would appear that buffalo also have a breeding season, albeit an extended one, which coincides with the more favourable grazing conditions prevailing during the summer months. It was therefore, significant that not a single new-born calf was seen in many of the large buffalo herds during the winter.

Should the permanent natural waterholes in this area dry up, then, as in the case of elephant breeding herds, the present complex of windmills will not suffice in the needs of the larger buffalo herds during a future bad drought. This fact should be borne in mind in the planning of future artificial water supplies, because with both elephant and buffalo the distribution and availabality of water and *NOT* grazing will be the ultimate limiting factor determining adverse population growth.

DISCUSSION

(i) *Productivity and Reproductive Potential of the Elephant Population in the Kruger National Park.*

The value of the recent aerial survey lies not only in determining the total number of elephant in the Kruger National Park, but in establishing, through interpretation of the excellent series of photographs (see Figs. 3, 4 and 5), also the number of young born during the past year (176), as well as the number of juveniles and sub-adults i.e. those between 1-11 years of age (667). This last figure was checked and rechecked but remained constant, and is of utmost importance, as it facilitates a number of interesting deduc-

tions. It is generally conceded by other workers that female elephants become sexually mature at the age of 12, and thereafter reproduce at intervals of four years up to the age of 70 or so. (Cf. Perry 1953, Carrington 1958, Spinage 1963, Bourlière & Verschuren 1960, Glover 1963, Buechner et al 1963, Simpson & Kinloch 1954, Buss & Brooks 1961 and others). An adult cow would thus produce about 15 young during her sexually active period. If, therefore, the number of young elephant calves (176) is considered in relation to the number of sub-adults (667), then the last figure appears to be much too low. This could be due to the fact that cows are not served immediately after weaning their last calves, and that a longer interval than four years therefore elapse between calving. There is also the possibility that young females might mature earlier. (A young elephant female was recently destroyed on the Lower Sabie road, and using Morrison-Scott's (1947) and Perry's (1953) tooth formula for determining age, this animal could not have been more than seven years old. Yet on microscopic examination of the ovaries, a number of *Corpora lutea,* in various stages of degeneration, were found. Whether this is a definite sign of sexual maturity or prepubertal ovulation is open to speculation and will only be clarified by further research.)

A higher mortality rate, particularly amongst newborn and very young calves in the large nomadic breeding herds, than has thus far been assumed for elephant in the natural state, is a more acceptable explanation for the disproportion in the above figures. To correlate the proportion of young calves to sub-adults counted would mean the postulation of a mortality rate amongst very young calves of as high as 33 per cent. It may be assumed that the majority would die during the first critical year of their lives. It would appear therefore that only two out of every three elephant calves reach maturity.

The question then arises why, if the mortality rate is that high, carcases are hardly ever found. If taken into consideration that an elephant weighs only 150-175 lbs. at birth, and that even with our large elephant population, no more than 50 calves would succumb annually, then it is more than likely that in the vast elephant habitat of the Kruger National Park, the majority of carcasses would never be found before being devoured by scavengers.

Future investigations on a series of developing sub-adult females will no doubt throw more light on this aspect.

Other workers in the field have also become conscious of the high mortality among young elephant calves, cf. Buss & Brooks (1961) in respect of elephant in Uganda:

"The 2,859 immature (approx. 24 percent) females in year 0 represents about a 36 per cent juvenile mortality. This appears to be a realistic mortality, considering that it is distributed over a nearly 12-year period."

In assessing the productivity of the elephant population in Uganda, Simpson & Kinloch (1954) have accepted the following seven hypotheses:

(1) Females become sexeually mature at 12 years of age.

(2) The gestation period is approximately 22 months.

(3) The interval between birth and the next conception, i.e. the suckling period, is about 2 years.

(4) The mortality amongst young elephant is 15%.

(5) The mortality amongst adult elephant is 10-20%. (Elephant are hunted in Uganda).

(6) 72 years is the maximum reproductive age.

(7) The basic sex ratio is 1 : 1.

It is important to determine the exact mortality rate of young elephant, as this will have to be considered in any cropping program that might be contemplated.

An analysis of the age structure of the elephant population in the Kruger National Park provides the following figures:—

Total number of elephant counted	2,374
Number of calves less than one year old	176
Juveniles and sub-adults from 1-11 years in breeding herds	667
Total number of elephant in breeding herds	1,900
Nomadic bulls (solitary or in groups)	474
Large bulls in breeding herds	59
Adult cows and young bulls in breeding herds = (1900—(667 + 59 + 176)	998
Number of adult breeding cows in breeding herds = 4 x 176 = 704 + 19 (i.e. 12-year-olds in calf and which will drop their young in their 13th year)	723
Number of senile cows in breeding herds (cf. Life table below)	18
Total number of adult cows	741
Number of young adult bulls in breeding herds (998—741)	257
Total number of adult bulls (257 + 59 + 474)	790
Surplus number of bulls over cows (despite present control at a rate of ± 40 bulls p.a.) = 790 — 741	49

The actual sex ratio here is probably also 1 : 1, but the surplus male animals represents an influx of nomadic bulls over the years from Southern Rhodesia (cf. Pafuri) and Moçambique (cf. the Lebombo Flats).

Glover (1963) has some interesting comments to make in this respect:

"If the sex ratio in the population is approximately 1 : 1 as is suggested by the present data there may be an 'excess' of males in the adult population. Since only one quarter of the adult females are likely to breed in any one year, then one-quarter of the adult males would be sufficient

to serve them. This means that from the breeding point of view three-quarters of the male population is redundant. This apparent excess of males in the population may be the reason why a moderately heavy toll of males by hunting or poaching can continue for long periods without seriously affecting population increase. It may also explain in part the all-male herds encountered in our surveys. However, until more data are obtained this must remain as little more than speculation."

The issue here is whether all-male herds and solitary bulls refrain from joining the breeding herds or whether they do periodically compete for the favours of cows in season. This would facilitate a rotation of sires and enhance natural selection which, in turn, could only benefit the population. The only way to solve this particular problem would be to mark a sufficient number of solitary bulls and study their subsequent movements accurately.

The aerial census totals were compared and checked with observations of elephant breeding herds made on foot over the years. These comparisons revealed a striking correlation:

	Aerial census totals	Ground observations
GROUP A.		
Number of animals counted	1900	1433
Number of adults and young animals in breeding herds	1724	1276
Number of small calves in breeding herds	176	157
% Small calves in breeding herds	9.26%	10.95%
GROUP B.		
Number of animals counted	1900	570
Adult cows, old and young adult bulls in breeding herds	1057	324
Juveniles and Sub-adults 1-11 years old	667	185
Small calves less than one year old	176	61
% Adult cows and bulls in breeding herds	55.63%	56.84%
% Juveniles and Sub-adults in breeding herds	35.10%	32.45%
% Small calves in breeding herds	9.26%	10.70%
GROUPS A AND B.		
Grand total of animals in breeding herds	1900	2003
Number of small calves in breeding herds	176	218
% Small calves in breeding herds	9.26%	10.88%

The percentage of small calves less than one year old of the grand total of elephant counted during the aerial census amounts to 7.4% (cf. Table 1.)

The above analysis of the age structure of breeding herds in the Kruger National Park conforms remarkably well with figures relating to other parts of Africa.

The annual increase in parts of the Belgian Congo is 9.2% (Bourlière and Verschuren (1960)).

Buechner, Buss, Longhurst and Brooks (1963) remark about elephant in the Murchison Falls National Park in Uganda: "As a guide to regulation of numbers, an increment of 7 to 8 percent provides a conservative basis for determining annual harvests. Three (aerial) counts in which a concerted effort was made to ascertain the number of calves showed 7.1, 7.2, and 7.3 per cent young, with no indication of any significant peaks of parturition during the calender year."

Buss and Brooks (1961) also hold the opinion that: "On the basis of 3,221 ground and aerial observations, the proportion of calves to other elephants observed in this region of Uganda during 1959 was approximately 7.5%."

It is, however, pointed out by Spinage (1963) that: "In Uganda it is estimated that the annual production of calves is of the order of 7.5% of the total population, but this does not necessarily mean that the population rate of increase is as high as that. It is likely to be much less."

Glover (1963), quoting Sheldrick and Parker on elephant in the Tsavo Park in Kenya, found that "A statistical analysis of the records showed that there is a close correlation ($r=0.90$) between the number of adult females and the number of juveniles within the nursery herds, and that on the average there would be some 8 juveniles of different ages up to about 12 years to every 10 adult females, and in addition there could be 4 young males which were difficult to classify as adult or juvenile."

This compares well with the local situation where for every ten adult cows in a breeding herd, we find 9.0 young animals (1-11 years old), 11.4 young animals plus year-old calves and 3.5 young adult bulls.

From the above-mentioned data, it is evident that reproduction of elephant in the Kruger National Park follows the same basic pattern which prevails throughout the rest of Africa.

The information obtained in respect of herd composition during the aerial survey may therefore be used as a safe and reliable basis for future estimates of expected annual increase, and would also function in the determining of quotas for any envisaged cropping operations.

A simple and practical method whereby accumulative annual increases in the elephant population for the next twenty years may be deduced, is set out in the life table below. This was compiled with the knowledge at our disposal. To simplify computations, bulls were left out altogether and only the population growth of 1162 elephant cows is figured. As the sex ratio here is also 1 : 1, however, the figure for annual increase obtained from the table, should be doubled.

Should it be decided to implement elephant control in the Kruger National Park immediately, it is obvious that only 59 x 2, i.e. 118, animals of all age groups, and an equal number of both sexes, i.e. 4.9 per cent

LIFE TABLE OF 1,162 ELEPHANT COWS (741 ADULTS OF WHICH 723 WERE SEXUALLY ACTIVE: 88 YOUNG CALVES) IN THE KRUGER NATIONAL PARK OVER A PERIOD OF 20 YEARS

AGE GROUP IN YEARS	TIME-LAPSE IN YEARS																				
	1964	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Calves of present season	88	94	94	94	94	105	105	105	105	121	121	121	121	146	148	148	148	173	179	179	179
1	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99	99	99	115	120	120
2	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99	99	99	115	120
3	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99	99	99	115
4	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99	99	99
5	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99	99
6	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97	99
7	28	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81	97
8	28	28	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81	81
9	19	28	28	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81	81
10	19	19	28	28	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81	81
11	19	19	19	28	28	28	28	41	41	41	41	59	63	63	63	63	70	70	70	70	81
12	19	19	19	19	28	28	28	28	41	41	41	41	59	62	63	63	63	70	70	70	70
13	**18**	**19**	**19**	**19**	**19**	**28**	**28**	**28**	**28**	**41**	**41**	**41**	**41**	**59**	**63**	**63**	**63**	**63**	**70**	**70**	**70**
14	18	18	19	19	19	19	28	28	28	28	41	41	41	41	59	63	63	63	63	70	70
15	18	18	18	19	19	19	19	28	28	28	28	41	41	41	41	59	63	63	63	63	70
16	18	18	18	18	19	19	19	19	28	28	28	28	41	41	41	41	59	63	63	63	63
17	**17**	**18**	**18**	**18**	**18**	**19**	**19**	**19**	**19**	**28**	**28**	**28**	**28**	**41**	**41**	**41**	**41**	**59**	**63**	**63**	**63**
18	17	17	18	18	18	18	19	19	19	19	28	28	28	28	41	41	41	41	59	63	63
19	17	17	17	18	18	18	**18**	**19**	**19**	**19**	**19**	28	28	28	28	41	41	41	41	59	63
20	17	17	17	17	18	18	18	18	19	19	19	19	28	28	28	28	41	41	41	41	59
21	**16**	**17**	**17**	**17**	**17**	**18**	**18**	**18**	**18**	**19**	**19**	**19**	**19**	**28**	**28**	**28**	**28**	**41**	**41**	**41**	**41**
22	16	16	17	17	17	17	18	18	18	18	19	19	19	19	28	28	28	28	41	41	41
23	16	16	16	17	17	17	17	18	18	18	18	19	19	19	19	28	28	28	28	41	41
24	16	16	16	16	17	17	17	17	18	18	18	18	19	19	19	19	28	28	28	28	41
25	**15**	**16**	**16**	**16**	**16**	**17**	**17**	**17**	**17**	**18**	**18**	**18**	**18**	**19**	**19**	**19**	**19**	**28**	**28**	**28**	**28**
26	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19	19	19	19	28	28	28
27	15	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19	19	19	19	28	28
28	15	15	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19	19	19	19	23
29	**14**	**15**	**15**	**15**	**15**	**16**	**16**	**16**	**16**	**17**	**17**	**17**	**17**	**18**	**18**	**18**	**18**	**19**	**19**	**19**	**19**
30	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19	19	19
31	14	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19	19
32	14	14	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18	18	18	18	19
33	**13**	**14**	**14**	**14**	**14**	**15**	**15**	**15**	**15**	**16**	**16**	**16**	**16**	**17**	**17**	**17**	**17**	**18**	**18**	**18**	**18**
34	13	13	14	14	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18	18	18
35	13	13	13	14	14	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18	18
36	13	13	13	13	14	14	14	14	15	15	15	15	16	16	16	16	17	17	17	17	18
37	**12**	**13**	**13**	**13**	**13**	**14**	**14**	**14**	**14**	**15**	**15**	**15**	**15**	**16**	**16**	**16**	**16**	**17**	**17**	**17**	**17**
38	12	12	13	13	13	13	14	14	14	14	15	15	15	15	16	16	16	16	17	17	17
39	12	12	12	13	13	13	13	14	14	14	14	15	15	15	15	16	16	**16**	16	17	17
40	12	12	12	12	13	13	13	13	14	14	14	14	15	15	15	15	16	16	16	16	17
41	**11**	**12**	**12**	**12**	**12**	**13**	**13**	**13**	**13**	**14**	**14**	**14**	**14**	**15**	**15**	**15**	**15**	**16**	**16**	**16**	**16**
42	11	11	12	12	12	12	13	13	13	13	14	14	14	14	15	15	15	15	16	16	16
43	11	11	11	12	12	12	12	13	13	13	13	14	14	14	14	15	15	15	15	16	16
44	11	11	11	11	12	12	12	12	13	13	13	13	14	14	14	14	15	15	15	15	**16**
45	**10**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**	**13**	**13**	**13**	**13**	**14**	**14**	**14**	**14**	**15**	**15**	**15**	**15**
46	10	10	11	11	11	11	12	12	12	12	13	13	13	13	14	14	14	14	15	15	15
47	10	10	10	11	11	11	11	12	12	12	12	13	13	13	13	14	14	14	14	15	15
48	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**	**13**	**13**	**13**	**13**	**14**	**14**	**14**	**14**	**15**
49	**10**	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**	**13**	**13**	**13**	**13**	**14**	**14**	**14**	**14**
50	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13	13	13	13	14	14	14
51	10	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13	13	13	13	14	14
52	10	10	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13	13	13	13	14
53	**9**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**	**13**	**13**	**13**	**13**
54	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13	13	13
55	9	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13	13
56	9	9	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12	12	12	12	13
57	**9**	**9**	**9**	**9**	**9**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**	**12**	**12**	**12**	**12**
58	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12	12	12
59	9	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12	12
60	9	9	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11	11	11	11	12
61	**8**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**11**	**11**	**11**	**11**
62	8	8	9	9	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11	11	11
63	8	8	8	9	9	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11	11
64	8	8	8	8	9	9	9	9	9	9	9	9	10	10	10	10	10	10	10	10	11
65	**7**	**8**	**8**	**8**	**8**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**10**	**10**	**10**	**10**	**10**	**10**	**10**	**10**
66	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10	10	10	10	10	10	10
67	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10	10	**10**	10	10	10
68	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10	10	10	10	10
69	**7**	**7**	**7**	**7**	**7**	**8**	**8**	**8**	**8**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**9**	**10**	**10**	**10**	**10**
70	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10	10	10
71	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10	10
72	7	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9	10
Senile 73	6	7	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9	9
Senile 74	6	6	7	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9	9
Senile 75	6	6	6	7	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9	9
Dead	6	6	6	6	7	7	7	7	7	7	7	7	8	8	8	8	9	9	9	9	9
TOTALS: Calves	88	94	94	94	94	105	105	105	105	121	121	121	121	146	148	148	148	173	179	179	179
TOTALS: Juveniles and Sub-adults	333	373	417	461	496	531	573	615	644	673	713	753	775	793	827	863	899	928	973	1023	1073
TOTALS: Adults	741	754	767	780	801	822	843	864	898	932	966	1000	1051	1106	1161	1216	1270	1331	1392	1453	1514
TOTALS: Totals	1162	1221	1278	1335	1391	1458	1521	1584	1647	1726	1800	1874	1947	2045	2136	2227	2317	2432	2544	2655	2766
PERCENTAGES: Calves	7.6%	7.7%	7.4%	7.0%	6.8%	7.2%	6.9%	6.6%	6.4%	7.0%	6.7%	6.5%	6.2%	7.1%	6.9%	6.7%	6.4%	7.1%	7.0%	6.7%	6.5%
PERCENTAGES: Juveniles and Sub-adults	28.7%	30.5%	32.6%	34.5%	35.7%	36.4%	37.7%	38.8%	39.1%	39.0%	39.6%	40.2%	39.8%	38.8%	38.7%	38.7%	38.8%	38.2%	38.3%	38.6%	38.8%
PERCENTAGES: Adults	63.7%	61.8%	60.0%	58.5%	57.5%	56.4%	55.4%	54.6%	54.5%	54.0%	53.7%	53.3%	54.0%	54.1%	54.4%	54.6%	54.8%	54.7%	54.7%	54.7%	54.7%
PERCENTAGES: Total	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%	100.0%
	1964	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	1984

The figures in bold type indicate the cows of each age group that calve during that particular year.

Mortality amongst calves is estimated at 33%, and for the purpose of the Life Table this loss is expected during the first critical year.

Mortality amongst adults and older calves is as yet insignificant in the Kruger National Park and is disregarded.

Among adult bulls a few are killed annually in fights.

A few also died of anthrax and accidents.

of the total number of elephants, needs be cropped to maintain the present population level of 2,374.

Petrides and Swank (1965 in press) also calculated the rate of hunting that could be sustained by an elephant population in the Queen Elizabeth National Park in Uganda as 4.8% of the standing crop biomass.

Where the kill is restricted to adults, only 2.6% of all elephants should be harvested per year, according to these workers.

The desirability of, and to what lengths the elephant population growth should be allowed to proceed unchecked in the Kruger National Park, will be discussed in the chapter on carrying capacity and grazing potential hereunder.

CARRYING CAPACITY AND GRAZING POTENTIAL FOR ELEPHANT IN THE KRUGER NATIONAL PARK

In calculating the carrying capacity of a specific area or vegetational zone in a National Park, in respect of a particular herbivore or group of herbivores, it is very necessary to distinguish between the theoretical and the practically applicable. In theory, an area may be assessed under the strictly controlled and often ideal conditions, which obtains in agricultural spheres. In practice, on the other hand, the carrying capacity of an area is not necessarily determined by available grazing, but often by the availability of water and distribution of watering points, the intensity of tourist traffic, the maintenance of boundaries, fences and so forth.

It would be futile to try and determine the carrying capacity of an enormous expanse such as the Kruger National Park on accepted agricultural standards, i.e. cattle units per morgen or other unit area. We are dealing here with a vast area of divergent and changing vegetational zones, each with adequate or less adequate water supplies, network of roads and tourist camps, unnatural boundaries and a variety of competing herbivorous species (including small mammals and insects, the impact of which on the available food supply may be vast).

The agriculturalist would compute the optimum stocking rate of his farm or experimental plot in terms of one, or at most, a few animals not in direct competition for grazing. Agriculturally speaking, an even distribution and intensity of grazing could also be arranged by means of a camp-system and artificial watering points, and it would not be feasible to compare the carrying capacity of land for cattle to that for, say buffalo, where these animals naturally graze uncontrolled and in an area with unstable water supplies. It is obvious that under natural conditions the carrying capacity for buffalo would be much lower on the same veld type than for cattle under controlled management.

Attempts have already been made to determine the carrying capacity of land for elephant in terms of cattle units per morgen or other unit area. Glover (1963) speculates as follows with regard to Eastern Tsavo, an area

of ± 5,000 square miles and harbouring 7,000 - 10,000 elephant: "In the neighbouring, better-watered region of Ulu-Machakos, the Agricultural Department of Kenya has estimated that the carrying capacity of the bush for free-ranging cattle is about 15 acres to the beast, although Pereira et al (1961) have shown that with very intensive management some 4-6 acres a beast can be attained. However, elephants cannot be managed in the same way as cattle, so it seems reasonable to accept 15 acres per beast for domestic cattle as a starting point. An average elephant at some 6,000 lbs. weighs about 10 times as much as local cattle at some 600 lbs., so one elephant may be taken as the equivalent of 10 of the local cattle. If the elephant eats as much in proportion as domestic stock, and the data provided by Buss (1961) and Napier-Bax and Sheldrick (1963) would support this, then it would require 150 acres or one quarter of a square mile to maintain it.

In other words, four elephants could apparently be maintained on one square mile of this type of range. But an elephant is a very rough feeder and spoils much more than it eats, so by assuming that the damage done is equal to the amount eaten, such range could be estimated to support only two elephants per square mile. Much, if not most, of the Park is not so well watered as the Ulu-Machakos range, so that one elephant per square mile is apparently about the highest stocking rate possible in the Park throughout the year, and it may be less, particularly when one remembers that other animals use the same range. Obviously more could be carried during and immediately after the rains, but as already mentioned, any figure based on only the best conditions would be unreal and unwise as a foundation of management practice.

The elephant problem of Tsavo now becomes clearer. The eastern part of the Park may be able to carry only some 5,000 elephants in reasonable safety. The June and September 1962 counts show that between 5,400 and 9,400 of these animals may be found there and even more recent counts suggest that there is a semi-permanent population of about 7,000 beasts in the area. If the habitat is to be preserved in its present form, for all inhabitants of the Park, then the number of elephants will have to be controlled".

Burton (1963) believes that 4 elephant to the square mile is not an excessive figure for areas with sufficient variety of vegetation types and an ample distribution of watering points.

Buechner, Buss, Longhurst and Brooks (1963) found that the Murchison Falls National Park (± 1,500 sq. miles) harboured an average of 7,000-8,000 elephant over 32 months, i.e. 4.5 to 5.5 sq. mile. These workers, however, point out that elephant have here exceeded the optimum carrying capacity of the land and have contributed significantly in changing the vegetation from a forested aspect to open grassland: „Seemingly, the elephants have been concentrating in ever-increasing numbers in the Park area, and it was evident at the termination of the study that their numbers must be regulated

Total elephant counted during the census	2,374
Number of calves less than one year old	176
If a basic sex ratio of 50 : 50 is accepted, then the number of female calves less than one year is	88
Total juveniles and sub-adults in the breeding herds (i.e. 1-11 year olds)	667
Therefore the number of juvenile and sub-adult female calves of 1-11 year old is	333
Adult cows and young adult bulls in breeding herds	998 (1057-59)
Large bulls in breeding herds	59
Nomadic bachelor bulls	474
Number of adult cows ± = 4 x 176 = 704 (breeding cows) + 19 (12-year old sexually mature cows, but which only calve in their 13th year on account of the 22 month gestation period)	723
Number of senile cows	18
Total adult cows	741
Number of young adult bulls in breeding herds = 998 — 741	257
Total number of adult bulls = 474 + 257 + 59	790
Surplus bulls over cows (despite present rate of control of ± 40 annually) = 790 — 741	49*

* Immigrant bulls through the years from Southern Rhodesia (cf. Pafuri) and Portguese East Africa (cf. the Lebombo Flats) probably represent the surplus.

to avoid damage to the vegetation, and the future welfare of the population of elephants".

The Wankie Game Reserve in Southern Rhodesia covers an area of some 5,000 sq. miles and carries a total semi-residential population of about 5,000 elephants, i.e. 1/ sq. mile. The authorities are concerned about the available water supplies. The extensive destruction and changing of the vegetation prevalent in Tsavo and Murchison Falls are, however, here restricted to the areas surrounding the watering points.

It would appear that theoretically a carrying capacity of 1-4 elephants per sq. mile, depending on the existing vegetation, available water and size of the area, obtains for the majority of elephant habitats in Africa.

To arrive at a more exact figure of absolute carrying capacity for elephants of any particular area, it would be necessary to know more about their daily food requirements, food preferences, seasonal movements and so on, than is the case at present.

It is known that full-grown elephants in circusses and zoos can subsist on about 100 lbs. hay per day together with smaller amounts of additional food such as oats, vegetables, etc. (Carrington, 1958). These are resting animals, however, and in most cases, cows. The dry weight of food consumed by an adult bull per day would undoubtedly be at least twice this amount, and in the natural state where the animal is continually on the move, even more. It would, therefore, not be excessive to expect that under normal conditions an adult elephant would consume some 300 lbs. dry food material per day, i.e. nearly 15 times as much as adult domestic cattle.

This massive appetite is supplemented by an equally huge thirst and an adult elephant can drink from 30-50 gallons per day. It seems possible though, that elephants do not drink every day.

Whilst cattle, sheep or horses digest 50-70% of their food intake, elephants only digest 44% (Benedict 1936).

Buss (1961) during an extensive study of the feeding habits of elephants in Uganda, found that the stomach contents of a fully fed animal constituted about 5-6% of the total body weight. Stomach contents weighed as much as 325 lbs. (The stomach and contents of a 13,248 lbs. elephant bull shot in the Kruger National Park, weighed 524 lbs.)

Napier-Bax and Sheldrick (1963) found that the stomach of a tame elephant at Voi was emptied every 12 hours, and elephant would therefore, presumably consume at least double the weight of their stomach contents over a period of 24 hours.

Buss (1961) determined that 88% of the total food mass of 71 elephants in the Murchison Falls National Park in Uganda, consisted of grass. A mere 10% of the food material that was utilised consisted of leaves, twigs, bark and fruits of trees and shrubs, whilst herbs and bulbs made up 2% of the total food intake. Woodland areas were mainly utilised as shelter and for shade, but not as an important source of food. With the onset of the rain, elephants immediately returned to their favourite grazing areas (the open grassland savanna).

In Tsavo, Napier-Bax and Sheldrick (1963) also found that grass creepers and herbs constituted the main bulk of ingested food. The most extensive damage to trees and shrubs occurred during the dry season when herbs were absent and when the nutritive value of grasses was at its lowest ebb.

Nicholson (1954) states that the food of elephants in Tanganyika, during the early rainy season, consists of 75% grass, and that grass is likewise an important item of food during the rest of the year.

It has been found over the years that elephants in the Kruger National Park exhibit the same food affinities and grazing cycles as elephants elsewhere in Africa. Here, grass and certain herbs are also utilised in excess during the rainy season, whilst roots and bulbs are also dug from the ground. Many varieties of wild fruits, particularly marula and palm nuts are purposely selected. Leaves, bark and even whole twigs are browsed particularly during fall, although large quantities of grass, such as *Panicum* and other species that retain their nutritive value in the dehydrated state, are still eaten. During the dry winter months elephants concentrate mainly along the rivers and permanent waters, where they consume large quantities of reed (*Phragmitis communis*), waterloving grasses, sedges and the leaves, bark and twigs of riverine trees and shrubs. Trees and shrubs away from the water, which retain dry leaves long after the onset of the winter, such as *Colophospermum mopane* and others, are also heavily browsed. In areas where veld fires have destroyed the grazing, it is noticeable that elephants almost immediately set to pushing over trees that have escaped the fire

and retained their leaves. They soon leave such areas however, and do not return until the lower vegetation strata have recovered.

Elephants will often seek out and eat the charred tips of twigs and branches of trees and shrubs in areas ravaged by veld fires before wandering off to more favourable pastures.

In the mopaniveld, covering most of the northern portions of the Kruger Park, *Colophospermum mopane* is one of the staple foodplants of elephants. Here it is significant that the scrub form is much more heavily browsed by the mass of the population i.e. the breeding herds. Nomadic lone bulls and small bachelor herds that remain in one area for any length of time, are more inclined to inflict damage to the tree stratum than is evident in the habitats of the breeding herds. In other vegetation types, such as the strips of *Combretum*-veld, that alternate with the Mopani-covered areas, and where scrub forms or coppice growth is less prevalent, greater damage is done to the trees.

A list of well over a hundred trees, shrubs, herbs and grass species that are utilised by elephants to a greater or lesser degree, has been recorded by Brynard and Pienaar (1960). The list will most certainly be extended once the results of the present microscopic examination and qualitative analysis of stomach contents are published. Pending such detailed information regarding the food habits of elephants, it is not possible to provide a complete check list of food plants utilised, in order of preference, indicate seasonal variations and to determine the relative proportions (% bulk) of each species utilised.

Should it be possible to obtain an indication of the expected yield of each utilised plant species per unit area during the growing season (a virtual impossibility in an area of the extent of the Kruger National Park), it may be possible to arrive at an absolute figure of carrying capacity for elephants in respect of each vegetation type. Even then, this figure would be largely theoretical and of academic interest only, in view of the fact that other influences such as competing species, would be ignored. In any event, absolute utilisation in an area such as the Kruger National Park with its limited water supplies and heavy tourist traffic, would be quite impossible.

It is clearly evident from a recent study by Petrides and Swank (1965 in press) in the Queen Elizabeth Park in Uganda, that elephants eat relatively little per unit of body weight and that assimiliation is poor when compared for instance with beef cattle. They nevertheless maintain a phenomenally high standing crop and although their growth rate is low, their production of biomass per unit area is four-tenths that of beef cattle and they manage this on a coarse diet.

Because of limited food requirements per unit biomass of elephants, there is danger of overuse and damage to the range if these animals are replaced by an equal biomass of smaller herbivores which have greater caloric-intake requirements per unit of weight.

It seems safe to assume therefore that an optimum carrying capacity

figure for any given range in terms of elephant biomass would already (grossly) exceed the safe carrying capacity of the same range for an equal biomass of any smaller grazing or browsing species or group of species.

When all is considered and done, one aspect becomes abundantly clear, i.e. that there is as yet no evidence of an "overpopulation" of elephant in the Kruger National Park in the sense that they are destroying or changing the vegetational milieu of the habitat. Elsewhere in Africa where elephants are herded together in confined areas as a result of interference by man (hunting, development, etc.), mention is made by research workers of the fact that forested or woodland zones are slowly changing to open grassland savanna.

Buechner and Dawkins (1961) state that: "In Murchison Falls National Park, located in tropical Uganda, East Africa, luxuriant wooded grasslands, *Terminalia* woodlands, *Cynometra* rainforests, and riparian forests are in the process of conversion to treeless grasslands through the combined action of elephants and fire".

In Tsavo, Glover (1963) finds that: "The damage caused by the overcrowding of elephant after several years of drought has prompted the study of the number of distribution of the elephants within its confines and the possible "safe" carrying capacity.

Not all the damage is caused directly by the animals; some, probably the most permanent, is caused by fires which sweep over the regenerating vegetation — becoming increasingly devastating as the woody vegetation recedes".

With the exception of a few small areas (cf. Pafuri and portions along the Letaba and Shingwidzi rivers) there is not the slightest indication in the Kruger National Park of a change from woodland or bushveld to grassland, either as a direct or indirect result of elephants. The generally held view that elephants have passed their optimum number in the Kruger National Park (cf. Wager, 1963 and others) appears without ground and is completely contradicted by a recent very extensive survey of the general effect and damage by elephants on the different vegetational strata in the various veld types of the Kruger National Park. (A separate report on these findings will soon be published).

In fact, it would appear that the exact opposite to a state of habitat destruction prevails. There are ominous indications that bush encroachment and overgrowth of open grassland areas is proceeding on an increasing scale over large portions of the Park. Many more trees and shrubs germinate and may even reach maturity than are destroyed by elephants and all other causes.

The gradual encroachment of bush on once open grassy plains and tree-studded savannas may in part be the result of the total absence of elephant from the Transvaal Lowveld for nearly a century. Since the arrival of the white man, continuous injudicious burning has resulted in the thinning

out of trees, as well as the stimulating of coarse grass growth and coppice formation. Since 1946, when accidental veld-fires were conscientiously extinguished and even controlled burning was abandoned for a seven year period, the suppressed fire resistant shrubs were afforded the opportunity of developing into vigorous and thick coppices (cf. conditions around Pretoriuskop and on the Lebombo flats).

Burton (1963) rightly points out in this respect that: "Before the coming of the white man the elephant must have been, through sheer bulk and strength, undisputed lord of its terrain, free to wander where it fancied. In those unfenced days elephants could have been seen in true perspective as the chief assistants of fire in the conversion of forest to grassland.

Since they are equally at home in either, they can hardly be said to destroy their own habitat when they help one type to give way to another. Only man, by confining them to small isolated territories, can cause them to remain so long in one place as to destroy the vegetation there".

When it is considered that nearly half of the Park's elephants are found in a portion of the northern mopani veld which amounts to only one-seventh of the total area of the Park, and that there is no indication here of the vegetational aspect undergoing any marked change or is suffering irreparable damage from the depredations of elephant, then it becomes obvious that the theoretical carrying capacity of the Kruger National Park for these animals is vast, and that the numbers have not nearly reached saturation point.

It is also clear that such a stage of saturation, where elephants will be actively destroying their habitat, is but a fantasy, and can hardly develop nor will it be allowed to develop under present conditions in the Kruger Park.

In view of its immense size and strength the elephant represents a climax species in the mammalian community of the Lowveld. Should it be allowed to reproduce unabated until it reaches a state of delicate balance with its available food resources, it would oust all competing herbivorous species, not only as far as food supply is concerned but, at an even earlier stage, also for want of adequate water resources.

Considering all factors in their proper perspective, what would then be a practical approach towards the rapidly-growing elephant population in a sanctuary such as the Kruger Park?

It must be decided, in the first instance, whether the present numbers and distribution of elephant is such that their continued survival is assured. Secondly, cognisance should be taken of the fact that elephants are not the only animals which are protected in the Kruger National Park, but in addition, a host of other herbivorous species have found sanctuary within its boundaries. Furthermore, certain vegetational zones and types, the rare flora of which is unique for the Kruger Park and even for the Republic of South Africa, merit absolute protection, despite their loss as a possible source of food to the elephant population. Thirdly, it should be conceded that the

ultimate limiting factor determining population growth of elephant and other herbivorous species, is the poor distribution of ample and stable water resources, particularly during times of drought. This is a factor which can be regulated to some degree by providing permanent artificial watering points, but even such remedial measures have a limit, and particular care should be taken that large and abundant species such as elephant and buffalo do not suppress the smaller and rarer forms during crisis times.

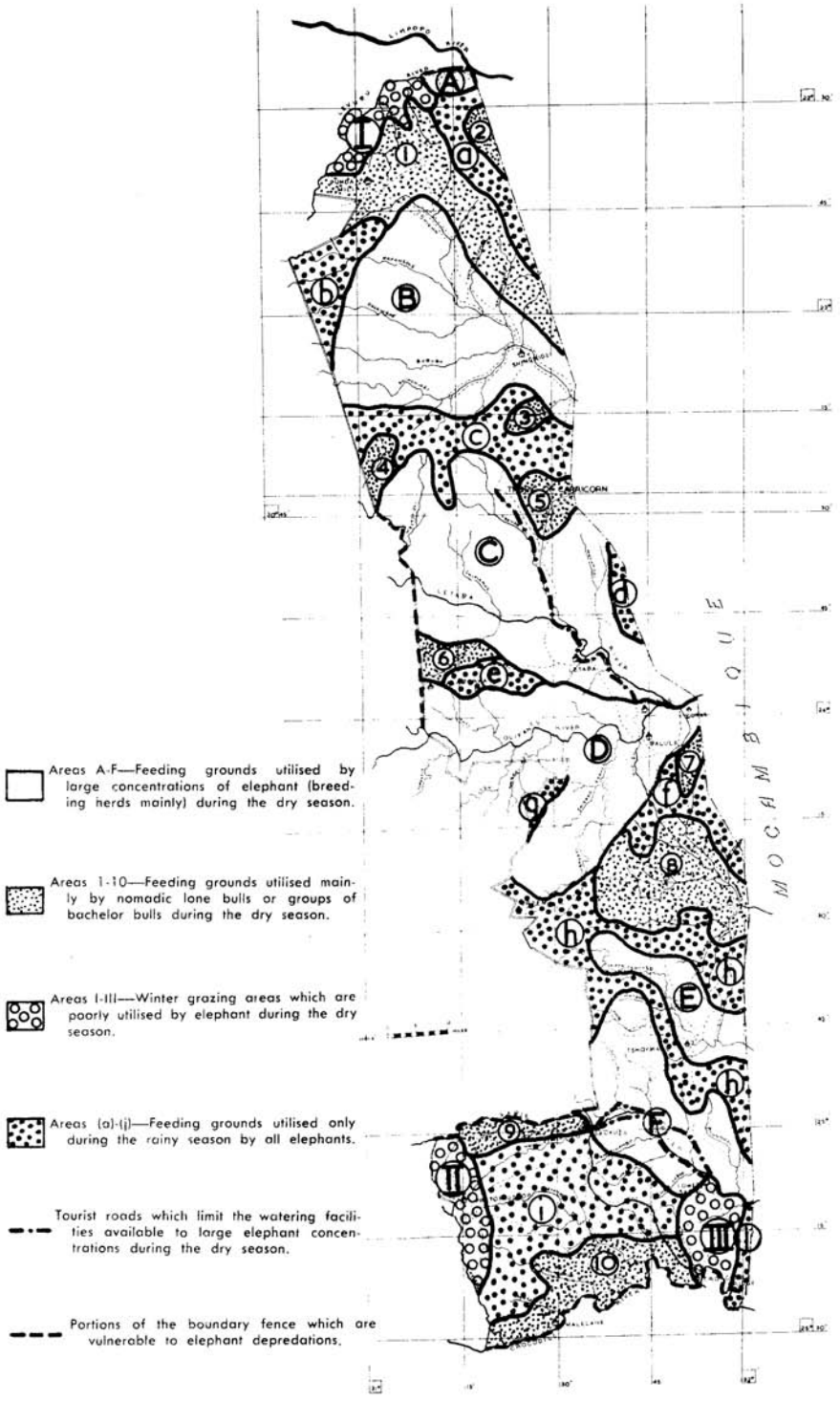
The risk aspect of huge and potentially dangerous animals such as elephants in respect of visitors, particularly where the Kruger National Park boasts a widespread and heavy tourist traffic, should certainly also be considered in any calculation of admissible limits of population-increase.

On the other hand, the participation of elephants in the economy of the natural biome should be investigated and acknowledged. It is essential and desirable that the important ecological function of elephants in each of the respective sections of the Park is properly valuated — amongst others, their role as natural "pruning shears" and eradicators of undesirable scrub; combatants of erosion by the trees and shrubs that they push over on denuded surfaces; agriculturists by virtue of the soil that is ripped open and aerated when they push over trees or dig up roots; distributors and establishers of new trees by the seeds germinating in their dung; road engineers and navigators by the communication routes which they tread out along the easiest gradients and shortest distance between e.g. watering points; as well as their considerable symbiotic function as benefactors of other species, such as the provision of food for lesser browsing species when trees are pushed down in overstocked and trampled areas, and also of water by the well-like pits that they dig in the dry beds of seasonal rivers; the creators of habitats for a legion of lesser forms of life including insects, reptiles, rodents, ground-nesting birds, etc. in or under the decaying trees uprooted by them; the conservators of grass seeds in overgrazed areas by the impenetrable crowns of, particularly, felled thorny trees, etc.

Against the setting of all the above considerations, the elephant problem in the Kruger Park becomes more clearly defined, and a more objective and realistic assessment of the applicable carrying capacities of the various vegetational zones in respect of elephants, now becomes possible.

In order to obtain an indication of what may be regarded as a "safe" saturation level for elephant in any particular area within the Kruger Park, reference should be made to a page in nature's own handbook and prevailing conditions in the area marked C in the accompanying Map (4) may be examined.

This is the area which occupies primarily the large tract of country between the Tsende- and Letaba rivers, as well as a strip along the Letaba river as far as the eastern boundary. By far the largest proportion of the Park's elephant population is accommodated within this confine, together with a rich assortment of other game species which differ markedly in numerical strength. No serious shortage of food or water occurs in this area (even during times of drought) and it appears well capable of pro-



Map 4.—Differentiation of seasonal feeding grounds of elephants in the Kruger National Park.