OBSERVATIONS ON DEVELOPMENTAL BIOLOGY, GROWTH AND SOME ASPECTS OF THE POPULATION ECOLOGY OF AFRICAN BUFFALO (Syncerus caffer caffer Sparrman) IN THE KRUGER NATIONAL PARK

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INTRODUCTION

An aerial census of elephant and buffalo populations in the Kruger Park during the dry season of 1964, revealed a total buffalo count of 10,514 (Pienaar et al. 1966b). The largest single concentration of buffalo was found in the Crocodile Bridge section in the south-eastern sector of the Park, where a tally of 2,024 was obtained in an area of about 100 sq. miles. In view of additional heavy grazing pressure by other species such as wildebeest, zebra and impala, as well as the fact that the winter range in this area already showed distinct signs of over-utilisation during dry periods, it was considered that culling of excess numbers would soon become necessary. Data on which culling rates could be based were fairly adequate for the other species, but our records concerning buffalo population dynamics were singularly lacking in detail.

With the object of establishing a safe and efficient culling technique for these animals, and to acquire additional knowledge about the population ecology of buffalo, a pilot culling scheme was initiated during March, 1966. A representative cull sample of 100 animals was scheduled for the buffalo herds on the Lemombo flats of Crocodile Bridge section and the project was successfully terminated during August of the same year.

A group of veterinarians from the Onderstepoort research centre joined the team of local workers in the field, and a mass of data was systematically collected. The results obtained will form the basis of a number of papers by other authors on such specialized subjects as reproduction, carcase composition, parasitic infestations, disease conditions, gross pathology, etc., and I will concern myself in the present paper only with data relating to developmental biology, growth and some aspects of population ecology.

TECHNIQUES

In order to minimize disturbance amongst our relatively tame but timid breeding herds of buffalo, it was decided to use only a crossbow and drugged darts for culling purposes. The advantages of using this technique soon became evident because culling was achieved with a minimum of fuss and disturbance. In many instances where buffalo herds are systematically hunted with rifles, they become very wary and take flight at the least sign of danger. The disturbance caused during the present culling operation was therefore minimal when it is considered that the herds could still be approached without difficulty after the last buffalo of the series was destroyed some 5 months after commencing the hunt. An additional advantage of the drugging technique is that no animals are left wounded. Of all the victims darted, only two were not found subsequently — probably due to a faulty dart mechanism or poor absorption of the injected drug.

The buffalo herds were usually tracked by means of a Land Rover from their favourite watering places in the area, and when located, the selected beasts were darted from the vehicle. A standard dose of 100 mgm. of Succinylcholine chloride was used for immobilizing purposes. Complete muscular paralysis was induced in a surprisingly short time and darted buffalo usually collapsed within 3-5 minutes. As a rule the jugular vein of the stricken animal was severed immediately after collapsing and the gushing blood was collected in a bucket and subsequently weighed. It was noted that the blood pH of buffalo immediately after collapse was 7.6. Dyspnoea, brought about by the paralysing effect of the drug on the muscles of respiration, and the resulting anoxia, soon changed this to 7.4, upon which the beast became unconscious. In animals in which the jugular vein was not cut, the heart usually stopped beating some 16-21 minutes after darting, and the blood pH was then down to 7.1. A few buffalo received chance intravenous injections of the drug and dropped within seconds after darting.

A sample of 100 animals representative of the prevailing population structure in the area was achieved in the following manner:

When a herd was located, the leading Land Rover would circle the herd a few times in order to break up any possible herd organization when in transit, during grazing, or defence patterns at watering places, etc. A point of reference relative to the herd was then selected by someone in the vehicle. Another helper would then draw a numbered disc from a tin containing 20 numbers which would indicate one out a group of 10 buffalo to the left or right of the point of reference, as the case may be. The selected beast would be carefully observed through binoculars, and if possible, it would be sexed and aged as accurately as possible. All attempts would then be made to dart the selected beast. In cases where this was not possible, a similar animal was selected in a more advantageous position and darted. In cases where a selected beast could not be identified with certainty, lots were drawn again and a new animal selected. A total of 5 herds were eventually involved in the sampling.

The number of animals destroyed and examined during a day averaged from two to three. Immediately after death the animals were photographed and measured and external parasites were collected. Young buffalo (up to 363 kgm. in body weight) were weighed whole on the hanging platform of a spring balance suspended from a portable gantry. The carcases were subsequently skinned, opened and quartered according to accepted procedures, and the individual parts were again weighed separately, in order to obtain an indication of fluid loss during the weighing procedure. This was necessary, as it was the only means possible by which adult buffalo could be weighed, and the conversion factor thus obtained was used in correcting the body weights obtained for adult beasts (Table 1).

A complete autopsy was performed on all beasts by the team of veterinarians and a detailed study of the reproductive organs was also conducted. Internal parasites were collected, and histological, pathological and gross anatomical material was preserved for subsequent examination. All skulls and lower jaws were carefully numbered, cleaned and preserved for subsequent study of tooth replacement, ageing, etc. The stomach contents were weighed separately and samples were taken for microscopic qualitative analysis, as well as for establishing the moisture content and dry weight of food in the stomach. A number of animals were darted immediately after watering, and others were destroyed en route to their watering points in order to obtain a rough estimate of the amount of water consumed by the animals during this time of the year (winter).

All field observations and measurements were recorded on special data sheets and filed for subsequent analysis and elaboration.

RESULTS:

1. SEX RATIOS, SIZE-CATEGORY CHARACTERISTICS, GROWTH AND FIELD AGE CRITERIA.

Of the 100 buffalo in the sample from the Crocodile Bridge population, 47 were males and 53 females. This is not surprising as groups of bachelor and lone bulls which comprised 6.98% of the total population numbers during the time of study were perhaps not completely represented in the sample. Male animals also form the bulk of buffalo that are destroyed in this section annually for raiding on adjoining farmlands, fence-breaking and aggressive tendencies. There is also evidence of differential mortality between sexes due to predation: lions appear to take considerably larger numbers of male than female animals.

The adult sex ratio in an undisturbed population could therefore be very close to unity, despite the fact that there is always a preponderance of females in the breeding herds. The primary (prenatal) sex ratio is not known in buffalo, but in our small sample of 9 foeti in which the sex could be determined without doubt, 6 were male and 3 female.

The body measurements, weights and other vital statistics relating to each individual in the series are provided in Table 1. From an analysis of the relevant data it becomes evident that the different individuals are grouped into a number of well defined categories, which are interpreted as age groups. This is substantiated by the fact that buffalo in the Kruger Park appear to have a distinct and clearly demarcated breeding season (see below).

The relative age groups have been classified according to Ansell's scheme (1966) into 'infants' or suckling calves, which include all calves of the latest calving season and up to a year in age; 'juveniles', which include calves of 12-24 months old; '2-year old and 3-year old sub-adults'; young adults of 4 and 5 years old and adults over 5 years of age. The latter group was again arbitrarily subdivided according to tooth wear and horn measurements into individuals of 6-7 years old, ca. 8-15 years old and over 15 years of age.

The average life expectancy (ecological longevity) of buffalo under natural conditions is not known, but Flower (1931) mentions a bull that was sold by the Zoological Gardens of London after 15 years, 5 months and 27 days. A female lived in the New York Zoological Gardens for 18 years, 5 months and 5 days (Crandall, 1964). Jones (1958) reports that a specimen received at the Philadelphia Zoological Gardens on October 8, 1929, lived until January 30, 1956, or 26 years, 3 months, 22 days. Although the potential longevity of buffalo may therefore be 25 years or more, it is doubtful whether many buffalo in the natural state attain a greater age than twenty years. Animals in the older age categories are the first to show signs of weakness during adverse seasons and fall easy prey to lions and even hyaenas.

It will be noted from Table 1 that buffaloes grow most rapidly during the first 12 months of life and that the period of slowest growth of sub-adult buffaloes corresponds with the period of maximum tooth replacement (i.e. during the 3-5 year old period).

Ansell's field age criterion for 'infants', in which the height at the withers of the calf is compared to the cow's elbow level, does not hold good for buffalo. The shoulder height of new-born buffalo calves (measured at the withers) varies from 76-81 cm., and the elbow level of adult cows is rarely more than 70 cm. (average 66-69 cm.) above the ground. A more reliable level for separating the 'infant' class, would be a line through the inguinal fold at its highest point on the flank of the cow. An imaginary line may easily be drawn through this level, which is a good 91 cm. or more off the ground. All calves of which the height at the withers fall below this line, may be reliably classed as 'infants'. This would be a more realistic classification, as calves of greater shoulder height are usually weaned (5 to 6 months old) and should really be classified with the next group, i.e. 'juveniles'. A horizontal line mid-way between the shoulder height of

adult cows and the inguinal fold line would separate juveniles from sub-adults, and here Ansell's criterion is valid enough for field application.

In buffalo there are other characteristics which may be used more accurately under field conditions in separating the various age groups in a mixed population:

(i) *Colour of Coat:*

The colour of the hair of new-born calves is black or dark olive-brown, but this soon changes to a dirty yellowish-brown when the calf is a few months old. The coat also subsequently becomes rough and grizzled and loses its smooth appearance. The colour again darkens with age to a reddish or chocolate brown, but the brown colour is retained in the case of cows, particularly on the hindquarters, up to their third year and in the case of bulls into their 4th and even 5th year, before the colour changes to the black or dark brown of the adult hair coat.

The hair becomes smooth once more during the 2nd year of life but it is significant that the hair of old bulls becomes distinctly wavy in texture. Very old animals become almost hairless in parts and many hairs lose their pigment and become white, particularly on the face and neck.

(ii) *Horns:*

In young calves the horns are straight and project from the head in the shape of a V (Figs. i, ii, xix and xx). In the year-old class (juveniles) the horns are from 30-46 cm. long and curve slightly outwards, but the growth is still upwards and the tips are widely separated (Figs. iii, iv, xxi and xxii). In two-year old sub-adults the horns are usually 41-69 cm. long (measured along the curvature), and the tips begin to grow towards one another (Figs. v, vi, xxiii and xxiv). In three-year old sub-adults, the process mentioned above is continued and the horns complete much of the outward curve and attain a length of 61-86 cm. In the case of bulls there is considerable thickening of the horns around their bases and the first indications of the boss being shaped (Figs. vii, viii, xxv and xxvi).

In four-year old cows the adult shape of horn is attained and the tips of the horns begin their backward sweep — this process continues, and the horns also dip and widen, so that in many older adult cows the tips are widely separated and there is a wide, flat span (Figs. x, xii, xiv, xvi and xviii). In old cows the tips of the horns wear and are often broken or blunt. In four-year old bulls the tips of the horns also sweep backwards and the horn bases are further enlarged (Figs. ix, xxvii). The boss is well-shaped in 5-year old bulls, but is still covered with hairy skin, and the backward sweep of the horns is completed. Bulls in this age class have particularly well-shaped and graceful horns (Figs. xi and xxvii).

In young adult bulls of 6-7 years old, the horny layers of each horn grow forward around the boss, but have not yet met in the centre of the

skull, and there is a patch of variable size on the forehead still covered with skin (Figs. xiii and xxvii). In older bulls the horny boss on each side is much thickened and rough and meets its opposite number in the centre of the forehead. The horns are also worn away at the tips, and although the widest span is attained in this age class (maximum span measured was 104.1 cm.), the length of the horns along the curvature is often less than in the younger age classes (Figs. xv and xvii).

It was also noticed that from the side, young heifer calves presented a straight nasal profile, whereas bull calves, and particularly adult bulls, showed a distinctly convex nasal profile (Figs. xix - xxxvi).

The face of old buffalo cows appears bony and shrunken, whereas that of old bulls becomes very wrinkled, particularly around the eyes (Figs. xxxv and xxxvi).

(iii) *Body Measurements:*

The most reliable body measurement to establish the age group of a particular buffalo appears to be the chest girth and this varies as follows:

Infant bull calves 81-124 cm.

Juvenile bull calves 124-163 cm.

2-year old sub-adults (♂) 157-185 cm.

3-year old sub-adults (♂) 183-196 cm.

4 and 5-year old young adults (♂) 193-208 cm.

Adult bulls older than 5 years 201-221 cm.

Infant heifer calves 76-114 cm.

Juvenile heifer calves 114-157 cm.

2-year old sub-adults (♀) 157-165 cm.

3-year old sub-adults (♀) 165-188 cm.

4-year old — mature cows — 188-206 cm.

Body length (along curvature) is also a good standard measurement, particularly in the case of male buffalo, as the animals grow in length even after attaining maturity, and the oldest bulls also show the longest body length (see Table 1).

(iv) *Weight and Growth:*

The weights of a series of new-born calves varied from:

♂ ♂ 26-42 kgm. (Average of 6 was 37.2 kgm.)
♀ ♀ 36 kgm. and 32 kgm.

Growth rates measured in a number of captive buffalo calves, reared in captivity at Skukuza after having been caught very soon after birth and not yet more than a year old are as follows:

(a) Sex: female. (3 days old). Birth weight ca. 35.8 kgm. Birth date 18th January, 1966.

The animal had 6 deciduous incisors present in the lower jaw at birth. The 7th and 8th milk incisors were just cutting after 4 months and 3 weeks.

Weight:	1 month old	39.9 kgm.
	2 months old	49.0 kgm.
	3 months old	54.4 kgm.
	4 months old	63.5 kgm.

(b) Sex: male. Birth weight ca. 36.0 kgm.
(4 days old.) Birth date 15th January, 1966.

Weight after	1 month	43.5 kgm.
	2 months old	54.4 kgm.
	3 months old	65.3 kgm.
	4 months old	76.0 kgm.
	$7\frac{1}{2}$ months old	117.0 kgm.

Animal had only 4 deciduous incisors in the lower jaw at birth and 8 months later still had only 4 present.

(c) Sex: male. Birth weight 38.1 kgm.
(soon after birth). Birth date 22nd April, 1966.

Weight after	1 month	49.4 kgm.
Weight after	4 months	83.5 kgm.

There were 6 deciduous incisors present in the lower jaw at birth and the 7th and 8th were cutting after only 1 month and 2 weeks.

(d) Sex: male. Birth weight 40.8 kgm. (soon after birth).

Birth date: 15th April, 1966.

Weight after	1 month	53.2 kgm.
Weight after	$4\frac{1}{2}$ months	99.8 kgm.
Weight after	12 months	193.7 kgm.
Weight after	2 years	362.8 kgm.

There were 6 deciduous incisors present in the lower jaw at birth and the 7th and 8th cut after 2 months.

The average weights of known-age buffalo (both sexes) reared in captivity at Panfontein Experimental Station were as follows: (after Van Zyl, 1966).

1	Year old	216.4 kgm.
3	Years old	494.9 kgm.
5	Years old	684.5 kgm.
8	Years old	680.8 kgm.

The weights of these buffalo of known age correspond very well with those of the age classes separated in Table 1 and provide further confirmation for the age criteria used in their classification. From the combined data obtained from the weights in Table 1 and those from the buffalo of known age, it is possible to construct a growth curve for both male and

female buffalo from birth to old age (maximum longevity under natural conditions taken as 20 years) (Fig. A). It is evident that the period of maximum growth for both sexes is during the first 12 months of life. During the period of maximum tooth replacement (3-5 year old groups) the growth rate is slowed down, but in the case of females, the adult weight is attained during the 4th year, when the animal is also sexually mature and usually calves for the first time. In the case of males however, growth is maintained and weight is gained even during old age. It is significant that the group of oldest bulls had the largest body measurements and attained the heaviest weights of all adult males measured. The maximum weight for an adult cow in the sample group was 636.8 kgm. and for an adult bull in good condition, 767.5 kgm. The largest bull ever weighed in the Park (an old animal in prime condition) measured 802.4 kgm. This compares favourably with weights recorded by Meinertzhagen (1938) for adult male buffalo in East Africa (678.6 - 835.1 kgm.).

The average weight of a buffalo, irrespective of sex and considering the complete sample of 100 animals, was 489.89 kgm., which shows a close correlation with our previous estimate of 498.96 kgm. (Pienaar et al. 1966b).

It should be noted that the majority of buffalo comprising the 100 animal sample were in good physical condition, ample winter grazing having been provided by a bountiful summer season.

(v) *Dentition:*

When the dentition of the various relative age groups is examined, a definite and regular sequence of tooth eruption and replacement becomes evident.

Calves are usually born with six deciduous incisors present in the lower jaw, as well as three milk-premolars on both sides of the upper and lower jaws. Some new-born calves have been found with only four deciduous incisors present. The fourth deciduous incisor (canine) on either side is usually cut by the end of the second month (Figs. xxxvii and xLvi). The first lower permanent molar is usually evident by the end of the fourth month and is followed soon after by the 1st upper permanent molar.

Juveniles of twelve to eighteen months old, show a full complement of eight deciduous incisors in the lower jaw, as well as three milk-premolars in both the upper and lower jaws (Figs. xxxviii and xLvii). In old animals the fourth deciduous incisor (canine) does not develop and this state persists until the permanent teeth emerge. In most juvenile animals the first two permanent molars in both upper and lower jaws have emerged and in older animals of this group, the third permanent molar is also being cut (usually first in the lower jaw).

At about 2 years of age or soon after, the first milk-incisors are replaced by permanent teeth (Figs. xxxix and xLviii). At this stage also the first deciduous premolars in the lower jaw are replaced by permanent teeth or are in the process of being shed. This process is again repeated soon afterwards in the upper jaw. By this time all the permanent molars in the lower

jaw have emerged but the third permanent molar in the upper jaw is often still cutting.

During the third year of life, the second milk-incisors are replaced by permanent teeth and when the animal is three years old, the first and second permanent premolars in the lower jaw have also erupted and the third permanent premolar is also replacing the worn remnants of its deciduous predecessor (Figs. xL and xLix). The first permanent premolar in the upper jaw is also firmly established, and the second and third are in different stages of replacing their deciduous counterparts. The third permanent incisor emerges after four years and by this time all the permanent premolars and molars have erupted in the lower jaw, and it is usually only the third permanent premolars of the upper jaw that have not completely replaced the deciduous teeth (Figs. xLi and L). The last permanent incisor (canine) emerges soon after the animal attains 5 years of age and the full complement of permanent teeth is then present (Figs. xLii and Li).

The only change in the teeth structure after the fifth year of life, is the progressive wearing away of the enamel and dentine layers, and the incisors of old animals particularly, show very gross signs of wear (Figs. xLv and Liv).

It will be noted that the tooth replacement schedule adheres closely to the pattern recorded by Parvulescu and quoted by Marsboom (1950) for known-age buffalo in Rumania.

2. FEEDING HABITS AND WATER REQUIREMENTS.

(a) *Feeding habits:*

Buffalo are grazing animals, but all stomach contents examined contained at least some traces of plants other than grasses. Individual buffalo have also been observed browsing the leaves of a variety of woody shrubs. Although buffalo are attracted, like most grazing ungulates, to young grass on fresh, green burns, these animals are less partial to young, short grass than most grazing animals, and will feed on old, cured grass with equal relish. They are also much less prone to selective overgrazing than other animals such as wildebeest and zebra, and utilise the available food supplies within their chosen habitats in a much more economical and less destructive manner than most of the other important grazing species.

Buffalo herds range over a very large area and rarely linger in a trampled or depleted zone while there are still good stands of grass in their habitat. Herds have been found to roam as much as 11 miles away from their watering places in their nomadic grazing routines. In this manner, the grazing habits of buffalo actually complement the requirements of species with more restricted feeding habits and others which shun old or tall grassland such as tsessebe, wildebeest, zebra, etc., in that additional grazing range suitable to the selective requirements of these animals is opened up in the wake of buffalo herds.

An appreciation of particular and seasonal food preferences in the case of buffalo must await the detailed qualitative analysis of samples taken from the stomach contents of animals killed during the culling operation.

The following grasses and monocotyledonous species have thus far been recorded as food items of buffalo in actively grazing herds:

*Themeda triandra**
*Panicum coloratum**
Digitaria spp.*
*Panicum maximum**
*Heteropogon contortus**
Brachiaria nigropedata
Bothriochloa insculpta (young, after burns)
Phragmitis communis (young shoots)
Typha capensis (near water)
Sporobolus robustus (in vleis)
Cenchrus ciliaris (particularly in winter)
Schmidtia bulbosa
Enneapogon cenchroides
Hyparrhenia dissoluta (young, after burns)
Andropogon gayanus
Andropogon amplectens
Setaria flabellata
Eragrostis superba
Cyperaceae spp. (near water)
Echinochloa stagnina (near water)
Sorghum verticilliflorum (in vleis)

* The species marked with an asterisk appear to be preferred during all times of the year.

The leaves of *Vellozia retinervis* and *Scilla cooperi* are also eaten on spring burns.

During the culling project, leaves of *Grewia bicolor* were found in practically all stomachs examined during the months from April to August, and leaves of the following dicotyledonous plants have also been recorded in buffalo stomach contents on occasion:

Grewia messinica, Grewia monticola, Dichrostachys cinerea spp. *cinerea, Combretum hereroense, Heeria insignis, Euclea divinorum, Diospyros mespiliformis, Securinega virosa* and *Colophospermum mopane* (in the north).

A 450 gm. sample of the stomach contents was taken from each buffalo and sealed in a plastic bag after the addition of a few cc's of formalin to stop bacterial action. These samples were subsequently washed, filtered, and the solid residue was dried in a drying oven to a constant weight. The dry weights thus obtained were used to calculate the dry weight of the stomach content of each animal and the results are presented in Table 1.

Annison and Lewis (1959) have calculated that the daily food consumption of an ungulate is very near 50 per cent of the stomach contents' dry weight, and in Table 1, the daily food consumption for each age group of buffalo has been estimated in this manner. It has been determined that a 453.6 kgm. domestic steer requires about 9.1 kgm. of dry range forage per day and it is significant that the estimated consumption of even the largest buffalo bulls (average body weight 717.64 kgm) was only 8.39 kgm. per day and that of an average buffalo of 489.9 kgm. body weight (the average weight for the total population sample), was only 6.12 kgm. of dry food per day. It must be stressed here that during the time of study, the large majority of sample animals were in good condition, and there was no lack of food in the habitat.

These figures are of interest, and provide a basis for estimating the productivity and energy relations of a wild buffalo population in comparison with that of domestic stock on similar dry range.

(b) *Water intake:*

An attempt was made to estimate the water requirements of adult buffalo during the period of study (March-August). For this purpose, a number of buffalo were darted en route to their watering places (i.e. immediately prior to drinking). Others were again purposefully allowed to drink undisturbed and were darted when walking away from the watering point.

The average weight of stomach and contents of a total of 6 adult buffalo in the first group was 115.2 Kg. The average weight of stomach and contents of 5 adults in the second group was 146.5 kgm. A rough estimate of the average water consumption of adult buffalo under similar conditions would, therefore, be 31.3 Kg or 31.3 litres.

The average consumption of a group of 5-year old animals was similarly calculated to be 30.46 Kg or 30.46 litres per day. In another case 40.0 Kg water was obtained from the wet stomach content of a cow that had just drunk her fill.

3. REPRODUCTION.

The reproduction of the African buffalo will form the basis of a separate treatise by Dr. V. de Vos, but for the purpose of calculations which follow, certain findings must be briefly mentioned here:

(i) Contrary to earlier beliefs, it has now been established that buffalo in the Lowveld of the Transvaal have a definite and clearly demarcated breeding season. Although out of season births are not uncommon, it is now evident that the majority of buffalo calves in the Kruger Park are dropped during the period January to April, with a peak in January and February (Fairall 1967).

The rutting season extends from March to May and mating activity peters out during the winter months. This confirms the seasonal pattern of reproduction and indicates a gestation period of about 11 months (vide 330 days, Kenneth & Ritchie 1953).

The increasing size of embryos from pregnant cows which were obtained after the operation was commenced in March, provides additional proof of a confined breeding season (Ref. Table 2).

These findings have since been confirmed in other populations of buffalo in the Park and are in contrast to what has been reported for buffalo breeding activity elsewhere. Zuckerman (1953), in reporting fourteen single births in the Zoological Gardens of London, notes their occurrence in every month, except April and September. Brand (1963), likewise finds no evidence of seasonal breeding activity in the Pretoria Zoo and both Ansell (1960) and Dasmann and Mossman (1962) report similar findings for wild buffalo populations in Zambia and Rhodesia. This is indeed surprising, and the reason for the seasonal pattern in the Kruger Park is still not understood.

There may be some correlation here with the state of nutrition and grazing conditions.

(ii) Van Zyl (1966) recorded 16 oestrus cycles during a period of 12 months in each of two sexually mature buffalo cows 4 and 7 years old respectively in captivity. The average cycle is of 23 days duration and the cow is in oestrus for 5 to 6 days during this period. Ovulation occurred more often and in longer succession from the left ovarium than the right. Whether regular oestrus cycles also occur amongst mature female buffalo in the wild state, has not been established, but there is certainly very little visible evidence of oestrus activity in the sex organs of cows at times other than during the breeding season. There may be several cycles in succession during the mating season, and a cow is not necessarily fertilized during the first of these. In the present sample several non-pregnant specimens were collected in which the ovaries contained corpora lutea of previous oestrus cycles.

A buffalo cow in oestrus is attended by several herd bulls in succession or simultaneously, and is served many times while in this state.

(iii) Cows do not calve every year, and there appears to be a period of lactation anoestrus after parturition, when little sexual activity is displayed and with follicular growth at a low ebb. Of the 40 sexually mature female buffalo in the population sample, 16 were pregnant (non-lactating) or had aborted (1), 6 were in oestrus (some of which may yet have been fertilized during the current rutting season), 8 were lactating and suckling calves, while 9 were non-lactating and not pregnant (these included animals which may have lost their calves). Only one individual (No. 91 in Table 2), was suckling a calf of about 5 months old and was pregnant. If 50 per cent of the cows in oestrus became pregnant, this would mean 17 + 3 pregnant cows and 8 + 9 + 3 non-pregnant cows observed during a period of 5 months, which covered both the peak calving as well as the rutting period. The evidence derived from our small sample is therefore fairly substantial that wild, free-roaming buffalo cows calve only every alternate year. It appears likely however, that this pattern is largely determined by prevailing environmental conditions and buffalo cows may well calve twice every three years during a succession of particularly favourable seasons (De Vos, priv. comm.).

(iv) Buffalo cows become sexually mature after three years and may have their first calf soon after their 4th birthday (vide No. 86, Table 2).

Male buffalo may already be sexually mature after $2\frac{1}{2}$-3 years, but are rarely, if ever, allowed to take part in breeding activity by the older herd bulls, until they are at least 7-8 years of age.

(v) Implantation of embryos occurs in both the left and right horns of the uterus, and two cases of twin foeti were recorded amongst 17 pregnant cows (in the one case one of the embryos was in a state of resorption). In the 9 cases where the sex of the unborn calf could be distinguished, 6 were male calves and 3 females.

(iv) In cows the number of mammae was usually 4 but sometimes there were 2 extra rudimentary teats. The posterior pair of mammae was often fused in bulls, so that only 3 mammae could be distinguished. Calves are suckled for four to five months and are then gradually weaned. Young calves commence taking herbaceous food at an early age. Calves of four months old were found to have substantial amounts of grass in the stomach and the rumen was already well-developed.

(vii) The fecundity amongst sexually mature buffalo cows is high and even amongst a group of 9 very old cows, one was pregnant, three were in oestrus, and three were suckling calves. Whereas the sexually mature female segment of the present population sample is 40 animals and only 50 per cent of these calve during a particular year, the expected natality rate, particularly during adverse seasons, appears to be of the order of 20 per cent. (Vide 17 pregnant and 23 non-pregnant individuals in table on Reproduction data.)

4. MORTALITY FACTORS.

Infant mortality amongst buffalo calves is high and judging from population age analyses and the results of the present random sample, only 6 to 9 out of every 20 new-born calves reach reproductive maturity. Mortality factors which determine the recruitment rate to the population and are instrumental in the regulation of numbers in all age groups of the population include intraspecific competition for food and water, predators, diseases and miscellaneous accidents.

It has been regularly observed during years of low rainfall, when the winter range becomes severely depleted, that the mortality rate amongst young calves is appreciably higher than during favourable seasons. This is particularly true in the large herds, which number from 300 to 700 individuals. The reason for this severe decimation in the number of young calves may be sought in the food shortage precipitated by the gregarious habit of these animals. During periods of drought, the grazing in the immediate vicinity of permanent waters becomes badly trampled by the churning hooves of the large herds of buffalo and other animals during their daily treks to and fro from the watering places. The larger herds must, of necessity, then move much greater distances (up to 11 miles and more) to reach substantial grazing and the young, suckling calves find these long journeys very tiring and rapidly lose condition. In their weakened state they lag behind or drop out of moving herds, and eventually fall easy prey to such predators as lions and hyaenas. During such times, also, diseases and parasitic infections exert their most profound influence on the population.

It has been frequently noted that the percentage survival of young calves in smaller herds (< 100 animals), with less nomadic grazing routines, is much higher than in the larger herds (see below). There is obvious survival value therefore in the splintering of the big herds, and this is a phenomenon which has become increasingly evident in recent years amongst the larger herds of buffalo on the Lebombo flats.

Although the high mortality rate is therefore primarily attributable to undernourishment, debilitation and disease, it is reasonable to assume that the large majority of calves lost are eventually caught by carnivora (lions and hyaenas). Of a total of 153 buffalo carcases found during the last year which had been caught by lions, only 5.2 per cent were of calves less than 1 year of age, but this is probably an under-representation of the actual percentage caught in view of the small size of the carcase, which is more often than not completely devoured by lions. This is even more true of hyaena kills however, and there is considerable suggestive evidence that most stray calves are caught by these predators and not by lions. A similar fate also befalls disease-weakened calves, although in the case of adult buffalo, disease-ridden individuals lagging behind the herds will obviously attract the attention of lion prides which follow the herds.

The latest estimate of the lion population in the whole of Crocodile Bridge section is 84, and of this number, about half have a direct influence on the buffalo herds in the study area. For long periods, particularly during the winter months ,the buffalo herds are constantly followed by these lion prides, and most kills are made near the watering places.

The average annual kill per lion is variously estimated to range from 20 (Guggisberg 1961), 26 (Stevenson-Hamilton 1925), 35 (Talbot and Talbot 1963) to 36.5 prey animals (Wright 1960), but where large numbers of bulky animals such as buffalo are caught, the figure is probably lower. According to carcase data collected over a period of 13 years, buffalo represent 26.41 per cent of all lion kills in the study area (as against an average of 9.12 per cent in the Park as a whole). The average annual kill per lion in this area is probably not more than 20 and the lions on the Lebombo flats of Crocodile Bridge section thus probably take some 220 buffalo every year. Of this number, about 150-170 would be adult animals. It is significant that of 120 buffalo kills recently recorded, lions killed twice as many bulls as cows. The former are usually lone bulls, which are pulled down by hunting prides, or old animals from bachelor groups which are waylaid in their permanent abodes near water. This heavier predation on male animals away from breeding herds is probably due, in part, to their sedentary habits and relative weakness (in the case of old individuals), but may also testify to the defensive success and survival value of the herd structure. The differential predation on the two sexes may also explain the lower number of adult bulls than adult cows obtained in the population sample.

Lions are sometimes unsuccessful in their attempts to pull down buffalo, and a number of animals in the sample bore wounds inflicted by lion claws. Only two animals suffered detrimental effects and in the others the wounds healed remarkably well. A young calf was found wandering around aimlessly with a wound inflicted by a lion, a tooth of which had pierced its skull some days previously and caused a severe inflammatory meningitis.

In some of their more hazardous encounters with buffalo, the lions came off second best, and several cases have been recorded where lions have been gored and trampled to death.

The only other predators which inflict mortality on buffalo in the Kruger Park are leopards, which pull down the occasional young calf, and large crocodiles, which are capable of capturing and drowning even full-grown buffalo. One animal in the sample group had been seized by the nose by a crocodile, but managed to free itself. The regulating influence of both leopards and crocodiles on the buffalo population in the Park is relatively very small, however. (Of 1,234 buffalo carcases recorded since 1954 in the Park as a whole, 1,124 were caught by lions and only 5 by leopards, 2 by crocodiles and 3 by hyaenas.)

Some of the highly contagious and rapidly fatal epidemic diseases such as the great rinderpest epidemic of 1897-98 and the anthrax epidemics of the 1920's and 1960-61, are known to have inflicted massive mortality amongst the buffalo herds of the Kruger Park at various stages in the past. (Pienaar 1961). Neither of these drastic epizootic diseases have caused mortality amongst the Crocodile Bridge population in recent years. The regulatory effect of disease has been imposed here more indirectly, particularly during adverse times, through the action of erosive diseases and parasitic infestation.

Although some of the enzootic diseases recorded amongst buffalo in this area obviously run a fatal course, it is doubtful whether many cause direct mortality, as weakened or sick individuals would almost invariably fall prey to predators, and be eliminated from the population *before* they succumb to the disease.

During normal years, the sanitary effect of predation is obviously benificial to the population, but the decimating effect of this group of diseases, as well as of parasitism, should not be underestimated, as they may have a considerable influence on the rate of predation during unfavourable seasons, in that larger numbers of buffalo would then fall prey to predators than would be the case in a virile and healthy population.

Instances have been recorded where a pride of lions have killed three and more animals out of an emaciated group of buffalo, and proceeded to consume only one.

A large number of internal as well as external parasites were collected during the culling operation and these have subsequently been identified and reported on by parasitologists of the Onderstepoort Research Centre.

A number of buffalo (particularly old bulls that spend a lot of time in or near water) were heavily infested with intestinal schistosomes (cf. *S. matheei*).

Erosive diseases such as foot- and mouth disease, naval ill, lumpy skin disease, blue-tongue, mange, malignant catarrhal fever and ephimeral fever have been found to affect buffalo and manifest different morbidity rates.

Serological evidence of *brucellosis* has been found in buffalo of the present population sample. Higromata resembling those produced in cattle infected with brucellosis have also been observed in several buffalo. Serological complement fixation tests have also revealed antibodies to Wessels-

bron disease in serum samples from Park buffalo. This virus can, like Rift valley fever, cause drastic perinatal mortality in sheep, but its effect on unborn wild animals has not been established. *Corridor disease* may also cause death in buffalo (Neitz, 1957), and signs of this disease have also been found in individual buffalo of the present sample. It is also expected that an unknown virus disease, the symptoms of which resemble that of *Sporadic bovine encephalomyelitis* of cattle, may cause mortality in buffalo calves in the Park. Buffalo in the Kruger Park are carriers of *Theileria parva* which causes *East Coast fever* of cattle, but there is no evidence of direct disadvantage of these protozoans to their wild hosts.

Other mortality factors which have a direct bearing on the numbers of buffalo populations in the Park include human predation and fatal injuries accidentally incurred. Not many buffalo are killed by poachers in the Park, but increasingly larger numbers are destroyed by Park staff annually in operations to protect the southern border fence, and by adjoining farmers in dealing with crop raiders and carriers of East Coast fever which infect their cattle. Odd buffalo are also destroyed in the protection of human life and when displaying persistant aggressive tendencies. In this manner 102 buffalo were shot during the period August 1964—July 1966. (An average of more than 50 p.a.)

Several buffalo were noticed amongst the larger herds with broken legs and other self-inflicted wounds, and young calves are sometimes fatally injured and trampled during stampedes.

During freak cold spells and severe winters mortality has also been experienced amongst, particularly, the weaker calves and old animals.

Old buffalo are sometimes trapped in mud wallows and die a lingering death.

5. POPULATION AGE STRUCTURE, ANNUAL RECRUITMENT RATE AND DETERMINATION OF PROVISIONAL CULLING RATE FOR THE CROCODILE BRIDGE POPULATION.

An analysis of the age structure of the random sample of 100 animals obtained from the Crocodile Bridge population, and shown in Table 1, revealed the following composition:

Infants (sucking calves) less than 12 months old	8%
Juveniles (between 12 and 24 months old)	6%
Two-year old sub-adults	6%
Three-year old sub-adults	7%
Four-year old young adults	9%
Five-year old young adults	10%
Adult cows older than 5 years	29%
Adult bulls older than 5 years	25%
Total	100%

For purposes of comparison with herd age structure obtained from a study of good quality aerial photographs of other herds (see Figs. Lv and Lvi) and ground observations in the field, the four- en five-year old categories in the above analysis may be grouped with the adults as in Table 3 below.

TABLE 3.

Comparison of age structure of sample from Crocodile Bridge population with age composition of other herds in the Kruger National Park.

Buffalo herd analysed.	*Number of animals*	*Age composition of Population (%)*				
		Infants	Juveniles	2 & 3 yr. old sub-adults	Adult bulls	Adult cows
1. Population sample from Crocodile Bridge area	Random sample of 100	8%	6%	13%	35%	38%
2. Shabin herd (Pretoriuskop)	97	9.3	9.3	17.6	30.9	32.9
3. Large herd (Makamba), Lebombo flats.	204	4.0	2.0	9.3	39.2	45.5
4. Small herd (Bob), Lebombo flats.	91	12.0	8.8	18.7	24.2	36.3
5. Portion of Sabi-Sand herd	116	12.0	12.0	15.6	27.6	32.8
6. Large herd (Saliji)	527	10.6	89.4			

It will be noticed from Table 3 that the age structure of the population sample from Crocodile Bridge is a good average between the extremes of herds in which young animals are poorly represented and others, (particularly the smaller herds), in which there are an abundance of young animals.

The sampling technique therefore appears to be quite valid, and provides an acceptable picture of the age structure of the entire Crocodile Bridge population.

The available data indicate a gross annual recruitment rate varying between 6 and 12 per cent, according to prevailing conditions.

Reproductive data at our disposal make it reasonable to expect from a population of 2,132 buffalo (810 adult cows) a minimum calf crop of about 400 to 410 even during years of bad drought (see Table 4). Depending on prevailing environmental conditions, the mortality rate amongst calves may vary from 40 to 70 per cent and only 120 to 250 may survive the first critical year (vide percentage of yearling category in Table 3).

When it is considered that lions alone may take as many as 220 buffalo (including many calves) from the population per annum (representing a natural annual mortality rate of about 6 per cent in all age groups from juveniles onwards), it will be appreciated that the nett annual increment to the population is significantly lower than was at first expected.

Under very adverse conditions, such as during period of prolonged drought, there will almost certainly be a decline in population numbers, and it is evident that the population growth curve is in fact appreciably slower than that of other grazing species with higher reproductive rates, such as wildebeest, particularly in areas where the population is approaching saturation level with regard to available food and water supplies.

An accurate aerial census completed towards the end of the culling operation (July) yielded a tally of 2,132 for the Crocodile Bridge buffalo population. At the time of the aerial count, the population was composed of 7 breeding herds numbering respectively 454, 384, 670, 158, 172, 91 and 54 animals. In addition, 149 adult males were counted singly or in bachelor herds numbering as many as 30 individuals. The latter comprised 6.98 per cent of the total population. A significant feature of all breeding herds was the preponderance of adult females (see Table 3 above), and this was probably due to the withdrawal from the breeding herds of many adult males after the rutting season. It was noticed that the number of adult bulls in the large breeding herds steadily diminished after the termination of breeding activity, and, during the late winter months particularly, considerable numbers of adult male buffalo could be found roaming about in groups of a few to 30 animals or more. The overall preponderance of females in the population may also be due to the larger number of adult male buffalo captured by lions and which are destroyed by human interference along the borders.

During a previous aerial census of the buffalo population on the Lebombo flats during August 1964, a total of 2,024 animals were counted (Pienaar et al 1966b). Seasonal immigration of buffalo from other areas does not play a role in the study area and the present population total of 2,123 represents a nett annual increment of about 2.6 per cent. This annual rate of increase has been maintained over the last two favourable years despite an exploitation level of about 4.8 per cent (102 destroyed during control operations + 100 removed during the culling scheme), and all the losses due to predation, disease, and other natural causes.

TABLE 4.

Age Structure and Growth of the Female Segment of the Crocodile Bridge Buffalo Population.

Time in years	*Number of mature breeding females*	*Number of female calves in annual crop*	*Immature females*			*Recruitment to breeding population. (Four year old cows)*	*Annual adult mortality ± 6%*	*Total (nett) Female population before next breeding season*
			1 Year old	*2 Years old*	*3 Years old*			
1	810	202	64	60	56	53	48	1,192
2	815	204	70	64	60	56	49	1,213
3	822	206	71	70	64	60	49	1,233
4	833	209	72	71	70	64	50	1,255
5	847	212	73	72	71	70	51	1,275
6	866	217	74	73	72	71	52	1,302
7	885	221	76	74	73	72	53	1,329

65% Calves die before attaining one year of age. Mortality rate after one year is about 6% p.a. Adult cows breed every alternate year and 50% of calves are females.