

STUDIES ON THE BIOLOGY AND PRODUCTIVITY  
OF THE GIRAFFE *GIRAFFA CAMELOPARDALIS*

by

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'The sight of a herd of giraffes walking leisurely across an open piece of ground, or feeding through a park-like country of scattered trees and bush, is one which, once seen, must ever linger in the memory; for there is something about the appearance of some few of the largest mammals still extant upon the earth which stirs the imagination as the sight of smaller but more beautiful animals can never do.'

Frederick Courtenay Selous

"African Nature Notes and Reminiscences"

1908

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ABSTRACT

This study was carried out in the eastern Transvaal Lowveld in an area with a giraffe population density of 2,6 per km<sup>2</sup>. Lions are the only predators and it was estimated that 48% of the calves die in their first year. The sex ratio departs significantly from unity in favour of females.

Plant fragments in the rumen were identified. Giraffe subsist on the leaves of trees and shrubs, though fruit, flowers, twigs and grass were also utilised. Marked seasonal changes in the plant species selected were determined by availability and different habitats were utilised accordingly. Chemical analysis of rumen content showed correlations of nutritional value with species eaten and seasonal phenological changes of the vegetation.

Tooth eruption, wear and incremental layers in the cementum were found to be suitable criteria for age determination.

Total body mass was measured and carcasses dressed out at 61,9% for males and 56,6% for females. Lower mass and lower proportion of fat was found in the dry season. Meat yield was similar to other African ungulates, buttock and bone proportion was high, but fat was low.

A gestation period of 457 d and birth mass of 102 kg (higher than in the literature) was used to determine the age of foetuses whose growth was similar to other uniparous mammals. Postnatal increase in mass, height, length and chest girth followed the usual mammalian growth curve. Mass could be predicted from buttock or foreleg mass or from body measurements.

There is evidence that hypertrophy of the foetal testis occurs. Parameters of male sexual function were correlated with age, but no seasonal effects were apparent. Puberty was found to be dependant on physiological status. Androstenedione was the dominant testicular hormone in the foetus and testosterone in the adult. Most conceptions occurred during the humid months of the year when conditions are good for the females.

Vesicular and haemorrhagic follicles and corpora lutea were common in foetal ovaries. Numerous corpora lutea were also found in immature ovaries, but they regressed at puberty. The corpus luteum of pregnancy underwent a decrease in size in early gestation followed by an increase to term. Both ovaries are equally active, implantation is ipsilateral and the placenta is polycotyledonary of the syndesmochorial type. Gonadotrophic activity could not be demonstrated in the urine of pregnant females. Lactation endured for about 13 months, the milk was relatively rich but its composition changes with time. There was a reduction in stomach fill in late gestation but lactating females had a significantly greater fill than others.

## PREFACE

The work described in this dissertation was carried out in the Mammal Research Institute of the University of Pretoria and the Wellcome Institute of Comparative Physiology, London under the supervision of Prof. J.D. Skinner M.Sc., Ph.D., and Dr. I.W. Rowlands M.Sc., Ph.D., who supervised the work on the ovary.

Some parts of the work which required specialised techniques or equipment, not available in the abovementioned institutes were carried out in collaboration with colleagues in other Institutes. Their help is acknowledged accordingly.

Some aspects of the work reported in Chapter 2 of this dissertation have already been published, but are not cited separately as their contents have been incorporated in this chapter. The relevant papers are:

HALL-MARTIN, A.J. 1974. A note on the seasonal utilisation of different vegetation types by giraffe.

*S. Afr. J. Sci.* 70, 122-123.

HALL-MARTIN, A.J. 1974. Food selection by Transvaal Lowveld giraffe as determined by analysis of stomach contents.

*J. sth Afr. Wildl. Mgmt Ass.* 4, 191-202.

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Most of the material used in this study was collected while the writer was employed as Game Warden of the Timbavati Private Nature Reserve. The co-operation, interest and support of the owners and staff was greatly appreciated. Thanks are also due to Mr. Aubrey Cooper of the Sandringham Private Nature Reserve and to the owners of the Buffelshoek Private Nature Reserve for contributing material.

Many colleagues and collaborators have contributed to this study and it is pleasant to thank them all for their assistance. In particular mention must be made of the interest and assistance rendered by Dr. I.W. Rowlands formerly Senior Research Fellow at the Wellcome Institute and his staff. Other scientists with whom collaboration has been most fruitful are Mr. W.D. Basson, Prof. J.M.R. Geerthsen, Dr. J. Hanks, Dr. J. Labuschagne, Dr. J. Morris, Miss G. Rosch, Prof. A. Smith, Dr. J.D.G. Steenkamp, Dr. G.K. Theron, Mr. K.L. Tinley, Dr. M. van Dijk and Dr. M. von La Chevallerie.

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## CHAPTER 1

GENERAL INTRODUCTION

## INTRODUCTION

Game cropping schemes in Africa have over the past few years provided a wealth of biological data on several animal species. Large numbers of animals have usually been involved and it has been possible to gather data from adequate samples of different sex and age classes. A total of 39 giraffes *Giraffa camelopardalis giraffa* were shot in the eastern Transvaal Lowveld between April 1970 and July 1971 for commercial purposes, and were made available for investigation. There is a need for biological and ecological information on the giraffe which has been relatively little studied (Dagg 1971) and opportunities for gathering such information are rare; especially in southern Africa where land development and restricted park size are factors which could limit the future abundance and range of this species. Wherever possible, therefore, data was collected from this small number of culled giraffe and an additional 54 animals which died of natural causes or accidents, or were killed by predators. Data from seven giraffes which were donated to the Mammal Research Institute of the University of Pretoria for research purposes are also included in this study.

As the availability of most of this material was usually dictated by considerations other than research priorities it was not possible to ensure that adequate material and observations were always obtained. For example, while studies on carcass composition, aspects of reproduction, nutrition and age determination were possible, equally important studies on behaviour could not be attempted. The results from the various investigations are synthesized here in appropriate chapters and these data contribute to hitherto little studied facets of the biology of the giraffe.

## STUDY METHODS

Wherever possible recognised methods for conducting empirical research were followed. Appropriate details of such methods are given where applicable in each chapter. In some cases, such as in the identification of plant fragments or the dissection of giraffe carcasses non-standard techniques were used. In these cases the justification for these deviations are discussed.

The sample of giraffe available, though almost entirely from a single population, was not collected at random, nor was the collection evenly spread over the seasons. The reasons for this have been explained. However, for the purposes of this study it has been assumed that the samples were adequate. Where comparisons between different classes of animals have been made it has also been assumed that the frequency of occurrence of a particular characteristic within the sample is, within the accepted limits of probability, an accurate reflection of its distribution within the population. Conventional statistical methods have, therefore, been applied, though occasionally with reservations. Mean values have been given with the standard error.

For comparison of the means of two samples and for paired comparisons the Students *t* - test (Simpson, Roe & Lewontin 1960) has been used throughout. The test for the significance of binomial proportions used is the  $\chi^2$  distribution, also discussed by the above authors. Standard correlation and regression procedures have been used to measure the degree of correlation between two variables, to provide predictive functions and to judge the accuracy with which the one variable may be predicted from another. Both linear and polynomial regressions have been used where appropriate. The statistical background to these techniques, methods of calculation, methods of testing regression coefficients and the significance of correlation coefficients which have been followed throughout are those discussed in detail by Simpson. *et. al.* (1960), and by Sokal & Rohlf (1969). Where more complex statistical procedures such as principal components analysis have been used a more detailed discussion has been given in the text.

## STUDY AREA

### LOCATION, TOPOGRAPHY AND WATER

The main study area was the Timbavati Private Nature Reserve and its environs, centred approximately on 24°24' S and 31°21' E in the eastern Transvaal Lowveld at an altitude of 300-450 m above sea level. It is a privately owned 550 km<sup>2</sup> wilderness area and its eastern boundary adjoins the Kruger National Park. A 1,8 m game fence enclosing the Reserve was erected in 1960/61 and effectively prevents any movements of ungulates across these artificial boundaries. The Reserve supports most of the indigenous large mammal species, including predators, of the southern savanna biome.

The topography is gently undulating and soils are mostly derived from granite (acid, sandy soils) or basalt (base rich clay loams). Numerous drainage lines and small watercourses feed the Timbavati and Shlralumi Rivers which flow intermittently during the wet season. Only the Timbavati River which

until about 20 years ago was perennial, holds scattered pools of water throughout the dry season. Perennial water supplies in the Reserve have been supplemented by dams and boreholes.

### CLIMATE

No reliable climatic data are available from within the Reserve. Data\* from nearby recognised weather stations at Phalaborwa and Skukuza with similar vegetation and climatic conditions to the northern and southern parts of the Reserve respectively, have therefore been used. There is a clearly defined rhythm in rainfall and temperature resulting in three well defined seasons, a hot wet season from November to March; a cool dry season from April to July and a hot dry season from August to October.

The mean annual rainfall is 532,0 mm at Phalaborwa and 576,0 mm at Skukuza but is extremely variable. At Phalaborwa 78% and at Skukuza 77% of the rainfall occurs from November to March in storms of short duration and high intensity. Mean monthly temperature varies from 9,0°C to 33,0°C at Phalaborwa and from 6,0°C to 32,0°C at Skukuza. Relative humidity is high during the wet season and evaporation usually exceeds rainfall. Frost is infrequent.

The climate is thus a tropical type with a unimodal temperature, radiation and rainfall peak per annual cycle, as opposed to an equatorial climatic regime with bimodal temperature, radiation and rainfall peaks. This has important consequences as climate influences the phenology of plants which in turn influences the ecology of mammals.

Rainfall and temperature data can be effectively summarised by a modified climate diagram (Gausson 1955, Walter 1971). The same scale is used for 10°C and 20 mm to show the arid period prevailing when the rainfall curve falls below the temperature curve, and the humid period when the rainfall curve rises above the temperature curve (Fig.1). When rainfall is above 100 mm it is referred to as a perhumid period. The horizontal extension of the different areas on the diagram shows the duration of these periods, while the vertical extension shows the intensity of the humidity or aridity respectively. These comparisons are valid because evaporation is related to temperature (Walter 1971) and radiation, which in turn is controlled by cloud cover during the annual cycle.

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\*Monthly Weather Reports, Weather Bureau, Pretoria.

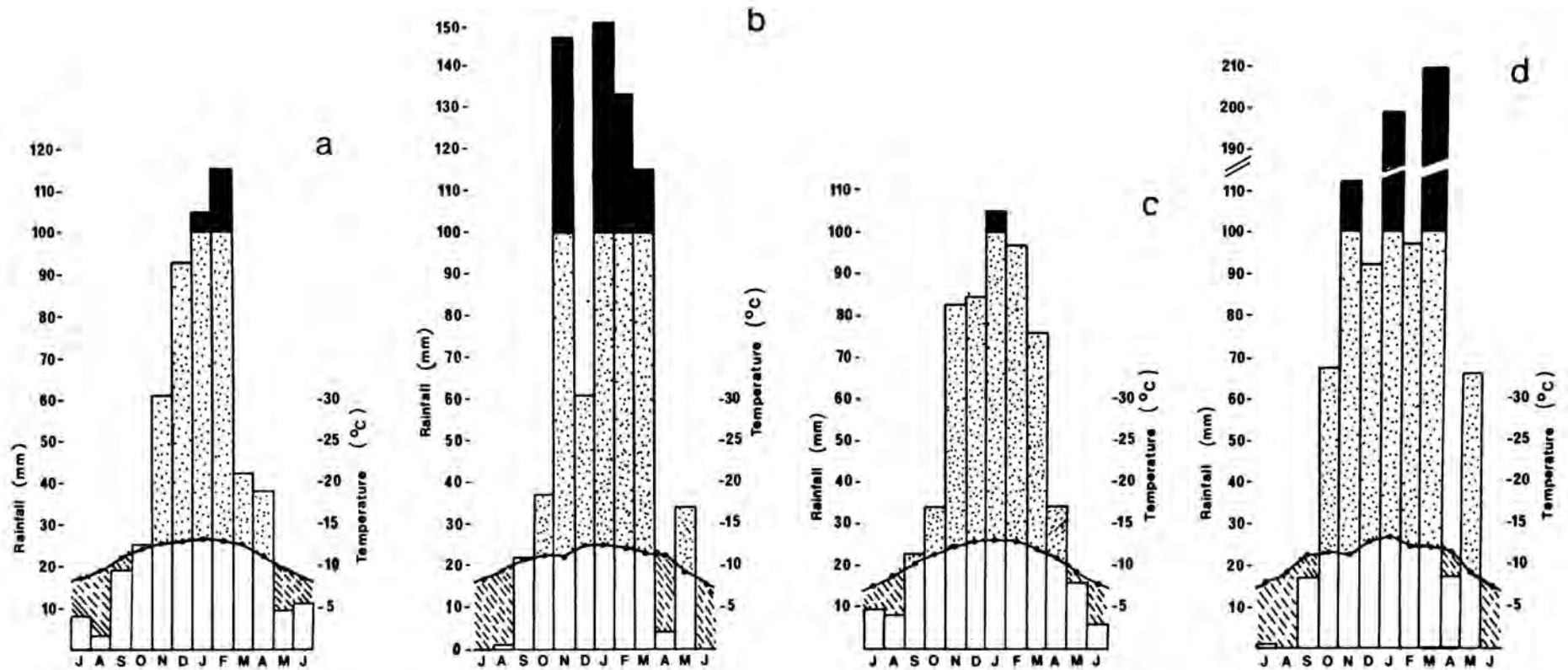


FIG. 1 — Climate diagrams for Phalaborwa (a — 20y mean, b— 1971/1972 season) and Skukuza (c— 20y mean, d— 1971/1972 season). Data from Weather Bureau, Pretoria



## VEGETATION

The vegetation can be classified into major types on a physiognomic (Tinley 1969) and floristic basis. Only woody plants are discussed here.

### *Combretum apiculatum* tree savanna

This is the most widespread type which occurs throughout the central and northern sections of the Reserve. It is usually found on shallow reddish or greyish brown granite soils, especially where the topography is undulating. A quartz pebble layer is often exposed. The dominant species is *Combretum apiculatum* which forms a generally closed, sometimes stratified layer from 2 m to 4 m high. Scattered *Sclerocarya caffra*, *Lannea stuhlmannii* and *Acacia nigrescens* trees occur as emergents. Important associated trees and shrubs are *Grewia* spp., *Combretum hereroensis*, *Peltophorum africanum*, *Euclea undulata* and *Acacia gerrardii*.

### *Combretum zeyheri* tree savanna

This is the dominant vegetation type in the southern part of the Reserve. The topography is flatter than in the north with less clearly eroded drainage lines. The deep, pale grey soil is derived from granite. The tree stratum is occupied by several species the most important of which are *Combretum zeyheri*, *C. apiculatum* and *C. collinum*. Other common woody species are *Terminalia sericea*, *Pterocarpus rotundifolius*, *Acacia gerrardii*, *Acacia hereroensis*, *Dalbergia melanoxylon*, *Sclerocarya caffra*, *Bolusanthus speciosus*, *Euclea divinorum*, *E. undulata* and *Dichrostachys cinerea*.

### *Acacia nigrescens* open tree savanna

This vegetation type occurs on greyish or reddish granite soils throughout the Reserve and on basaltic soils in the central and southeast sections of the Reserve. This is also the typical vegetation of the heavy clay soils derived from dolerite dykes in the south and east. The dominant woody plant species is *Acacia nigrescens* which occurs as a thick-stemmed shrub up to 2 m tall, probably maintained in this growth form chiefly by the pressure of giraffe browsing, and as a tree usually about 10 m tall. Associated trees and shrubs are *Sclerocarya caffra*, *Grewia subspathulata*, *Combretum hereroensis*, *Dalbergia melanoxylon*, *Ormocarpum trichocarpum*, *Acacia senegal* and *Acacia exuvialis*.

### *Colophospermum mopane* shrub savanna and woodland:

True woodland dominated by *Colophospermum mopane* covers large tracts of the

northern section of the Reserve. Elsewhere isolated patches of this vegetation type occur, sometimes associated with extensive areas of *C. mopane* shrub savanna. These vegetation types are usually associated with granite soils. The shrub mopane is usually from 1 m to 2 m high, while the trees are up to 10 m or 15 m high. Associated trees or shrubs are *Euclea undulata*, *Combretum imberbe*, *Acacia* spp. and *Commiphora* spp.

#### Riverine thicket

Most of the larger watercourses in the Reserve support a belt of thicket along their banks. This vegetation type is closed and stratified. The canopy trees can be up to 20 m high. The most important species along the Timbavati River and its tributaries (Porter 1970) are *Diospyros mespiliformis*, *Trichilia emetica*, *Dombeya rotundifolia*, *Ficus ingens*, *Ekebergia capensis*, *Albizia versicolor* and *Lonchocarpus capassa*.

Along the banks of the northern rivers *Schotia brachypetala*, *Diospyros mespiliformis*, *Acacia welwitschii*, *Sclerocarya caffra*, *Combretum imberbe*, *Lonchocarpus capassa* and *Spirostachys africana* are the most important species. The palm *Phoenix reclinata* is widespread along watercourses.

#### Termitaria thickets

Termitaria soils usually differ in their water relations and nutrient status from the soil catena around them (Wild 1952, van der Schijff 1965). They are usually better developed in the southern section of the Reserve which has deeper soils and higher rainfall than the north and are absent from the black clay soils of the dolerite dykes. These mounds support a closed, stratified, thicket. Canopy trees up to 20 m high include species such as *Xanthocercis zambesiaca*, *Berchemia zeyheri*, *Diospyros mespiliformis* and *Sclerocarya caffra*. A large variety of shrubs is found on termitaria.

#### RANGE CONDITIONS

There has been a significant change in the vegetation of substantial parts of the Reserve over the past few decades (Porter 1970 and pers. comm.\*). On the granite soils large scale encroachment by *Acacia exuvialis*, *Dalbergia melanoxylon*, *Ormocarpum trichocarpum* and *Albizia harveyi* is occurring. On the heavy clay soils *Acacia nigrescens* and *Grewia* spp. dominate over large areas.

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\*Mr. R.N. Porter, Hluhluwe Game Reserve, P.O. Box 25, Mtubatuba. Natal.

The reasons for this change in the grass/woody plant balance can probably be ascribed to overgrazing and trampling, brought about partly through the elimination of game migrations leading to year round use of the same range, the total exclusion of fire for over 20 years in most areas and other factors.

These changes have probably led to the depletion of the climax grass cover and perhaps also to the extinction of the attendant grazing herbivores such as roan antelope *Hippotragus equinus*, sable antelope *Hippotragus niger* and tsessebe *Damaliscus lunatus*. The number of other grazers such as blue wildebeest *Connochaetes taurinus* and Burchell's zebra *Equus burchelli* have also decreased. These range conditions are however ideal for browsing animals such as impala *Aepyceros melampus* and giraffe - the populations of which are increasing.

## STUDY POPULATION

### POPULATION DENSITY

The size and crude density of the giraffe population was determined by using the road strip census technique of Hirst (1969a). It was found that there were approximately 1434 giraffe in the Reserve in October 1971, with a crude population density of approximately 2,6 giraffe per km<sup>2</sup>. This figure is considerably higher than any given in the literature for other giraffe populations (Table 1), though to what extent this is due to man's influence eg. fences and water holes, is not known. It is likely though, that this high crude population density results in considerable intra-specific competition for food, especially during the dry season when leaf production has virtually ceased but no data are available to prove this.

There are indications that the population of giraffe in the Timbavati exceeds the carrying capacity of the area. Thus during the late dry season of 1965, which was preceded by a season of low rainfall and the population density of giraffe was only 2,18 per km<sup>2</sup> there were 182 recorded deaths from starvation and malnutrition in the Reserve (Hirst 1969b) amounting to over 15% of the population. Hirst (1969b) also noted deaths from starvation and malnutrition to a lesser extent during the late dry seasons of 1964 and 1966. He also mentioned that during these periods of nutritional stress the incidence of lion *Panthera leo* predation on giraffe rose considerably.

TABLE 1: CRUDE POPULATION DENSITY OF GIRAFFE IN DIFFERENT REGIONS OF AFRICA

No. of giraffe per km <sup>2</sup>	Locality	Area sampled km <sup>2</sup>	Source
0,01 - 1,45	Various localities in Africa	-	cited by Foster & Dagg 1972
0,09 - 0,13	Garamba National Park, Zaire 1960 - 1963	4 800	Bourlière 1965
0,88 *	Akira Ranch, Kenya	316	Blankenship & Field 1972
0,16	Kruger National Park, R.S.A.	19 500	National Parks Board 1970
0,99 *	Sabie Sand Wildtuin, R.S.A.	550	Graupner 1971
1,23 *	Hans Merensky Nature Reserve, R.S.A.	52	Oates 1970
2,60 *	Timbavati Private Nature Reserve, R.S.A.	550	This study

\* Fenced areas where artificial build up of population density is possible.

Further evidence for an excessive giraffe population in Timbavati is indicated by the large proportion of trees and shrubs which show distinct browse lines and pruning effects as a result of giraffe feeding.

## PREDATION AND MORTALITY

During the study period at Timbavati 54 carcasses were recovered during routine patrols of which 44 (81%) could be ascribed to lion kills; six (11%) were due to natural causes, these included four very old males, two of which died after a cold spell in January 1972, and two young calves; three (6%) were killed after they had become entangled in the boundary fence and one male (2%) died after breaking a front leg in a fight with another giraffe.

The number of giraffe killed by lion in each month is shown in Table 2 and probably only represents a sample of the total number of giraffe killed during the period. The data for the period July 1970 - June 1971 were provided by Mr. D. Jackaman (pers. comm.)\*. Most calves were killed in their first few weeks of life following the peak calving period which lasts from March to June (Chapter 7). The greatest number of adults were killed in October at the end of the winter period of food shortage (Chapter 2). Giraffe kills due to lion have been grouped into three-monthly periods (Table 3a). From this table it can be seen that there are no significant differences in the relative number of giraffe killed during the four different periods of the year between this study and Hirst's (1969b) study. A comparison of giraffe age class proportions killed by lion between these studies also shows no significant differences (Table 3b). The proportion of calves is likely to be under-represented in the kill data as lions often leave very little evidence of a calf kill and this could easily be missed. Nevertheless, they still form a significant part of the collected material (41%). As juveniles accounted for only 21% (n=1007) of the population during the study period the data from the kills examined suggest that there is significant predation pressure on calves in their first few months of life, the proportion of calves in the recorded kills being significantly greater ( $P < 0,001$ ) than the proportion in the population. The proportion of immature animals was the same in both sets of data (11%) while the proportion of adults in the recorded kills (48%) was significantly less ( $P < 0,001$ ) than the proportion of adults in the population (68%).

## SEX RATIO

A disparate sex ratio in giraffe has been reported for several different areas in Africa. In woodland habitat in a fenced cattle ranching area Innis (1958) reported 28% females (n=141). Bourlière (1961) reported 41% females (n=85)

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\* Mr. D. Jackaman, Punda Milia Restcamp, P.O. Skukuza, Transvaal.

TABLE 2: NUMBER OF GIRAFFE OF DIFFERENT AGE CLASSES KILLED BY LION IN THE TIMBAVATI PRIVATE NATURE RESERVE BETWEEN JULY 1970 AND JULY 1972

Age Class	Months												Total
	J	F	M	A	M	J	J	A	S	O	N	D	
Juvenile	1	2	-	-	2	4	4	-	1	-	3	1	18
Immature	-	-	-	-	1	-	2	2	-	-	-	-	5
Adult	4	3	-	-	3	1	1	1	-	7	-	1	21
Total	5	5	-	-	6	5	7	3	1	7	3	2	44

TABLE 3A: COMPARISON OF NUMBER OF GIRAFFE KILLED BY LION IN THE TIMBAVATI PRIVATE NATURE RESERVE FOR THREE-MONTHLY PERIODS FROM JUNE 1964 - MAY 1967 (HIRST 1969b); AND JULY 1970 - JULY 1972 (THIS STUDY)

	Dec. - Feb.	Mar. - May	June - Aug.	Sep. - Nov.	Total
1964 - 1967	15	8	43	37	103
1970 - 1972	12	6	15	11	44
$\chi^2$	3,32	1,23	0,75	1,67	
P	*n.s.	n.s.	n.s.	n.s.	

TABLE 3B: COMPARISON OF AGE CLASS PROPORTIONS OF GIRAFFE KILLED BY LION IN THE TIMBAVATI PRIVATE NATURE RESERVE DURING THE PERIODS JUNE 1964 - MAY 1967 (HIRST 1969b) AND JULY 1970 - JULY 1972 (THIS STUDY)

	1964 - 1967	1970 - 1972	$\chi^2$	P
Juveniles	15 (35%)	18 (41%)	0,335	*n.s.
Immature	2 (5%)	5 (11%)	1,324	n.s.
Adult	26 (60%)	21 (48%)	1,420	n.s.
Total	43 100%	44 100%		

\*n.s. = no significant difference

from Amboseli in Kenya and he presented statistical evidence that significantly more males are born in captivity (61,5% of 117 births). Bourlière also reported that 61% of giraffes counted over a period of 5 months from October 1960 - February 1961 in Nairobi National Park were females. However, Foster (1966) suggested that the disparate sex ratio of giraffe in Nairobi could be explained by habitat preferences. Here, as well as in the Serengeti National Park (Foster & Dagg 1972) males predominated in heavily wooded and forested areas and females predominated in more open habitats. In two different areas in Rhodesia investigated by Dassman (Foster & Dagg 1972) females made up 66% and 56% of the populations (sample size not given). Oates (1971) reported a sex ratio of 1 : 1,45 in favour of females (n=172) in an area of reasonably homogenous vegetation in the eastern Transvaal. Graupner (1971) reported sex ratios of 1 : 1 north of the Sand River in the Sabi Sand Wildtuin, eastern Transvaal, which is enclosed by a game proof fence and 4,3 : 1 in favour of males south of this river. He attributed this marked difference to the restriction on movement posed by the Sand River which was more easily crossed by males. Berry (1973) reports a 1 : 1,67 ratio in favour of females in the Luangwa Valley, Zambia (n=264). Child (1968) classified 257 adult giraffe according to sex in the Chobe area of Botswana and found a ratio of 1 : 2,05 in favour of females. A significantly disparate sex ratio of 1 : 1,2 ( $P < 0,001$ ) in favour of females is apparent for Timbavati giraffe from Hirst's (1969b) data (n=6468). In the present study a sex ratio of 1 : 1,3 which is also significantly disparate in favour of females was found (n=820;  $P < 0,001$ ). However the sex ratio of calves (n=38) and immature animals (n=86) did not differ from 1 : 1. A total of 23 fetuses was sexed of which 13 were male and 10 were female, but these data are insufficient for meaningful statistical analysis. There is thus no evidence from the Timbavati population that the sex ratio at birth differs from the expected 1 : 1. (The sex ratio of giraffe born at Taronga Zoological Park, Australia, did not differ significantly from 1 : 1, n=63. However it should be noted that of four stillborn calves recorded, all were male, R. Strahan pers. comm. \*) As the sample of giraffe which were sexed comes from all available habitats, all having similar visibility, it is unlikely that the difference could be explained on the basis of different habitat selection by the sexes. Of the lion kills which could be sexed (all adult or immature) it was found that nine were males and 14 were females. If these data can be interpreted as suggesting that more females than males are killed (which is not statistically justified) then it would rule out selective predation pressure as a factor influencing the sex ratio of giraffe

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and makes the explanation of the disparate sex ratio even more difficult unless there is selective predation pressure against male calves. Only four adults were found that had died from natural causes other than predation and all were very old males. Emigration cannot be invoked as an explanation as the Reserve is fenced and giraffe seldom break through successfully. There is thus no satisfactory explanation as yet for the disparate sex ratio among giraffe in the Timbavati and further study is required.



## CHAPTER 2

FEEDING, NUTRITION AND HABITAT SELECTION

## INTRODUCTION

Food selection by giraffe has been studied by several workers in Africa. Most of these studies relied on visual observations of feeding animals and lists of plant species eaten in various areas have been published. Other studies have been more quantitative and the frequency with which certain plant species were eaten has been given.

Innis (1958) related the availability of leaves to the preference shown for them. In a later study she investigated nutrient content of leaves of several species commonly eaten by giraffe (Dagg 1960). Leuthold & Leuthold (1972) compared the frequency of occurrence of plant species in the habitat during the dry season with the frequency in the giraffe's observed diet, revealing selection for or against certain species. Oates (1972) calculated the quotient of percentage frequency of the species taken by giraffe and the percentage frequency of occurrence of the species in the field, to give a preference rating.

In the present study stomach contents were analysed. The material was collected over a period of one year from July 1971 to June 1972, from giraffe culled, or killed by lions.

CLIMATE AND PLANT GROWTH

Environmental and historical factors will determine what vegetation type occurs in a particular area. Factors of short term duration such as intra- and inter-specific competition between both animals and plants and temporary climatic extremes influence the availability of plant foods to specific animal species. How some of these factors have influenced the habits, population size and structure of the giraffe studied are briefly discussed below.

Most of the plants utilised by giraffe in the study area are adapted to an active growth phase during the wet season and a deciduous dormant phase which coincides with the advent of the dry season. Several studies on the phenology of plants in tropical and subtropical Africa have reported an abundance of leaves, flowers and fruit in the humid period with a diminishing availability during the arid period (Huntley 1970, Oates 1971, Hall-Martin 1972, Hall-Martin & Fuller 1975). Histograms depicting the availability of leaves, flowers and fruits of several species, in different areas and under different climatic

regimes, are given by these authors. These figures indicate that in the deciduous species e.g. *Acacia nigrescens*, *Combretum apiculatum*, *Combretum imberbe* and *Albizia harveyi* and the semi-deciduous *Colophospermum mopane* fewer leaves are available from June to November, with minimum availability from July to October in all three study areas, there usually being some trees in the samples which had leaves throughout the year. Only *Combretum imberbe* in southern Malawi showed complete deciduousness. The leaf, flower and fruit regimes of those species studied in different areas were similar.

These authors also discuss the importance of rainfall to the onset and intensity of the leaf flush, flowering and fruiting periods of several species. It has also been noted that temperature, light intensity, photoperiod, water stress, shortage of mineral nutrients and other internal factors also play an important part in the timing of the flush of new leaves (Eyre 1968, Kozłowski 1971, Longman & Jeník 1974). Moreover late summer peaks in rainfall may also influence plants to flower twice in the same season (Huntley 1970).

No similarly detailed phenological studies were undertaken in the Timbavati, but climatic and floristic observations suggest that similar findings to those quoted above would result from such a study. The conclusions drawn from these studies have therefore been considered applicable, at least for purposes of discussion, to the present study.

## MATERIAL AND METHODS

The material used in this study was collected and treated as follows:

### COLLECTION OF MATERIAL

Grab-samples amounting to approximately 10% by mass of the total wet stomach contents were taken from the rumens of from three to five giraffes per month. Sometimes the unavoidable mixing of ruminated material with the rumen contents took place, particularly in the case of animals killed by lions. The material was sun-dried and stored in sealed plastic bags.

### MONTHLY SAMPLES

As there is considerable variation between the diets of individual animals of the same species (Hofmeyr 1970, Stewart 1971) the material was examined on a monthly basis rather than an individual basis. To achieve this, randomly

selected portions of the stomach contents from each individual animal collected during a particular month were combined to give 12 approximately equal-sized samples, one for each month. A standardised procedure for the constitution of these monthly samples was followed, part of the material collected from each animal being spread out evenly, in a square. The square was quartered and one quarter was contributed to the sample for that month. The quarters from consecutive samples were taken in a consecutive order starting from the top left quarter in the first sample and working in a clockwise direction through the rest.

### SUBSAMPLING

Field observations showed that giraffe utilised a wide range of plants. These can be divided arbitrarily into two groups on the basis of leaf type or leaflet size. Group I consisting of all simple-leaved species and compound-leaved species with leaflets longer than 1 cm. Group II consisting of all compound-leaved species with leaflets less than 1 cm in length. Because of the significant difference in size of leaves in the two groups, a simple comparison of the frequency of occurrence of different species in the samples is not a valid means of assessing the importance of these different species in the diet of the giraffe (see also Stewart 1967). It was therefore considered necessary to confine comparisons of relative species importance within the two major groups. Furthermore, because of the range of size of leaves within each group relative frequency alone was not considered adequate for assessing the importance of species; comparisons were therefore made on the basis of relative mass or relative surface area.

#### Group I

The sample for the month was spread about 1 cm deep on a flat surface and quartered. One quarter was selected, starting with the top left quarter in the first month and working in a clockwise direction through the other 11 months. From the selected quarter approximately 50 ml of material was randomly collected for the determination of Group II species. The remaining material was then mixed up again with the other three quarters and spread out again as before. The midpoint of the square was determined by observation and marked. From this point the material was sorted through and leaf or fruit fragments larger than  $0,5 \text{ cm}^2$  were picked out. The sorting was carried out in small concentric circles around the midpoint until 50 fragments of a suitable size had been collected. The remaining material was then mixed up and the sorting procedure repeated three more times.

These fragments were identified where possible to species level using a dissecting microscope and detailed diagnostic keys for the identification of over 50 species compiled for this study from reference material collected in the study area. After oven-drying for at least 12 hours at 60°C the mass of the material of each species was determined.

#### Group II

The 50 ml of material collected from the monthly sample was agitated over a sieve with a 1,0 mm<sup>2</sup> mesh. The material which did not pass through the mesh was examined microscopically and all Group II leaflets and fragments, all Group I fragments larger than 2,0 mm<sup>2</sup>, as well as all woody material, flowers and seeds were removed. The remaining material was soaked overnight in water and then teased apart under the microscope and classified. It was not necessary to wash the sample in acetic acid (Sinclair & Gwynne 1972) as particle aggregates bound by dried saliva and rumen fluids separated easily after soaking in water. The material which had passed through the mesh was examined microscopically and all fragments or whole leaflets of the Group II species, and flowers, were removed.

The leaflets were identified as far as possible to species using a diagnostic key prepared for the 13 most important Group II species occurring in the study area. Fragments of leaflets or leaflets which had been partially digested were usually classified as far as genus or as unidentified material. Due to the small size of the leaflets of several species, and the small number involved, it was impractical to work on the basis of mass for comparative purposes. The mean leaflet surface area for each of these species was, therefore, calculated from a random sample of 25 leaflets, and this figure was used to determine the total surface area for each species in each monthly sample of 50 ml.

#### Woody material.

All woody material from the 50 ml sample which did not pass through the mesh was dried in an oven at 60°C for at least 12 hours and its mass determined. This material included twigs, petioles, spines, thorns and large midribs.

#### Flowers

All flowers or flower fragments found in the 50 ml sample were dried in an oven at 60°C for at least 12 hours and their mass determined.

### SAMPLES FOR CHEMICAL COMPOSITION STUDIES

Part of the remaining material of each of the samples from individual animals was spread out as before and quartered. One of these quarters was contributed to the chemical analysis sample for that month. The consecutive order for selecting quarters was the same as that followed before. The resulting samples for each of the 12 months were ground through a 1,5 mm sieve in a cross beater laboratory mill. The material was well mixed and quartered and only sufficient material for the chemical analysis was retained. These samples were dried to constant mass in a force draught oven at 100°C. Crude protein (N x 6,25), ether extract (fat), crude fibre and ash were determined on triplicate sub-samples (approx. 5,0 g each) by standard (Horwitz 1970) procedures for animal feeds. The heat of combustion (gross energy content) of the samples was determined using an automatic adiabatic calorimeter.

### MULTIVARIATE STATISTICAL ANALYSIS

The multivariate statistical analysis used in this study is known as principal components analysis (PCA). A brief, though comprehensive description of the technique is given by Gittins (1969) and a more mathematical description is given by Seal (1964). The PCA technique has found a wide range of users in quantitative plant ecological studies (Yarranton 1967, Hall-Martin 1972, 1975, Theron 1973) in plant taxonomic studies (Ross & Morris 1971) and in studies on animals (Machin 1974). In the context of this study the object of using the technique was to extract sets of components from the plant species identified in stomach contents x sampling months matrices for the Group I and Group II leaves which would account for as much as possible of the variation between the different plant species eaten by giraffe during the different months of the year.

Eight component analyses were performed, one normal and one inverse for each of the Group I relative percentage mass, Group I relative percentage frequency, Group II relative percentage surface area and Group II relative percentage frequency data respectively. The raw data are given in Tables 5 - 8. Only species which occurred in stomach samples for at least three months were included. In some cases, e.g. *Acacia* spp. flowers and *Combretum* spp. fruits, the data for more than one species were lumped together. The code numbers for the different species used in the analyses are given in the tables.

Both normal and inverse PCA's were carried out, in the case of the normal analyses the first step was the computation of correlation coefficients between

each month and each other month over all species values for each of surface area, mass or relative frequency resulting in a symmetrical 12 x 12 matrix. The principal components were extracted from this matrix. The inverse analysis correlation coefficients were calculated between each species and each other one over all months.

An eigenvalue and eigenvector are associated with each principal component. The value indicates the proportion of the total variation accounted for by the component and thus the 'importance' of the component, and the vector gives the weighting of each parameter (month in the case of the normal analyses or species in the case of the inverse analyses). Components are extracted in descending order of eigenvalues. The vector is scaled so that the highest value is unity.

Two-dimensional scatter diagrams were constructed from the analyses. The position of a species along an axis in a normal analysis is found by summing the products of the eigenvector and parameter (month) vector for the species. Conversely the position of a month along an axis in an inverse analysis is found by summing the products of the eigenvector and species value means for each month.

#### HABITAT SELECTION

Hirst (1964) noted the seasonal distribution of giraffe in the course of an ecological survey of the Timbavati Reserve. He found that they were concentrated in two regions of the Reserve during the dry season. One of these was the north-western block of the Reserve where the vegetation is predominantly a mosaic of *Combretum apiculatum* tree savanna, *Acacia nigrescens* open tree savanna and *Colophospermum mopane* communities with thicket along watercourses. The other important area was a broad strip along the Timbavati River in the south east of the Reserve. The vegetation here is predominantly *Combretum zeyheri* tree savanna, *Acacia nigrescens* open tree savanna and extensive riverine thickets. It was found that after the rains the giraffe population was dispersed over a much wider area and their habitat preference was less marked (Hirst 1964).

Observations were therefore made on giraffe distribution in different habitats in the Reserve from June 1971 to July 1972. These data were then analysed and provide a quantitative basis for assessing the seasonal movements of the giraffe.

## RESULTS

### FOOD SELECTION

A total of 8099 plant fragments, including leaves, leaflets, flowers, flower buds, pod fragments and seeds were examined and classified (Table 4). It was convenient to use the term 'unit' to refer to any leaf fragment or plant part regarded as an individual record of the occurrence of a particular plant taxon.

#### Validity of samples

The adequacy of the number of Group I fragments sampled in each month could be tested by examining a graph with the number of species found plotted on one axis and the number of fragments on the other (Fig. 2). These curves are similar to the species/area curves used by Morris (1969) to test the adequacy of sample sizes in plant ecological studies. The number of new species found in each of the four subsamples of 50 fragments can be read off these curves.

Five out of the 12 curves (March, May, June, August and October) tended to flatten after the 50 fragment level. This indicated that for these months a sample of 200 fragments was probably adequate to account for most of the Group I species actually present in the stomach. The remaining seven curves were still rising at the 200 fragment level indicating that not all the species variation within the sample had been accounted for. However, it can be seen from Table 5 that in any month over 75% of the total number of fragments represented not more than five species of plants. This indicates that most of the other species found in each month were contributing relatively little towards the total nutrition of the giraffe. The effort to account for all the species actually present in the samples was, therefore, not justified for the purposes of this study. There is a tendency for the dry month curves (May to October) to be flatter than the wet month curves (November to April) indicating a less diverse diet during this period.

To test the validity of the Group II samples a second 50 ml sample was drawn from the May material and the Group II fragments recovered. It was found that the concentration of 1,68 fragments per ml derived from the first 50 ml sample was increased but not significantly, when the two samples were combined, by only 0,06 fragments per ml to 1,74 fragments per ml ( $\chi^2 = 0,0467$ ). The concentration of 0,18 units per ml decreased to 0,10 units per ml. These data and an assessment of the time involved in sorting and identifying this material

TABLE 4: CLASSIFICATION OF GIRAFFE STOMACH CONTENTS, TRANSVAAL LOWVELD, JULY 1971 - JUNE 1972

													Totals	Percentage of row totals within sections
<b>1. Group I fragments:</b>														
Identified to species	193	192	186	199	161	189	183	191	199	187	190	192	2262	94,2
Identified to genus	-	2	-	-	35	5	14	2	1	8	7	5	79	3,3
Identified to family	-	-	-	-	3	4	1	1	-	1	-	-	10	0,4
Unidentified	7	6	14	1	1	2	2	6	-	4	3	3	49	2,0
<b>TOTALS</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>200</b>	<b>2400</b>	<b>99,9</b>
<b>2. Group II leaflets and fragments (50 ml samples):</b>														
Identified to species	80	117	30	94	122	461	502	263	291	198	37	168	2363	61,6
Identified to genus	34	16	6	13	87	124	179	471	81	151	47	66	1275	33,2
Unidentified leaflets	6	-	-	-	-	-	45	82	-	5	-	2	140	3,6
Unidentified flowers	-	-	35	3	-	-	4	-	-	-	-	-	42	1,1
Flowers and seeds to genus	-	-	10	4	-	-	-	-	-	-	-	2	16	0,4
<b>TOTALS</b>	<b>120</b>	<b>133</b>	<b>81</b>	<b>114</b>	<b>209</b>	<b>585</b>	<b>730</b>	<b>816</b>	<b>372</b>	<b>354</b>	<b>84</b>	<b>238</b>	<b>3836</b>	<b>99,9</b>
<b>3. Group I fragments from 50 ml sample:</b>														
	73	176	282	113	119	128	113	69	170	228	235	157	1863	-
<b>4. Totals of all units examined each month:</b>														
	393	509	563	427	528	913	1043	1085	742	782	519	595	8099	



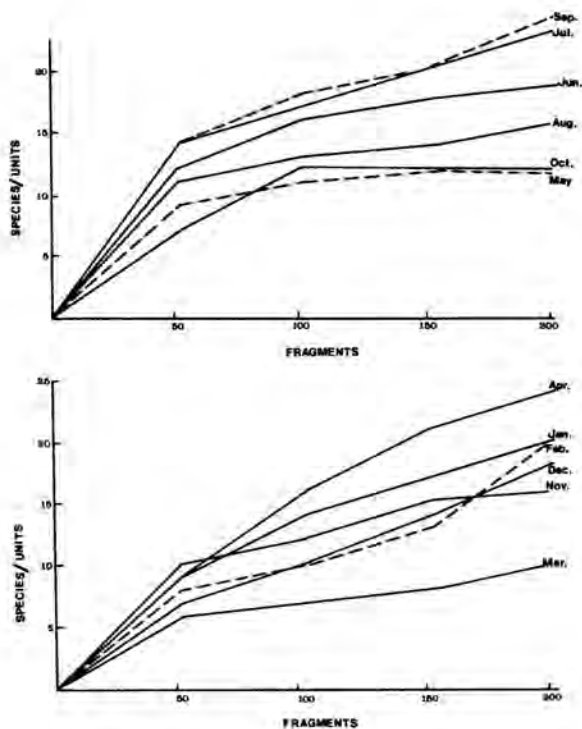


FIG. 2

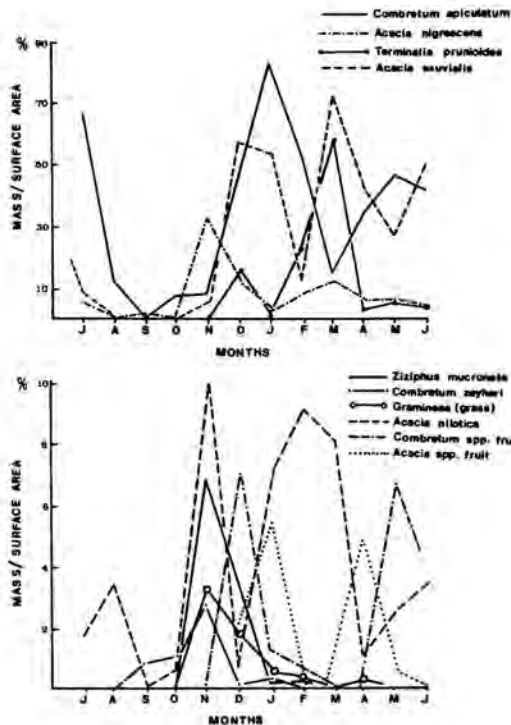


FIG. 3

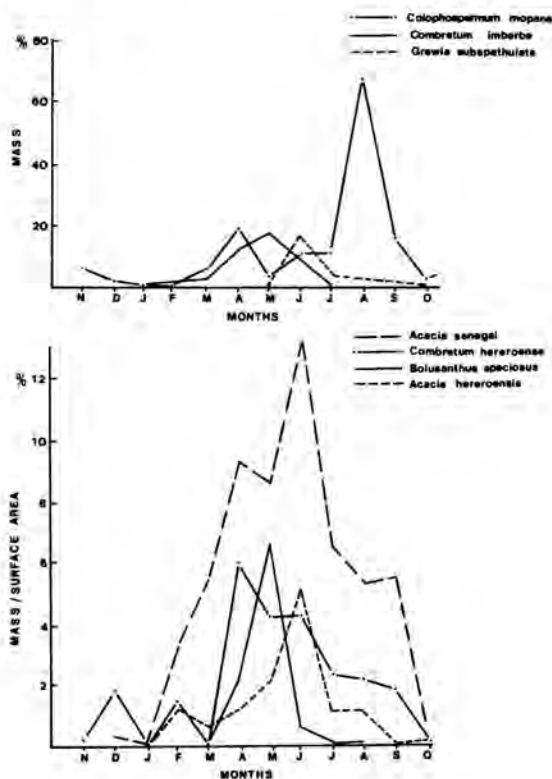


FIG. 4

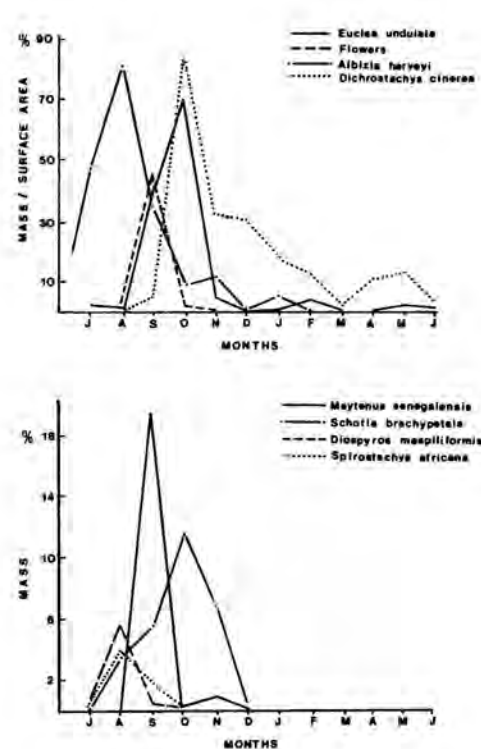


FIG. 5

FIG. 2 – The number of plant species/units and number of fragments of Group I material from giraffe stomach contents, July 1971 – June 1972.

FIG. 3 – Relative percentage mass or surface area of selected plant species from giraffe stomach contents, July 1971 – June 1972.

FIG. 4 – Relative percentage mass or surface area of selected plant species from giraffe stomach contents, July 1971 – June 1972.

FIG. 5 – Relative percentage mass or surface area of selected plant species in the stomach contents of giraffe, July 1971 – June 1972.

indicated that the 50 ml sample was adequate for the purposes of this investigation.

#### Validity of climatic data

The study period can be considered to be a representative year for purposes of discussion. The Phalaborwa and Skukuza rainfall curve, however, rose above the temperature curve about two weeks earlier than normal, and total rainfall was higher (Fig. 1). At both stations there were abnormal dry spells in April and wet spells in May which may have influenced the vegetation, and thus the feeding of the giraffe to some extent (Fig. 1).

#### Utilisation of leaves, flowers, fruit and grass

The relative percentage frequency of occurrence and relative percentage mass of Group I units, are given in Tables 5 and 6 respectively. The relative percentage frequency of occurrence and the relative percentage surface area of Group II units are given in Tables 7 and 8 respectively. The relative percentage mass and relative percentage surface areas of the most important Group I and II species are presented graphically in Figs. 3, 4 and 5.

In these figures three distinct phenological peaks were found which appear to coincide with the climatic seasons: leaf fall peak, a flowering and fruiting peak, and a leaf flush peak.

#### The hot wet season (November to March)

From Tables 5 and 7 it can be seen that the preferred deciduous species were utilised to a maximum at this time. These plants produce new leaves shortly before, or after, the commencement of the rains (October/November).

The most important species utilised during the early part of this season were *Combretum apiculatum*, *Terminalia prunioides*, *Acacia nigrescens*, *Ziziphus mucronata* and *Combretum zeyheri* (Fig. 3). It was during this period of abundance that giraffe made limited use of tall grasses (Fig. 3). The onset of leaf flush in Group II species and their consequent utilisation is also indicated by peaks in the occurrence of various *Acacia* spp. in the samples, in particular *Acacia exuvialis* and *Acacia nilotica* (Fig. 3). The level of utilisation of most of the abovementioned species fluctuated considerably throughout the year. Nevertheless, they constituted the major portion of the giraffes' diet during this time (Tables 5 & 7).

TABLE 5 : THE RELATIVE PERCENTAGE FREQUENCY OF OCCURRENCE OF GROUP I LEAVES AND FRUITS, IN STOMACH CONTENTS OF TRANSSVAAL LOWVELD GIRAFFE, JULY 1971 - JUNE 1972

	PCA Code	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May	June
<i>Gramineae</i>	20	-	-	-	-	1,5	2,0	0,5	0,5	-	0,5	-	-
<i>Olacaceae</i>													
<i>Ximenia caffra</i>	d <sup>+</sup> 10	1,5	0,5	2,0	-	-	-	-	-	-	1,0	-	-
<i>Mimosaceae</i>													
<i>Albizia anthelmintica</i>	d	-	-	-	-	0,5	-	-	-	0,5	1,0	-	-
<i>Albizia versicolor</i>	d	0,5	-	-	-	-	-	-	-	-	-	-	-
<i>Albizia sp.</i>	d	-	-	-	-	16,5	-	-	-	-	-	-	-
<i>Acacia senualis</i> - fruit	22	-	-	-	-	-	1,0	3,0	-	-	1,0	0,5	0,5
<i>Acacia nigrescens</i>	d 3	11,0	2,0	3,5	2,0	45,5	25,5	13,5	20,5	25,5	12,0	13,0	6,5
<i>Acacia welwitschii</i>	d	0,5	0,5	-	-	-	-	-	-	-	-	-	-
<i>Acacia sp.</i> - fruit	22	-	-	-	-	-	1,0	1,5	-	-	1,5	-	-
<i>Caesalpiniaceae</i>													
<i>Colophospermum mopane</i>	d 2	15,0	68,0	19,5	5,0	5,5	3,5	2,0	0,5	3,0	23,0	6,0	14,5
<i>Schotia brachypetala</i>	sd 13	-	2,0	1,5	8,5	4,0	-	1,0	-	-	-	-	0,5
<i>Papilionaceae</i>													
<i>Bolusanthus speciosus</i>	d 9	0,5	0,5	-	-	-	-	-	-	-	1,5	7,0	0,5
<i>Mundulea sericea</i>	d	-	-	-	-	-	-	-	-	-	0,5	-	-
<i>Pterocarpus rotundifolius</i>	d	0,5	-	-	-	-	-	-	-	-	-	-	-
<i>Zygophyllaceae</i>													
<i>Balanites maughami</i>	d	-	-	-	-	-	-	-	-	-	-	-	0,5
<i>Euphorbiaceae</i>													
<i>Pseudolachnostylis maprouneifolia</i>	d	0,5	-	-	-	-	-	-	-	-	-	-	-
<i>Securinega virosa</i>	sd	-	-	-	-	-	-	0,5	0,5	-	-	-	-
<i>Spirostachys africana</i>	d 11	0,5	4,5	3,5	1,0	-	-	1,0	-	-	-	-	-
<i>Anacardiaceae</i>													
<i>Sclerocarya caffra</i>	d 18	-	-	2,0	-	-	2,5	0,5	5,0	-	-	-	-
<i>Celastraceae</i>													
<i>Maytenus senegalensis</i>	e 8	1,5	-	18,5	4,5	8,0	-	-	0,5	0,5	1,0	-	1,5
<i>Cassine transvaalensis</i>	e	-	-	-	2,0	-	-	-	0,5	-	-	-	2,0
<i>Rhamnaceae</i>													
<i>Ziziphus mucronata</i>	d <sup>+</sup> 19	-	-	-	-	10,0	4,5	0,5	1,0	-	-	-	1,0
<i>Tiliaceae</i>													
<i>Grewia flava</i>	d	-	-	-	-	-	0,5	-	-	1,0	-	-	-
<i>Grewia monticola</i>	sd	-	-	-	-	-	-	-	-	-	1,0	-	-
<i>Grewia occidentalis</i>	d	-	-	0,5	-	-	-	-	-	-	-	-	-
<i>Grewia subspatulata</i>	d 6	4,0	0,5	2,0	0,5	0,5	1,0	1,0	-	-	-	-	12,0
<i>Grewia spp.</i>	d	-	-	-	-	-	-	-	0,5	-	-	-	-
<i>Combretaceae</i>													
<i>Combretum apiculatum</i>	d 1	55,5	7,5	-	2,5	3,0	35,5	60,0	29,5	13,0	26,0	38,0	37,0
<i>Combretum apiculatum</i> - fruit	21	-	-	-	-	-	1,5	-	-	-	-	-	-
<i>Combretum hereroense</i>	d 4	3,0	1,5	2,5	-	-	1,0	-	0,5	-	7,0	1,5	3,0
<i>Combretum imberbe</i>	d 16	-	-	3,0	-	0,5	0,5	1,0	2,5	2,5	14,0	18,0	10,0
<i>Combretum imberbe</i> - fruit		-	-	-	-	-	-	-	-	-	0,5	-	-
<i>Combretum zeyheri</i>	d 17	-	-	0,5	1,0	1,5	0,5	1,0	0,5	-	-	-	-
<i>Combretum spp.</i>	d 15	-	1,0	-	-	1,0	-	0,5	-	0,5	2,5	-	-
<i>Combretum spp.</i> - Fruit	21	-	-	-	-	-	1,5	5,0	0,5	-	-	3,5	2,5
<i>Terminalia prunioides</i>	d 7	0,5	0,5	-	-	0,5	17,0	6,0	32,0	53,0	4,0	10,0	6,0
<i>Terminalia prunioides</i> - fruit		-	-	-	-	-	-	-	-	0,5	-	-	-
<i>Ebenaceae</i>													
<i>Euclea divinorum</i>	e	0,5	-	0,5	-	-	-	-	-	-	-	-	-
<i>Euclea natalensis</i>	e	-	-	0,5	-	-	-	-	-	-	-	-	-
<i>Euclea undulata</i>	e 5	1,0	0,5	32,5	71,5	1,0	-	0,5	2,0	-	-	1,0	0,5
<i>Diospyros mespiliformis</i>	e 14	-	7,5	0,5	1,0	-	-	-	-	-	-	-	-
Unidentified spp.	12	3,5	3,0	7,0	0,5	0,5	1,0	1,0	3,0	-	2,0	1,5	1,5
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

d = deciduous      sd = semi-deciduous      e = evergreen

TABLE 6 : THE RELATIVE PERCENTAGE MASS OF GROUP I LEAVES AND FRUITS, IN STOMACH  
 CONTENTS OF TRANSSVAAL LOWVELD GIRAFFE, JULY 1971 - JUNE 1972

	PCA Code	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
<i>Gramineae</i>	20	-	-	-	-	3,29	1,75	0,47	0,29	-	0,31	-	-
<i>Olaaceae</i>													
<i>Ximelia caffra</i>	10	1,46	0,13	0,58	-	-	-	-	-	-	3,02	-	-
<i>Mimosaceae</i>													
<i>Albisia anthelmintica</i>		-	-	-	-	0,59	-	-	-	0,52	0,33	-	-
<i>Albisia versicolor</i>		0,45	-	-	-	-	-	-	-	-	-	-	-
<i>Albisia</i> spp.		-	-	-	-	16,51	-	-	-	-	-	-	-
<i>Acacia emuialis</i> - fruit	22	-	-	-	-	-	1,31	1,25	-	-	0,35	0,63	0,20
<i>Acacia nigrescens</i>	3	6,19	0,95	1,61	0,45	33,11	13,13	2,88	8,87	12,85	7,19	6,66	4,90
<i>Acacia welwitschii</i>		0,09	0,02	-	-	-	-	-	-	-	-	-	-
<i>Acacia</i> sp. fruit	22	-	-	-	-	-	0,79	4,21	-	-	4,55	-	-
<i>Caesalpiniaceae</i>													
<i>Colophospermum mopane</i>	2	10,51	67,83	15,03	1,86	5,10	1,91	0,52	0,06	5,45	19,41	3,11	10,36
<i>Schottia brachypetala</i>	13	-	3,21	5,42	11,54	6,83	-	0,15	-	-	-	-	0,20
<i>Papilionaceae</i>													
<i>Bolusanthus speciosus</i>	9	0,07	0,26	-	-	-	-	-	-	-	2,08	6,53	0,60
<i>Mundulea sericea</i>		-	-	-	-	-	-	-	-	-	0,35	-	-
<i>Pterocarpus rotundifolius</i>		0,30	-	-	-	-	-	-	-	-	-	-	-
<i>Zygophyllaceae</i>													
<i>Balanites maughanii</i>		-	-	-	-	-	-	-	-	-	-	-	0,42
<i>Euphorbiaceae</i>													
<i>Pseudolachnostylis maprouneifolia</i>		1,63	-	-	-	-	-	-	-	-	-	-	-
<i>Securinega virosa</i>		-	-	-	-	-	-	0,58	0,03	-	-	-	-
<i>Spirostachys africana</i>	11	0,76	3,79	1,36	0,13	-	-	0,17	-	-	-	-	-
<i>Anacardiaceae</i>													
<i>Sclerocarya caffra</i>	18	-	-	4,43	-	-	2,05	0,29	4,11	-	-	-	-
<i>Celastraceae</i>													
<i>Maytenus senegalensis</i>	8	0,88	-	19,49	2,69	7,99	-	-	0,61	2,11	0,82	-	1,24
<i>Cassine transvaalensis</i>		-	-	-	3,86	-	-	-	0,04	-	-	-	0,54
<i>Rhamnaceae</i>													
<i>Ziziphus mucronata</i>		-	-	-	-	6,90	3,73	0,23	0,23	-	-	-	0,32
<i>Tiliaceae</i>													
<i>Grewia flava</i>		-	-	-	-	-	0,17	-	-	0,93	-	-	-
<i>Grewia monticola</i>		-	-	-	-	-	-	-	-	-	0,19	-	-
<i>Grewia occidentalis</i>		-	-	0,56	-	-	-	-	-	-	-	-	-
<i>Grewia subaphatulata</i>	6	4,14	2,32	1,38	0,33	0,87	0,67	0,34	-	-	-	-	15,04
<i>Grewia</i> spp.		-	-	-	-	-	-	-	0,61	-	-	-	-
<i>Combretaceae</i>													
<i>Combretum apiculatum</i>	1	67,22	12,24	-	7,55	7,71	48,34	83,39	53,85	15,56	35,81	47,42	42,87
<i>Combretum apiculatum</i> - fruit	21	-	-	-	-	-	4,38	-	-	-	-	-	-
<i>Combretum hereroense</i>	4	2,32	2,22	1,85	-	-	1,82	-	1,43	-	5,99	4,13	4,25
<i>Combretum imberbe</i>	16	-	-	1,81	-	0,97	0,97	0,73	1,49	2,47	12,48	17,14	8,65
<i>Combretum imberbe</i> - fruit		-	-	-	-	-	-	-	-	-	0,04	-	-
<i>Combretum zeyheri</i>	17	-	-	0,85	1,01	2,76	0,19	0,34	0,10	-	-	-	-
<i>Combretum</i> spp.	15	-	0,34	-	-	0,85	-	0,42	-	0,41	1,89	-	-
<i>Combretum</i> spp. - fruit	21	-	-	-	-	-	2,49	1,31	0,77	-	-	6,72	4,72
<i>Terminalia prunioides</i>	7	0,49	0,10	-	-	0,35	15,74	1,87	22,90	59,03	3,22	5,86	3,96
<i>Terminalia prunioides</i> - fruit		-	-	-	-	-	-	-	-	0,69	-	-	-
<i>Ebenaceae</i>													
<i>Euclea divinorum</i>		0,44	-	0,64	-	-	-	-	-	-	-	-	-
<i>Euclea natalensis</i>		-	-	0,78	-	-	-	-	-	-	-	-	-
<i>Euclea undulata</i>	5	1,25	1,06	38,93	69,03	5,78	-	0,26	3,28	-	-	1,46	1,11
<i>Diospyros mespiliformis</i>	14	-	5,40	0,65	1,42	-	-	-	-	-	-	-	-
Unidentified spp.	12	1,87	0,20	4,70	0,17	0,44	0,64	0,63	1,40	-	1,07	0,56	1,41
TOTAL		100,07	100,07	100,07	100,04	100,05	100,08	100,04	100,07	100,02	99,10	100,22	100,79

TABLE 7 : RELATIVE PERCENTAGE FREQUENCY OF OCCURRENCE OF GROUP II LEAFLETS AND FRAGMENTS IN 50 ML SAMPLES FROM STOMACH CONTENTS OF TRANVAAL LOWVELD GIRAFFE, JULY 1971 - JUNE 1972

	PCA Code	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June
<i>Mimosaceae</i>													
<i>Albizia harveyi</i>	d 9	37,5	69,2	25,9	9,6	9,6	0,7	5,1	0,6	0,5	-	-	-
<i>Acacia exuvialis</i>	d 1	3,3	-	-	-	2,4	38,3	33,6	3,8	46,8	20,1	10,7	23,1
<i>Acacia gerrardii</i> var. <i>gerrardii</i>	d 7	1,7	1,5	1,2	-	1,4	-	1,1	0,3	-	-	4,8	0,8
<i>Acacia hereroensis</i>	d 4	4,2	4,6	-	0,9	1,0	-	0,3	4,2	3,8	4,8	7,2	20,6
<i>Acacia karoo</i>	d	-	-	-	-	0,5	-	-	-	-	-	-	-
<i>Acacia luederitzii</i> var. <i>retinens</i>	d 5	1,7	-	-	-	-	-	-	0,1	-	-	-	0,4
<i>Acacia nilotica</i> subsp. <i>kraussiana</i>	d 2	1,7	3,8	-	0,9	10,5	1,4	10,1	7,4	12,6	1,1	2,4	3,8
<i>Acacia senegal</i> var. <i>rostrata</i>	d 3	6,7	6,0	4,9	-	-	0,5	0,4	2,7	8,6	10,5	8,3	14,7
<i>Acacia sieberana</i> var. <i>woodii</i>	d 8	-	-	2,5	-	5,8	-	-	0,4	-	-	-	-
<i>Acacia tortilis</i> subsp. <i>heteracantha</i>	d 6	7,5	3,0	-	-	1,9	0,2	-	2,8	3,8	3,7	2,4	5,1
<i>Acacia</i> spp.	d	28,3	12,0	7,4	11,4	41,6	21,2	24,5	57,7	21,8	42,7	56,0	27,7
<i>Acacia</i> spp. - flowers	15	-	-	12,4	3,5	-	-	-	-	-	-	-	-
<i>Acacia</i> seeds	-	-	-	-	-	-	-	-	-	-	-	-	0,8
<i>Dichrostachys cinerea</i> subsp. <i>africana</i>	d 11	-	-	-	-	3,8	15,2	3,2	7,0	0,5	11,9	2,4	-
<i>Dichrostachys cinerea</i> subsp. <i>argillicola</i>	d 10	-	-	2,5	71,1	21,1	22,4	14,4	3,1	1,6	2,0	6,0	2,1
<i>Caesalpiniaceae</i>													
<i>Peltophorum africanum</i>	sd 13	-	-	-	-	0,5	0,2	-	-	-	-	-	-
<i>Papilionaceae</i>													
<i>Ormocarpum trichocarpum</i>	d 12	2,5	-	-	-	-	-	0,7	-	-	2,0	-	-
Other spp. - flowers	15	-	-	19,8	2,6	-	-	0,6	-	-	-	-	-
Flower buds	15	-	-	23,5	-	-	-	-	-	-	-	-	-
Unidentified leaflets	14	5,0	-	-	-	-	-	6,2	10,1	-	1,4	-	0,8
TOTAL		100,1	100,1	100,1	100,1	100,1	100,1	100,2	100,2	100,0	100,2	100,2	99,9

TABLE 8 : RELATIVE PERCENTAGE SURFACE AREA OF GROUP S AND FRAGMENTS IN 50 ML SAMPLES FROM STOMACH CONTENTS OF TRANSVAAL LOWVELD GIRAFFE, JULY 1971 - JUNE 1972

	PCA Code	July	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	March	Apr.	May	June
<i>Mimosaceae</i>													
<i>Albizia harveyi</i>	9	47,88	80,41	37,63	8,57	11,40	0,55	4,30	0,96	0,44	-	-	-
<i>Acacia exuvialis</i>	1	8,12	-	-	-	5,44	57,85	54,31	11,32	72,72	43,45	27,45	51,08
<i>Acacia gerrardii</i> var. <i>gerrardii</i>	7	1,31	1,07	1,10	-	1,05	-	0,57	0,24	-	-	3,92	0,60
<i>Acacia hereroensis</i>	4	1,06	1,10	-	0,16	0,22	-	0,05	1,38	0,65	1,16	2,03	5,04
<i>Acacia karroo</i>		-	-	-	-	0,33	-	-	-	-	-	-	-
<i>Acacia luederitzii</i> var. <i>retinens</i>	5	0,41	-	-	-	-	-	-	0,04	-	-	-	0,10
<i>Acacia nilotica</i> subsp. <i>kraussiana</i>	2	1,70	3,48	-	0,61	9,97	0,87	6,84	9,13	8,19	1,02	2,55	3,49
<i>Acacia senegal</i> var. <i>rostrata</i>	3	6,51	5,35	5,48	-	-	0,31	0,27	3,22	5,36	9,08	8,56	13,03
<i>Acacia sieberana</i> var. <i>woodii</i>	8	-	-	3,01	-	5,74	-	-	0,49	-	-	-	-
<i>Acacia tortilis</i> subsp. <i>heteracantha</i>	6	1,97	0,72	-	-	0,47	0,03	-	0,91	0,63	0,86	0,66	1,20
<i>Acacia</i> spp.		20,45	7,91	6,08	5,72	28,03	9,50	11,76	50,96	10,04	27,39	42,49	18,17
<i>Acacia</i> spp. - flowers	15	-	-	8,35	1,45	-	-	-	-	-	-	-	-
<i>Acacia</i> seeds		-	-	-	-	-	-	-	-	-	-	-	3,63
<i>Dichrostachys cinerea</i> subsp. <i>africana</i>	11	-	-	-	-	2,78	7,34	1,63	6,64	0,27	8,21	1,95	-
<i>Dichrostachys cinerea</i> subsp. <i>argillicola</i>	10	-	-	4,60	82,36	32,65	23,14	15,92	6,25	1,72	2,93	10,43	3,18
<i>Caesalpinaceae</i>													
<i>Peltophorum africanum</i>		-	-	-	-	1,89	0,45	-	-	-	-	-	-
<i>Papilionaceae</i>													
<i>Ormocarpum trichocarpum</i>	12	7,19	-	-	-	-	-	1,31	-	-	5,06	-	-
Other spp. - flowers	15	-	-	28,94	1,08	-	-	0,22	-	-	-	-	-
Flower buds	15	-	-	4,76	-	-	-	-	-	-	-	-	-
Unidentified leaflets	14	3,47	-	-	-	-	-	2,85	8,53	-	0,88	-	0,53
TOTAL		100,07	100,04	99,95	99,95	99,97	100,04	100,03	100,07	100,02	100,04	100,04	100,05

As the fruits of various species, in particular the *Combretum*<sup>spp.</sup> and *Acacia* spp., became available, they were also utilised (Fig.3).

The relative percentage of the total numbers of Group I and Group II units in the 50 ml samples during this period showed the same relationship to each other (Fig. 6) as the rainfall and temperature curves (Fig. 1). During the months with a favourable available water balance for plants i.e. rainfall curve above temperature curve, there was a marked increase in the relative numbers of Group II, leaflets taken in comparison with the relative numbers of Group I units taken (Fig. 6).

#### The cool dry season (April to July)

This was a period of falling temperature and little or no rain. The onset of leaf fall occurred in many species of trees and shrubs during this time, of which some were the summer food staples (i.e. those species which were eaten in greatest quantities, irrespective of whether they were taken because of palatability or availability). Several species which were available throughout the wet season, but seldom utilised, assumed an increasing importance in the cool dry season diet of the giraffe. Some of these Group I species were *Bolusanthus speciosus*, *Combretum hereroense*, *Grewia subspathulata*, *Combretum imberbe* and *Colophospermum mopane* (Fig. 4), and fruit of *Acacia* spp. and *Combretum* spp. (Fig. 3). There were also peaks in the relative surface area of *Acacia senegal* and *Acacia hereroensis* among the Group II species (Fig. 4).

The relationship between the relative percentage of total numbers of Group I and Group II units in the 50 ml samples again followed the climatic curves. As an unfavourable water balance for plant growth became established, indicated by the rainfall curve falling below the temperature curve at the end of March (Fig. 1), the curve of the Group II relative percentage of total numbers fell below the Group I curve (Fig. 6). This may be due to the tendency of the *Acacia* spp. to lose their leaves earlier in the dry season than the simple-leaved deciduous species. There would then be relatively less Group II material available for utilisation.

#### The hot dry season (August to October)

During these months the availability of leaves was drastically reduced with the completion of leaf fall by most species in the study area. This resulted in a marked change in diet of the giraffe, as they then utilised the evergreen or semi-deciduous species such as *Euclea undulata*, *Maytenus senegalensis*, *Schotia brachypetala* and *Diospyros mespiliformis* (Fig. 5).

During the early part of the hot dry season two species, *Colophospermum mopane* (semi-deciduous) and *Albizia harveyi* (deciduous) which were only occasionally taken during the wet season but increasingly utilised during the early dry season (Figs. 4 & 5) were particularly important among the Group I and Group II species respectively. The other important Group II species at that time of the year was *Dichrostachys cinerea* (Fig. 5). The deciduous *Spirostachys africana* was also utilised in the hot dry season (Fig. 5). The onset of flowering in many species before the commencement of the rains (Huntley 1970, Oates 1971, Hall-Martin 1972, Hall-Martin & Fuller 1975) was clearly shown by the recorded peaks in flower utilisation (Fig. 5). Giraffe made sufficiently intensive use of *Acacia nigrescens* flowers to produce distinct browse lines on flowering trees in the study area during August and September 1971.

The curve of relative numbers of Group I species in the 50 ml samples was well above the Group II curve for this season (Fig. 6) corresponding to the temperature curve which was above the rainfall curve for most of this period (Fig. 1).

#### Woody material in the diet

It was found that during the hot, dry season, giraffe ingested a much greater amount of woody material than at other times of the year (Fig. 6). The peak of woody material found in the monthly 50 ml sample covered the period August to November when the least amount of leaves was available to the giraffe. Giraffe were seen at this time of the year to chew and swallow thin branches of various species. Similar behaviour has also been noted by Innis (1958).

#### Stones in the stomach contents

Small stones were found throughout the year in the 50 ml samples of stomach contents. The largest quantity, (0,4lg), was found in the sample for October, 1971. These stones are possibly swallowed with water particularly at the height of the dry season when most waterholes are reduced to muddy pools.

#### Osteophagia

On several occasions osteophagia was seen, and Porter ( *loc. cit.* ) has noted similar behaviour in the study area in the dry season.



### General

The above results can be summarised by means of combined relative percentage mass and surface area curves of some of the hot wet season, cool dry season and hot dry season food staples (Fig.7) to emphasise the seasonal peaks found in the utilisation of different plant species. The intensity of utilisation of several species during the study period can be compared with the assumed availability of leaves of the same species (Fig.8). This shows clearly that some seasonally available species e.g. *Combretum apiculatum* and *Acacia nigrescens* are utilised when available, other seasonally available species e.g. *Combretum imberbe* are only utilised for part of the available season and other species e.g. *Euclea undulata* and *Maytenus senegalensis*, though always available are only utilised when the other food staples are not available.

### CHEMICAL COMPOSITION

Because of the relatively large seasonal variation in some of the constituents and the small number of samples no average values have been calculated for the chemical analysis of the monthly samples (Table 9). These variations are discussed in relation to the food selection by giraffe as described above and also to rainfall and temperature (Fig.1).

TABLE 9: MEAN COMPOSITION OF COMBINED GRAB-SAMPLES OF GIRAFFE RUMEN CONTENTS ON A DRY MATTER BASIS, TIMBAVATI, JULY 1971 - JUNE 1972

Month	Protein %	Ether extract %	Crude fibre %	Ash %	Heat of Combustion (kg/g) (kj/g)
July 1971	14,38	5,66	24,04	21,64	19,25
August	15,88	5,26	26,92	14,27	21,88
September	12,18	3,66	25,54	20,87	17,74
October	12,50	2,06	23,18	35,38	14,10
November	22,17	4,11	24,81	10,81	20,09
December	21,19	3,43	22,88	15,63	19,96
Jan 1972	19,19	2,64	25,18	12,58	19,39
February	20,34	4,01	26,58	12,52	19,94
March	21,55	3,25	23,38	14,90	18,64
April	16,64	3,13	25,07	14,40	19,14
May	18,62	3,91	24,40	15,23	18,90
June	18,50	4,70	25,50	12,55	19,98

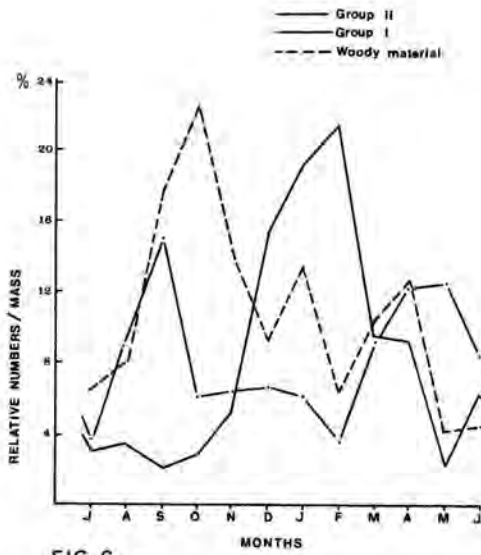


FIG. 6

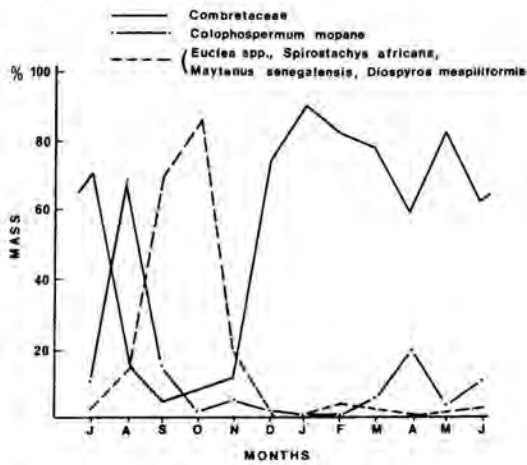


FIG. 7

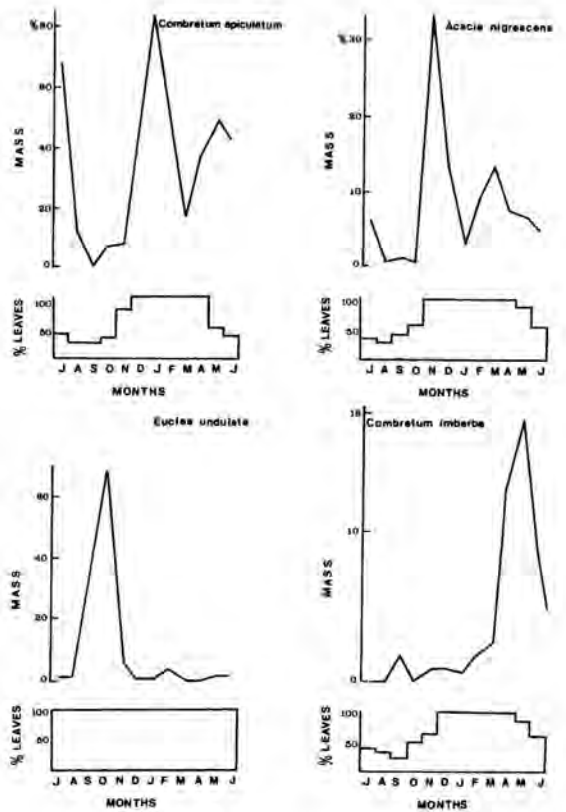


FIG. 8

- FIG. 6 – Relative percentage of total numbers of Group I and Group II units, and percentage mass of woody material, from 50 ml samples of giraffe stomach contents, July 1971 – June 1972.
- FIG. 7 – Relative percentage mass of predominantly wet season food (Combretaceae), cool dry season food (*Colophospermum mopane*) and hot dry season food (*Euclea* spp., *Spirostachys africana*, *Maytenus senegalensis* and *Diospyros mespiliformis*) from stomach contents of giraffe, July 1971–June 1972.
- FIG. 8 – Relative percentage mass of selected plant species in the stomach contents of giraffe, July 1971–June 1972, and the expected percentage availability of leaves of these species (based on data of Huntley 1970, Oates 1971 and Hall-Martin 1972)

### Crude Protein

The mean protein content of the rumen samples during the hot wet season (November to March) was 21%, representing the highest values recorded during the study period. At that time the giraffe were feeding mainly on the new leaf growth of deciduous shrubs and trees such as *Acacia nigrescens*, *A. exuvialis*, *A. nilotica*, *Combretum apiculatum*, *C. zeyheri*, *Terminalia prunioides* and *Ziziphus mucronata*. During the first month of the cool dry season (April, Table 9) there was a marked decrease in the rumen protein content. This might have been related directly to the low rainfall experienced during April (Fig. 1) but it is also possible that the feed intake *per se* may have been reduced because the giraffe population exceeded the carrying capacity of the study area. The increase in protein content during May and June may have resulted from the late rains in May (Fig. 1) or from a normally higher protein content in the species then being utilised. The most important plants taken during this period were *Colophospermum mopane*, *Bolusanthus speciosus*, *Combretum hereroense*, *C. imberbe*, *Acacia senegal* and *A. hereroensis*. During the hot dry season (August to October) the availability of leaves was drastically reduced by the completion of leaf fall in most of the species preferred by giraffe in the study area. There was a marked change to a diet of predominantly compound leaved evergreen or semi-deciduous species which are generally low in protein at that time of the year, such as *Euclea undulata*, *Colophospermum mopane*, *Maytenus senegalensis*, *Schotia brachypetala*, *Diospyros mespiliiformis* and *Albizia harveyi*. The lower protein values recorded from the rumen samples at that time are related to the effect of season on the species utilised. Towards the end of the hot dry season there was a marked increase in woody material ingested. This material normally has a low protein content (Dougall, Drysdale & Glover 1964).

### Ether extract

The seasonal variation in the fat content of the rumen samples was relatively small except for the low value of 2,64% in January and the relatively high values for the June, July and August samples. Inspection of the data on the plant fragment identifications failed to provide any obvious explanation for the high and low values.

### Crude fibre

The crude fibre content of the samples are remarkably constant throughout the study period, the difference between the highest and lowest values was only 4,0%. The plant fragment identifications, however, showed a marked increase in

woody material ingested from September to November, which might have been expected to result in a related increase in crude fibre intake. However the probability of restricted food intake and the unknown effect of digestive processes make the interpretation of the results difficult.

#### Ash

The ash content of the samples show marked variation with the highest value (35,38%) recorded during October when the diet contained relatively large amounts of woody material and when the largest amounts of gravel were found in the stomachs. Osteophagia is also more prevalent at this time. The lowest value 10,81% was recorded during the following month when the giraffe were feeding on new leaf growth which normally has a low ash content (Dougall *et. al.* 1964, Groenewald, Joubert & Tölken 1967, Joubert & Eloff 1971).

#### Heat of combustion

The heat of combustion or calorific value of the rumen samples show relatively little variation for the greater part of the year with the exception of October and to a lesser extent September during the dry season when staple foods were scarce. These low values appear to be related to the increased intake of woody material with a high ash content.

### MULTIVARIATE STATISTICAL ANALYSIS

As the components are extracted in descending order of importance it is possible to ignore all but the first few. The eigenvalues for the first three components in all eight analyses accounted for most of the variation present in the data (Table 10).

#### Inverse analysis

The geometrical distances for the first three components were plotted against each other in pairs for each analysis. All the plots showed the same trends but only one diagram (the clearest) of each has been shown (Figs. 9 & 10). The positions of the months of the year are represented in relation to each other on the basis of presence and abundance of species. In these figures the climatic conditions pertaining to each month have also been indicated by symbols: the hot wet season (November to March) has been indicated by triangles; the cool dry season (April to July) by squares; the hot dry season (August to October) by circles.

TABLE 10a: EIGENVALUES (%) AND CUMULATIVE % FOR THE FIRST THREE COMPONENTS FOR EACH INVERSE ANALYSIS

Component	Group I				Group II			
	*Fr.	*C.	M.	C.	Fr.	C.	*S.A.	C.
1	24	24	24	24	25	25	26	26
2	20	44	19	43	19	44	19	45
3	11	55	13	56	14	58	14	59

TABLE 10b: EIGENVALUES (%) AND CUMULATIVE % FOR THE FIRST THREE COMPONENTS FOR EACH NORMAL ANALYSIS

Component	Group I				Group II			
	Fr.	C.	M.	C.	Fr.	C.	S.A.	C.
1	51	51	55	55	49	49	47	47
2	17	68	16	71	19	68	21	68
3	13	81	10	81	12	80	15	83

\* Abbreviations: Fr. = Relative percentage frequency, M. = Relative percentage mass, C. = Cumulative value, S.A. = Relative percentage surface area.

Group I

A cumulative variability of 55% was accounted for by the first three components of the analysis on the basis of relative percentage frequency (Table 10a). The plot of the first and third components is shown in Figure 9a. It can be seen that the first component has separated the hot dry season months (August to October) from the other months. The hot wet season months (November to March) are grouped loosely together and the cool dry season months (April to July) also lie together in this loose group, but are not as clearly separable from the former as both are from the hot dry season group.

The first three eigenvector components for the ordination of relative percentage mass of the Group I leaves accounted for a cumulative variability of 56% (Table 10a). The plot of the second and third components illustrating the grouping of the months of the study period is shown in Fig. 9b.

The clustering of the months follows much the same pattern as that described

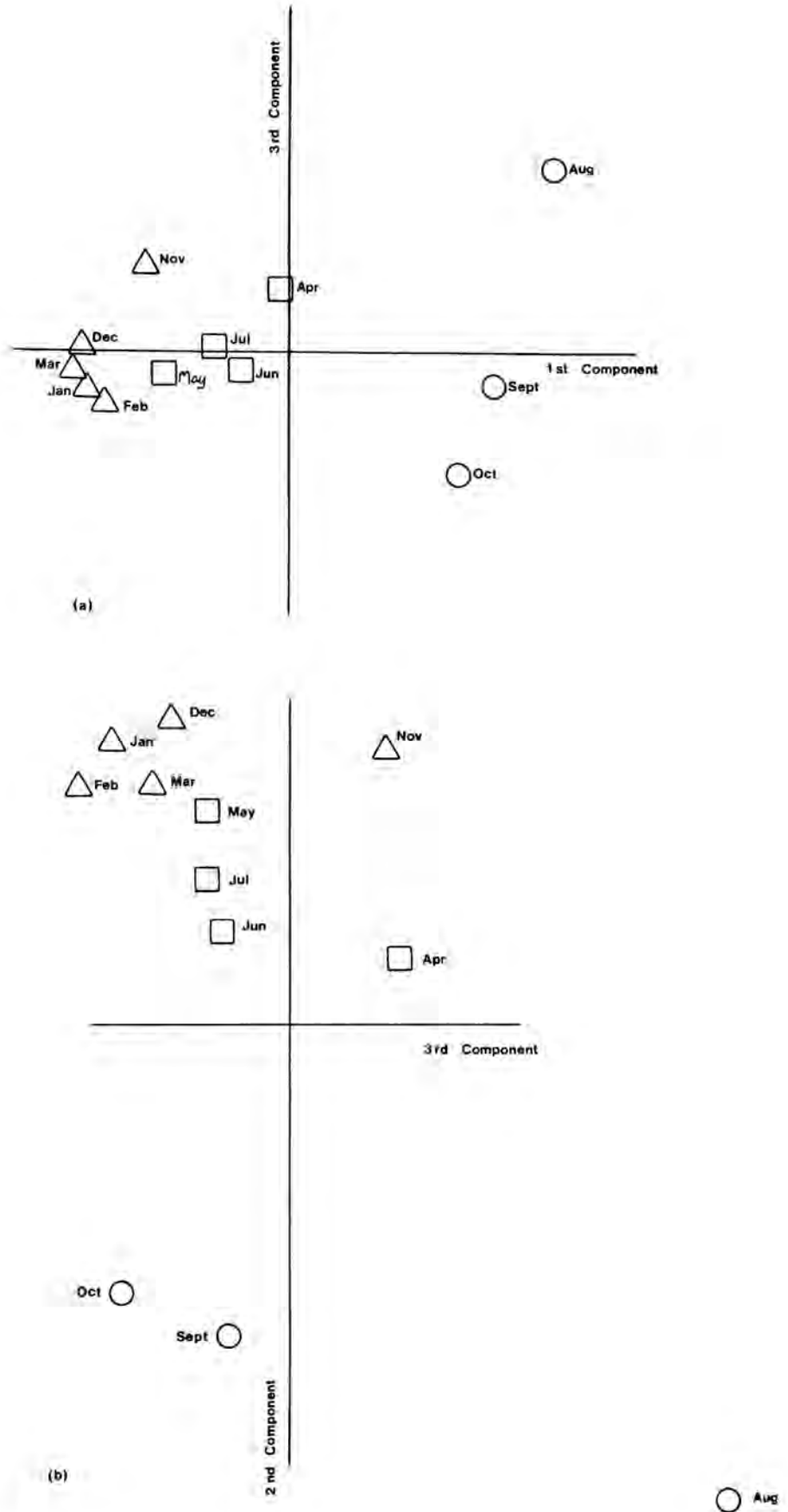


FIG. 9 — Positions of the months plotted against: (a) the first and third components of the Group I relative frequency inverse analysis, (b) the second and third components of the Group I relative mass inverse analysis.

above on the basis of relative percentage frequency, in this case (Fig. 9b) it is the second component which has separated the hot dry season months away from the rest. These three groupings of the months on the basis of stomach contents coincide with the classification derived from the climate diagrams as discussed previously (Chapter 1) and also justify the arrangement of the discussion of feeding preferences in these three periods.

### Group II

The first three components of the analysis of relative percentage frequency accounted for a cumulative variability of 58% (Table 10a), and the first three components of the relative percentage surface area inverse analysis accounted for a cumulative variability of 59% (Table 10a). The positions of the months as located by the first and second components of both these analyses are shown (Fig. 10a & b). In these plots a distinct grouping together of the months of November to June is seen. A second rather loose grouping of July to October could also be discerned from both plots though the first component of the relative percentage frequency analysis separated October from the other three months in the group. These groupings do not compare as closely with the climatic status of the months as indicated by the Group I inverse analyses (Fig. 9a & b) but they nevertheless effectively separate the months in which non-*Acacia* species are most prominent in the diet (July to October) and those in which *Acacia* spp. are most important.

### Normal analysis

The geometrical distances derived from the analyses were plotted on axes to give a graphical representation in two dimensions of the relationships between the 22 species used in the data matrix.

### Group I

The first two components of the analysis of relative percentage frequency of Group I species (accounting for a cumulative variability of 68% - Table 10b) are plotted in Fig. 11a. Because some species separate away from the main group, especially along the first component the scale on this axis has been broken where appropriate. The species typical of the three seasons discussed above were not clearly grouped together. The greatest distances, as could be expected, separated the predominantly wet season staples such as *Combretum apiculatum* (1) *Acacia nigrescens* (3) and *Terminalia prunioides* (7) from the hot dry season staple *Euclea undulata* (5) along the first component; the cool dry season staples *Colophospermum mopane* (2) and *Combretum imberbe* (16) were placed in an intermediate position. The second component placed *Euclea undulata* (

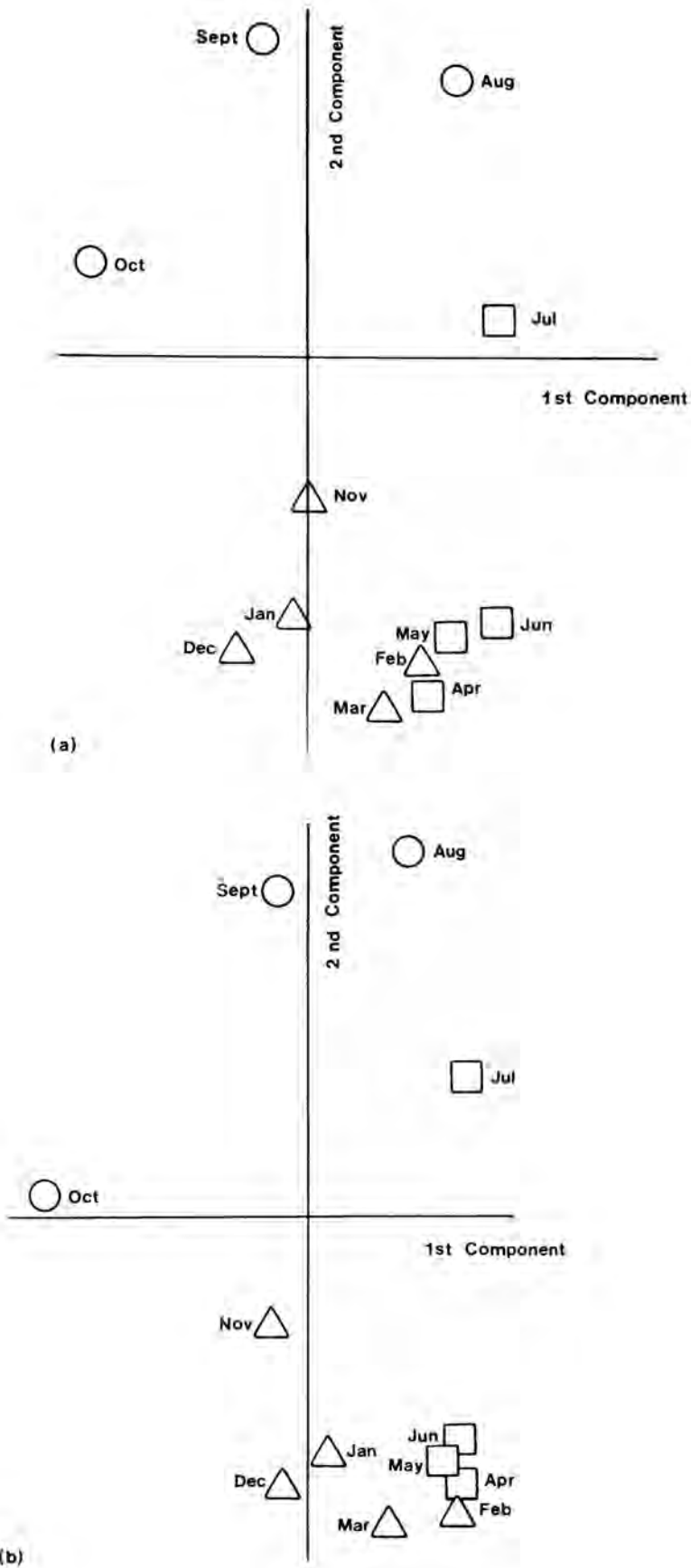


FIG. 10 – Positions of the months plotted against the first and second components of:  
(a) the Group II relative frequency inverse analysis;  
(b) the Group II relative surface area inverse analysis.



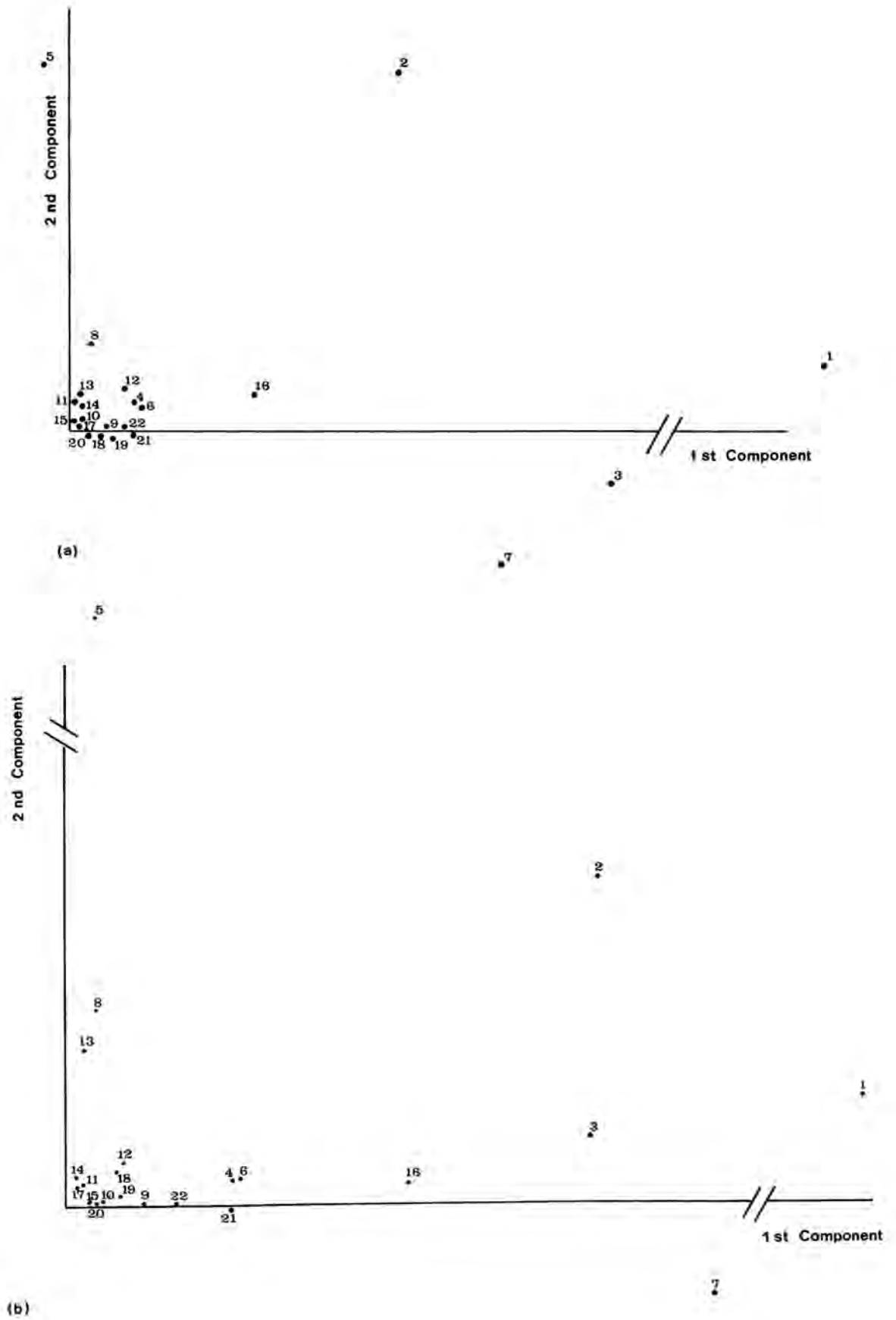


FIG. 11 — Positions of the species plotted against the first and second components of:  
 (a) the Group I relative frequency normal analysis,  
 (b) the Group I relative mass normal analysis. Species code numbers are given in Table 5.

and *Colophospermum mopane* (2) well away from all the other species.

The first and second components of the ordination of relative percentage mass of Group I leaves are plotted in Fig. 11b. A cumulative variability of 71% is accounted for (Table 10b) by these components. The staples of the three seasons occupied similar positions relative to each other as in the relative frequency ordination. The less frequently utilised species were clustered together.

### Group II

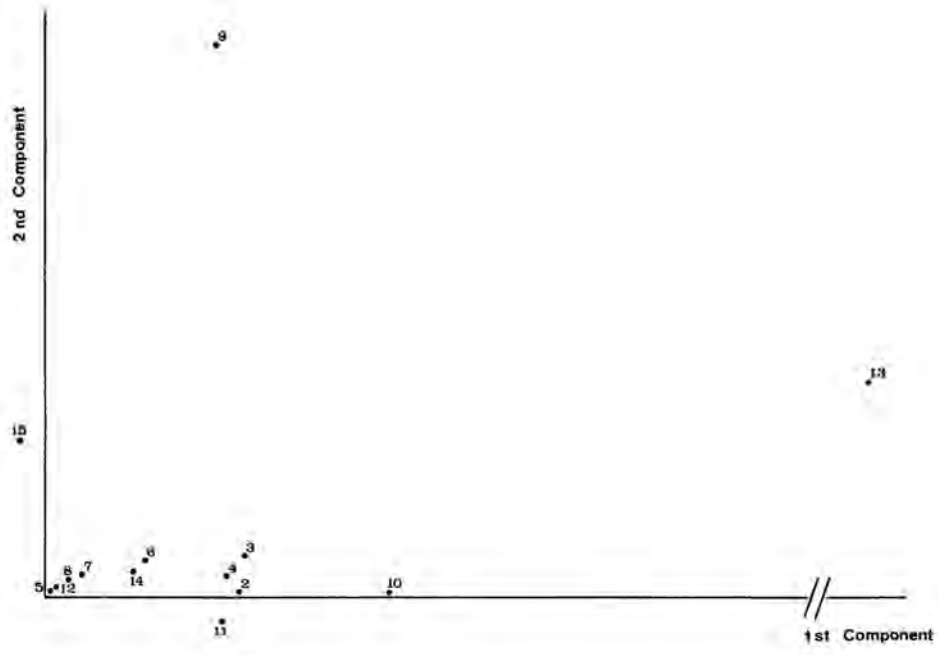
The first and second components of the analysis of relative percentage frequency of Group II species (accounting for a cumulative variability of 68% - Table 10b) are plotted in Fig. 12a. For convenience of illustration the horizontal axis has again been broken. The main hot wet season species of this group were separated from the rest by the first component. *Acacia exuvialis* (1) could thus be grouped with *Peltophorum africanum* (13) which though unimportant was eaten only in November and December. The major hot dry season species *Albizia harveyi* (9), together with *Acacia* flowers (15) which were available only at the end of the dry season were separated from the other species by the second component. The remainder of the species were clustered together.

The first and second components of the ordination of relative surface area were plotted (accounting for a cumulative variability of 68% - Table 10b) as shown in Fig. 12b. The same general pattern is revealed by this plot as in the previous figure, though the relative positions of *Acacia exuvialis* (1) and *Peltophorum africanum* (13) along the first component were reversed probably because *Peltophorum africanum* has a much higher surface area per leaf fragment than *Acacia exuvialis*.

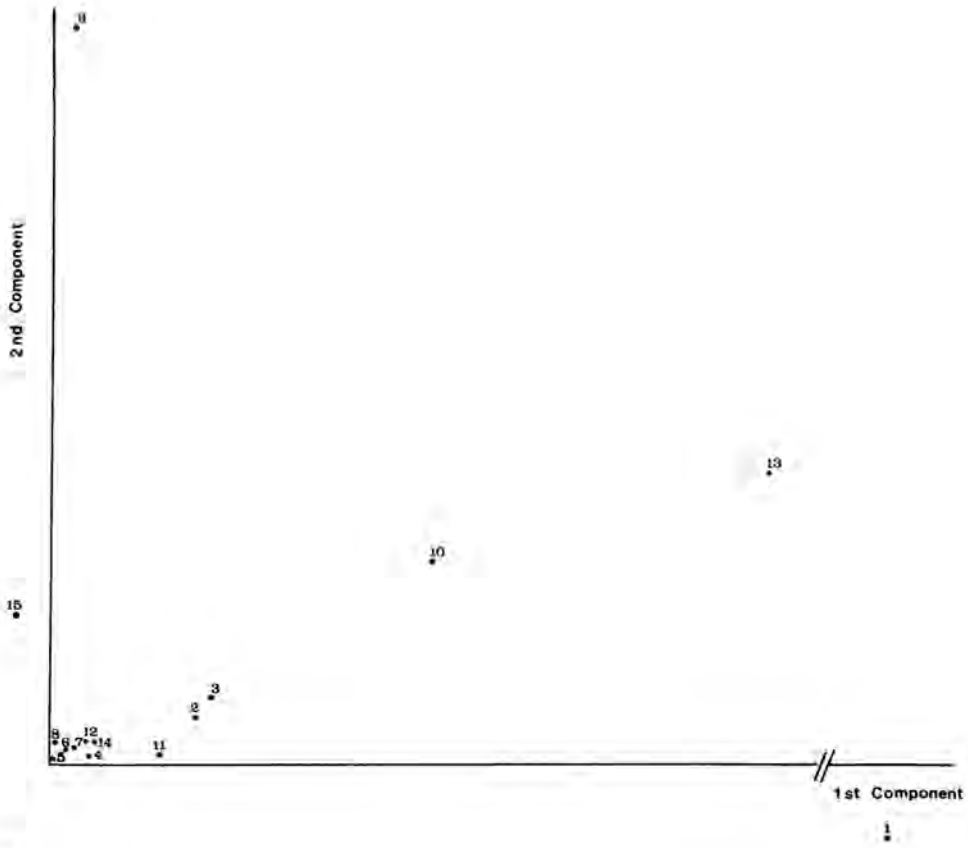
### HABITAT SELECTION

A total of 1087 giraffe observations were recorded during the study period and these data are summarised in Table 11. The data have been grouped so as to compare them with Hirst's (1964) data on wet and dry season concentrations. The June to October group can be regarded as representative of the dry season and the November to May group as representative of the wet season.

There are significant differences in the observed occurrence of giraffe in *Acacia nigrescens* open tree savanna, *Combretum zeyheri* tree savanna, *Colophospermum mopane* communities and riverine thicket, between the wet and dry seasons ( $\chi^2$  values given in Table 11). On the other hand, the observed



(a)



(b)

FIG. 12 — Positions of the species plotted against the first and second components of:  
(a) the Group II relative frequency normal analysis,  
(b) the Group II relative surface area normal analysis. Species code numbers are given in Table 7.

seasonal occurrence of giraffe in the *Combretum apiculatum* tree savanna and other plant communities was not significantly different.

TABLE 11: NUMBERS OF GIRAFFE OBSERVED IN DIFFERENT VEGETATION TYPES, TIMBAVATI PRIVATE NATURE RESERVE, JULY 1971 - JUNE 1972

	Apic.	Nig.	Zey.	Mopane	Riv.	Other	Total
Nov. - May	183	378	52	32	33	144	822
June - Oct.	59	79	27	37	20	43	265
$\chi^2$	,0 <sup>6</sup> 2	21,5	4,44	34,18	5,39	0,24	
P	,995	,001	,050	0,001	,02	,50	

- \* Apic. = *Combretum apiculatum* tree savanna  
 Nig. = *Acacia nigrescens* open tree savanna  
 Zey. = *Combretum zeyheri* tree savanna  
 Mopane = *Colophospermum mopane* shrub savanna and woodland  
 Riv. = Riverine thicket  
 Other = Other vegetation types

From Table 12 it can be seen that the concentration of giraffe in the dry season in the areas described by Hirst (1964) is clearly reflected by increases in the percentage occurrence of giraffe in the *Combretum zeyheri*, *Colophospermum mopane* and riverine thicket communities with a concomitant decrease in the *Acacia nigrescens* community.

TABLE 12: THE PERCENTAGE GIRAFFE OBSERVED IN DIFFERENT VEGETATION TYPES, TIMBAVATI PRIVATE NATURE RESERVE, JULY 1971 - JUNE 1972

	No.	Apic.*	Nig.	Zey.	Mopane	Riv.	Other	Total
Nov. - May	822	22,3	46,0	6,3	3,9	4,0	17,5	100,0
June - Oct.	265	22,3	29,8	10,2	14,0	7,5	16,2	100,0

\* Abbreviations as used in Table 11

METHODS

There are several possible sources of error in the methods used in this study. The diagnostic keys were based almost entirely on trees or shrubs which the giraffe were seen to eat over the study period. Fragments of herbs or other plants which the giraffe may have eaten could have remained unidentified due to their absence from the keys used. The relative rates of digestion of different species, and the degree of digestion rendering fragments unidentifiable have not been investigated. However, over 94% of the Group I material, and over 61% of the Group II material was identified to species, and a further 33% of Group II material was identified to genus. It seems unlikely therefore that these sources of error would have invalidated the results presented.

The arbitrary imposition of a minimum size limit on the Group I fragments examined may have influenced the results if there was a tendency for the leaves of some species to be broken into smaller pieces than others. No experimental data is available to confirm this. The minimum size limit imposed on Group I fragments recovered from the 50 ml sample could also have influenced the conclusions drawn from Fig. 6.

Even though the individual plant species eaten by giraffe were not subjected to comparable chemical analyses, and no corrections could be made for the effect of digestive processes, most of the variation in chemical content of the rumen samples could be related to the phenology of plants due to seasonal changes in climatic conditions (i.e. temperature and rainfall) resulting in different patterns of intra- and inter-species selection by giraffe. McCullagh (1969) analysed the stomach contents of African elephants *Loxodonta africana* from Uganda and also found seasonal changes in the chemical composition of the diet which could be attributed to seasonal phenological changes in the vegetation. Because the giraffe is a highly selective browser rumen sample analyses might not be reliable indicators of the overall quality of available herbage in the giraffe habitat though the seasonal depression in protein values found in this study coincide with the well known seasonal depression of nutritional value of African vegetation (e.g. Groenewald, *et. al.* 1967, McCullagh 1969, Joubert & Eloff 1971, Myre 1972, Field & Blankenship 1973). Moreover, due to the activities of rumen microbes and processes such as urea recycling such samples might not be reliable indicators of the nutritional value of the ingested forage.

Some other shortcomings of the methods are also apparent. The samples taken represent food that has been subjected to an unknown amount of digestion and solubilization in the rumen and an unknown amount of the various chemical fractions have been absorbed. The increase in the intake of woody material during the September to November period was not reflected in the crude fibre content of the samples. Sullivan (1962) has indicated that crude fibre as determined in the proximate or Weende scheme of analysis as was used in this study, is an empirical substance and does not have the same composition in different kinds of forages. When considering the large variety of plant species available to giraffe and included in their diet, this is a serious shortcoming. Preference should therefore be given to more specific analytical methods for structural carbohydrates, which would indicate both cellulose and lignin content (Crampton & Maynard 1938, van Soest 1963).

The protein values found for the hot wet season (November to March) agree with protein values for the same period of the year reported by Bonsma (1942) for common bushveld trees and shrubs observed to have been eaten by cattle. The lower values found during the dry months are also in accord with the reports of Dagg (1960) who analysed leaves of various species eaten by giraffes from Klaserie, 20 km west of the study area. A decline in protein content of *Colophospermum mopane* leaves from 14,2% early in the year to 7,9% in September/October has been reported from the Save Valley in Mocambique by Myre (1972). Groenewald *et al.* (1967) also reported similar declining protein values in *C. mopane*, *Combretum apiculatum* and *Grewia* spp., they found, in addition, that the protein content of the first spring leaves was low in these species. Similar results have been reported by Joubert & Eloff (1971).

The difficulties in interpreting ether extract, crude fibre and ash were also experienced by Dagg (1960). She also found that from an analysis of six sets of giraffe droppings collected at monthly intervals that the crude fibre content did not rise with the increased intake of woody material during the dry months. As far as is known there is no special feature of the giraffe's digestive tract or its microbes which might explain these points (van Hoven, pers. comm.)\* In their studies on giraffe in Kenya, Field & Blankenship (1973) also analysed rumen contents. They found a mean protein content of

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\*Dr. W. van Hoven, Dept. of Zoology, University of Pretoria, Pretoria 0002

12,73% which is lower than all months except September and October in the Transvaal Lowveld; their crude fibre content is more than twice as great, ash is about one quarter and only ether extract is in the same range of values. As their results are mean values it is not possible to draw any conclusions as regards seasonal fluctuations from their data. The apparently low protein content of their material may result in lighter animals as the mean mass of female giraffe ( $676 \pm 12$  kg) from their study area (as given by Kayanja & Blankenship 1973) is significantly lower ( $P < 0,001$ ) than that of Transvaal giraffe ( $792 \pm 18$  kg. - Table 18, Chapter 4).

#### FOOD AND HABITAT SELECTION

The results show that giraffe in the Timbavati select the bulk of their food from deciduous plant species during the wet period of the year mostly as leaves, but also fruit when available. Early in the dry season the food supply diminishes as the deciduous species begin to lose their leaves due to an increasingly unfavourable water balance and their natural seasonal cycle, as well as the effect of heavy browsing pressure by the large giraffe population. Feeding patterns then change. Species which were largely ignored during the wet season are then utilised. Later, during the hot dry season months (August to October) even less of the preferred wet season food is available and giraffe subsist on the leaves of evergreen species, usually not utilised at other times of the year, Early in the spring they also eat flowers.

Marked seasonal differences in the diet of giraffe in Tsavo National Park in Kenya were also found by Leuthold & Leuthold (1972). The Tsavo giraffe subsisted mainly on deciduous trees, shrubs and vines during the wet and early dry season with a change to mainly evergreen plants in the late dry season.

The distribution and seasonal movements of giraffe in the Timbavati as discussed here and by Hirst (1964) can be partly explained as a response to feeding preferences. The greatest density of giraffe is found, throughout the year, in the central part of the Reserve where the dominant vegetation types are *Combretum apiculatum* tree savanna and *Acacia nigrescens* open tree savanna. It is in these plant communities that the giraffe find most of their staple foods such as *Combretum apiculatum*, *Acacia* spp. and *Terminalia prunioides*. The peaks shown in the utilisation of *Acacia nigrescens* and *Acacia exuvialis* reflect the wet season concentration of giraffe in the *Acacia nigrescens* community. The *Combretum apiculatum* tree savanna is widely distributed elsewhere in the

12,73% which is lower than all months except September and October in the Transvaal Lowveld; their crude fibre content is more than twice as great, ash is about one quarter and only ether extract is in the same range of values. As their results are mean values it is not possible to draw any conclusions as regards seasonal fluctuations from their data. The apparently low protein content of their material may result in lighter animals as the mean mass of female giraffe ( $676 \pm 12$  kg) from their study area (as given by Kayanja & Blankenship 1973) is significantly lower ( $P < 0,001$ ) than that of Transvaal giraffe ( $792 \pm 18$  kg. - Table 18, Chapter 4).

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The results show that giraffe in the Timbavati select the bulk of their food from deciduous plant species during the wet period of the year mostly as leaves, but also fruit when available. Early in the dry season the food supply diminishes as the deciduous species begin to lose their leaves due to an increasingly unfavourable water balance and their natural seasonal cycle, as well as the effect of heavy browsing pressure by the large giraffe population. Feeding patterns then change. Species which were largely ignored during the wet season are then utilised. Later, during the hot dry season months (August to October) even less of the preferred wet season food is available and giraffe subsist on the leaves of evergreen species, usually not utilised at other times of the year, Early in the spring they also eat flowers.

Marked seasonal differences in the diet of giraffe in Tsavo National Park in Kenya were also found by Leuthold & Leuthold (1972). The Tsavo giraffe subsisted mainly on deciduous trees, shrubs and vines during the wet and early dry season with a change to mainly evergreen plants in the late dry season.

The distribution and seasonal movements of giraffe in the Timbavati as discussed here and by Hirst (1964) can be partly explained as a response to feeding preferences. The greatest density of giraffe is found, throughout the year, in the central part of the Reserve where the dominant vegetation types are *Combretum apiculatum* tree savanna and *Acacia nigrescens* open tree savanna. It is in these plant communities that the giraffe find most of their staple foods such as *Combretum apiculatum*, *Acacia* spp. and *Terminalia prunioides*. The peaks shown in the utilisation of *Acacia nigrescens* and *Acacia esuvialis* reflect the wet season concentration of giraffe in the *Acacia nigrescens* community. The *Combretum apiculatum* tree savanna is widely distributed elsewhere in the



Reserve and is intensively utilised by giraffe for feeding throughout the year, there is thus no change in frequency of occurrence of giraffe in this community in different seasons.

During the dry season there is greater utilisation of the *Colophospermum mopane* shrub savanna and woodland patches and of the *Combretum zeyheri* tree savanna of the southern parts of the Reserve. There is also a noticeable concentration of giraffe along watercourses where considerable use is made of the mostly evergreen species of the riverine thicket and senile floodplains such as *Euclea undulata* and *Maytenus senegalensis*. The effect of water availability on giraffe habitat selection and movements has not been taken into account. Although surface water may be a limiting factor for about two months following leaf fall when the giraffes are forced to eat more woody vegetation it is less important than food as giraffe can survive for long periods without access to surface water (Foster & Dagg 1972).

It is evident from this study that the late dry season (August to October) is a critical period in the ecology of giraffe in the Transvaal Lowveld. The effect of the declining quality of the food ingested and possibly also the expenditure of energy necessitated by the increasing distances which the giraffe were required to move between feeding and watering sites under conditions of increasing food scarcity appear to be related. Observations suggest that giraffe drink regularly while water is available and presumably this is necessary for the maintenance of an adequate water balance while subsisting on increasingly drier food. These effects are further manifested in the poor physical condition of giraffe at this time of year resulting in an increase in the number of giraffe killed by lions. This increased predation on giraffe is especially high after seasons of low rainfall (Hirst 1969b) or during periods of cold drizzling weather (this study) when giraffe are probably subjected to the additional stress of having to draw on their body reserves to maintain an increased metabolic rate for efficient thermoregulation. Even when in peak condition giraffe carcasses contain only about 1,5% fat. Deaths from starvations and malnutrition also occur more frequently during the late dry season (Hirst 1969b). This critical period of low nutrition in giraffe is probably a population limiting factor, both directly through starvation and malnutrition and indirectly through its influence on susceptibility to predation and the animals' vulnerability to climatic stress. These factors will assume increasing importance in areas where the giraffe population density is high or the habitat marginal.

Studies on food selection and the quality of ingested food by wild ungulates are extremely interesting but are of limited practical value in terms of studying food in relation to maintenance and production requirements. In order to quantify the intake of food in terms of utilisable material, further information is required on both the daily intake and the digestibility of food. Even if the digestibility of the food selected could be determined by *in vitro* techniques (Hopson, Johnson & Dehority 1963, Tilley & Terry 1963) the accurate quantitative determination of food intake would still not be feasible with wild animals. Tamed animals in pens (Arman & Field 1973) or tamed animals fitted with oesophageal fistulae (Van Dyne & Torell 1964, Basson 1971) could, however, be used on a small scale to provide some information on both the qualitative and quantitative aspects of food intake.

#### MULTIVARIATE STATISTICAL ANALYSIS

The use of a principal components analysis of the data was proved justifiable on several grounds. First, the Group I inverse analysis supported the division of the year into three seasons which is what was suggested on the basis of the climate diagrams. Even though the climatic divisions were not as clearly supported by the Group II inverse analysis the hot dry season with *Albizia harveyi* and *Dichrostachys cinerea* predominant was clearly separated from the rest of the year where *Acacia* spp. predominate. Within the latter group the wet season months lay close together.

The second point is that in the normal analyses the wet season staples were far removed from the dry season staples (Figs. 11 & 12) thus emphasising the change in the utilisation of different plant species by giraffe at different times of the year. Also, even within the tight cluster of all the other species those which were mostly utilised in the wet season lay closer to *Combretum apiculatum* (1) and the dry season species lay closer to *Albizia harveyi* (9).

The third point to be considered is the relative positioning of the months and species by means of relative frequencies as opposed to the other measures used. The similarity of distribution of points by the different systems is striking (*cf.* Figs. 9 to 12). From this one can tentatively conclude that the measurements of relative surface area and relative percentage mass were closely correlated with relative percentage frequency. Furthermore this suggests that the assessment of species importance within the two groups on the basis of one measure alone would have been adequate. This conclusion could not otherwise have been reached except by the tedious means of calculating correlation coefficients for the data for each species, comparing relative percentage frequency and the other measures used.

## CHAPTER 3

DENTITION AND AGE DETERMINATION

## INTRODUCTION

The purpose of these studies was to develop a reliable method of age determination of giraffe to enable a more precise evaluation of carcass composition, growth and reproductive status to be made. A method of age determination might also be of use to other workers.

The only reported age determination criteria for giraffe are those of Singer & Boné (1960). Relevant parts of their study are discussed fully where necessary and their data have been supplemented.

In the present study tooth replacement and wear, annual layers in the teeth, mandible growth and eye lens mass, were investigated.

## MATERIAL AND METHODS

SOURCE OF MATERIAL

Material was collected from giraffe shot or killed by lions in Timbavati, and adjacent nature reserves (Sandringham and Buffelshoek), and giraffe which died of natural causes in the Hans Merensky Nature Reserve 70 km to the north-west of Timbavati. The vegetation and climate of all these areas are similar. Several known-age skulls from other areas where vegetation and climate are not the same were also included.

KNOWN-AGE ANIMALS

Absolute age of tooth eruption in giraffe as given in this study has been based on skulls and jaws from several sources, whose ages at death were approximately known. In only two cases were the exact date of birth and death known, these were a 5½-y old female (J.H. Grobler pers. comm.)\* and a 1-d-old female (Wilson 1969) from the Matopos National Park, Rhodesia. The ages of the other animals used as 'known-age' standards were only approximately known to within a few months, or days in the case of neonates. These were a 4-month-old male,

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a 10-month-old female, a 1-y-old female, a 1½-y-old female, a 6½-y-old female and a 20-y-old female from the Hans Merensky Nature Reserve (S.M. Zaayman pers. comm.);\* a 8½-y-old male from Matopos National Park (Wilson 1969); a 13-y-old female from the Daan Viljoen Game Park, South West Africa (J.M. Hofmeyr pers. comm.);\*\* and a 7-y-old female from West Nicholson, Rhodesia (D. Cowie pers. comm.);\*\*\*. Two neonates were collected in the Timbavati and the remains of several calves killed by lions were estimated to be only a few weeks old.

#### DENTITION AND TOOTH ERUPTION

In their monograph on the extant giraffes and fossil giraffids of Africa, Singer & Boné (1960) describe the dentition of giraffe and the stage of tooth eruption reached in 32 giraffes which did not yet have the full complement of permanent teeth. Some of this material was collected in the field but many specimens from zoological gardens were included. In addition, they attempted to establish the absolute age at eruption of the teeth.

The present study is based on a sample of skulls and jaws of 46 giraffe (including 5 fetuses) with immature dentition and a further 75 mature skulls. The stage of tooth eruption was examined in all the material and a classification of this data was prepared.

#### TOOTH SECTIONS

##### Introduction

The method of age determination of mammals by examining the rate of deposition of dentine and cementum in thin sections was largely developed by Laws (1952, 1953). Since then this method has been widely used and several reviews have appeared (Laws 1962, Sergeant 1967, Klevezal' & Kleinenberg 1969, Morris 1972, and Spinage 1973).

Most of the work reported has dealt with studies on temperate zone animals, and relatively few have dealt with African species (Spinage 1973).

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Age determination by counting cementum layers or incremental lines in decalcified sections of teeth has been reported in southern Africa on kudu *Tragelaphus strepsiceros*, springbok *Antidorcas marsupialis*, black-backed jackal *Canis mesomelas* and cattle *Bos indicus* and *Bos taurus* by Simpson & Elder (1969), Rautenbach (1971), Lombaard (1971) and Steenkamp (1974) respectively. The successful use of undecalcified sections has also been reported by Smuts (1972) working on Burchell's zebra.

The tooth selected for study was the upper first molar ( $M_1^1$ ) as this is the first permanent maxillary tooth to erupt. This tooth is also easier to extract than its lower counterpart ( $M_1$ ). The teeth were first measured for tooth wear studies and then fixed in 10% neutral formalin buffered to pH 7,0 for periods varying from 1 to 4 weeks. The tooth was then divided into three using a hacksaw. With the tooth clamped in a vice the first cut was made along the mesio-distal line between the roots; the buccal half of the tooth was then divided by a labio-lingual cut between the roots. One buccal cusp and root was used for the preparation of undecalcified sections, and one for decalcified sections.

#### Undecalcified sections

The undecalcified sections were prepared following the technique of Steenkamp (1966). The formalin-fixed teeth were washed in running tap water for at least 15 minutes before dehydration through a graded series of alcohols (30% alcohol - 15 min, 50% alcohol - 30 min, 70% alcohol - 30 min, absolute alcohol I - 30 min, absolute alcohol II - 30 min, absolute alcohol III - 30 min). The specimens were dried in an oven at 40°C and then embedded in a clear polyester resin in a glass mould. They were then placed under a vacuum of 0,003 to 0,005 Hg/mm<sup>2</sup> until all air bubbles had been withdrawn and left to harden overnight at 40°C. Longitudinal and transverse sections as thin as 50/μm were cut on an electric motor driven machine using a diamond dusted disc of 0,6096 mm thickness at 1500 r.p.m. under a continuous water jet. The machine was designed and built by Steenkamp and has been fully described elsewhere (Steenkamp 1966, 1969). The sections were further thinned by grinding on waterproof emery paper of decreasing coarseness (Numbers 320, 400A and 600A respectively) and finally polished on a superfine Aloxite water hone, No 201 A.

These thin sections were then stained using alcian blue, haematoxylin and eosin, or Pollak trichrome stain (Lunt 1958), mounted in DPX and examined under bright field illumination. Unstained sections were examined using polarised light.

## Decalcified sections

### Decalcification techniques

Specimens were decalcified using several techniques.

1. Most teeth were decalcified following Steenkamp (1969, 1974). The decalcification process commenced by soaking the specimens for 12 days in 5% nitric acid diluted 1 : 4 with 10% neutral formalin. The teeth were then placed in ethylene diamine tetracetic acid (disodium salt) (EDTA) until decalcification was completed after 2 to 4 weeks. The EDTA was dissolved in 0,1M phosphate buffer at pH 7,0 to make a 10% solution. The pH was adjusted with NaOH initially. After decalcification the specimens were washed for 12 hours in running tap water prior to dehydration and clearing.
2. An ultrasonic vibrator (Dreyer 1965) was also tried but good results were not achieved, possibly due to faulty equipment.
3. A selection of specimens which had been soaked in the nitric acid/formalin solution were further decalcified at 60°C in EDTA made up as a 0,5 M solution buffered with NaOH to a pH of 7,4 (D.H. Retief pers. comm.)\*. The specimens were agitated daily and the fluid was renewed every 5 days. After decalcification the specimens were washed for 12 hours in running tap water and then transferred to 70% or 90% alcohol prior to dehydration and clearing.
4. Specimens were soaked in 5% aqueous trichloroacetic acid at room temperature (Disbrey & Rack 1970). The fluid was changed daily until complete decalcification was achieved. After decalcification specimens were either washed for 12 hours in running tap water or transferred directly to 70% or 90% alcohol for dehydration and clearing.
5. Decalcification of several specimens was also attempted using Gooding & Stewarts fluid (Lockard 1972). The fluid is made up from 10 ml formic acid, 5 ml 10% formalin and distilled water to 100 ml. After decalcification the specimens were neutralized in a saturated solution of lithium carbonate in 70% alcohol for 12 hours prior to dehydration and clearing.

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In all the decalcification procedures used the volume of fluid was always of the order of 20 times that of the tissue. The specimens were either treated whole, trimmed by removal of the crown or were longitudinally split.

The end-point of decalcification was determined radiographically by using a dental X-Ray apparatus. If the specimens were radio-opaque then further decalcification was required (Steenkamp 1969, 1974). Once familiarity with decalcified tissue had been acquired the end-point was determined by palpation (Disbrey & Rack 1970). This method was preferred above the chemical method of Culling (1963).

#### Dehydration and clearing

After washing or neutralizing, the specimens were dehydrated and cleared using an automatic tissue processor. Two schedules were used and gave good results, though schedule I proved more satisfactory.

#### Schedule I

#### Schedule II

(after Disbrey & Rack 1970)

- |   |  |
|---|--|
| 1. 70% alcohol - 1 hour                         | 1. 90% alcohol - 2 hours                             |
| 2. 70% alcohol - 1 hour                         | 2. 90% alcohol - 2 hours                             |
| 3. 80% alcohol - 1 hour                         | 3. Absolute alcohol I - 2 hours                      |
| 4. 80% alcohol - 1 hour                         | 4. Absolute alcohol II - 2 hours                     |
| 5. 90% alcohol - 1 hour                         | 5. Absolute alcohol III - 2 hours                    |
| 6. Absolute alcohol - 2 hours                   | 6. Absolute alcohol equal parts<br>Toluene - 2 hours |
| 7. Absolute alcohol - 2 hours                   | 7. Toluene I - 2 hours                               |
| 8. Xylene or Toluene - 1 hour                   | 8. Toluene II - 2 hours                              |
| 9. Xylene or Toluene - 1 hour                   | 9. Toluene III - 2 hours                             |
| 10. Molten paraffin wax<br>52 to 53°C - 6 hours | 10. Molten paraffin wax<br>52 to 53°C - 2 hours      |
| 11. Molten paraffin wax<br>56 to 58°C - 6 hours | 11. Molten paraffin wax<br>56 to 58°C - 3 hours      |

#### Preparation of sections

After clearing, the specimens were embedded in paraffin wax with a melting point of 56 to 58°C. Whole teeth that had a pulp cavity were embedded in a vacuum oven. Serial sections were cut on a rotary microtome at 5 µm and good ribbons were produced. When ambient temperatures were high the blocks were cooled in a refrigerator before cutting. At low ambient temperatures the blocks were not refrigerated but the face of the block was frozen with a spray of freon or

dichlorodifluoromethane if necessary. Cutting was carried out under conditions of high relative humidity, maintained by using a humidifier. It was necessary to take particular care with trimming and facing blocks. Each section of the knife edge was used only once and was then stropped on a microtome knife sharpener. The knife edge was regularly inspected under a binocular microscope and was honed when necessary and regularly cleaned with xylene. A high angle knife tilt was found to be necessary as compression of the sections was the chief difficulty in cutting. It was not necessary to soak the blocks in water (Grimsdell 1973) or Mollifex (Steenkamp 1974) before cutting.

Several trial counts were made on both transverse and longitudinal sections (mesio-distal and labio-lingual planes) and it was found that longitudinal sections cut in the mesio-distal planes produced the most satisfactory results. All teeth were then sectioned in this way and mounted on labelled slides using Haupt's adhesive.

### Staining

Several different stains were tried and produced mediocre or poor results. These included Delafield's haematoxylin and eosin, Grams' stain, the Gram-Twort method, Harris's haematoxylin and eosin and Heidenhain's haematoxylin and eosin; safranin, safranin and fast green, Mallory trichrome; and 1% aqueous solution of neutral red alone or in combination with carbol fuchsin (Disbrey & Rack 1970). The haematoxylin stains were used with and without mercuric chloride mordanting (Disbrey & Rack 1970). Ehrlich's haematoxylin as described by Disbrey & Rack (1970) in combination with aqueous eosin gave the clearest and most consistent results. The staining schedule was modified with experience and the final schedule used was as follows:

1. Dewaxing: Xylene I, 2 to 4 minutes } Slides must be gently  
                   Xylene II, 2 to 4 minutes } agitated
2. Rinse in absolute alcohol I, 1 minute
3. Rinse in absolute alcohol II, 2 minutes
4. Rinse in absolute alcohol III, 4 minutes
5. Ehrlich's haematoxylin 60 to 90 minutes
6. Rinse in running tap water 5 minutes
7. Differentiate in 0,5 to 1,0% acid alcohol (concentration depending on staining time and stain efficacy) until sections show a salmon pink flush, 1 to 2 seconds
8. Blue in running tap water 20 to 30 minutes
9. Aqueous eosin 15 minutes



10. Rinse in tap water 1 second
11. Dehydrate:
  - 70% alcohol < 1 second
  - 80% alcohol < 1 second
  - 100% alcohol < 1 second
  - Xylene - until coverslipped

After staining the sections were mounted in Canada Balsam and oven dried. Sixty three first molars, 25 assorted incisors and 17 canines were prepared in this way.

#### Counting cementum layers of decalcified specimens

The slides were examined microscopically at magnifications of x63, x160 and x400. After several trial counts had been conducted it was found that rigid rules of counting would have to be adhered to. In giraffe there was a high degree of accessory and split bands, especially in the root tip and in the molar pad. Counts were therefore confined to the zone lying approximately half-way between the apex and the cervical margin on the mesial edge. It was also apparent that in many sections each layer was composed of two dark staining bands with a clear layer between separated from the next band by a wider clear band. The separation of the two dark bands was not always clear under a magnification of x160, but could usually be seen at a magnification of x400.

A minimum of two cementum layer counts were made on at least five sections, taken from different levels of the tooth. Counting from the dentino-cemental junction outwards, twenty counts per tooth were routinely made at a magnification of x160 of the maximum number of bands, but excluding bands of very faint and discontinuous appearance. Counts were repeated at a magnification of x400 when it was possible to clearly distinguish the double bands. All specimens were counted using these procedures and the maximum modal count, rather than a mean, was used for age determination.

Rapid counting was achieved using a Zeiss projection microscope at a x120 magnification. This microscope was set up so as to project an enlarged image of the tooth section on to a piece of white paper placed next to the instrument. The image obtained was very clear and the position of the counted bands could be marked on the paper. It was also possible to move the section up and down to scan the lines to ensure their continuity and find the best site for counting. All counts were repeated using the projection method.

### Counting dentine layers

Where layers in the dentine stained clearly they were counted in order from the pulp cavity outwards. As the 'neonatal' and 'weaning' lines could seldom be identified with confidence all lines were counted.

### TOOTH WEAR AND MATURITY

The measurement of characteristics which change continually with tooth wear and can be related to chronological age have been widely used in large mammal studies. Examples of these are a ratio derived from the height and width of the molar teeth used for moose *Alces alces*, (Passmore, Petersen & Cringan 1955), mule deer *Odocoileus hemionus*, (Robinette, Jones, Rogers and Gashwiler 1957), and Thomson's gazelle *Gazella thomsonii*, (Robinette & Archer 1971). Tooth wear in giraffe was assessed by measuring the changing proportions of the maxillary first molar with age.

In order to measure this tooth accurately it was removed from the skull using a hammer and chisel to chip away the maxilla thus exposing the roots of the tooth which was then levered free. The following measurements were made using a steel vernier caliper accurate to 0,1 mm:

1. Crown height:- The maximum height of the anterior and posterior buccal as well as lingual cusps were measured from both sides of the jaw to allow for irregular wear. Results were recorded as mean heights of the buccal and lingual cusps respectively and as a mean of all cusps (crown height). The measurements were taken from the highest point on the occlusal (biting) surface of the cusp to the cingulum.
2. Occlusal surface width:- The maximum width across the occlusal surfaces of the four cusps for each maxillary first molar were measured and then recorded as the mean for both sets of lingual or buccal cusps to allow for uneven wear.

Several measurements of the total size of the tooth suggested by Steenkamp (pers. comm.\* and 1974) were also taken.

These were:

- I. The labio-lingual width of crown.

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- II. The mesio-distal width of the crown.
- III. The length of the root.
- IV. Crown height.
- V. Total length of tooth.
- VI. Crown index =  $\frac{\text{labio-lingual dimensions}}{\text{mesio-distal dimensions}} \times \frac{100}{1}$

As teeth grow older the deposition of dentine continues at a rate which gradually occludes the pulp cavity. The width of the pulp cavity should therefore decrease with increasing age (Spinage 1973). To check this the roots of all molars were examined and subjectively assessed as open, partly occluded or occluded.

#### MANDIBLE MEASUREMENTS

The use of mandible measurements for age determination has been reported for many mammal species (e.g. for moose, Passmore *et. al.* 1955; for red deer *Cervus elaphus* by Lowe 1967; for black wildebeest *Connochaetes gnou* by von Richter 1971; and for cottontail rabbits *Sylvilagus floridanus* by Bothma, Teer & Gates 1972). In his studies on bovines Steenkamp (1969) found that not only was there an increase in mandible length with age from 2½y to 4½y of age but also a decrease in the angle formed by the horizontal and vertical rami.

Measurements were made on all available giraffe mandibles using a steel caliper (accurate to 1,0 mm ) of the following:

1. Total length: measured from the anterior tip of the jaw (excluding teeth) to the posterior rim of the angle on the buccal side only. The mean of the left and right mandibles was used.
2. Length of diastema: the minimum distance between the posterior edge of the alveolus of the canine and the first premolar (P<sub>2</sub>), the mean of the two sides being taken.
3. Length of toothrow: greatest length from anterior edge of P<sub>2</sub> to posterior edge of M<sub>3</sub>.
4. Ramus height: the greatest length from the tip of the coronoid process vertically to the lower edge of the ramus.

5. Radiographs of a sample of jaws were made and from these the angle between the vertical and lower horizontal rami were measured as described by Steenkamp (1969).

### EYE LENS MASS

The use of eye lens mass for age determination in wildlife studies was developed by Lord (1959), based on the principle that the lens is an ectodermal structure and therefore growth continues throughout life. The use of the technique has been reviewed in depth by Friend (1968) and also by Morris (1972).

Whole eyes were dissected out of the skull as soon after death as practical and fixed in 10% formalin. An incision was made in the sclera to facilitate rapid penetration of the fixative. After a variable period of storage the sclera incision was enlarged and the lens gently squeezed out together with the vitreous humor. The lens was freed of any adherent suspensory ligament or ciliary tissue, mass measured and then placed in an open specimen tube. The tubes were placed in a forced-draught oven at 80°C. The lens mass was then measured weekly on a Mettler balance to the nearest 0,1 mg. A constant mass was not achieved as the lenses were still decreasing in mass after 120 d when the final measurements were made. Lenses were removed from the oven in batches of five to avoid post-drying mass increases. Damaged or partially decayed lenses, (discoloured, pockmarked or distorted in shape) were disregarded.

### RESULTS

#### DENTITION

The dentition of the giraffe previously described by Singer & Boné (1960), is similar to that of most living ungulates and was already present in the earliest recorded fossil material of the Giraffidae. The dental formula is:

$$2 \left( i \frac{0}{3} c \frac{0}{1} pm \frac{3}{3} \right) = 20 \text{ for the deciduous teeth, and}$$

$$2 \left( I \frac{0}{3} C \frac{0}{1} PM \frac{3}{3} M \frac{3}{3} \right) = 32 \text{ for the permanent teeth.}$$

In giraffe the arrangement of the incisors in the jaw describes a semi-circle and the canines shape and position fit them very closely to the incisors. The incisors have a flattened, triangular, spatular crown. The canines have a larger crown, are much more triangular and somewhat bilobed. These teeth all have a single root which slopes horizontally backwards.

The premolars are unilobed. The lower ones have two roots, an anterior and posterior one, while the upper premolars have three roots, the two on the buccal side are lateral, anterior and posterior; and the third is medially situated on the lingual side.

The deciduous premolars have a complex cusp pattern and  $PM_3$  has three distinct lobes. The upper deciduous premolars have three roots,  $PM_3$  has three roots,  $PM_2$  and  $PM_1$  have only two, but a rudimentary third fang is often found in  $PM_2$ . The permanent molars of giraffe typically have a double-crescentic double-lobed structure (Fig. 13). The upper molars have three roots, like the premolars but the lower molars have only two roots.  $M_3$  has an extra posterior lobe or talonid. The upper molars of giraffe are broader than long, the bucco-lingual dimensions being greater than the mesio-distal dimension in 166 out of 168  $M^1$  teeth, 64 out of 65  $M^2$  and 64 out of 65  $M^3$  measured. The lower molars are longer than broad (72  $M_3$  teeth measured).

The crown of the molars has a longitudinal valley or infundibulum which extends across the tooth mesio-distally separating the buccal and lingual cusps, but is confined by the posterior and anterior edges of the crown. There is also a transverse cleft which extends bucco-lingually which divides the tooth into an anterior and posterior lobe. This cleft continues down the root on the lingual side and ends between the cingulum on the buccal side in the upper molars. In the lower molars this cleft is particularly deep on the buccal side, being less marked on the lingual side. According to Singer & Boné (1960) the less marked groove on either surface is actually nothing more than the lateral depression resulting from the formation of a mesostyle by an elevation of the cingulum. The cusps of the molars are slightly angled through their transverse axes to the longitudinal axis of the jaw so that the cusp axes are rotated anteriorly and medially. As a result of this rotation the anterior cusps of the molars lie more laterally on the buccal side than the posterior lobe of the preceding molar.

Following Arambourg (1947) the cusps of mammalian teeth can be named in a logical way (Fig. 13). The main cusps are called cones (upper) or conids (lower). The lingual ones in the upper teeth are from front to back the protocone and the hypocone and in the lower teeth the paraconid, the metaconid and the entoconid. The buccal cusps are respectively the paracone and metacone, and the protoconid and hypoconid. Secondary cusps in the upper teeth are the median paraconule and metaconule and in the lower the hypoconulid. Other secondary cusps are also derived from elevations of the cingulum. These are the buccal parastyle, mesostyle and metastyle, and the protostylid, ectostylid and hypostylid of upper and lower molars respectively. On the lingual side these

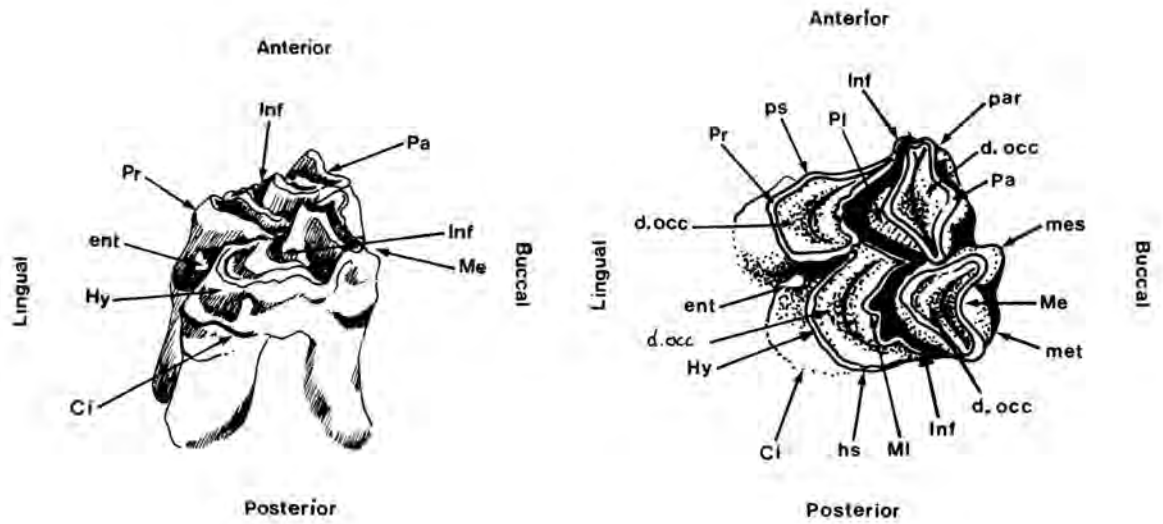


FIG. 13 — Sketches of a giraffe maxillary first molar (lateral and occlusal surface views) to show main features. Labelling follows Arambourg (1947).

Main cusps		Secondary cusps	Other features
Pr — Protocone	} Lingual	PI — Paraconule	Ci — Cingulum
Hy — Hypocone		MI — Metaconule	
Pa — Paracone	} Buccal	ps — protostyle	d. occ — dentine of occlusal surface
Me — Metacone		ent — entostyle	
		hs — hypostyle	
		par — parastyle	
		mes — mesostyle	
		met — metastyle	

are the protostyle, entostyle and hypostyle, and the parastylid, metastylid and entostylid on the upper and lower teeth respectively.

In the giraffe several cusps or styles lose their individuality and fuse into crests or lophs. These, as described by Singer & Boné (1960), are the paraconule (given as protoconule p.379 *op. cit.*) and protocone, metaconule and hypocone; parastyle, paracone and mesostyle; mesostyle, metacone and metastyle (or corresponding conids and stylids in the lower tooth) which are fused forming four crescentic ridges. The lingual ridges are more curved in the upper teeth and the concavity is on the buccal side, while the position is reversed in the lower teeth.

In newly erupted teeth the crescentic ridges, styles and stylids are very distinct. With the gradual attrition of the crests the apex of each loph becomes levelled mesio-distally while at the same time broadening in the buccal-lingual axis. A gradually increasing crescentic tract of dentine shows between the lips of enamel which progressively separate from one another. At the same time the infundibulum narrows by approximation of the buccal and lingual lips of the adjacent walls of the crescents. In very old teeth the infundibulum is reduced to a simple ridge of enamel or disappears completely.

All the teeth of giraffe are coated with very rugose enamel. This feature is characteristic of both extant and fossil Giraffidae (Singer & Boné 1960).

### TOOTH ERUPTION

#### Eruption sequence

Thirteen eruption stages in the lower jaw were recognized (Table 13). The last of these stages is when the full permanent dentition has come into wear. The observations on the state of eruption and wear lead to the following conclusions:

1. The eruption of corresponding molars and premolars in the upper and lower jaws is not synchronous. In six out of ten cases of asynchrony found there is a slight delay in the eruption of the lower tooth. This supports the contention of Singer & Boné (1960), based on 16 out of 18 observations, that the upper teeth erupt slightly ahead of the lower. Due to the damaged or deficient state of the material in a few cases the stage of eruption used for the compilation of Table 13 had to be taken from the upper jaw. As the asynchrony of eruption is slight the observations on these skulls were considered fairly representative of their lower jaws.

TABLE 13: TOOTH ERUPTION STAGES AND THEIR APPROXIMATE CHRONOLOGICAL AGE FOR THE LOWER JAW OF GIRAFFE

Stage	I <sub>1</sub>	I <sub>2</sub>	I <sub>3</sub>	C	PM <sub>2</sub>	PM <sub>3</sub>	PM <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>	(n)	Approximate age	Source of age determination	
													Known-age (n)	Cementum layers (n)
0	(D)	(D)	(D)	((D))	(D)	(D)	(D)	-	-	-	5	Late foetuses and at birth	3	-
1	D	D	D	(D)	D	D	D	-	-	-	5	up to 4 weeks	3	-
2	D	D	D	D	D	D	D	((P))	-	-	7	up to 10 months	2	-
3	D	D	D	D	D	D	D	(P)	-	-	2	up to 12 months	1	2
4	D	D	D	D	D	D	D	P	-	-	5	12 to 15 months	1	-
5	D	D	D	D	D	D	D	P	((P))	-	4	15 to 18 months	1	-
6	D	D	D	D	D	D	D	P	(P)	-	2	18 months to 2½ y	-	1
7	D	D	D	D	D	D	D	P	P	-	2	up to 3 y	-	1
8	D	D	D	D	D	D	D	P	P	(P)	3	up to 3½ y	-	1
9	<b>P</b>	D	D	D	D	D	D*	P	P	P	3	up to 4 y	-	-*
10	P	P or D	D	D	D or ((P))	(P) or D	(P)	P	P	P	2	up to 5 y	-	2*
11	P	P	P	D	P	P	P	P	P	P	3	up to 5½ y	-	2
12	P	P	P	(P)	P	P	P	P	P	P	3	up to 6 y	1	-
13	P	P	P	P	P	P	P	P	P	P	-	up to 6½ y	1	1

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D = deciduous tooth in wear; P = permanent tooth in wear; ( ) = tooth in advanced stage of eruption - not yet in wear; (( )) = cusps just emerging above alveolar margin; \* = permanents' cusps can be seen between roots of deciduous teeth.



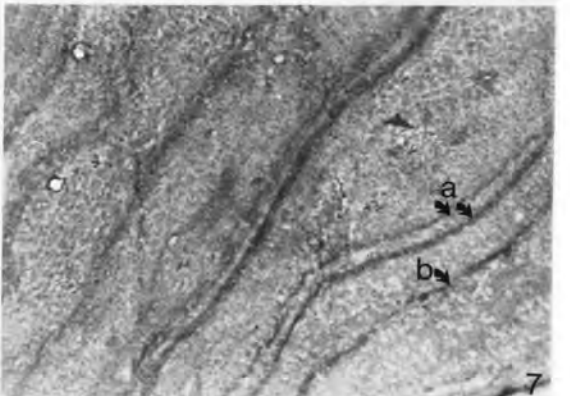
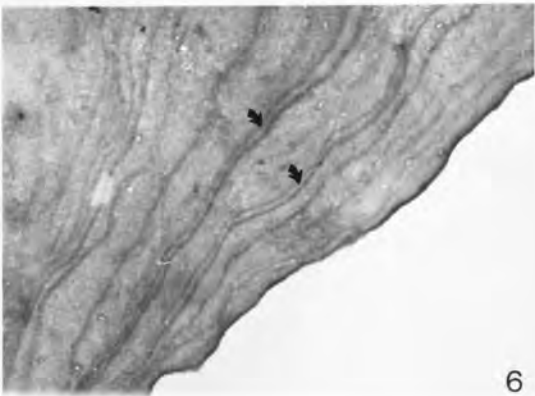
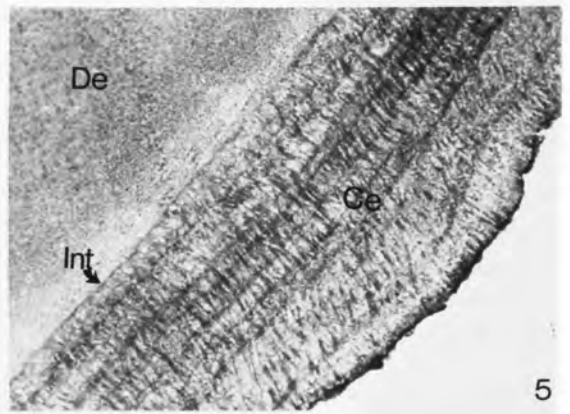
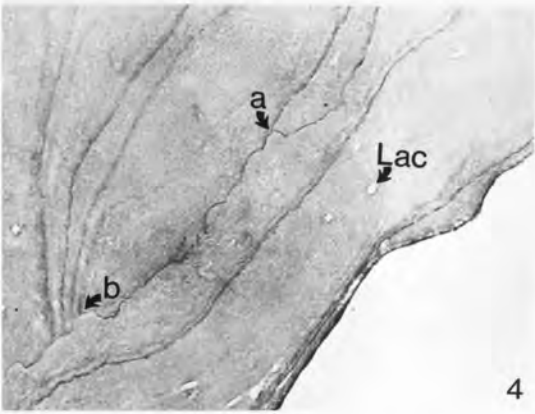
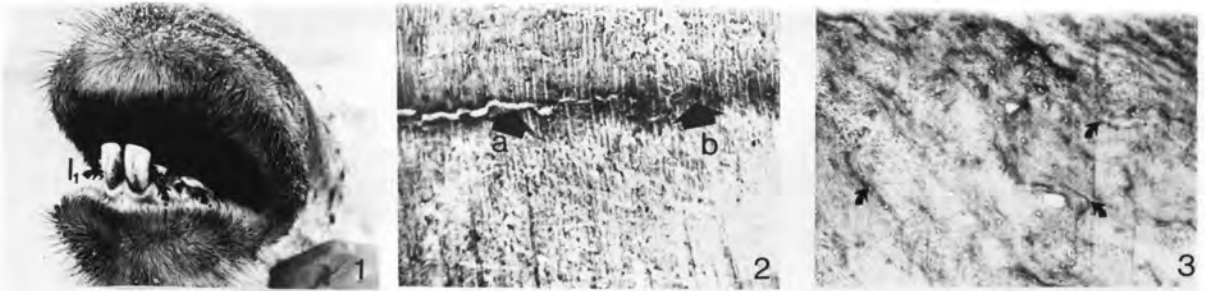
2. In giraffe the deciduous premolars erupt in regular succession, posterior to anterior in the mandible (based on 5 fetuses from this study and one from Singer & Boné (1960). In the maxilla the eruption sequence is not simply reversed as tentatively suggested by Singer & Boné (1960). The evidence from 5 fetuses is that  $PM^3$  erupts first, followed by  $PM^4$  (4 fetuses) and then  $PM^2$ . However, in one foetus  $PM^2$  preceded  $PM^4$ . The eruption of the deciduous incisors occurs in a regular succession from  $i_1$  to  $i_3$ .
3. The permanent molars erupt in regular succession from first to third in both maxilla and mandible. The premolars erupt in reverse order however from fourth to second (five observations). In one case  $P_2$  was the first to erupt indicating that, as suggested by Singer & Boné (1960) the sequence is less rigid in the premolars than the molars. Their observation that  $P_3$  is the first premolar to erupt is not supported (five observations). (In their discussion of this point p. 386 there is a misprint and a specimen cited as No. 25628 should read No. 35628).
4. The permanent incisors erupt in regular succession from  $I_1$  to  $I_3$ .  $I_1$  appears during the eruption and maturation of  $M_3$  and is always present by the time  $M_3$  has completed its growth.  $I_2$  appears only after all molars have erupted and at about the same time as the premolars appear. Singer & Boné (1960) state that  $I_2$  never erupts before the full development of all the molars and premolars, in one case in this study  $I_2$  has, however, completed its eruption before  $P_3$  and  $P_2$ .  $I_3$  only appears after all premolars have erupted. The complete eruption of  $I_1$  while worn  $i_2$  and  $i_3$  are still in place (stage 9, Table 13) is illustrated in Plate 1, Fig.1.
5. The permanent canine is the last tooth to erupt in the giraffe.
6. A total of four congenital absences of teeth was observed out of 83 skulls (with jaws) examined. These were one bilateral  $P_2$ , one unilateral  $P_2$  and two bilateral  $P^2$ . The not unusual absence of  $P_2$  was also observed by Singer & Boné (1960).

#### Chronological age of eruption stages

Reference was made to the available known-age material and the cementum layer counts to assign approximate chronological ages to some of the eruption stages described (Table 13).

PLATE 1

- Fig. 1. Mouth of approximately 4-y-old giraffe showing complete eruption of  $I_1$ , while remains of  $i_2$  and  $i_3$  are still in place. This condition corresponds to stage 9 (Table 13) X 0,25.
- Fig. 2. Undecalcified longitudinal section of giraffe  $M^1$  showing splitting (a) along a dark staining band (b) in the dentine. Formalin, 20  $\mu\text{m}$ , haematoxylin & eosin (H & E), X 113.
- Fig. 3. Decalcified longitudinal section through molar pad region of giraffe  $M^1$  showing indistinct, wavy, incremental bands (arrowed) unsuitable for counting. Formalin, EDTA, 5 $\mu\text{m}$ , H & E, X 71.
- Fig. 4. Decalcified longitudinal section through root tip (apex) of giraffe  $M^1$  showing splitting (a) and intersecting (b) incremental bands in the cementum and a lacuna (Lac) of Sharpey's fibres. Formalin, EDTA, 5  $\mu\text{m}$ , H & E, X 141.
- Fig. 5. Decalcified longitudinal section through giraffe  $M^1$  root midway between the cervical margin and apex showing dentine (De), cemento/dentinal interface (Int) and cementum (Ce) with incremental bands suitably stained for counting. Formalin, EDTA, 5  $\mu\text{m}$ , H & E, X 180.
- Fig. 6. Decalcified longitudinal section through giraffe  $M^1$  root near apex showing double bands (arrows) and single bands in the cementum. Formalin, EDTA, 5  $\mu\text{m}$ , H & E, X 89.
- Fig. 7. Decalcified longitudinal section through giraffe  $M^1$  root near apex showing double band (a) and single band (b). Same section as Fig. 6 above. Formalin, EDTA, 5  $\mu\text{m}$ , H & E, X 226.



The first permanent molar is formed prenatally but its postnatal growth appears to be slow. Cusps only appear above the alveolar margin at about 6 weeks of age (though still below the gum at that stage) and the process of eruption continues slowly until the tooth is fully emerged and in wear by the age of one year.

The eruption of the second molar apparently takes place over a longer period of time stretching from about 15 months until 3 y by which time the tooth is in wear. The eruption of the third molar takes place rapidly from about 3½ y of age and this tooth is in wear by the age of 4 y. By this time the first incisor has been replaced by its permanent (Plate 1, Fig.1) and the deciduous molars are well worn and loose (stage 9) and by 4½ y (stage 10) they have been lost or are often found as caps perched on top of the erupting crown of the permanent tooth.

In several cases it was possible to increase the accuracy of the assessment of age of a particular jaw by examining the degree of calcification as shown by radiography. This technique was especially useful when distinction had to be made between similar stages of eruption e.g. between stages 8 and 9 (Table 13), and the degree of mineralization of the unerupted permanent teeth could be assessed by the degree of radiopacity.

### TOOTH SECTIONS

#### Undecalcified sections

Though sufficiently thin sections were produced to allow of the structure of the cementum and dentine being studied and some dark staining bands were seen, no incremental layers suitable for age determination purposes were found in giraffe. Splitting was regularly observed to have occurred along the dark staining bands in the dentine, indicating a weakness or inconsistency in the homogeneity of the matrix (Plate 1, Fig. 2).

#### Decalcified sections

Stained sections from 63 maxillary first molars were examined for incremental lines in the cementum and dentine. In only 10 of these were the dentine lines sufficiently clearly distinguishable for counting. Of these none were in agreement with the results of the cementum line count, five showing fewer lines and five showing more lines than the cementum counts from the same teeth. The sample was too small to attempt a correlation between the dentine counts and other indications of age in the giraffe, though it was clear that older animals had more lines than younger ones.

Even though a seemingly unambiguous definition of what constituted a cementum line had been decided upon before commencing the counts, difficulties were experienced which undoubtedly contributed an unknown amount of error to the results. Some of these problems have been mentioned by other workers (Spinage 1967, Klevezal' & Kleinenberg 1969, Grimsdell 1973a). The degree of staining of cementum bands achieved varied between teeth and between sections from the same tooth resulting in a great deal of variability in the appearance of bands. Even within the same section the degree of definition of successive bands is variable as is the spacing between them (Plate 1, Figs. 4 & 5). Bands tend to coalesce on the sides of the tooth where the cementum layer is thinner and to part and split in the root tip area. (Plate 1, Fig. 4). In addition the bands become discontinuous and very markedly undulating in the molar pad (cervical) region (Plate 1, Fig. 3). The complexity produced by split bands in the apex (Plate 1, Fig. 4) is further compounded by the effect of the often large lacunae which in the living tooth contain Sharpey's fibres (Grimsdell 1973a) around which the bands often eddy, thus making this region, as well as the molar pad unsuitable for counting. It is because of the inconsistency in the number and clarity of lines throughout the length of the root that longitudinal sections are necessary if maximum counts are to be made. In general this situation is much the same as found by Grimsdell (1973a) in the buffalo *Syncerus caffer*.

The obvious 'eruption line' found by Spinage (1967) in the incisors of defassa waterbuck *Kobus defassa* was not found to be a feature of giraffe molars. The zone of cementum immediately adjacent to the dentino-cementum junction was found to be very wide, often wider than the rest of the cementum layer.

In 17 teeth the phenomenon of narrow double dark bands (Plate 1, Figs. 6 & 7) lying very close together was observed, in 3 of these the counts were double the number of broad 'annual' bands; in 6 they were close to double; in 5 much less than double and in 3 very much more than double in one case, treble. The explanation for this phenomenon is possibly related to reproductive endocrinology as it was only found in sexually mature animals (though only 10 immature giraffe's teeth were examined, either as part of this study or subsequently). The presence of multiple bands is not a sexually linked character ( $\chi^2 = 0,4854, P < 0,05$ ), but this would not necessarily mean that these are not 'rut' lines in males, as found by other workers (Low & Cowan 1963, Mitchell 1967) and lines marking parturition and lactation events in the case of females.

No obvious differences between ease of counting cementum lines in maxillary and mandibular molars, canines and incisors were found.

As there is only one dry season per year in Timbavati it was assumed that only one dark band would be laid down each year. This was confirmed by the correlation found between the number of cementum bands in immature teeth and their expected age as determined from tooth eruption, as well as from the known-age material. Multiple bands were found in two known-age animals, nevertheless when counting the broad bands a good fit with age was found. In 4 teeth (6%) the cementum line counts were obviously anomalous and discarded. In giraffe the first molar is fully erupted at one year of age and no cementum bands are formed prior to eruption. Several molars of calves younger than one year were sectioned and it was found that the cementum layer was homogenously stained, in older calves where  $M^1$  was erupting the newest cementum showed signs of layering. In an animal in its second year there would, therefore be a translucent, an opaque and then a second translucent band together giving a count of only one dark band. To compensate for the year which would be lost by this means of counting the counts were taken as the number of broad dark bands plus one.

It was concluded therefore that the age of a giraffe could be reasonably accurately determined from the number of broad cementum bands counted under  $\times 160$  magnification as confirmed by the counts of these incremental layers in the teeth of known-age specimens. However, it was appreciated that more than one band could be formed per year, these double bands usually being less easily seen under low magnification. Where doubt existed the age of the animal as suggested by the number of cementum bands could be checked against tooth wear as described below.

The phenomenon of the sections parting along dark staining bands in the cementum similar to the splitting observed in dentine (Plate 1, Fig. 2 was seen in several cases.

#### CORRELATION OF CEMENTUM LINES WITH TOOTH WEAR

The relationship between number of cementum lines and the various measures of tooth wear were investigated. Initially scatter diagrams were constructed for cementum lines against mean molar crown height, lingual crown height, buccal crown height, crown width, the ratio of crown width over crown height, the ratio of crown surface area over crown height, buccal occlusal surface

and lingual occlusal surface. These diagrams showed that there are close relationships between lingual crown height, mean molar crown height, lingual occlusal surface and number of cementum lines respectively. Nevertheless, all the data from all the measurements were investigated using linear regression and correlation analysis.

The most significant correlations were found between the two lingual wear measurements and number of cementum lines. As there is a marked sexual dimorphism in many other features of giraffe the data for both sexes were processed separately. The regression coefficients for the sexes were then tested and it was found that differences between the regressions are certainly not significant ( $t = 0,9537$  for lingual occlusal surface width and  $t = 0,0295$  for lingual crown height; with 49 degrees of freedom these values have probabilities greater than 0,9). The data were therefore pooled and new regressions calculated. The linear regression formulae, which can be used for predicting the number of cementum lines, and therefore age of giraffe, from these measurements are given in Table 14.

TABLE 14: REGRESSION COEFFICIENTS OF NUMBER OF INCREMENTAL LINES IN CEMENTUM (Y) ON VARIOUS DIMENSIONAL MEASUREMENTS (X) OF GIRAFFE MAXILLARY FIRST MOLARS

Measurement	Sex	Regression equation	r	P-value	n
Lingual occlusal surface	both	$Y = 1,3648X - 0,9404$	0,957	< 0,001	55
Lingual occlusal surface	m	$Y = 1,3998X - 1,2118$	0,960	< 0,001	27
Lingual occlusal surface	f	$Y = 1,2935X - 0,4469$	0,960	< 0,001	26
Lingual crown height	both	$Y = -0,9558X + 20,7986$	0,959	< 0,001	55
Lingual crown height	m	$Y = -0,9464X + 20,7400$	0,969	< 0,001	27
Lingual crown height	f	$Y = -0,9488X + 20,575$	0,942	< 0,001	26

In giraffe the paracone and metacone do not wear down as rapidly as the protocone and the hypocone. In several cases in old animals (15 y +) the enamel of the paracone and the metacone is still fairly high even when the paraconule and metaconule have been completely worn away. The regression of cementum lines on buccal cusp measurements is therefore unsuitable for prediction purposes. Mean crown height, though better than buccal measurements alone is nevertheless also less suitable than the lingual measurements and has a lower correlation coefficient than any of the regressions above. (Regression formula for mean crown height:  $Y = -0,9994X + 22,598$ ,  $r = 0,919$ ,  $P < 0,001$ ,  $n = 52$ ).

The scatter diagram of buccal occlusal surface against number of cementum lines was obviously less suitable than lingual measurements. Nevertheless the regression equations were calculated,  $r = 0,6485$  which is much less than the lingual coefficients and even though significant at  $P < 0,001$  it was decided to use lingual measurements alone for prediction purposes.

The scatter on either side of the regression lines of lingual tooth wear (Figs. 14 & 15) are of the order one might expect for such a relationship, except for very young animals and very old animals, but the sample size in these age classes is small. In the case of lingual crown height the minimum value has been taken as zero, but in fact the values should be less, as in very old animals the upper part of the root below the cingulum is exposed and worn away. The 95% confidence intervals for individual predicted values of  $Y_x$  have been calculated and are shown in the figures. As expected the intervals are narrower in the region of the mean  $X$  and  $Y$  values and wider further away from the means. These confidence limits indicate that any prediction of a value of  $Y$  could be made with marginally greater confidence using lingual crown height rather than lingual occlusal surface width. From these calculated tolerance points it can be seen that for any lingual crown height value the number of cementum lines cannot be predicted with greater accuracy than plus or minus 2,7 lines, 2,6 lines and 2,7 lines for crown heights of 5, 10 and 15 mm respectively. In the case of lingual occlusal surface width the accuracy of prediction is plus or minus 2,9 lines, 2,8 lines and 3,7 lines for occlusal surface widths of 5, 10 and 15 mm respectively. Nevertheless, it should still be noted that some of the scatter in the relationship presented is due to the variability in the number of lines laid down by animals, errors of counting and of interpretation of lines and possible inconsistencies in measurement, especially in older animals. It would seem therefore, that if it were possible to plot true age against lingual crown height or occlusal surface less scatter might be expected, although the mean regression line would probably remain much the same.

It has been suggested by Grimsdell (1973a) and Watson (1967) that the relationship between tooth wear and age is curvilinear, polynomial regressions up to the fourth degree were, therefore, calculated for the data on lingual crown height and occlusal surface of maxillary first molars against number of cementum lines to investigate the intensity of the curvilinear relationship in giraffe. It was found that in the case of the lingual occlusal surface regression there was only a slight improvement (F value only just significant at 0,05 level) by the second degree polynomial over the first degree. The



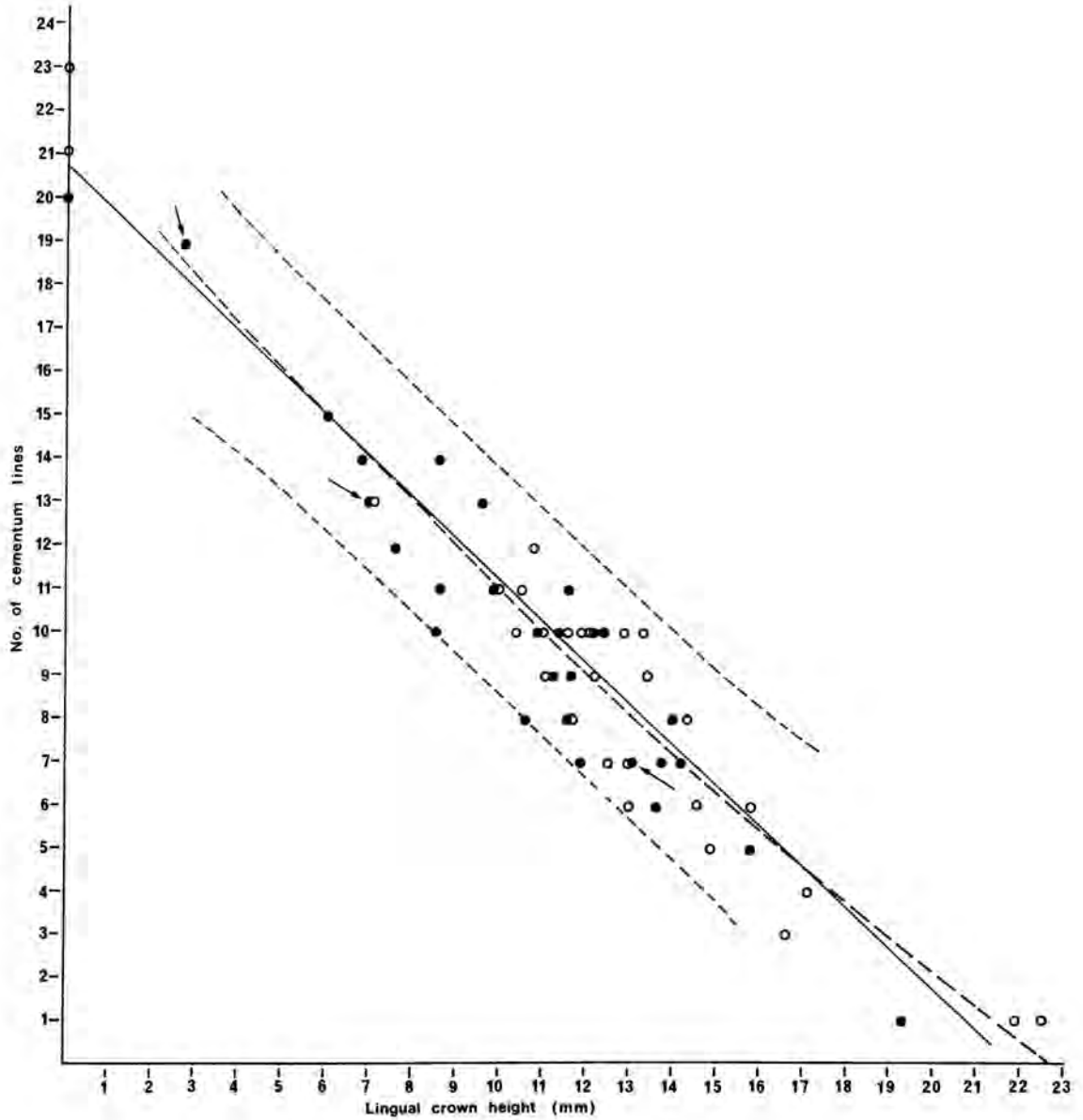


FIG. 14 — Relationship between lingual crown height of the giraffe first maxillary molar and number of cementum lines. Males (o), females (●). Arrows indicate known-age animals. Central solid and dashed lines indicate linear and polynomial regression lines respectively while the outer dashed lines are 95% confidence limits.

third degree gave no significant improvement and the fourth degree no improvement at all. The analysis of variance is given in Table 15a. In the case of lingual crown height there was no significant improvement above the first degree polynomial (Table 15b). These data show that the linear regression formulae (Table 14) are adequate for predictive purposes and that little or nothing was gained additionally by calculating a curvilinear regression. To further substantiate this point the highest order curvilinear regressions which gave an improvement over the linear regression were plotted as dashed lines in Figs. 14 & 15. It can be seen that the deviation from the linear regression is slight and the curve lies well within the 95% confidence limits for the linear regression.

TABLE 15: ANALYSIS OF VARIANCE OF POLYNOMIAL REGRESSIONS TO THE FOURTH DEGREE OF GIRAFFE MOLAR DIMENSIONS AT AGE

Source of variance	d.f.*	M.S.*	F	Significance
(a) Lingual occlusal surface width of maxillary first molar				
Degree 1 component	1	1054,4587	575,7736	$P < 0,001$
Residual (Degree 1 regression)	53	1,8313		
Degree 2 component	1	10,7959	6,5076	$P < 0,05$
Residual	52	1,6589		
Degree 3 component	1	3,3305	2,0480	n.s.
Residual	51	1,6262		
Degree 4 component		No improvement		
(b) Lingual crown height of maxillary first molar				
Degree 1 component	1	1058,7263	604,6904	$P < 0,001$
Residual (Degree 1 regression)	53	1,7508		
Degree 2 component	1	4,4294	2,6066	n.s.
Residual	52	1,6993		
Degree 3 component	1	0,6970	0,4054	n.s.
Residual	51	1,7190		
Degree 4 component	1	5,2951	3,2142	n.s.
Residual	50	1,6474		

\* d.f. = degrees of freedom

\*\* M.S. = mean square

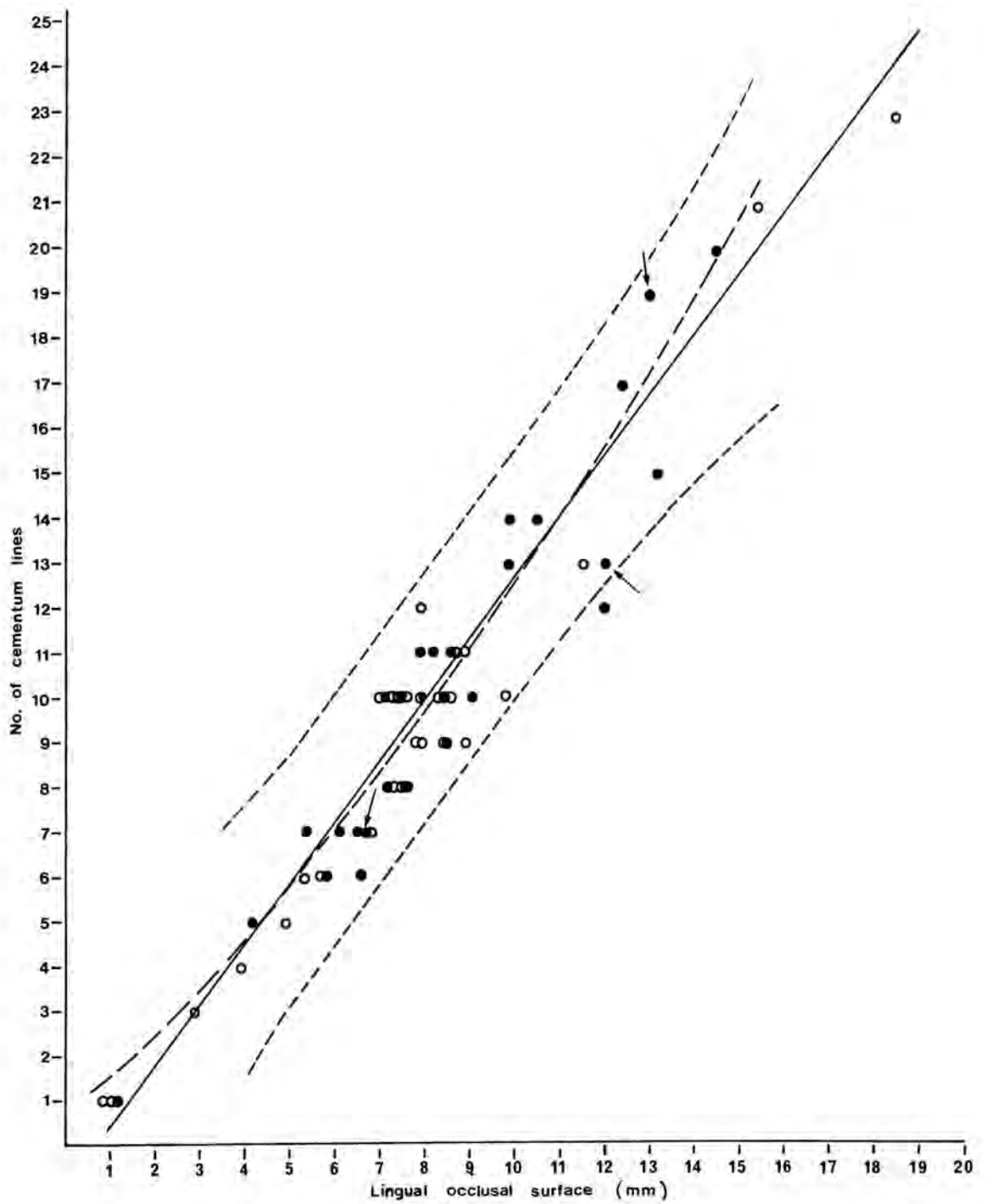


FIG. 15 — Relationship between lingual occlusal surface width of the giraffe first maxillary molar and number of cementum lines. Males (o), females (●). Arrows indicate known-age animals. Central solid and pecked lines indicate linear and polynomial regression lines respectively while the outer pecked lines are 95% confidence limits.

## TOOTH WEAR AND MATURITY

The results of measurements of crown height and occlusal surface width have been discussed in relation to age as determined by cementum layer counts.

It was found that root length was closely correlated with age in young animals and that root growth continued for several years after the eruption of  $M^1$ . During old age root resorption occurred. The measurement of root length was not, therefore, considered suitable as a criterion for age determination. The measure of total length of the tooth was also, therefore, unsuitable for age determination purposes.

Crown width measurements when used alone were not found suitable for age determination but when used in combination with some other measurement the relationship with age improved. Thus mean crown width alone (e.g. labio/lingual width) had a nonsignificant correlation of 0,103 with age as determined by cementum line counts, but when used as a component of a ratio such as crown width over crown height, crown surface area (labio-lingual x mesio-distal dimensions) over crown height or crown index the correlations rose to 0,813 ( $P < 0,001$ ), 0,796 ( $P < 0,001$ ) and 0,684 ( $P < 0,001$ ) respectively again confirming the value of the measurement of crown height.

Several such ratios were investigated but none were found to be as closely correlated with cementum line counts as the lingual crown measurements already discussed and are therefore not regarded as useful for age determination purposes.

The degree of occlusion of maxillary first molar roots from a sample of 47 teeth is shown in Table 16. Clearly occlusion of the roots is a crude measure of age. The buccal roots which are narrower than the lingual are first to close, and the posterior buccal root closes before the anterior one.

### Patterns of wear

A selection of maxillary first molars were arranged in year groups from 5 years upwards. It was found that there was a high degree of conformity in wear surface appearance in each group. These wear patterns were more distinctly differentiated in younger (less than 8 y) and older (12 to 14 y) teeth than in the intermediate age groups. In very old animals (over 15 y)

TABLE 16: OCCLUSION OF MAXILLARY FIRST MOLAR ROOTS IN GIRAFFE

Buccal		Lingual	Mean age (y)			
Ant.	Post.		Male Range	n	Female Range	n
*C	C	C	12,9(9-23)	8	13,8(10-20)	12
C	C	P			8,0	1
C	C	P	9,9(8-11)	8	8,5(7-10)	6
P	C	P			7,0	1
P	P	P	9,0 -	1	6,0(5-7)	3
P	P	O	5,5(4-7)	2	7,0	1
O	P	O			6,0	1
O	O	O	1,0	1	1,0(1)	2

\*C = pulp cavity occluded      P = pulp cavity partly occluded  
 O = pulp cavity open.

the wear on the occlusal surface, and especially on the paraconule and metaconule is very variable. A tooth regarded as typical of each year class was selected and used as a reference standard with which to compare other teeth (Plate 2). The changing wear patterns in the different age groups can briefly be described as follows:

5 years: The cones are all distinct, the infundibula are wide, the crescentic tracts of dentine exposed are approximately the same width, the tip of the mesostyle is still capped by enamel.

6 years: The enamel cap of the mesostyle has been worn away and dentine is exposed. The dentine surfaces of the protocone and hypocone are broader than those of the metacone and paracone.

7 years: The enamel loop connecting the anterior edges of the protocone and paracone has been worn down and a thin line of dentine runs up to the anterior lingual edge of the paracone. The enamel loop between the hypocone and metacone is not yet continuous at the wear surface.

8 years: A thin line of dentine has been exposed in the anterior enamel loop and the dentine of the protocone and paracone are now joined. The posterior loop is flush at its grinding surface.

## PLATE 2

Patterns of wear on maxillary first molars of giraffe according to known-age or age estimated from cementum line counts. Terminology follows Arambourg (1947) and is illustrated in Fig. 13. Salient features are indicated by arrows and discussed in more detail in the text. Age in years is shown next to each tooth, X 0,8. The sequential stages of wear are characterized by:

- 5 years: distinct cones, wide infundibula, mesostyle capped by enamel,
- 6 years: mesostyle dentine exposed,
- \* 7 years: anterior enamel loop worn down, posterior loop not,
- 8 years: anterior enamel loop dentine exposed, posterior not,
- 9 years: posterior enamel loop worn down, enamel of cones contiguous,
- 10 years: signs of wear on crown of entostyle,
- 11 years: posterior enamel loop dentine exposed,
- 12 years: wear in centre of tooth, entostyle dentine exposed,
- \* 13 years: dentine of protocone and hypocone continuous, infundibula narrow,
- 14 years: dentine of hypocone and metacone continuous,
- \* 19 years: all dentine surfaces continuous, enamel loops minimal,
- 21 years: no enamel on grinding surface, no entostyle,
- 23 years: root cavities exposed, enamel edges worn away.

\* known-age animals.



5



6



7



8



9



10



11



12



13



14



19



21



23

cm



- 9 years: The posterior enamel loop has been further reduced and the enamel of the hypocone and metacone are contiguous.
- 10 years: The first signs of wear appear on the crown of the entostyle.
- 11 years: The posterior enamel loop has been further flattened and the dentine of the hypocone and the metacone are continuous. The posterior edge of the protocone's enamel border and the anterior edge of the hypocone's enamel border are low between the paraconule and metaconule.
- 12 years: The crescentic tracts of dentine of the protocone and hypocone are in contact where their tips meet in the centre of the tooth. The enamel of the entostyle has been worn down and dentine is exposed.
- 13 years: The dentine of the protocone and hypocone are continuous. The infundibula are now very narrow.
- 14 years: The dentine of the hypocone and metacone are continuous and the posterior infundibulum has been isolated by a loop of enamel, being the remains of the lingual wall of the metacone and the buccal wall of the hypocone.
- 19 years: The infundibula have almost disappeared and the dentine of all four cusps is continuous. The enamel loop separating the paracone and metacone remains as a small ridge only.
- 21 years: No enamel is left on the grinding surface. The exterior loop of enamel, the remains of the walls of the cusps, is being worn away in parts, usually on the lingual surface first. The entostyle has been worn away.
- 23 years: The lingual enamel loop (the remains of the walls of the protocone and hypocone) has been worn away below the former level of the cingulum. Buccal enamel walls are still present. Four root cavities are exposed.

#### MANDIBLE MEASUREMENTS

Scatter diagrams were constructed to show mandible length, length of diastema,



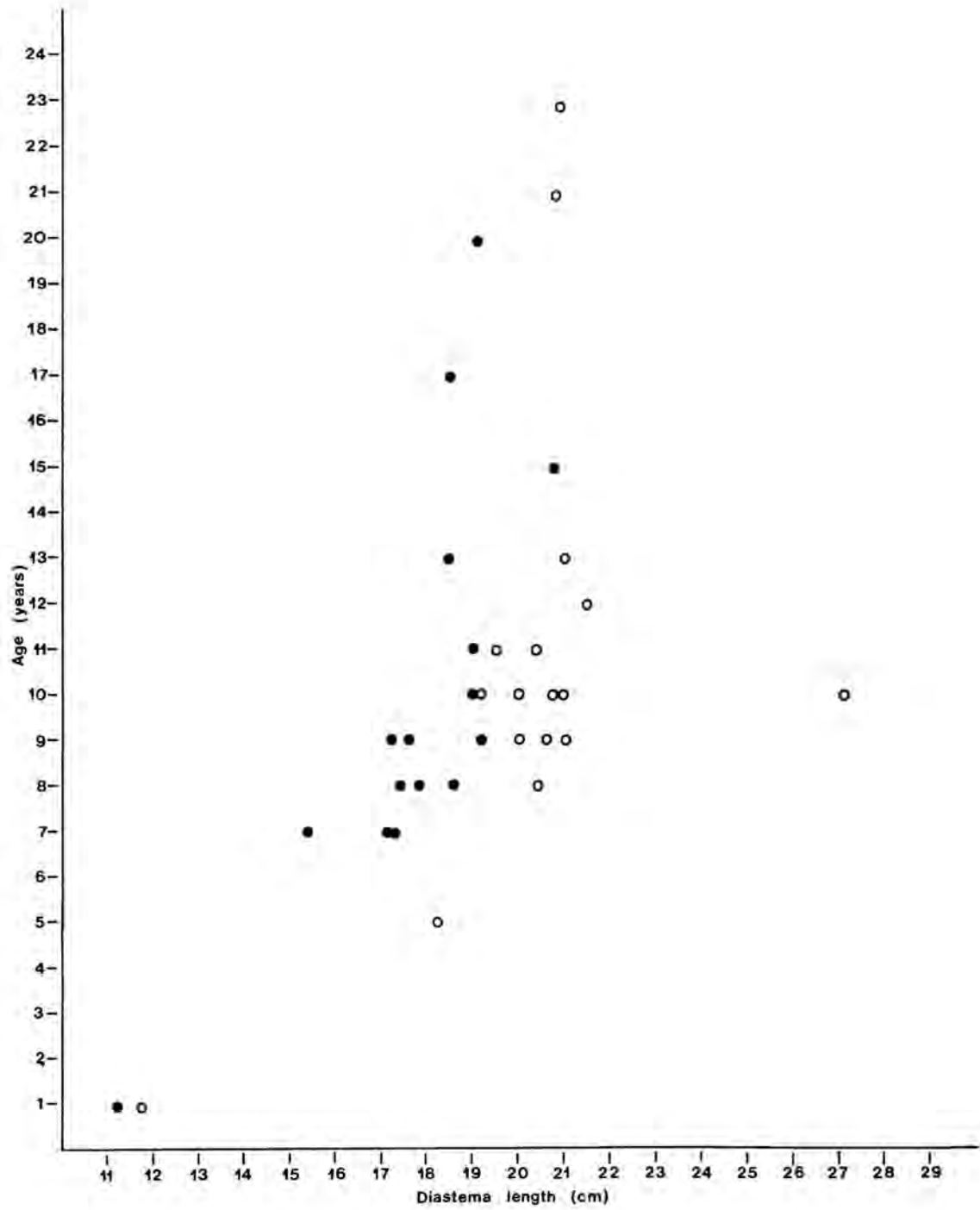


FIG. 16 — Relationship of diastema length to age (as determined from cementum lines) in giraffe. Male (o), female (●).

length of toothrow, ramus height and jaw angle plotted against age in years as determined from cementum lines. An example of these plots is shown in Fig. 16 for diastema length, which, like all the other features shows a normal growth curve except for the plot of jaw angles (Fig. 17) where no pattern can be discerned. In those features showing a normal growth curve, sexual dimorphism is clearly evident with males having the greater dimensions at age. Some use could be made of this kind of curve for age determination of immature animals if a sufficiently large sample were available to give size limits for these features for different age classes. The present data are inadequate for this purpose.

#### EYE LENS MASS

Of the 32 pairs of lenses that were measured, five (17%) did not differ left from right; 17 pairs (57%) differed by less than 1% from the mean, the remainder differed between 1% and 3% from the mean, the mean difference being higher in the heaviest lenses. Two singletons were included and two pairs with highly anomalous masses were rejected. A t-test for the difference between paired samples showed no significant difference between right and left eye lenses ( $t = 0,603$ ,  $P < 0,05$ ). The mean eye lens mass was therefore plotted against age as determined from cementum layer counts or tooth eruption stage (Fig. 18).

Although the sample size is small it can be seen from the scatter diagram that the growth falls into two phases. There is an initial period of rapid growth from birth to about 18 months of age and a subsequent phase showing a rectilinear relationship with estimated age. The paucity of samples from the older age classes tends to obscure the flattening of the curve with age which might be expected.

Linear regression lines could be fitted to the data for the range from 1,4 y to 12 y, for males and females together and separately. The regression equations are given in Table 17.

The regression line for both sexes combined is valid because there is no significant difference between the regression coefficients for males and females ( $t = 1,0338$  with 17 degrees of freedom has a probability of 0,4).

The sample is too small to allow of any meaningful discussion of the variability of lens mass at age. Nevertheless, in the age class 10 y in which there are 5 samples, inspection of the scatter diagram suggests that

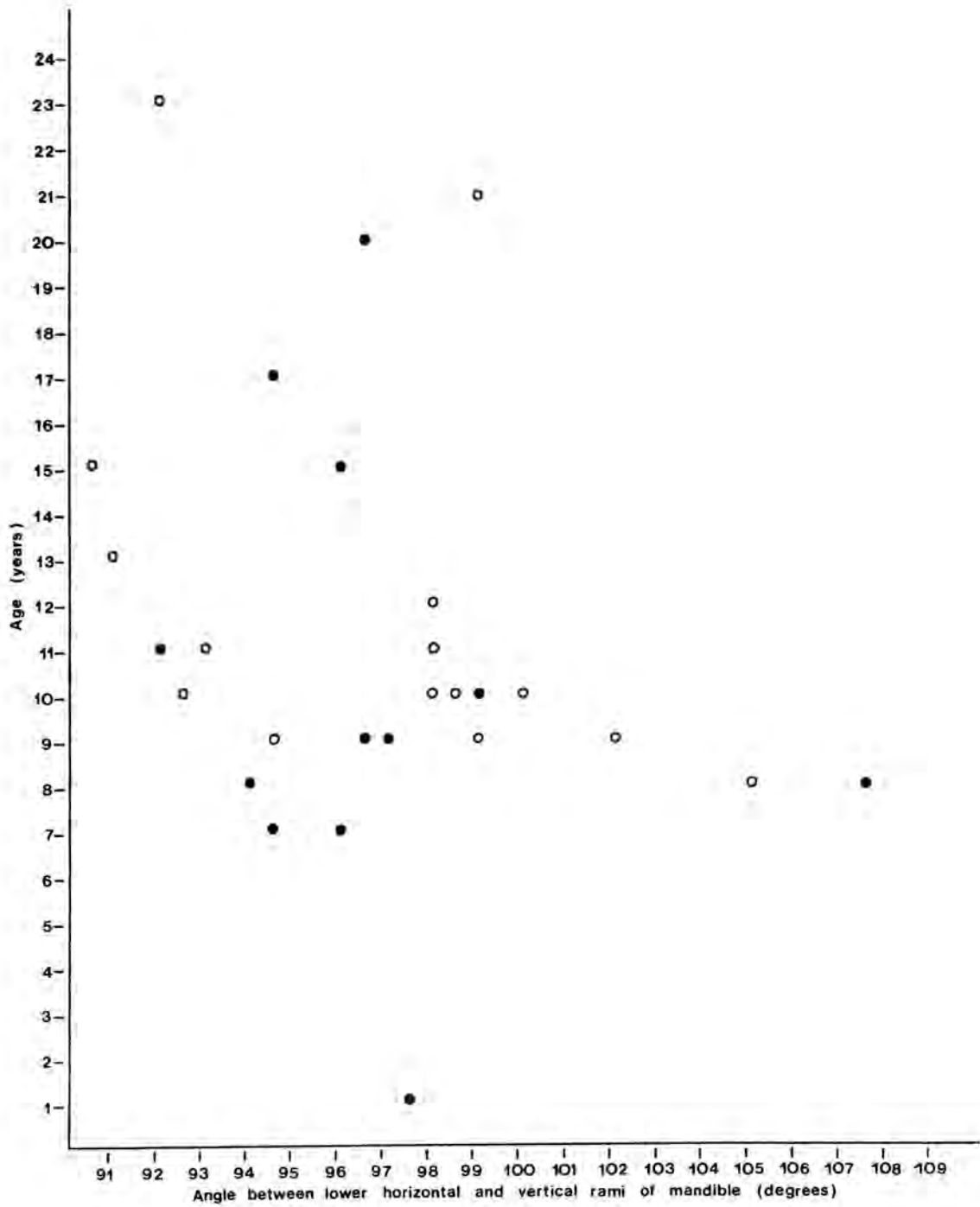


FIG. 17 — Relationship of the angle between the lower horizontal and vertical rami of the mandible to age (as determined from cementum lines) in giraffe. Male (o), female (●).

the variability would not be great. It should also be borne in mind that the variability found between lens mass may be due, not only to intrinsic biological variability, but also to the handling of the material. Poor technique can result in inaccurate results (Morris 1972).

TABLE 17: REGRESSION COEFFICIENTS OF NUMBER OF INCREMENTAL LINES IN CEMENTUM (X) ON EYE LENS DRY MASS (Y) OF GIRAFFE

Sex	Regression equation	r	P-value	n
Both	$X = 0,0199 Y - 10,9$	0,931	< 0,001	21
Male	$X = 0,0197 Y - 10,7$	0,967	< 0,01	7
Female	$X = 0,0201 Y - 11,0$	0,888	< 0,001	14

As the plot of dry lens mass against age was obviously curvilinear, polynomial regressions up to the fourth degree were computed for all the data. The second degree polynomial gave a significantly better fitting curve over the first degree (Table 18), but the improvement due to the third degree polynomial was only just significant at the 5% level. There was no significant improvement by the fourth degree. The third degree polynomial residuals were therefore plotted on Fig. 18 and show the degree of curvilinearity found.

TABLE 18: ANALYSES OF VARIANCE OF POLYNOMIAL REGRESSIONS TO THE FOURTH DEGREE FOR DRY EYE LENS MASS AGAINST NUMBER OF CEMENTUM LAYERS OF GIRAFFE MOLARS

Source of variance	df.	M.S.	F	Significance
Degree 1 component	1	1249471,0	82,36	P < 0,0001
Residual (Degree 1 regression)	29	15170,0		
Degree 2 component	1	354845,0	116,77	P < 0,001
Residual	28	3038,0		
Degree 3 component	1	11459,00	4,202	P < 0,05
Residual	27	2726,96		
Degree 4 component	1	6152,00	2,3705	n.s.
Residual	26	2595,23		

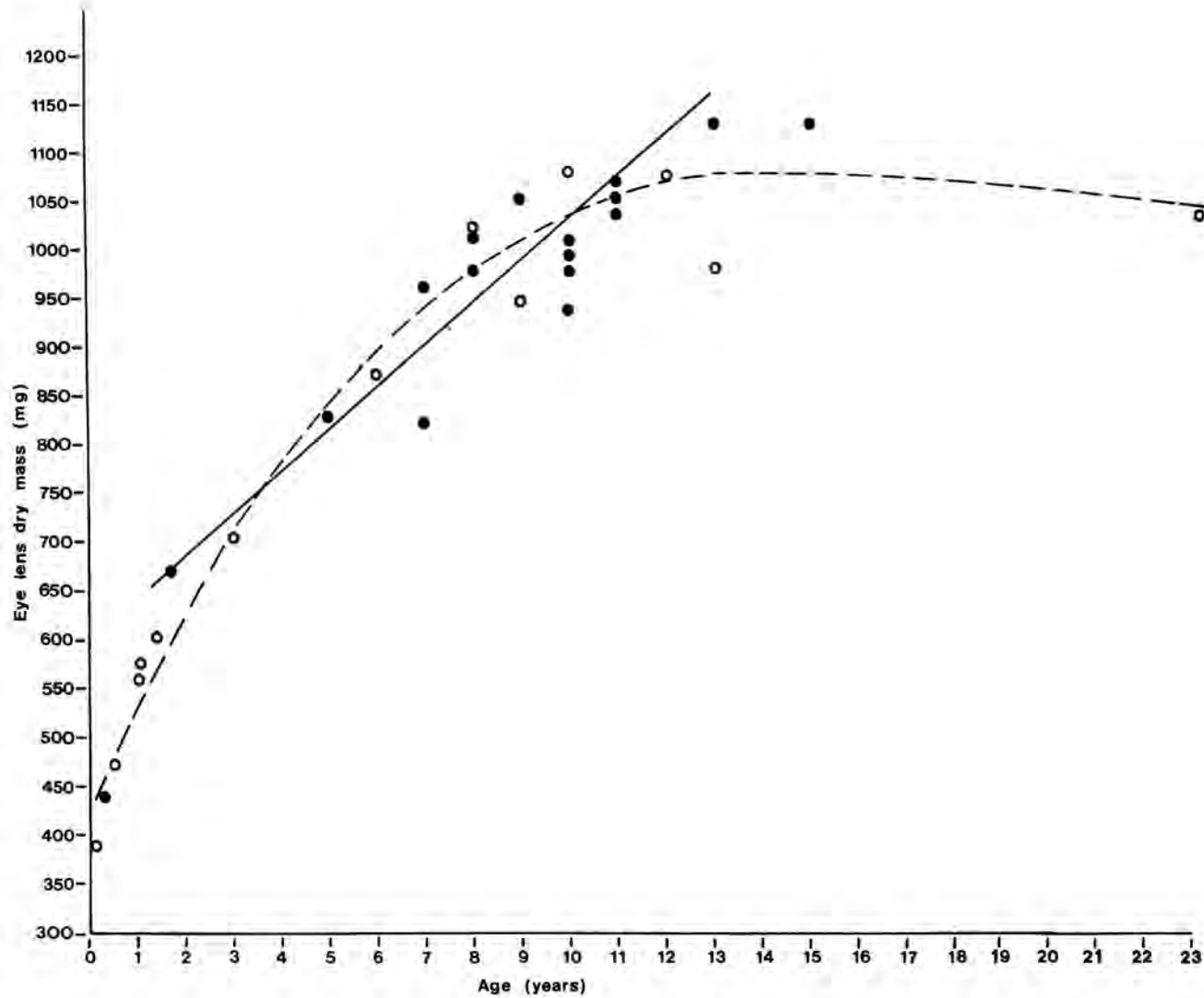


FIG. 18 — Relationship of dry eye lens mass to age (as determined from cementum lines) in giraffe. Males (o), females (●). Polynomial regression (pecked) and linear regression (solid) lines are shown ( see text for details).

## DISCUSSION

TOOTH ERUPTION

The conclusions summarised in Table 13 differ from those of Singer & Boné (1960) in the following respects:

1. They found that  $i_3$  did not begin to erupt until 2 months after birth, whereas in all the southern African giraffes this tooth was erupted at birth.
2. They found that the first molar was erupted at 4 months of age *cf.* 12 months in the present study. However, as their definition of 'fully erupted' does not entirely agree with that used in the present study, which takes into account whether the tooth is actually in wear or not, the actual difference may be less than the 8 months suggested.
3. Singer & Boné (1960) suggested that the second and third molars begin to erupt at about 4y and  $4\frac{1}{2}$  y respectively. From the present study these stages were thought to occur at about 2y and  $3\frac{1}{2}$  y respectively.

There is, however, close agreement with Singer & Boné (1960) on the eruption times suggested for the second premolar, the permanent canine, the time period over which the deciduous molars are lost, and the time period over which the incisors are replaced.

Singer & Boné (1960) described the eruption stage reached by two giraffes which were born, reared and died in zoological gardens. One of these specimens (No. 299998, U.S. National Museum, Washington, U.S.A.) came from the Sudan National Zoological Park, its age at death is given as 5 months 26 d, and it would fit into stage 2 as given in Table 13. The second specimen cited is No. 80146 (American Museum of Natural History, New York) originated from the New York Zoological Park and its age at death is given as 7 months. However, there are two skulls in the museum bearing this latter registration number and both are of immature animals. Singer & Boné (1960) refer to them as 80146<sup>1</sup> to which they attach the age of 7 months and 80146<sup>2</sup>. The dentition descriptions provided for the two specimens shows that 80146<sup>1</sup> has M<sup>1</sup> fully erupted and M<sup>2</sup> erupting, while 80146<sup>2</sup> has only reached the stage where M<sup>1</sup> has started to erupt. By these criteria in comparison with wild animals, 80146<sup>1</sup> would be placed in stage 5 of Table 13, and would therefore be between 12 and 15 months old (Table 13) while 80146<sup>2</sup> would fit into stage 2 and would be between 4 and 10 months old (Table 13). It seems unlikely that a captive animal would have a growth tempo so accelerated that its permanent teeth would erupt at half the age that is apparently normal in

the wild. The situation is further confused by the cranial measurements presented later in their paper where 80146<sup>2</sup> (having the junior dentition) is shown to be considerably larger than 80146<sup>1</sup> (with advanced dentition). Furthermore, the measurements given for 80146<sup>1</sup> (Table 4, Singer & Boné 1960) correspond with measurements of skulls from Timbavati classified as stage 2 (M<sub>1</sub> beginning to erupt) and the measurements given for 80146<sup>2</sup> correspond with those for stage 5 (M<sub>1</sub> erupted, M<sub>2</sub> erupting) from Timbavati. It would seem therefore as though Singer & Boné (1960) have transposed their labelling and that a correct summation of the situation is that the smaller of the two skulls has the junior dentition and is 7 months old (which would then correspond on all points with the wild material) and the larger skull has the more advanced dentition and is considerably older than 7 months.

The classification of immature giraffe into different age categories based on tooth eruption can only serve as an approximate measure of age since there are several factors which influence tooth eruption. Some of these are early loss of predecessors, crowding and nutrition, all of which can result in great variation between individuals of similar age and sex (Steenkamp 1970, 1974).

The eruption sequence of the different teeth of the giraffe differs from that found in other African mammals. The lower teeth erupt first in buffalo (Grimsdell 1973a) Thomson's gazelle (Robinette & Archer 1971) and grey duiker *Sylvicapra grimmia* (Riney & Child 1960) while in Burchell's zebra the upper and lower teeth erupt almost simultaneously (Smuts 1972).

As mentioned by Steenkamp (1974) the calcification of a tooth may be a more meaningful indication of somatic maturation than is its clinical emergence. Although this aspect of dentition requires more elucidation it was found useful as a criterion for separating skulls with similar tooth surfaces but having unerupted teeth at different levels of development as shown by radiography.

The nomenclature of Arambourg (1947) is useful when discussing tooth wear and Spinage (1973) has focused attention on this system. Unfortunately, Spinage (1973) transposed the buccal and lingual nomenclature of the mandibular teeth, transposed some of the labels of the cones in the bovid maxillary molar, orientated the bovid mandibular teeth lingually-bucally and not buccally-lingually, and used a symbol 'Pt' to label parts of the zebra maxillary teeth for which he gave no explanation (p. 168-169 and Fig. 1 *op. cit.*). In an erratum published later (*E. Afr. Wildl. J.* 1974, Vol 12, p. 167) the errors in the labelling of the bovid maxillary teeth and orientation of the bovid

mandibular teeth are noted and an arrangement of the descriptive terms of Arambourg (1947) is given. However, the error in the original text, and the omission in the figure are not mentioned. Moreover, in this erratum the buccal and lingual nomenclature of the mandible have again been transposed.

## TOOTH SECTIONS

### Undecalcified sections

It would appear that the use of undecalcified sections for age determination purposes in African mammals might be dependant on species characteristics or techniques. The successful use of undecalcified sections has so far only been reported by Watson (1967) for wildebeest and Smuts (1972) for Burchell's zebra. As in the case of giraffe Grimsdell (1973a) found these sections unsuitable for use in buffalo.

### Decalcification

The best sections were obtained from specimens which had been well-fixed in nitric acid/formalin and then decalcified by the chelating agent EDTA. Though trichloroacetic acid proved much faster for routine use, specimens tended to be more brittle than EDTA treated specimens. The use of an ultrasonic vibrator (Dreyer 1965, Steenkamp 1974) is promising as a rapid method but could unfortunately not be recommended on the basis of the present results. No success was achieved with Gooding & Stewart's fluid.

The efficacy of the decalcifying procedures followed in this study is further shown by the successful cutting of sections at  $4 \mu\text{m}$ , though  $5 \mu\text{m}$  was preferred for routine use. Other workers, with the exception of Steenkamp (1974), have had to use much thicker sections and have had to resort to soaking the blocks in water to achieve softening of the tissue.

### Dentine layers

The presence of layers in the dentine was well demonstrated in some specimens but not seen in most. This suggests that the absence of these layers is an artefact of the technique used. Improved staining might, therefore, lead to the development of age criteria using dentine layers.

### Cementum layers

The heterogeneity of the staining of cementum layers in giraffe indicates that further investigations into the nature of these layers, their formation and their staining properties are required. Ehrlich's haematoxylin meets most



of the requirements but refinements might improve results. This stain proved suitable not only on giraffe teeth but also on 30 other species representing six orders of Mammalia which were examined during the course of another study (Hall-Martin in prep.). Ehrlich's haematoxylin was also recommended by Klevezal' & Kleinenberg (1969) and Steenkamp (1974). Grams' stain used on giraffe teeth provided variable results, although the neutral red was well taken up by the cementum bands in some specimens. When used in combination neutral red and carbol fuchsin produced acceptable results. A more detailed investigation of these stains and possibly other basic stains should prove rewarding.

It is widely accepted that the calcification rhythm in teeth may be disturbed by a sudden and/or severe change in level of nutrition or during times of physiological stress particularly that associated with reproduction and lactation (e.g. Laws 1962, Klevezal' & Kleinenberg 1969, Morris 1972, Steenkamp 1974). It has also been suggested that critical levels of Vitamin D might play a role (Laws 1962). As far as African mammals are concerned several workers have postulated that the dark staining cementum lines represent areas of arrested growth or hypocalcification formed during the dry season when the animal may be under some nutritional stress (Spinage 1967, Laws 1968, Simpson & Elder 1969, Grimsdell 1973a, Lombard 1971, Rautenbach 1971).

Klevezal' & Kleinenberg (1969) also discussed these points and showed that the transparent bands are hypercalcified in comparison with the opaque ones. Additional evidence that the dark staining bands in dentine represent areas of hypocalcification formed as a result of disturbances of the calcification process is discussed by Steenkamp (1969, 1974) who worked on bovine incisors. In the present study the observations that splitting regularly occurred along these dark staining bands in the dentine of undecalcified sections and in the cementum of a few paraffin specimens indicate weakness or inconsistency in the homogeneity of the tissue matrix. Though a detailed discussion of these phenomena in conjunction with dentine and cementum formation and morphology is beyond the scope of this report, they must be viewed as evidence supporting the hypothesis that the dark staining bands represent lines of hypocalcification at least in the teeth of giraffe. The light-staining or transparent zones of cementum would then be formed during the wet season when nutritional conditions are optimal. The data presented in Chapter 2 do not provide any indication of a biphasic nutritional depression in giraffe in Timbavati, there is only the major nutritional depression in the late dry season. It would seem reasonable to suggest

therefore, that only one dark staining incremental layer per year is due to a nutritional effect, as found in immature animals. The second band which forms in most years in some adults, with no selection for sex, is likely to be associated with the endocrinology of reproduction or lactation as has been suggested by Laws (1962) in the case of seals. If the double bands were due to other environmental effects such as change in day length and temperature it might be expected that they would be present in all giraffe from the same area, or in all mature animals only, but this was not found to be the case.

The increased frequency with which cementum lines occur in the apical part of the root and their decreased frequency toward the cervical margin are features also noted in cattle teeth (Steenkamp 1974), and detracts from the use of this technique for age determination. However, even if this is so, the results of such studies would still "identify different ages, even though they do not provide an absolute measure of age" (Steenkamp 1974, p. 12). This problem can, however, be resolved as regression models with optimum prediction accuracy are developed.

#### LONGEVITY

Foster & Dagg (1972) reported males about 25 y, 26 y, 23 y and 21 y old and two females over 25 y old in the Nairobi National Park, Kenya. Captives have lived to 28 y (Flower 1931, King 1947), the oldest giraffes in New York Zoological Park lived to 21 y and 22 y respectively (Crandall 1964) while the oldest females at Taronga, Australia were at least 21 y and 26 y old and the oldest male 25 y old at death (Strahan *loc. cit.*). Spinage (1968) mentions a female that lived to the age of 23 y in the Zoological Gardens of London. The greatest ages determined for giraffe during this study were 23 y and 21 y for males and 20 y for a female. The known-age female skull from Hans Merensky was about 20 y old but only 19 cementum layers were counted. It seems likely then that giraffe in the wild regularly live to over 25 y. The oldest male and female shot in Timbavati were both still in good condition, the female being pregnant, and they probably would have lived for several more years. Though their first molars were badly worn, their other teeth were still in reasonably good condition.

#### CRANIAL SUTURES

Singer & Boné (1960) made observations on the closure of eight cranial sutures in their material. Though they found some correlation of suture fusion with tooth eruption order there were many exceptions. This method was therefore not examined in this study as it offered little hope of providing a more

accurate means of age determination than tooth eruption or cementum layers.

### EYE LENS MASS

Even though acceptable correlation coefficients for prediction purposes were found from this data, this technique cannot be considered for use as a means of age determination in the giraffe, except perhaps in immature animals. There is considerable overlap in lens mass for older animals. However, despite the overlapping, the linearity shown by the increase in mass of the eye lenses from about 1,4 y, to 12 y provides some confirmation of the validity of the age criteria used. A biphasic lens growth curve has been reported for several other African mammal species recently studied (Laws 1967, Lombaard 1971, Rautenbach 1971, Smuts 1972). Neither Laws (1967) nor Smuts (1972) used these curves for age determination purposes but argued, as here, that the linearity shown in the curves confirmed other age criteria. Eye lens mass was found unsuitable as a criterion for precise age determination in the springbok and black-backed jackal by Rautenbach (1971) and Lombaard (1971) respectively. Nevertheless, it has been used with success for small mammals (Morris 1972) and on a large sample of impala (Fairall 1969). Finally, it is worth noting that stress in the life of the animal (Myers & Gilbert 1968) as well as nutrition (Friend & Severinghaus 1967, Morris 1972) may effect the lens/mass/age relationship.

### CONCLUSIONS

The results of this study can be summarised in a few points. The age of a giraffe from the eastern Transvaal Lowveld and probably from anywhere else in southern Africa can be determined with sufficient accuracy for all practical purposes as follows:

1. The stage of tooth eruption can be examined from both jaws or from upper or lower jaw alone and the corresponding stage of eruption with its chronological age can be found from Table 13.
2. From the mean lingual crown height or mean lingual occlusal surface width the corresponding age can be read off the regression line in Figs. 14 and 15. The mean of the two ages found can be taken. Alternatively the regression equations can be solved for Y (the number of cementum lines) from a known X (the measurement of tooth wear).

3. The maxillary first molar wear pattern can be compared with the wear patterns of the selected reference teeth (Plate 2). Any necessary adjustments can then be made.

Using these procedures it is likely that the age of most animals can be determined to within approximately 1 y up to about 15 y of age. Thereafter the probable error increases because of the greater scatter found in older teeth and because tooth wear patterns are more variable, but the error in prediction is still unlikely to exceed 2 y.

## CHAPTER 4

CARCASS COMPOSITION AND MEAT PRODUCTION

## INTRODUCTION

The meat production potential of wild ungulates in Africa has been subjected to increasingly intensive investigations in recent years (Talbot, Payne, Ledger, Verdcourt & Talbot 1965; van Zyl, von La Chevallerie & Skinner 1969; von La Chevallerie 1970; Huntley 1971a; von La Chevallerie, Erasmus, Skinner & van Zyl 1971; von La Chevallerie & van Zyl 1971). The significance of live body mass in assessing this potential has been stressed by von La Chevallerie (1970). However, unless live body mass as a parameter of meat production is related to body composition, it may well be an inadequate or misleading indicator of the potential of animals and of the productivity of the flora on which they live (Ledger 1965). During the course of giraffe culling in the eastern Transvaal Lowveld data on body mass and body composition were obtained. Though inadequate for a definitive statement on meat production efficiency of the species, the data provide useful information on the carcass quality of giraffe and a basis for comparison with domestic stock and other wild ungulates.

## MATERIAL AND METHODS

CARCASS DISSECTION

Most of the giraffe used in this study were shot in the Timbavati, additional data were obtained from animals shot in the Sandringham and Buffelshoek Reserves. The three reserves are contiguous and vegetation and climate are similar over the whole area. A total of 25 females (over 6y old) and 19 males (over 8y old) were used in this study. The giraffe were shot in the head, usually soon after sunrise but occasionally much later, using a 30'06 calibre rifle and 180 gr soft nosed or expanding bullets. The animals collapsed instantly and their carotid arteries and jugular veins were severed within seconds. No animals were wounded and the carcasses were well-bled.

Various body measurements were taken and these are discussed in Chapter 5. Due to the large size of the carcasses, the field conditions under which these operations were carried out, and the lack of suitable scales, the animals were butchered where they fell and their mass measured in pieces. The butchering commenced by skinning the exposed side of the animal either in

panels or in one piece. It would have been desirable to follow the carcass dissection procedure proposed by Ledger (1963), but the limited equipment and manpower made this impossible. A procedure using only four men, based on the traditional butchery of the indigenous Shangaan people, modified to accord with Ledger (1963) where possible, was followed. After skinning the body was dissected as follows:

1. The exposed foreleg was first removed as suggested by Ledger (1963). A vertical cut was made commencing at the olecranon process of the ulna alongside the posterior edge of the *m. tensor fasciae antibrachii*, continued to the posterior angle of the scapula, cutting into the *m. latissimus dorsi* where it runs inferior to the posterior edge of the *m. triceps*. Then while the leg was lifted a lateral cut was made through the pectoral muscles close to their junction with the forelegs. This cut was continued along the leading edge of the forelegs as indicated by the anterior edge of the *m. biceps brachii* and the *m. supraspinatus* and then round the dorsal end of the scapular cartilage cutting through the *m. trapezius*. The foreleg could then be raised clear of the thorax and the final cut made by severing the connection of the scapular cartilage to the thorax so that the inferior surface of the scapular itself was clear of muscular tissue. The foot was then removed from the foreleg at the carpal joint.
  
2. The hindleg (buttock) was next removed in a manner similar to that described by Laws, Parker & Archer (1967) for the African elephant. This method is also used by the Shangaan people and it is the easiest way of removing the bulky and heavy legs of large animals. The hind leg was removed at the acetabulum and included the muscles lying exterior to the dorso-lateral surface of the pelvis and lateral to the sacrum. This muscle mass is made up of the *m. gluteus*, *m. biceps femoris*, *m. tensor fasciae latae*, *m. iliacus*, *m. semitendinosus*, *m. sartorius* and *m. semi-membranosus*. A cut was begun along the lateral edge of the sacrum and continued mesio-distally severing the muscle attachments between the *tuber coxae* and the *tuber ischii*, the muscles being cleanly removed from the bone and obturator membrane. As the muscle attachments were severed the muscle mass was reflected away from the bone. This cut was continued ventrally along the posterior edge of the *tuber coxae* severing the attachments of the *m. tensor fasciae latae* and the patellar ligament. It was possible then to rotate the leg so as to facilitate disarticulating the head of the femur. The leg was finally freed by a cut through the remaining muscle attachments and the foot removed at the tarsal joint.

3. Next the *m. longissimus dorsi* was removed from its attachments to the sacrum and ileum as far anteriorly as the seventh cervical vertebrae exposing the ~~heads~~ <sup>capitulae</sup> of the thoracic ribs.
4. The head was removed by severing it from the neck at the atlas joint and continuing the cut along the posterior line of the jaw.
5. A horizontal cut was then made through the heads of the thoracic ribs and vertically down through the sternum which was split ventrally. The cut was continued posteriorly through the abdominal muscles as far back as the pelvis and then a vertical cut was made along the anterior edge of the pelvis to join the dorsal cut. The rib cage with the attached flank and abdominal muscles was removed, cutting through the diaphragm as close to the ribs as possible, which exposed the viscera.
6. The body was then eviscerated and the genitalia removed. The oesophagus was ligated and severed close to the cardiac sphincter. The duodenum was also ligated near the pyloric sphincter and severed from the stomach. The rectum was ligated and severed. The kidneys and kidney fat were removed from the body cavity with the viscera.
7. The neck was severed from the thorax by a cut running between the seventh cervical and first thoracic vertebrae. When dealing with large bulls the neck also had to be divided between the fourth and fifth cervical vertebrae as it was too unwieldy to be handled in one piece.
8. The remainder of the carcass was then turned over and the foreleg, hind leg, *m. longissimus dorsi* and the rib cage of the other side removed.
9. The chine and pelvis were separated by a cut between the last thoracic and first lumbar vertebrae. The tail was removed at the junction of the sacral and coccygeal vertebrae.

The mass of all the body components was determined using a Salter spring balance with a capacity of 200 kg. The balance was regularly checked for accuracy against a known mass standard. The time elapsed between shooting and mass measuring varied according to the size of the animal. Blood and body fluids lost during butchery were not measured. The total body mass of giraffe used in this study is, therefore, the sum of the mass of the body components as determined on the spring balance with no correction being

introduced for blood and fluids lost and also includes the mass of the reproductive tract and its contents in females.

### BUTTOCK DISSECTION

The composition of the buttock closely approximates the composition of the whole carcass (Butterfield 1962). The left buttock of several giraffe were therefore dissected into muscle, fat, connective tissue and bone. Hindleg length was first measured in a straight line from the dorsal surface of the head of the femur to the ventral surface of the distal articulation surface of the tarsus. Circumference of the buttock was also measured using a flexible tape. Measurements were taken to the nearest 1,0cm. Bone is classified as that which remains after all muscular tissue and fatty tissue has been removed from a hindleg as dissected from the body in the manner described above. This component is similar to the butchers bone as defined by Ledger (1965) and consists of the femur, tibia, tarsus, patella plus the tendon ends, cartilage and coarse connective tissues thicker than 4mm such as the patellar ligaments.

### MUSCLE FIBRE DIAMETER

Meat samples were taken from the *m. longissimus dorsi* at the third lumbar vertebra before the removal of the muscle from the body. The samples were about 80cm<sup>3</sup> and were fixed in 10% formalin. Muscle fibre diameter was later measured from subsamples of these meat cubes according to the method described by Joubert (1956).

### MASS ESTIMATION

Ledger (1964) reported that the mass of the leg of a standard dressed carcass of Boran cattle *Bos indicus* bears a constant relationship to the animal's live mass irrespective of its age. This relationship was used as a means of predicting liveweight in Boran cattle and eight species of wild ungulates (Smith & Ledger 1965), and also by Laws *et al.* (1967) for African elephant. Because of the usefulness of such a technique for predicting live mass in a game cropping or ranching system, its applicability to giraffe was investigated.

## RESULTS

### BODY MASS

The mean total body mass of adult giraffe is shown in Table 19, together with the standard deviation, standard error and range for three different age groups.



These data are a close approximation to the live mass of the giraffe, but have been affected by several sources of bias - the most important of these being the blood and evaporation loss after shooting and during butchering. Small scraps of tissue were also lost and have not been accounted for. In addition to bias during mass determination there are several other factors which influence the total body mass of a given animal at a given time. Some of these were investigated and are briefly discussed.

TABLE 19: TOTAL BODY MASS (kg) OF ADULT GIRAFFE OF DIFFERENT AGE GROUPS FROM THE EASTERN TRANSVAAL LOWVELD, JUNE 1971 - JULY 1972

Group	Age (y)	n	Mean	SD*	SE*	Range
(a) Males						
I	8 - 9	8	1096,6	122,0	46,1	849 - 1250
II	10	6	1183,3	76,5	34,2	1202 - 1303
III	11 - 23	<u>5</u>	1287,6	120,9	60,4	1056 - 1395
All males		19	1174,3	133,8	31,5	849 - 1395
(b) Females						
I	6 - 8	9	752,0	76,9	27,2	636 - 884
II	9 - 11	10	773,3	91,7	30,5	635 - 895
III	12 - 20	<u>6</u>	863,1	62,9	28,1	779 - 950
All females		25	791,8	86,3	17,6	635 - 950

\* SD<sub>i</sub> = standard deviation  
 SE<sub>i</sub> = standard error

### Sex

There is marked sexual dimorphism in the giraffe with the heaviest males having a mass more than 150% of that of the heaviest female (Table 19). This dimorphism is a feature of most African ungulates (von La Chevallerie 1970).

### Age

As it could be expected that there would be an increase in body mass with age up to the inflexion point of the growth curve (Chapter 5), the differences in body mass found among the present study animals could have been due to this effect. However, because the majority of the specimens fell into the lower

age classes (8 y to 10 y in males, 6 y to 11 y in females) and the samples were small it seemed likely that the age effect would be masked. The data were therefore divided as nearly as possible into three equal-sized groups representative of young adults, prime adults and old adults (Table 19). When t-tests were done on total body mass of male giraffe in the three different groups it was found that there was no significant difference between the first and second group and the difference between the third and second groups was only significant at the 5% level ( $t = 2,534$ ; d.f. = 11). In the case of female giraffe the younger group was significantly lighter than the next older group ( $t = 5,1586$ ; d.f. = 17,  $P < 0,001$ ). There was no significant difference in mass between the two older groups. In view of these findings it becomes possible to examine mass differences on a seasonal basis with greater confidence.

#### Season

Several recent studies on production of wild ungulates in southern Africa have focused attention on the effects of season on live mass (van Zyl *et al.* 1969, Skinner, von La Chevallerie & Van Zyl 1971; von La Chevallerie & van Zyl 1971; Huntley 1971b; von La Chevallerie *et al.* 1971).

The total body mass data of adult giraffe were grouped into the three seasons as defined in Chapter 1 and are shown in Table 20. When t-tests were done on total body mass for the different seasonal groupings it was found that the August to October male group was significantly lighter than the April to July group, 1129,8 kg *cf.* 1152,3 kg ( $t = 3,115$ ; d.f. = 14;  $P < 0,001$ ) and the November to March group 1129,8 kg *cf.* 1329,0 kg ( $t = 3,029$ ; d.f. = 6;  $P < 0,02$ ). In the case of females the dry season group was significantly lighter than the April to July group 762,6 kg *cf.* 801,6 kg ( $t = 9,2938$ ; d.f. = 18;  $P < 0,001$ ) but not significantly different from the November to March group, irrespective of whether or not foetal mass is excluded.

The ages of the animals in the different seasonal groupings were compared and it was found that the ages of male giraffe shot during the cool dry season (April to July) were not significantly different from the ages of the hot dry season group (August to October) ( $t = 1,1288$ ; d.f. = 14). The April to July group also did not differ significantly in age from the hot wet season group ( $t = 2,0244$ ; d.f. = 12). The animals in the latter group were however, significantly older than the hot dry season group but only at the 5% level ( $t = 2,7556$ ; d.f. = 6). Among the females no differences in age between the three groups were found using the t-test. These data, in

addition to the small differences found in mass of adults of different ages, lend confidence to the suggestion that the lower masses of those shot during the dry season is an effect of lowered plane of nutrition.

TABLE 20: TOTAL BODY MASS (kg) OF ADULT GIRAFFE IN DIFFERENT SEASONS, EASTERN TRANSVAAL LOWVELD, JUNE 1971 - JULY 1972

Season	n	Mean	S.D.	S.E.	Range
(a) Males					
April - July	11	1152,3	136,4	43,1	849 - 1395
August - October	5	1129,8	95,7	47,9	973 - 1250
November - March	3	1329,0	30,4	21,5	1306 - 1372
(b) Females (including foetal mass)					
April - July	15	801,6	78,3	20,9	636 - 907
August - October	5	762,6	73,2	36,6	635 - 860
November - March	5	791,8	111,2	55,6	677 - 950
(c) Females (excluding foetal mass)					
April - July	15	793,2	70,9	18,9	636 - 885
August - October	5	730,4	71,7	35,9	626 - 835
November - March	5	741,4	65,7	32,9	673 - 843

#### Stomach fill

The mass of the stomach contents was measured for each animal and included in total body mass. In the case of adult males ( $n = 19$ ) the stomach fill as a percentage of total body mass ranged from 8,5% to 13,6%, in females there was a much wider range from 8,2% to 20,7%. It is clear that stomach fill would have a greater influence on total mass of females than of males (Table 21). Females were classified according to pregnancy and lactation status and it was found that there was a significant difference between stomach fill as a percentage of total body mass in lactating cows (greater fill) than non-lactating cows. Stomach fill was however less in pregnant than in non-pregnant cows ( $P < 0,05$ ). These results are discussed further in Chapter 9.

### BODY COMPOSITION

For studies of meat production the dressed carcass composition rather than body composition is judged. However, body composition data is useful in studies of the amount of meat, viscera and other body parts consumed by predators, scavengers or decomposers; and as a means of assessing live mass of an animal by prediction methods. The body components of adult giraffe as a percentage of total mass is given in Table 21.

TABLE 21: BODY COMPOSITION OF ADULT GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, JUNE 1971 - JULY 1972

	Males (n = 19)				Females (n = 25)			
	Mean	S.D.	S.E.	Range	Mean	S.D.	S.E.	Range
Total body mass	1174,3	133,8	31,5	849-1372	791,8	86,3	17,6	635-950
As % of total body mass								
Dressed carcass	61,9	1,4	0,3	58,7-64,3	56,6	2,4	0,4	53,2-60,2
Buttocks	17,7	0,9	0,2	16,5-19,4	17,7	0,8	0,1	16,4-20,0
Forelegs	15,9	0,5	0,1	15,1-17,1	14,4	1,6	0,3	13,5-16,9
Chine, pelvis fillets, ribs & <i>m.l. dorsalis</i>	20,7	2,1	0,5	17,0-23,7	18,2	1,3	0,2	16,7-21,1
Neck	7,6	1,4	0,3	5,1- 9,9	5,9	0,6	0,1	4,8- 7,7
Offal	38,1	1,4	0,3	35,7-41,3	43,4	2,4	0,4	39,7-48,6
Skin	11,2	0,9	0,2	10,0-13,3	10,1	0,8	0,1	8,0-11,7
Feet	4,2	0,2	0,05	3,8- 4,7	3,9	0,3	0,07	3,2- 4,5
Head	2,9	0,2	0,07	2,6- 3,5	2,5	0,2	0,05	1,8- 3,0
Intestines	5,0	0,4	0,1	4,1- 5,7	5,9	0,9	0,1	4,5- 8,6
Organs	3,3	0,4	0,09	2,6- 4,3	7,1	4,4	0,9	3,4-20,8
Stomach & contents	11,5	1,3	0,3	8,5-13,6	13,9	2,8	0,5	8,2-20,7

### CARCASS COMPOSITION

The data from dressed carcasses of adult giraffe can, for comparative purposes, only be discussed as four major components; these are buttock, foreleg, neck and a component referred to as 'rest of carcass'. This latter category includes pelvis, chine, *m.l. dorsalis*, ribs and fillets. The data are presented in Table 22. In females the buttock as a percentage of carcass mass is significantly greater than in the male ( $t = 7,7188$ ; d.f. = 42;  $P < 0,001$ ). There is no significant difference, however, in the foreleg's contribution to carcass mass ( $t = 0,8192$ ; d.f. = 42). The neck contributes a significantly greater

TABLE 22: CARCASS COMPOSITION OF ADULT GIRAFFE, TRANSVAAL LOWVELD, JUNE 1971-  
 JULY 1972.

	Males					Females				
	n	Mean	SD.	SE.	Range	n	Mean	SD.	SE.	Range
Total dressed carcass mass	19	726,7	84,4	19,9	502,1-857,2	25	447,2	46,1	94,2	360,7-514,8
Dressed carcass as % of total body mass	19	61,9	1,4	0,3	58,7- 64,3	25	56,6	2,4	9,5	51,3- 60,2
As % of dressed carcass mass										
<u>All adults</u>										
Buttocks	19	28,6	1,42	0,34	26,2- 31,1	25	31,4	0,98	0,20	29,8- 34,0
Forelegs		25,8	0,86	0,20	24,3- 27,1		26,0	0,60	0,12	25,2- 27,4
Neck		12,2	2,50	0,59	8,0- 16,9		10,4	1,24	0,25	8,2- 13,6
Rest of carcass		33,6	2,88	0,68	28,8- 38,5		32,1	1,51	0,31	28,1- 35,2
<u>Group I</u>										
Buttocks	8	29,4	1,44	0,54	27,4- 31,1	9	31,4	1,12	0,38	30,3- 34,0
Forelegs		25,6	0,90	0,34	24,5- 27,1		26,4	0,56	0,20	25,5- 27,4
Neck		12,7	2,01	0,76	8,2- 14,9		9,8	0,52	0,18	8,8- 10,6
Rest of carcass		32,4	2,40	0,91	28,8- 36,1		32,3	1,19	0,42	29,9- 33,9
<u>Group II</u>										
Buttocks	6	28,2	0,72	0,32	27,1- 29,1	10	31,6	0,72	0,24	30,0- 32,0
Forelegs		25,6	0,48	0,20	24,7- 26,1		25,6	0,44	0,14	25,2- 26,5
Neck		10,9	2,17	0,97	8,2- 14,6		10,9	1,21	0,40	9,8- 13,6
Rest of carcass		35,2	2,45	1,09	30,8- 38,5		31,8	1,73	0,58	28,1- 34,7
<u>Group III</u>										
Buttocks	5	27,3	0,60	0,30	26,2- 28,0	6	31,1	1,08	0,48	29,8- 32,9
Forelegs		26,3	1,00	0,50	24,3- 27,1		25,9	0,56	0,24	25,3- 27,0
Neck		12,9	2,88	1,44	8,0- 16,9		10,6	1,59	0,71	8,2- 11,6
Rest of carcass		33,4	3,12	1,56	29,0-37,2		32,3	1,49	0,67	30,8- 35,2

proportion to carcass mass in males ( $t = 3,038$ ; d.f. = 42  $P < 0,01$ ) and so do the rest of the carcass components ( $t = 2,0719$ ; d.f. = 42;  $P < 0,05$ ).

When carcass composition in the three different age groups was examined it was found that there were no significant changes in the relative importance of the different components with age in females. In the case of males, however, the buttock contributed significantly more ( $t = 3,1683$ ; d.f. = 11;  $P < 0,01$ ) to the carcass in the younger animals than in the oldest animals. This was due in part to the increase in size of the neck. There were no other significant differences.

When the amount of fat found in the buttock of cows shot during the three seasons was compared (Table 23a) it was found that there was significantly less fat present in the hot dry season ( $t = 4,0027$ ; d.f. = 4;  $P < 0,001$ ) than in the wet season and also less than in the cool dry season (April to May) ( $t = 1,9781$ ; d.f. = 7;  $0,05 < P < 0,1$ ). No differences in buttock fat could be ascribed to the physiological influence of pregnancy. No seasonal differences were found in the muscle, bone and sinew components of the buttock reflecting loss of condition of females (Table 23a). Seasonal comparisons could not be made for adult male giraffe as the sample was too small (Table 23b). When mass of kidney fat in nine adult male and 18 adult female giraffe was examined (Table 24a) it was found that there were no significant differences between the seasons in males or females. The mean value for the hot dry season was, however, lower than the other seasons. The kidney fat deposits of pregnant and non-pregnant females were compared and it was found that there was no significant difference at the 5% level.

Kidney fat mass as a percentage of total body mass was also calculated (Table 24b). It was found that there were no significant differences discernible at the 5% level of probability in the data. The ranges are, however, wide and samples are small. The kidney fat percentage was then compared between pregnant and non-pregnant females and it was found that the latter had significantly more kidney fat as a percentage of total body mass ( $t = 2,1969$ ; d.f. = 15;  $P < 0,05$ ).

The dressed carcass mass was plotted against age (as determined from tooth cementum counts) and a typical growth curve was found (Fig.19). Second degree polynomials were used to draw the curves which because of the small sample do not fit the points for older animals very well. Nevertheless it does indicate that the point of inflexion of the curve lies between 10y and 13y

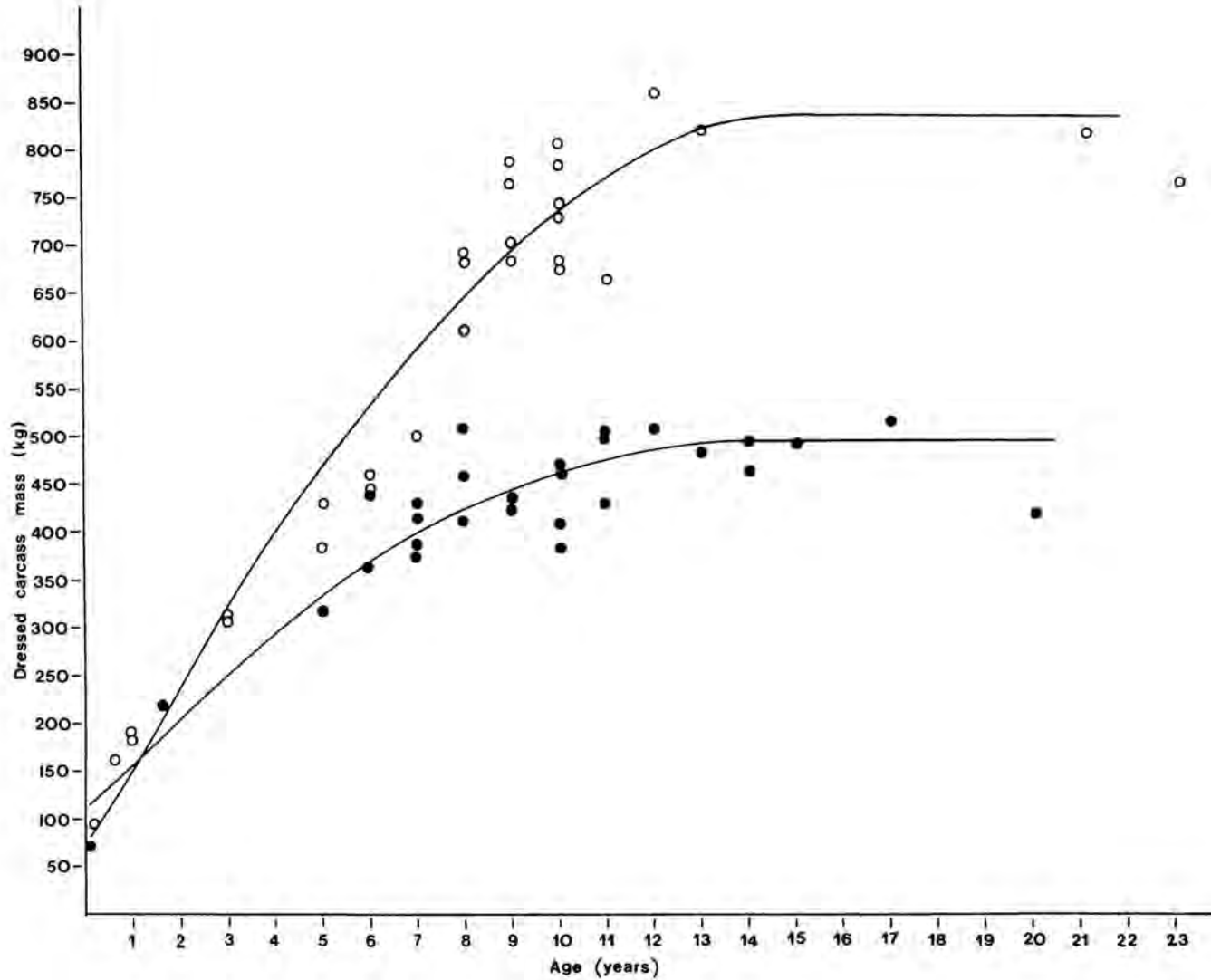


FIG. 19 — Carcass mass at age for Transvaal Lowveld giraffe. Males (○), females (●).

in males and probably 12y is a reasonable point to take for the asymptote. The data for females is better distributed and indicates that an asymptotic carcass mass is reached at about 11y

TABLE 23a: SEASONAL MASS CHANGES IN BUTTOCK COMPONENTS OF ADULT FEMALE GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, AUGUST 1971 - MAY 1972

Season	n	Cold buttock mass (kg)				As % of cold buttock			Buttock	
		Mean	SD	SE.	Range	Muscle	Bone & Sinew	Fat	Length (cm)	Circumference (cm)
August to October	4	69,0	4,0	2,3	64,5-74,7	77,0	21,5	0,52	115	121
November to March	5	67,2	6,6	3,3	59,4-75,5	77,1	21,4	1,39	110	121
April to May	8	68,5	3,3	1,3	66,2-72,6	78,3	20,6	1,17	112	122

TABLE 23b: BUTTOCK COMPOSITION OF ADULT MALE GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, AUGUST 1971 - MAY 1972

n	Mean	SD	SE.	Range	Muscle	Bone & Sinew	Fat	Buttock	
								Length (cm)	Circumference (cm)
6	106,0	7,0	3,1	92,3-115,7	75,6	23,9	0,46	123,2	147,0

#### MUSCLE FIBRE DIAMETER

The diameters of muscle fibres are presented in Table 25. Fibre diameter of the *m.l.dorsalis* in only one male foetus was measured and although it was less than in other males it was greater than a 1-week-old female calf which had a muscle fibre diameter of only 320µm. With increasing age in both males and females the muscle fibre diameter increased. Though the samples are small the differences between the means of the various groups were tested. It was found that the difference between male calves and males up to 6y old was not significant at the 5% level;



the difference between the young group and adults 7 y to 10 y old was significant ( $t = 7,4853$ ; d.f. = 4;  $P < 0,01$ ). The difference between the 7 y to 10 y old group and the oldest animals was not significant. When all males over 7 y old were pooled their mean muscle fibre diameter differed significantly from the younger animals (1-7 y) ( $t = 4,7363$ ; d.f. = 7;  $P < 0,01$ ).

TABLE 24a: KIDNEY FAT MASS (g) IN ADULT GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, AUGUST 1971 - JUNE 1972

Season	n	Mean	S.D.	S.E.	Range
<u>Males</u>					
August - September	3	1,133	0,381	0,269	0,595 - 1,417
November - February	3	1,285	0,292	0,207	0,879 - 1,559
April - June	3	0,680	0,220	0,155	0,397 - 0,935
<u>Females</u>					
August - September	4	0,886	0,254	0,146	0,624 - 1,304
November - March	5	0,935	0,327	0,163	0,510 - 1,474
April - June	9	1,067	0,337	0,119	0,595 - 1,644

TABLE 24b: KIDNEY FAT (g) AS A PERCENTAGE OF TOTAL MASS OF ADULT GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, AUGUST 1971 - JUNE 1972

Season	n	Mean	S.D.	S.E.	Range
<u>Males</u>					
August - September	3	0,096	0,029	0,021	0,055 - 0,124
November - February	3	0,096	0,020	0,014	0,067 - 0,114
April - June	3	0,060	0,019	0,013	0,035 - 0,083
<u>Females</u>					
August - October	4	0,110	0,025	0,148	0,083 - 0,152
November - March	5	0,121	0,043	0,021	0,074 - 0,196
April - June	9	0,133	0,046	0,162	0,068 - 0,202

Although there is an increase in mean muscle fibre diameter with age, in females the ranges in the different age groups show considerable overlap. No statistically significant differences were found between the age groups, except between calves and adults over 6 y old ( $t = -4,3118$ ; d.f. = 12  $P < 0,01$ ).

No facilities were available for objectively measuring other parameters of meat quality such as colour, tenderness, moisture content and flavour (von La Chevallerie 1972). However, giraffe meat was regularly eaten during the course of this study. It was found that there was more flavour and juiciness in the meat of young animals. The colour of giraffe meat varied from a pale pink in calves through gradually deepening shades of red to a dark maroon, almost black, in old animals. The dark meat of old males also had a characteristic strong musky odour, when fresh. The meat of adults was tougher than young animals and was less easy to chew than beef or impala. Giraffe biltong (air dried meat) was found to be tasty but considerably tougher than impala. It probably has a higher collagen content but this remains to be tested.

TABLE 25: MUSCLE FIBRE DIAMETER ( $\frac{MM}{EM}$ ) FROM *M. LONGISSIMUS DORSALIS* OF GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, JULY 1971 — JULY 1972

	n	Mean	SD.	SE.	Range
<u>Males</u>					
Foetus	1	43,6			
Calves (< 1 y old)	3	50,4	1,7	1,2	48,2-52,4
1 - 6y	4	53,2	1,0	0,6	52,0-54,4
7 - 10y	2	61,8	1,2	1,2	60,6-63,0
10 <sup>+</sup> y	3	65,5	4,4	3,1	61,6-71,6
<u>Females</u>					
Calves (< 1 y old)	3	37,6	7,6	5,4	32,0-48,4
1 - 6y	3	50,3	5,9	4,2	43,0-57,6
7 - 10y	6	50,3	3,0	1,3	46,2-54,2
10 <sup>+</sup> y	5	54,0	3,0	1,5	52,6-58,0

### MASS ESTIMATION

Buttock, foreleg and total body mass from 19 adult male and 25 adult female giraffe were used in this study. The mean mass of the paired legs of each animal was used as t-tests for differences between paired samples showed there were no significant differences between left and right forelegs or hindlegs respectively.

The regression equations for the prediction of total mass from hindleg or foreleg mass, together with the coefficient of correlation ( $r$ ) are given in Table 26. It is clear from this table and from the scatter diagrams drawn from the data (not shown) that there are differences between the relationship of leg mass to total mass in male and female giraffe. Greater accuracy can also be achieved in predicting dressed carcass mass from hindleg or foreleg mass than predicting total mass, as the correlation coefficients are greater. All correlations were found to be highly significant at the 0,001 level. Much better correlations were found in females inclusive of the reproductive tract contents than in females where the mass of the reproductive tract contents was subtracted from the total body mass (Table 26) possibly due to the compensating effect of decreased stomach fill in pregnant animals (Chapter 9).

TABLE 26: REGRESSION EQUATIONS OF HINDLEG AND FORELEG MASS ON BODY MASS, CARCASS MASS AND CORRECTED BODY MASS AND COEFFICIENTS OF CORRELATION FOR ADULT GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD, JUNE 1971 - JULY 1972

	<u>n</u>	<u>Regression equation</u>	<u>r value</u>	<u>Signi- ficance</u>
(i) Hindleg/body mass				
Adult female	25	$X = 11,803Y - 39,1$	0,905	***
Adult male	19	$X = 13,42Y - 209,3$	0,924	***
(ii) Foreleg/body mass				
Adult female	25	$X = 12,2065Y + 78,9$	0,876	***
Adult male	19	$X = 11,44Y + 103,5$	0,925	***
(iii) Hindleg/carcass mass				
Adult female	25	$X = 7,1532Y - 53,95$	0,959	***
Adult male	19	$X = 8,4996Y - 149,61$	0,932	***
(iv) Foreleg/carcass mass				
Adult female	25	$X = 7,717Y - 1,01$	0,974	***
Adult male	19	$X = 10,66Y + 44,22$	0,967	***
(v) Hindleg/body mass less reproductive tract				
Adult female	25	$X = 10,861Y + 9,38$	0,889	***
(vi) Foreleg/body mass less reproductive tract				
Adult female	25	$X = 11,1592Y + 122,17$	0,859	***

\*\*\*  $P < 0,001$

## DISCUSSION

BODY MASS

The mass of adult male giraffe *G.c. thornicrofti* given by Wilson (1968) for a specimen from the Luangwa Valley, Zambia (1269,4 kg) and by Sachs (1967) for a Masai giraffe *G.c. tippelskirchi* from the Serengeti, Tanzania (1096,6 kg) fall within the range of mass of the eastern Transvaal giraffe. The mass of an adult female given by Wilson (1968) also from the Luangwa Valley (1126,4 kg) is considerably greater than the heaviest female from the eastern Transvaal. The mass of a Masai giraffe female is reported as 797 kg, and a 10y-old female Nubian giraffe *G.c. camelopardalis* in the New York Zoological Park had a mass of 605 kg (Crandall 1964). The mean mass of 28 adult female Masai giraffe collected by Kayanja & Blankenship (1973) was  $676 \pm 12$  kg. An adult female *G.c. giraffa* collected in Rhodesia had a mass of 785 kg (V. Wilson pers. comm)\*.

The data given in Table 19 are however, not an accurate reflection of live mass due to several sources of mass loss inherent in the techniques used in this study such as blood loss and evaporation loss during dissection. As the most important carcass components such as legs and neck have a relatively small surface area to volume ratio, the evaporation loss from them is likely to be less than from the viscera which have a large surface area. Several studies which investigated evaporation loss have been reported, thus Smith & Ledger (1965) working on East African ungulates found that this loss rarely exceeded 4% of the live mass. Laws *et al.* (1967) report a blood and evaporation loss of 3% of body mass in hippopotamus *Hippopotamus amphibius* from Uganda. Skinner (1970a) states that game carcasses lose approximately 3% of live body mass on cooling. Huntley (1971a) found decreases of 1,4% and 1,8% of body mass in blesbok *Damaliscus dorcas phillipsi* and kudu respectively after cooling for at least 8 hours.

In a study on dressing percentages in the springbok, impala and sheep *Ovis aries* by van Zyl *et al.* (1969) mass losses of 6,7% to 13,2% were ascribed to the loss of blood, the mass of kidneys and kidney fat and mass lost during cooling. The amount of blood in *Bos taurus* varies from 5,8% to 8,5% of the total mass of the animal (Smith 1959) while Callow (1961) states that blood lost during slaughtering dairy cattle was 3,3% to 3,9%

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\* V.J. Wilson, National Museums of Rhodesia, Bulawayo, Rhodesia.

live mass. It seems reasonable therefore that if 4% of the mass in Table 19 is added to total body mass this will be a close estimate of live mass in eastern Transvaal giraffe.

The variation in live mass of ungulates due to differences in digestive tract fill is a factor which can vary due to the eating and drinking habits of a particular species and the time of day relative to these habits when its mass is measured (McCulloch & Talbot 1965; van Zyl 1968). Smith & Ledger (1965) discuss these variations in several East African ungulates. They found that the mass of the digestive tract as a percentage of total body mass could vary from as little as 8,2% in lesser kudu *Tragelaphus imberbis* to 29,4% in the hippopotamus. The variation found in giraffe in this study (8,5% to 13,6% in males, 8,2% to 20,7% in females - Table 21) falls within the range for the ungulates from East Africa. The range for adult female giraffe is greater than the range for adult males, however this is due to the physiological requirements of lactation (Chapter 9).

The mass of the gravid uterus is often subtracted from the total live mass of females so as to eliminate the effect of varying stages of pregnancy (Ledger 1963; Smith & Ledger 1965; Sachs 1967; Grimsdell 1973b; Sinclair 1974). Other reported live body masses either include the mass of the gravid uterus or else make no mention of its subtraction (Laws 1966; Laws *et.al* 1967; Skinner *et.al.* 1971; Robinette & Archer 1971). Some workers distinguish between mass of pregnant and non-pregnant females (Robinette 1963; Wilson 1968). In a comprehensive review of meat production from wild ungulates von La Chevallerie (1970) presents a table of live mass of different species which does not include pregnant females.

Hanks (1969a) reported that the live mass of an adult female elephant in Zambia can vary by 500 to 750 kg depending on the stage of pregnancy reached. In the present study on giraffe it was found that the uterus and its contents could have a mass of up to 169 kg and comprise up to 18,8% of the live mass of the female. The mass of adult females as given in this report is always intended as the closest approximation to the total live mass (= liveweight) of the animal in the field at the time of collection. Therefore the mass includes the reproductive tract and its contents. In all cases where the mass of a large foetus might have biased the range of data for a particular grouping e.g. age, or season, separate computations were done excluding foetal mass. No change in the significance of any data was noted.

Seasonal fluctuation in body mass is a feature of African ungulates (von La Chevallerie 1970; Skinner 1973) and usually reflects the decline in nutritive value of the veld. In the case of giraffe the data presented on lower body mass during the hot dry season (Table 20) and lower proportion of fat in the buttock (Table 23a) correspond with changes in diet (due to decreased availability of preferred species) and a decrease in the nutritive value of the species eaten (Chapter 2).

#### CARCASS COMPOSITION

It is unfortunate that the carcass cuts in giraffe did not conform to the standard cuts used by other workers (e.g. Ledger 1965; von La Chevallerie *et. al.* 1971; von La Chevallerie & van Zyl 1971; Huntley 1971a) but this was impossible under the circumstances pertaining to the field butchery of large carcasses and the unskilled labour available. However the dressing percentages in Table 22 refer to the same parts of the body as other workers and giraffe fall within the range for most African ungulates summarised by von La Chevallerie (1970). Male giraffe having a markedly higher dressing percentage than females.

As the composition of the buttock closely approximates the composition of the whole carcass (Butterfield 1962) the data in Tables 23a and 23b can be used to assess the meat yield of giraffe. The range of lean meat in females (77,0% to 78,3%) is close to that given by Ledger, Sachs & Smith (1967) for 17 wild ungulate species. The meat yield of male giraffe of 75,6% covers a range of 74,0% to 78,5% and thus it is also close to the range for other species. These figures are however lower than the 80% found in male eland *Taurotragus oryx* (von La Chevallerie *et. al.* 1971), 82% in male blesbok and 80,3% in male kudu (Huntley 1971a) and 82,3% in female and 84,0% in male springbok (von La Chevallerie & van Zyl 1971). The fat content of the giraffe carcasses (0,46% to 1,39% - Table 23) is also lower than that found in other species. Comparative data are 2,4% in male eland (von La Chevallerie *et. al.* 1971), 1,4% in male blesbok and 1,3% in male kudu (Huntley 1971a), and 1,7% and 2,5% in adult male and female springbok (von Chevallerie & van Zyl 1971). The fat content of the giraffe buttocks is also lower than that of any of the wild ungulates given by McCulloch & Talbot (1965), Ledger *et. al.* (1967) and von La Chevallerie (1972).

The giraffe carcass contains a relatively much higher proportion of bone and sinew (Table 23) than other species. Comparative data are 17,4% in male eland (von La Chevallerie *et. al.* 1971), 16,6% in male blesbok, 18,4% in male kudu

(Huntley 1971a), 14,3% and 15,2% in male and female springbok (von La Chevallerie & van Zyl 1971). This situation is partly explained by the long limbs and therefore longer bones of giraffe as compared with the other species mentioned. The neck, which in all animals has a relatively high percentage of bone, is extremely massive in giraffe and substantiates the general tendency that giraffe seem to have a higher percentage of bone in the carcasses than other game species.

Though the sample of animals for which kidney fat mass was available is small it nevertheless seems as though this fat deposit may not be as suitable an index of condition in the giraffe as in other species (von La Chevallerie & van Zyl 1971, Huntley 1971b).

The buttock, which is considered a high quality cut, comprised 28,6% of the mature male giraffe carcass and 31,4% in the mature female carcass (Table 22). These values are of the same order as those found in other species. Von La Chevallerie *et. al.* (1971) found 24,9% in male eland, Huntley (1971a) found 25,6% in male blesbok and 29,2% in male kudu, and von La Chevallerie & van Zyl (1971) found about 32,5% for adult male and female springbok respectively. The foreleg of giraffe, which is not a desirable cut, as it contains flat muscles, lots of tendon and connective tissue and a high percentage of bone, comprises a much higher proportion of the carcass than any of the other wild ungulates investigated in South Africa. Thus the 25,8% in adult male and 26% in adult female giraffe (Table 22) can be compared with 18,1% in male eland (von La Chevallerie *et. al.* 1971), 18,6% in male blesbok and 17,4% in male kudu (Huntley 1971a).

The giraffe can therefore be considered as having a fairly good carcass conformation in so far as it yields a high proportion of a good quality cut, the buttock, but the relatively low fat and high bone content of the carcass and relative late maturity (Fig. 19) are disadvantages.

#### MUSCLE FIBRE DIAMETER AND MEAT QUALITY

From the data presented in Table 25 it can be seen that muscle fibre diameter increases relatively slowly in females above 1y of age. In the case of males there is a relatively greater increase after the age of about 6y. By contrast, in springbok the major increase in muscle fibre diameter takes place early in the animals' life (von La Chevallerie & van Zyl 1971).

The data on muscle fibre diameter can be compared with those of von La Chevallerie (1972) on seven wild ungulate species. Giraffe females compare favourably with male blesbok (53,8  $\mu\text{mm}$ ), red hartebeest *Alcelaphus buselaphus* (52,6  $\mu\text{mm}$ ), impala, (56,7  $\mu\text{mm}$ ), and black wildebeest (53,9  $\mu\text{mm}$ ). The muscle fibre diameters of giraffe females are also less than eland (66,3  $\mu\text{mm}$ ) and gemsbok *Oryx gazella* (69,0  $\mu\text{mm}$ ) males, but much greater than springbok (43,2  $\mu\text{mm}$  in males and 40,2  $\mu\text{mm}$  in females - von La Chevallerie & van Zyl 1971). In comparison with these other species male giraffe do not fare as well though the mean muscle fibre diameter of giraffe over the age of 10y is nevertheless lower than that of eland and gemsbok bulls.

Muscle fibre thickness is a most important determinant of meat quality as experienced by the consumer as it determines the coarseness of grain and texture of the meat (von La Chevallerie 1972). From a consumer viewpoint giraffe meat would be most acceptable if it comes from males less than 6y old or from females. The differences in flavour and colour between young and old giraffe; and the odour of old males, must in any case favour the use of younger animals in any programme which seeks to market giraffe meat.

The observation that fibre diameter increases with body mass (viz. males against females, old against young) is in agreement with the findings of Joubert (1971) and von La Chevallerie (1972).

#### MASS ESTIMATION

Smith & Ledger (1965) found that the mass of either foreleg or hindleg as a percentage of total mass is constant and little affected by either sex, age or degree of fatness in the species they examined with the exception of adult male waterbuck *Kobus defassa* in which hindleg percentage decreased with age. In their work on elephant Laws *et. al.* (1967) found a decline in the percentage of hindleg in females and young males with increasing body size, and an increase in adult males. Ledger (1965) working with Boran steers found no change in the contribution of the hind leg to total mass with increase of age, but found a marked decrease relative to both total mass and carcass mass. In the springbok von La Chevallerie & van Zyl (1971) found that the percentage which different joints constituted of the carcass mass did not change markedly with age.

The mass of the foreleg or buttock of giraffe as a percentage of total mass was constant regardless of age or season (Tables 22 & 23). There was, however, a significant sex difference as males are much heavier than females and separate prediction equations were therefore calculated.



## CHAPTER 5

GROWTH

## INTRODUCTION

The change in an animal's dimensions over time comprises growth in its strictest sense (Simpson *et al.* 1960). Some data on these changes in both foetal and postnatal giraffe were collected and it is the primary purpose of this chapter to present and discuss some of these.

No account of the growth and development of the giraffe foetus has yet appeared in the literature, although development of the foetal ovary has been discussed (Kellas, van Lennep & Amoroso 1958, Kayanja & Blankenship 1973). Growth data for captive giraffe have been given by Gijzen (1958), Backhaus (1961) and Krumbiegel (1971). Foster & Dagg (1972), also give some data on growth rates of six wild giraffe in the Nairobi National Park, Kenya, based on measurements taken from photographs. In this chapter, in addition to discussing growth, methods of estimating foetal age in the field are given. Further methods of mass estimation based on the allometric growth of giraffe (allometry - change of proportions with increase of size - Reeve & Huxley 1945) were sought from data on body measurements.

## MATERIAL AND METHODS

A total of 21 foetuses from the eastern Transvaal were collected between July 1971 and May 1973. In addition one foetus from the Daan Viljoen Game Reserve, South West Africa and two from the Rhodesian Lowveld were available for study. The mass of each foetus was measured soon after collection. Crown/rump lengths (C/R) and vertebral column length (V/C) were measured where practical as described by van Zyl & Skinner (1970). A mean gestation period of 457 d has been calculated for giraffe from the available literature (Table 26). This does not include a recorded gestation of 394 d for a small animal which died shortly after birth (Lang 1955) and which appears to have been premature.

Linear body measurements were obtained from 53 giraffes (27 males, 26 females) soon after death. The measurements were taken from the animal in lateral recumbency and were as follows:

1. Total body length (L). The maximum length from the tip of the upper lip to the tip of the last caudal vertebra. This measurement was taken along the contours of the body.
2. Shoulder height (H). The front leg was held at right angles to the body with the hoof in a standing position i.e. its lower surface held parallel to the anterior/posterior line of the body. The maximum measurement was then taken from the sole of the hoof along the line of the leg to the highest point of the spine of the third thoracic vertebra. This is a straight measurement, not along the curves of the body and the terminal point was established by placing a board on the tip of the third thoracic vertebra, at right angles to it, and measuring to the board.
3. Chest girth (G). The maximum measurement along the contours of the body from the mesio-distal centre of the sternum to the mesio-distal centre of the third thoracic vertebra. The measurement is taken along the posterior edge of the *m. tensor fasciae antibrachii*, and was doubled to give total chest girth.

The total body mass is as used in Chapter 4. The ages are those derived from cementum layer counts or in a few cases from the prediction formulae given in Chapter 3. The relationships between body measurements and age were plotted as scatter diagrams, curves were then drawn in from the most significant polynomial regressions for the data.

As pointed out in Chapter 4 studies on meat production of an animal species requires a knowledge of the body mass of the animal at a particular age or time when collected. The estimation of body mass from dissected hindleg and foreleg mass was described. However, for many purposes such as studies on growth rates, general condition, drug dosage rates, transport and other aspects of wildlife management it is convenient to be able to assess the body mass on restrained live animals. The relationship between the various linear body measurements and body mass were examined in the giraffe and reliable criteria for mass estimation were sought.

## RESULTS

FOETAL GROWTH

The ages of the foetuses were derived from the expression of Huggett & Widdas (1951):  $W^{1/3} = a(t - t_0)$  where  $W^{1/3}$  is the cube root of foetus mass in grams;  $a$  is the specific foetal growth velocity, calculated as 0,114 using the gestation time of 457 d (Table 27) and a birth mass of 102 kg;  $t$  is the age of the foetus in days;  $t_0$  is a numerical estimate derived from the expression  $t_0 = 0,1 \times t_g$  for animals with a gestation time ( $t_g$ ) over 400 d. For the giraffe, therefore,  $t_0 = 45,7$ . The mass of 102 kg used in this study is an approximation based primarily on a 454-d-old (calculated) foetus which had a mass of 101,2 kg and which would presumably have had a mass of at least 102 kg at birth. This estimate is supported by records of a birth mass of 97,5 kg at the Hans Merensky Nature Reserve (S.M. Zaayman - *loc. cit.*), a new born calf (at least one day old) of 99,8 kg and a two-week-old calf of 106,1 kg from Timbavati (Table 28). The extra-territorial records (Table 28) were not used to calculate a mean birth mass as the 77 kg calf from Rhodesia was abandoned after birth and died the next day, it might therefore have been premature. The 84,4 kg calf from Zambia belongs to the subspecies *G.c. thornicrofti* and the 83,9 kg animal from Rhodesia was a late-term foetus. These records do, however, establish a definite minimum birth mass for wild giraffe well above those given for captives (Table 28), though it is not known why this should be so. It was also found (Table 29) that the mass of the giraffe neonate was much greater, relative to the mass of its dam, than other large African animals.

The cube root of foetus mass is plotted against age in Fig. 20 and this can be used for foetal age determination.

The crown/rump length, vertebral column length, mass and age of the foetuses are graphically illustrated in Fig. 21. Due to the large size of foetuses older than 340 d, and unavoidable *post-mortem* movement which might have changed their foetal position, reliable crown/rump measurements greater than 55 cm could not always be taken. In view of these difficulties, this measure is not regarded as reliable for age estimation of foetuses. The increase in vertebral column length followed a straight line having the equation  $X = 1,96 Y + 29,3$  (where  $X$  = age in days and  $Y$  = vertebral column length in cm). The correlation coefficient is 0,994 and it is highly significant ( $P < 0,001$ ). This expression can therefore be used with confidence for predicting foetal age. As was to be expected, the increase in mass

TABLE 27: GESTATION PERIOD IN THE GIRAFFE

Days	Locality	Source
* 455, 455, 461, 450	Cheyenne Mountain Zoo, Colorado, U.S.A.	Jarvis & Morris 1960
** 488	Regents Park, London	Robinson Gribble, Page & Jones) 1965
468	U.K.	Wilkinson & de Fremery 1940
*465, 459, 462	Columbus Zoo, U.S.A.	Savoy 1966
434	Matopos National Park, Rhodesia	Wilson 1969
$\pm$ 460	Matopos National Park, Rhodesia	J.H. Grobler ( <i>loc. cit.</i> )
$\pm$ 440	Zoological Gardens, London, U.K.	Roberts 1951
*** $\pm$ 455	Europe	Backhaus 1961
457	New York Zoological Park, U.S.A.	Crandall 1964
447	Hans Merensky Nature Reserve, R.S.A.	S.M. Zaayman ( <i>loc. cit.</i> )
Mean 457		

\* These records refer to *G.c. reticulata*

\*\* This record refers to *G.c. antiquorum*

\*\*\* Based on 35 pregnancies in captive giraffe

followed a 'J' shaped curve, with the increase being in an exponential phase during the last third of gestation.

The height of new born wild and captive giraffe are compared in Table 30.

#### POSTNATAL GROWTH

Many different mathematical functions describing growth can be found in the literature (von Bertalanffy 1938, Walford 1946, Beverton & Holt 1957, Simpson *et al.* 1960). However, it is possible to obtain a purely empirical representation of growth with age by means of a polynomial expression (Simpson *et al.* 1960). As the present data are from a

TABLE 28: BIRTH MASS OF GIRAFFE

Birth mass kg	Sex	Subspecies	Locality	Source
Captive animals				
70,0	♀	<i>G. c. antiquorum</i>	Antwerp Zoological Gardens	Gijzen 1958
63,6	♀	<i>G. c. reticulata</i>	Columbus Zoo, U.S.A.	Savoy 1966
50,4	♂	<i>G. c. reticulata</i>	Columbus Zoo, U.S.A.	Savoy 1966
48,6	♀	<i>G. c. reticulata</i>	Columbus Zoo, U.S.A.	Savoy 1966
67,2	♂	<i>G. c. reticulata</i>	Columbus Zoo, U.S.A.	Savoy 1966
48,5	-	<i>G. c. tippelskirchi</i>	New York Zoological Park (died 5 d after birth)	Crandall 1964
39,5	-	Subspecies not stated	New York Zoological Park (died 1 d after birth)	Crandall 1964
54,5	-	Mean of 16 captives	Europe	Dagg 1971
50,0	-	Captive animals		Hediger 1955
Mean 54,7				
Wild animals				
84,4	♂	<i>G. c. thornicrofti</i>	Luangwa Valley, Zambia	Wilson 1968
77,0	♀	<i>G. c. giraffa</i>	Matopos, Rhodesia	Wilson 1969
83,9	♀	<i>G. c. giraffa</i>	Southern Lowveld, Rhodesia	Records of the Bulawayo Museum
97,5	-	<i>G. c. giraffa</i>	Hans Merensky Nature Reserve, E. Transvaal	S.M. Zaayman ( <i>loc. cit.</i> )
106,1	♀	<i>G. c. giraffa</i> (calf 14 d old)	Timbavati	This study
99,8	♂	<i>G. c. giraffa</i>	Timbavati	This study
101,2	♂	<i>G. c. giraffa</i> (foetus 454 d old)	Timbavati	This study
Mean 92,8				

Giraffe  $W^{1/3} = 0,114 (t - 45,7)$

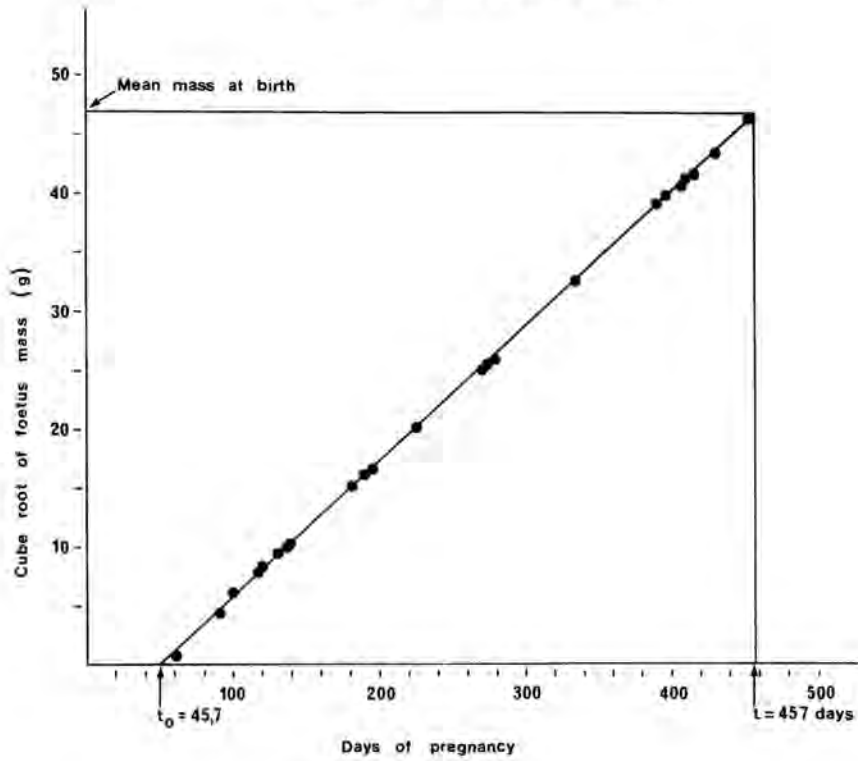


FIG. 20 — Plot of cube root of foetus mass against conception age for giraffe from southern Africa (see text for details of formula).

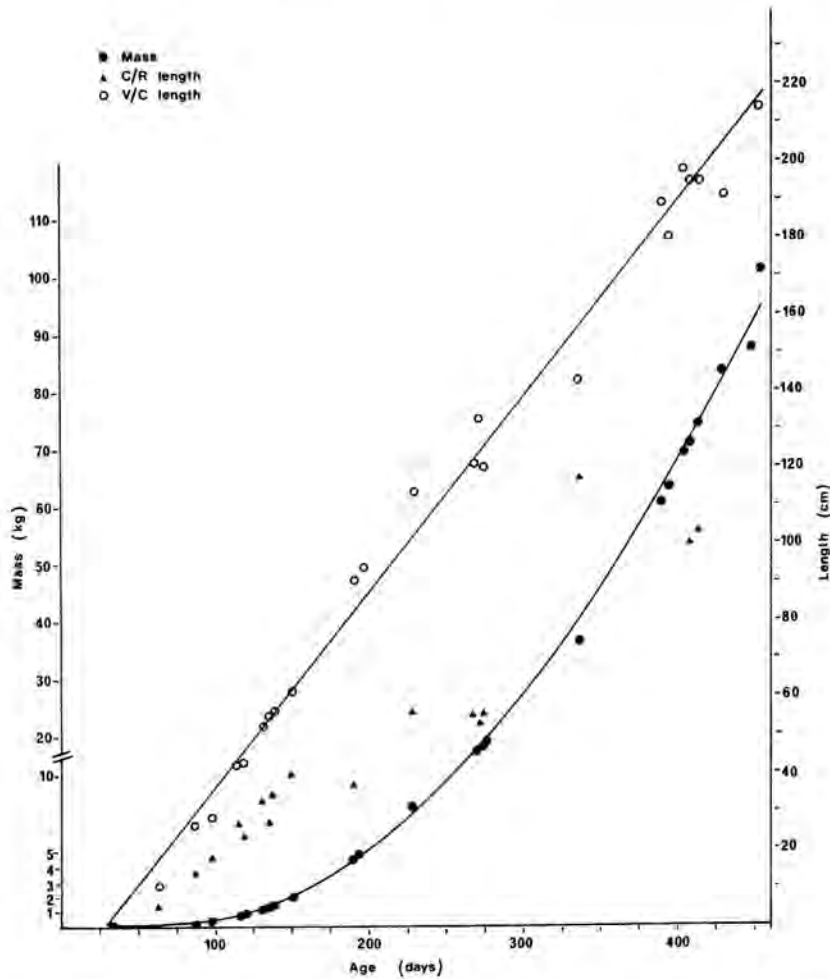


FIG. 21 — The mass, crown/rump length (C/R) and vertebral column length (V/C) at age for giraffe foetuses from southern Africa (note change of scale on mass axis).

TABLE 29: A COMPARISON OF THE MASS OF THE NEONATE AND ITS DAM IN LARGE AFRICAN MAMMALS

Species	Mass (kg) of neonate (a)	Mass (kg) of adult female (b)	a/b
Hippopotamus	50,0 <sup>1</sup>	1652,5 <sup>2</sup>	0,030
Black rhinoceros ( <i>Diceros bicornis</i> )	35,7 <sup>3</sup>	964,4 <sup>2</sup>	0,037
African elephant	120,0 <sup>4</sup>	2479,5 <sup>5</sup>	0,048
Eland antelope	29,5 <sup>6</sup>	445,4 <sup>5</sup>	0,066
Afrikander cattle ( <i>Bos indicus</i> )	31,8 <sup>7</sup>	470,2 <sup>8 &amp; 9</sup>	0,068
African buffalo	45,0 <sup>10</sup>	486,0 <sup>10</sup>	0,092
Giraffe	102 <sup>11</sup>	788 <sup>11</sup>	0,129

Sources: <sup>1</sup> Laws & Clough 1966, <sup>2</sup> von La Chevallerie 1970,  
<sup>3</sup> Dittrich 1967, <sup>4</sup> Hanks 1969a, <sup>5</sup> Wilson 1968,  
<sup>6</sup> Skinner 1967<sup>a</sup>, <sup>7</sup> Skinner & Joubert 1963,  
<sup>8</sup> Renzhorn & Meintjes 1972, <sup>9</sup> Steenkamp & van der Horst 1974,  
<sup>10</sup> Sinclair 1974, <sup>11</sup> This study.

small sample, biased in favour of animals 8 to 10y old, the computation of growth functions was not attempted. Instead, polynomial regression coefficients were used to fit curves to the scatter diagrams.

#### Growth in mass

Growth in total body mass with age was plotted (Fig. 22) and it appears that a typical growth curve is followed. It is clear from these data that growth curves for males and females differ. Polynomial regressions to the fourth degree were computed separately for both sexes and an analysis of variance made for each degree. Significant improvement in terms of the sum of squares was found for the second degree only for both males and females. The curves in Fig. 22 have been plotted from these regressions. Because there are few old animals in the samples, and these tend to be lighter than others the points for these lie below the line. Even though the inflexion points on the curves are not clearly seen because of the small sample and the method used for drawing the curves,

TABLE 30: HEIGHT OF GIRAFFE NEONATES

Height (cm)	Sex	Subspecies	Locality	Source
Captive giraffe				
178	♂	<i>G. c. tippelskirchi</i>	New York Zoo. Park	Crandall 1964
170, 173, 175	♂	not stated	New York Zoo. Park	Crandall 1964
168	♀	not stated	New York Zoo. Park	Crandall 1964
185, 182	♂	<i>G. c. antiquorum</i>	Antwerp Zoo. Gardens	Gijzen 1958
168	♀	<i>G. c. antiquorum</i>	Antwerp Zoo. Gardens	Gijzen 1958
Wild giraffe				
194, 212 *	♂	<i>G. c. giraffa</i>	Timbavati	This study
213 *	♀	<i>G. c. giraffa</i>	Timbavati	This study
ca. 183	-	<i>G. c. thornicrofti</i>	Luangwa Valley, Zambia	Berry 1973
ca. 183	-	<i>G. c. angolensis</i>	South West Africa	J.M. Hofmeyr, (loc. cit.)

\* Measurements taken on dead animals laid on their sides, and this may account for the greater height than measurements taken on standing animals.

it can be concluded that the asymptotic mass is reached at an earlier age in females (about 11y) than in males (about 12y).

The degree of scatter of the points (Fig. 22) is partly explained by individual biological variation in addition to seasonal effects. Also in the case of females some of the observed scatter may be ascribed to pregnancy.

#### Growth in height, length and chest girth

The data on shoulder height, total body length and chest girth were plotted against age (Figs. 23, 24, 25). A typical growth curve appeared to fit the points adequately. Polynomial regressions to the fourth degree were run for the data, separately for both sexes, and an analysis of variance was carried out. Significant improvements in F-values were found at the



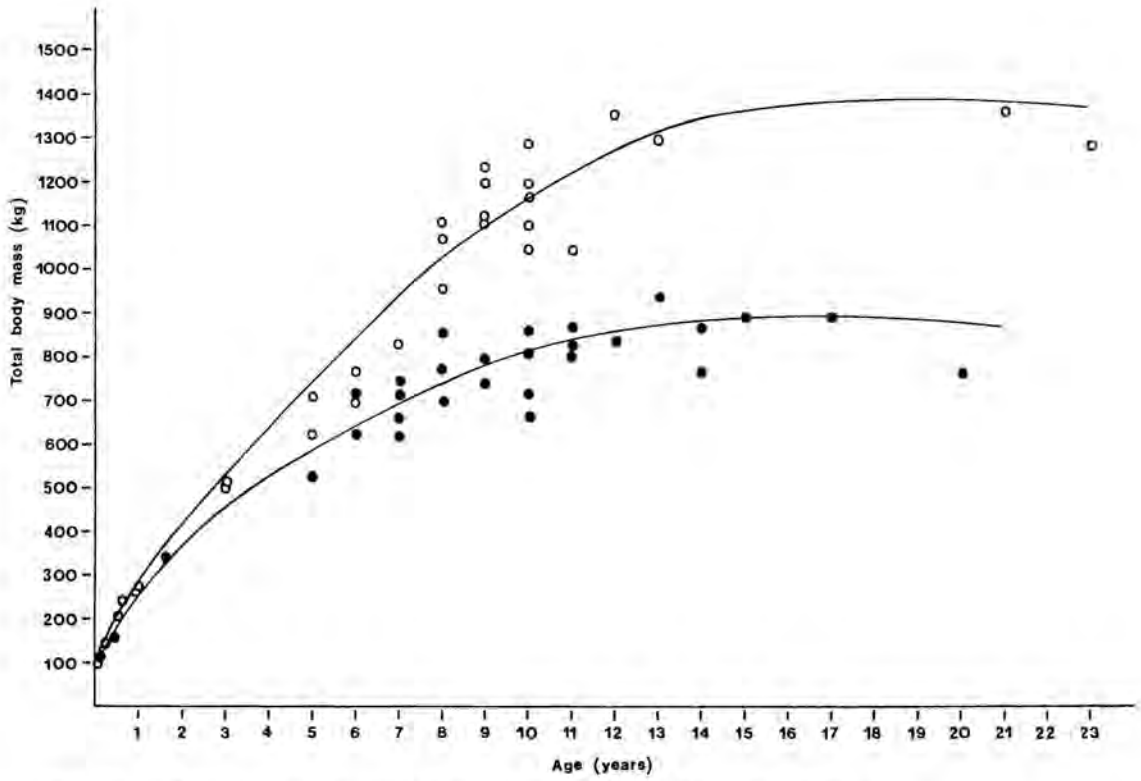


FIG. 22 — Total body mass at age for Transvaal Lowveld giraffe. Males (o), females (●).

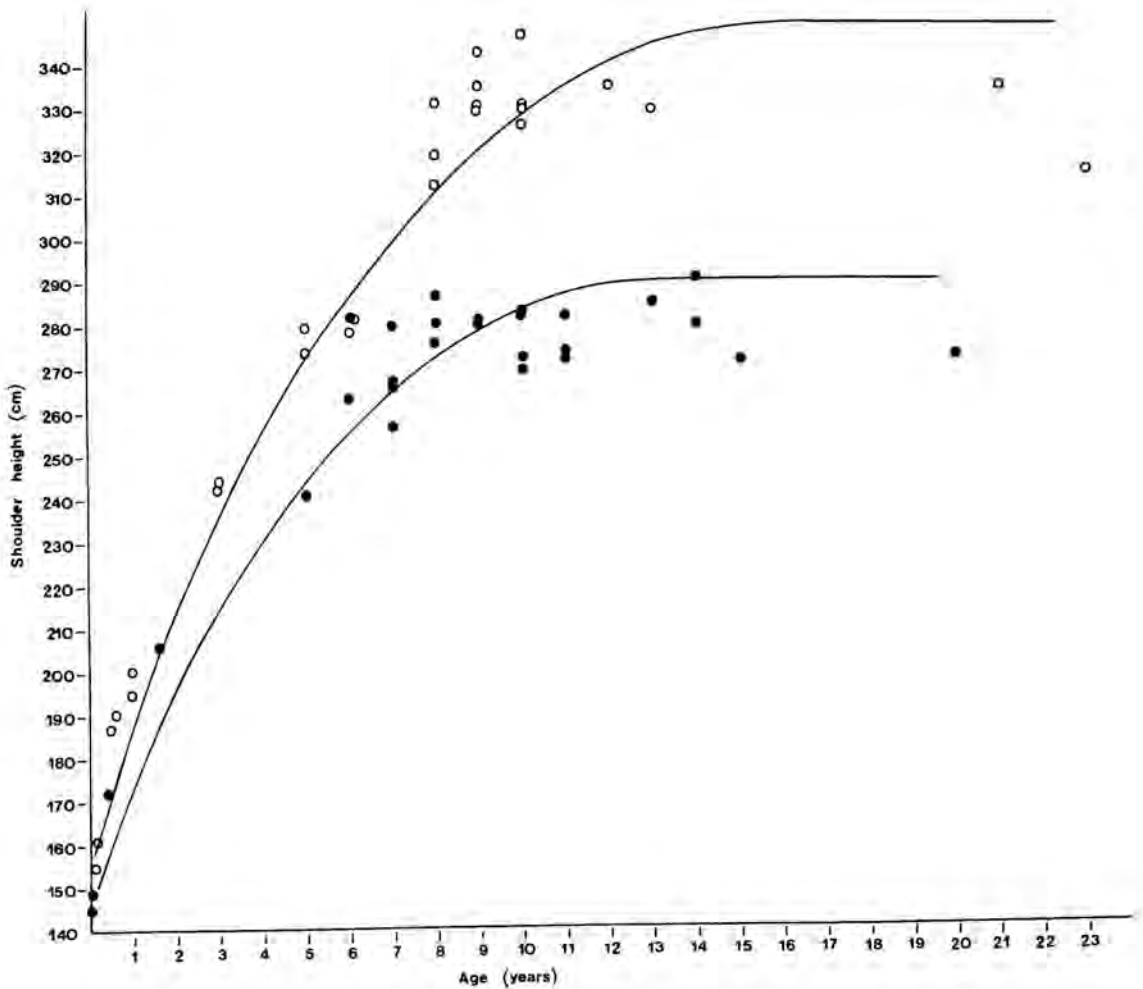


FIG. 23 — Shoulder height at age for Transvaal Lowveld giraffe. Males (o), females (●).

second degree level for shoulder height in males, and at the third degree for all the other relationships examined. From these coefficients curves were drawn which give a reasonable fit to the data. Due to the small number of smaller old animals in the sample, the plateau levels have probably been affected and the inflexion points of the curves are also not clearly defined.

The two measurements of total size i.e. shoulder height and body length were found to show markedly less scatter than chest girth. The F-values for the third degree polynomials were also lower and less significant ( $P < 0,05$ ) for chest girth than for the other measurements ( $P < 0,001 - P < 0,025$ ). This is presumably due to the decrease in subdermal fat deposits in the dry season and probably also in lactating females.

Sexual dimorphism is again seen in the age at which asymptotic height, (12y in males, 11y in females) and girth (i.e. about 10y for females, 12y for males) are reached. The approximate age at which asymptotic length is reached (11y) is the same for both sexes.

#### ALLOMETRIC GROWTH

From the measurements obtained and the total body mass, scatter diagrams were drawn. The relationships revealed that, as in the case of the black rhinoceros (Freeman & King 1969), there was good correlation between mass and the linear measurements. The regression equations and correlation coefficients were first calculated for males and females separately for several of these relationships. The regression coefficients for the sexes were then tested (assuming a 5% rejection criterion) and it was found that the regressions were all significantly different (t - and P - values were: girth  $t = 8,6136$ ;  $P < 0,001$ ; height  $t = 2,3368$ ;  $P < 0,05$ ; length  $t = 7,7869$ ;  $P < 0,001$ ). The data for the males and females were nevertheless pooled to improve the sample size and further regression coefficients calculated. These regression coefficients together with correlation coefficients are given in Table 31. All the regressions had very high correlation coefficients. This indicates that good predictions of body mass could be made from these linear measurements.

As Freeman & King (1969) pointed out it could be expected that there would be a good relationship between mass and volume in animals. In their studies on black rhinoceros and in other studies (McCulloch & Talbot 1965) the volume of the animal has been expressed as length  $\times$  girth<sup>2</sup>. This relationship was examined for the giraffe data and very high correlation

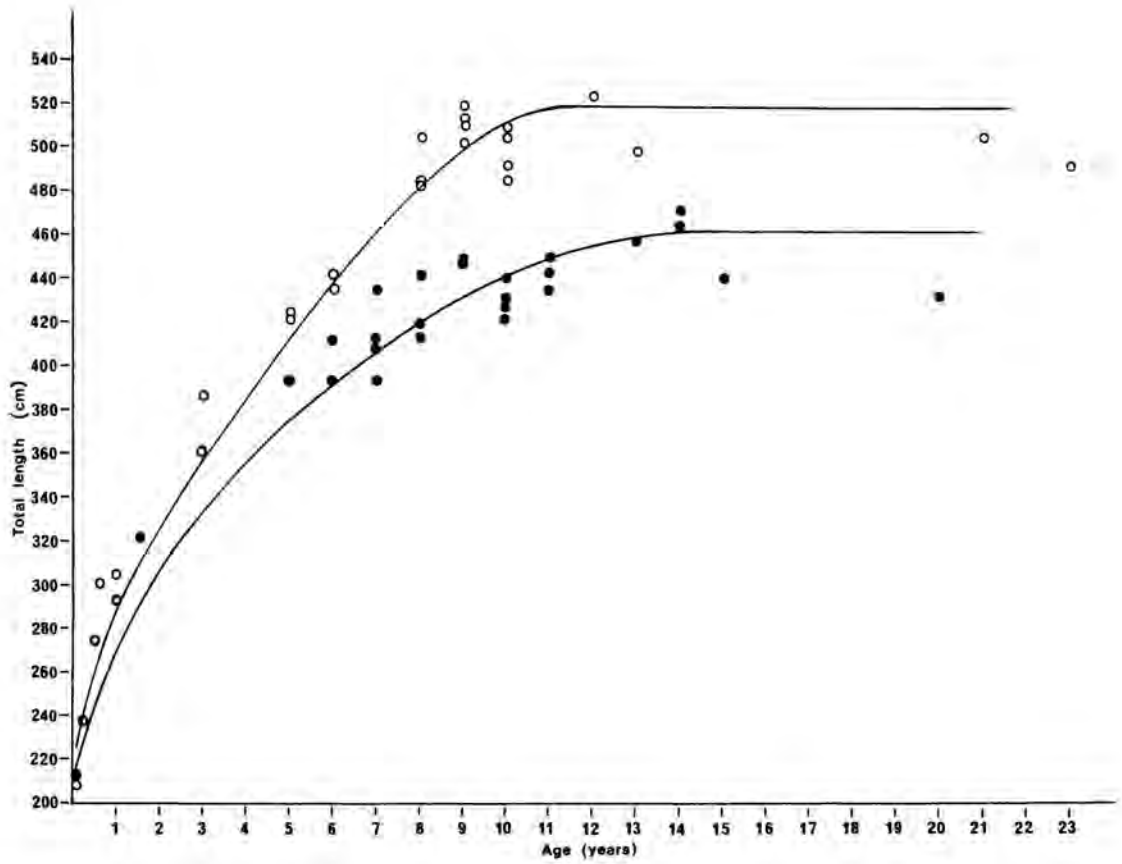


FIG. 24 — Total length at age for Transvaal Lowveld giraffe. Males (o), females (●).

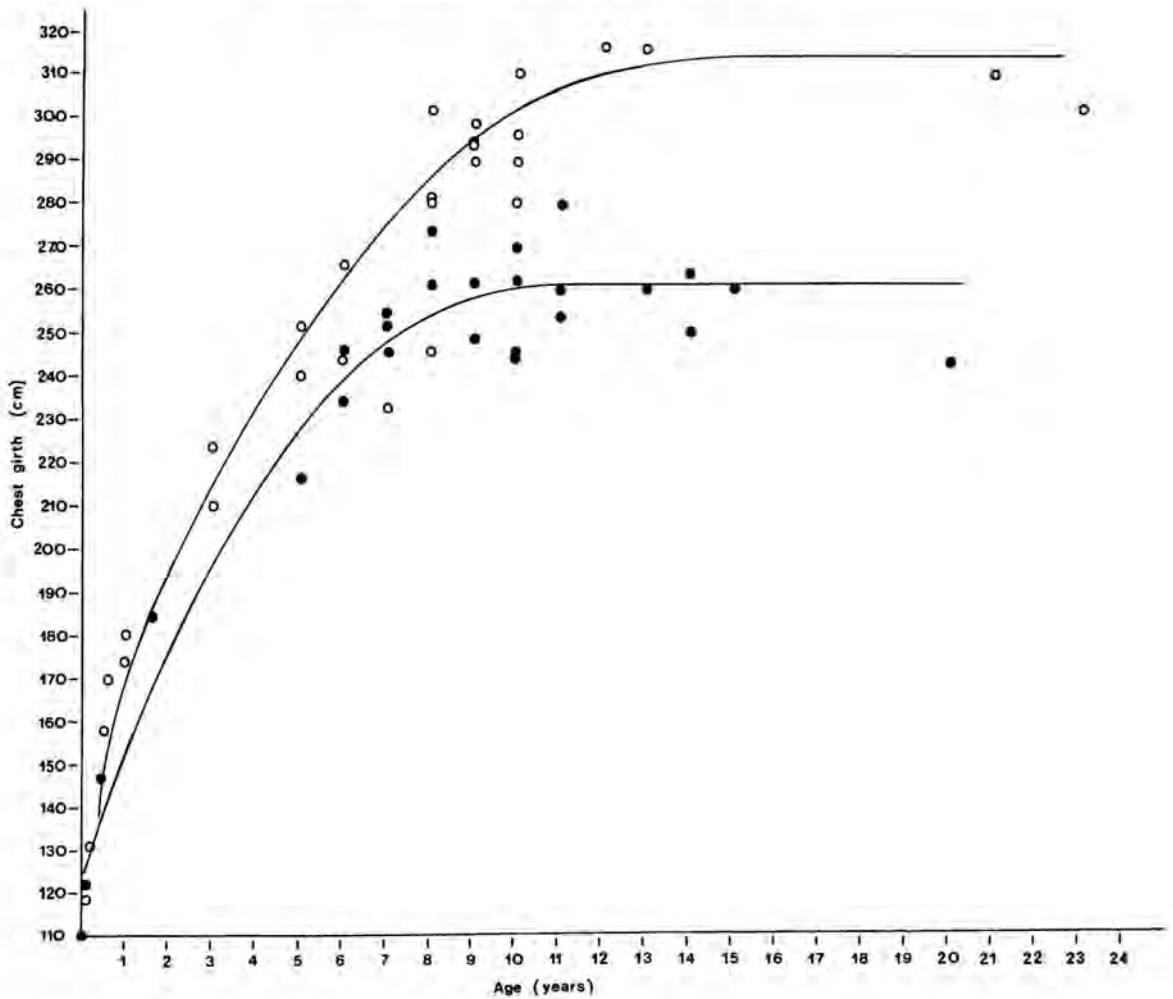


FIG. 25 — Chest girth at age for Transvaal Lowveld giraffe. Males (o), females (●).

coefficients were found (0,993 for males, 0,977 for females 0,990 for both sexes combined; Table 31). This relationship could therefore be used to give a much better prediction of mass than any of the measurements used alone.

This relationship is illustrated in Fig. 26.

TABLE 31: RELATIONS BETWEEN TOTAL BODY MASS (M), GIRTH IN CM (G), SHOULDER HEIGHT IN CM (H) AND TOTAL LENGTH IN CM (L) IN GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD

n	Sex	Relationship	r
27	male	$M = 6,989G - 904$	0,975
26	female	$M = 5,500G - 615$	0,965
53	both	$M = 6,748G - 881$	0,963
27	male	$M = 6,752H - 1051$	0,973
26	female	$M = 5,659H - 783$	0,932
53	both	$M = 6,604H - 1022$	0,965
27	male	$M = 4,223L - 964$	0,966
26	female	$M = 3,251L - 635$	0,938
53	both	$M = 4,061L - 934$	0,952
27	*male	$M = 26,117 LG^2 + 33,945$	0,993
26	*female	$M = 25,400 LG^2 + 66,109$	0,977
53	*both	$M = 25,902 LG^2 + 45,758$	0,990
27	male	$\text{Log } M = 2,676 \text{ Log } G - 3,543$	0,996
26	female	$\text{Log } M = 2,627 \text{ Log } G - 3,426$	0,989
53	both	$\text{Log } M = 2,664 \text{ Log } G - 3,514$	0,994
27	male	$\text{Log } M = 1,260 \text{ Log } H - 0,220$	0,951
26	female	$\text{Log } M = 3,104 \text{ Log } H - 4,686$	0,980
53	both	$\text{Log } M = 2,992 \text{ Log } H - 4,436$	0,986
27	male	$\text{Log } M = 2,573 \text{ Log } L - 3,882$	0,950
26	female	$\text{Log } M = 2,728 \text{ Log } L - 4,306$	0,979
53	both	$\text{Log } M = 2,778 \text{ Log } L - 4,439$	0,991

All r values are highly significant,  $P < 0,001$

\*  $\frac{\text{Girth in } m^3}{\text{Length} \times \text{girth}^2 \text{ in } m^3}$

Logarithmic and semi-logarithmic transformations gave much better correlation coefficients. The regressions of log body mass on log girth, log shoulder height and log length are also given in Table 32. The relations all give

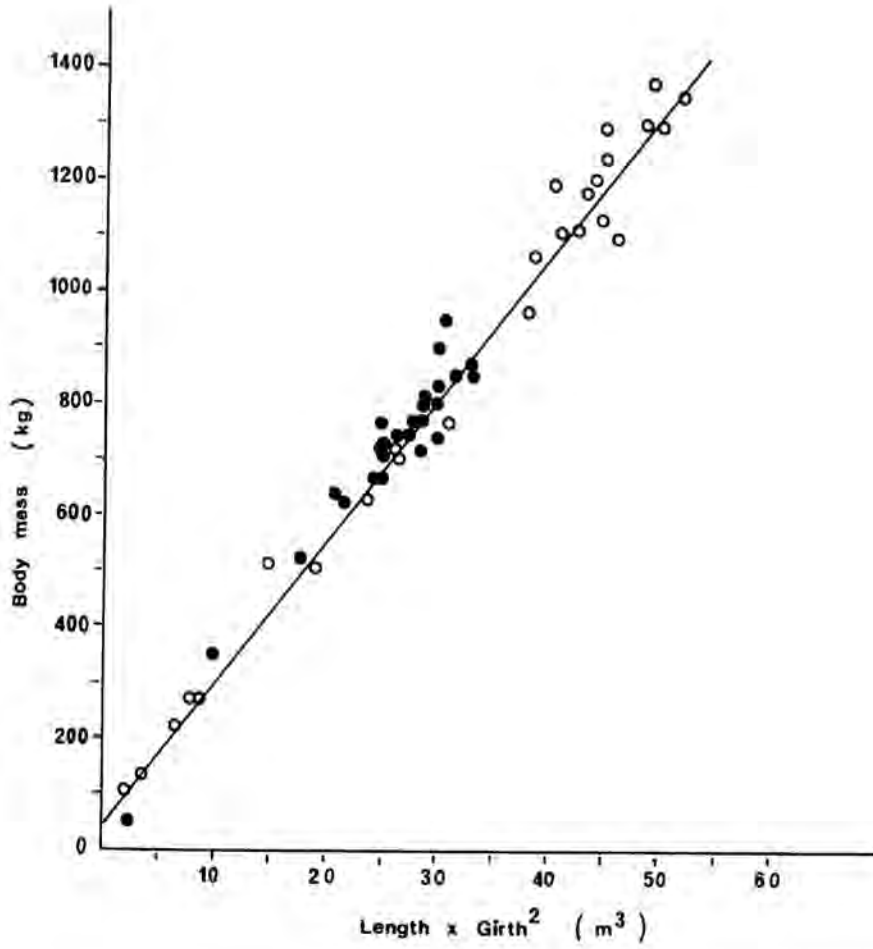


FIG. 26 — Regression of body mass on length x girth<sup>2</sup> for Transvaal Lowveld giraffe (see text for details). Males (○), females (●).

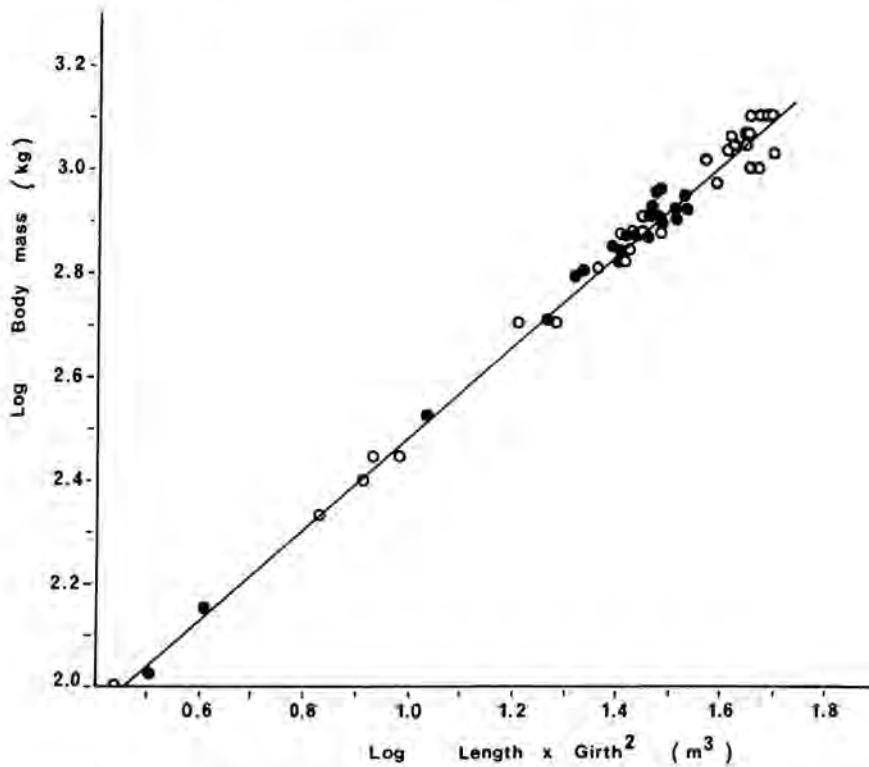


FIG. 27 — Regression of log body mass on log length x girth<sup>2</sup> for Transvaal Lowveld giraffe (see text for details). Males (○), females (●).

extremely good predictions of body mass from linear measurements, the least good still leaving less than 5% of variation in mass unaccounted for. There is little difference in predictive efficiency between the different relations.

TABLE 32: RELATIONS BETWEEN LOGARITHMIC FUNCTIONS OF TOTAL BODY MASS (M), GIRTH IN CM (G) AND LENGTH (L) IN GIRAFFE FROM THE EASTERN TRANSVAAL LOWVELD

n	Sex	Relationship	r
27	male	$\text{Log } M = 1,371(\text{Log } L + \text{Log } G) - 4,025$	0,997
26	female	$\text{Log } M = 1,363(\text{Log } L + \text{Log } G) - 3,984$	0,994
53	both	$\text{Log } M = 1,369(\text{Log } L + \text{Log } G) - 4,015$	0,996
27	male	$\text{Log } M = 0,907(\text{Log } LG^2) + 1,578$	0,997
26	female	$\text{Log } M = 0,901(\text{Log } LG^2) + 1,588$	0,994
53	both	$\text{Log } M = 0,906(\text{Log } LG^2) + 1,580$	0,996

All r values are highly significant,  $P < 0,001$

A maximum correlation coefficient of 0,996 was found (both sexes together) for combinations of log length plus log girth, and for log length x girth<sup>2</sup> (Table 32). The correlation coefficients for these relationships for males only were both 0,997, a very good correlation indeed. The relationship of log body mass and log length x girth<sup>2</sup> is illustrated graphically in Fig. 27.

## DISCUSSION

### FOETAL GROWTH

It has been shown above (Fig. 21) that growth in length and mass of giraffe foetuses follow the expected straight line and 'J'-shaped curve respectively. These results are in agreement with those for other uniparous mammals (Everitt 1968).

### NEONATAL MASS AND HEIGHT

Records for birth mass vary considerably (Table 28). For example Dagg (1971) gives 54,5 kg for animals born in captivity but it is not known how each animal's mass was measured and sometimes the mass was estimated. (Dagg pers. comm.)\*. Calves born in captivity are apparently lighter than calves born

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in the wild (Table 28). The reports of Gijzen (1958) and Savoy (1966) would seem to confirm this, but different subspecies were involved. That of Gijzen (1958) was *G.c. antiquorum*, those of Savoy (1966) were all *G.c. reticulata*. Of the records from wild populations, that of Wilson (1968) was *G.c. thornicrofti* and Wilson (1969) was *G. c. giraffa* while those from the Transvaal are all *G.c. giraffa*. There are not enough data to determine the influence of sex on birth mass. Though the results presented above are few it is important to note that the range and maximum birth mass is considerably greater than previously believed. Kayanja & Blankenship (1973) have stated that a foetus of 52 kg was 'shortly before birth', while Field & Blankenship (1973) used a birth mass of 54,5 kg whereas from our data these foetuses would have been < 30 d old. Though it has been shown (Chapter 2) that adult females in Kayanja & Blankenship's (1973) sample were lighter than those from Timbavati and it might therefore be expected that foetuses in their sample are also lighter; the regressions of C/R length against mass are not significantly different for the two populations up until C/R measurements become unreliable ( $t = 0,556$ ;  $d.f. = 16$ ,  $P < 0,5$ ).

Though the data are scanty it seems that captive giraffe are shorter at birth than wild giraffe (Table 30). The shoulder height (150 cm) of a neonate from Rhodesia (Wilson 1969) agrees well with three measurements from the Transvaal Lowveld of 149 cm for a female and 139 cm and 155 cm respectively for two males.

#### POSTNATAL GROWTH

The growth curves might have been considerably different if a larger and better distributed sample was available. It is therefore difficult to attach absolute confidence to the inflexion points as interpreted from these curves (Figs. 22 to 25). The data are also too few to have fitted the curves by eye with confidence, though it is likely that if the latter method were used the inflexion points in most cases would be situated at earlier ages. In this respect it should be borne in mind that according to the literature summarized by Dagg (1971) giraffe approach their full size at 4 y but may continue to grow until 7 y or 8 y of age. These ages are considered too low but Crandall's (1964) observation that a captive male giraffe did not increase in stature after 11 y is close to the results of the present study. In studies on buffalo, Sinclair (1974) also found a decline in mass during old age.

The relationships between mass and linear measurements given in Tables 31 & 32 are much closer than those reported by McCulloch & Talbot (1965) for several species. The relationships for giraffe are, however, not as good as those reported for female elephant (Krumrey & Buss 1968). The log relations are usually close to or slightly better than the  $r^2$  values given for the black rhinoceros by Freeman & King (1969) and the  $r$  values given for elephant by Hanks (1972). All the equations given in the tables can be used for mass estimation purposes with considerable confidence, even if only a single measurement is available. In practice it would probably be best to calculate more than one estimate of mass and use the mean.

As these data were all derived from the same population of giraffe it is likely that the results will be most accurate when used locally. However, in the absence of other data the methods can probably be used with confidence for any other population of giraffe in southern Africa including Zambia. (No statistically significant differences have been found in cranial measurements of giraffe from South Africa, South West Africa, Botswana, Rhodesia, Zambia and Angola - Hall-Martin unpublished).

The body shape of the different species for which the equation relating mass to length x girth<sup>2</sup> has been applied appears to have little influence on the correlation coefficient. Thus the correlation coefficients derived from a compact bodied animal like the black rhinoceros (Freeman & King 1969) and a long-necked, long-limbed animal like the giraffe are similar.

To what extent the relationships have been influenced by fluctuating mass due to seasonal effects, pregnancy, different stomach fill etc. has not been investigated. Although McCulloch & Talbot (1965) have shown that in general the natural variations between individuals are as important as differences in fill, they also showed that the body measurements provided estimates of mass that are independent of variation in fill, or body condition.

Freeman & King (1969) found no differences between the sexes in linear measurements in black rhinoceros. While McCulloch & Talbot (1965) found that for species they worked on subdivision of the data into classes did not result in any marked increase in accuracy of the prediction derived. In the case of the giraffe it is evident (Fig. 26 & 27) that



subdivision into sexes would only subdivide the range of the data due to the different ranges of mass in adult males and females respectively. The pooling of the data not only effectively increases the range of mass variation but also doubles the sample size. The higher correlation coefficients for the pooled data also indicate that the overall relation is a more precise means of providing an estimate of mass than are the individual sex relationships. The advantages of having a single prediction equation of high precision applicable to all giraffe, regardless of age or sex and time of collection, are obvious.

## REPRODUCTIVE BIOLOGY OF MALE GIRAFFE

### INTRODUCTION

There are few references to the reproductive biology of male giraffe in the literature though several papers mention breeding seasons and related topics (Foster & Dagg 1972, Field & Blankenship 1973). The testicular artery and characteristics of epididymal spermatozoa of giraffe have been described by Glover (1973) and the male tract has been briefly described by Velhanker, Hukerie, Deshpande & Sane (1973). Nothing has yet been reported on the development of the reproductive tract, its endocrinology, nor on seasonal changes.

### MATERIAL AND METHODS

Material for this study (including four foetuses) was collected from 31 male giraffe, all from the Timbavati or its environs. Reproductive tracts were dissected out of freshly killed animals and stored in 10% formalin. The mass of the paired testes, epididymes and bulbo-urethrae respectively was determined in the laboratory. Slices of testes taken for histology were fixed in Bouin's fluid or Zenker-formol solution. The Bouin-fixed material was dehydrated in alcohol, cleared in xylol and embedded in paraffin wax; sections 6  $\mu\text{m}$  thick were stained with Delafield's haematoxylin using either chromatrope 2R or aqueous eosin as counterstain. The Zenker-formol fixed tissue was postchromed in potassium dichromate, washed, dehydrated, cleared, embedded in paraffin wax, sectioned and treated with Sudan black as described by Threadgold (1957) in his method I. Seminiferous tubule diameters were the mean of 25 tubules measured in cross-section with a Zeiss micrometer eyepiece.

The ages of the postnatal giraffe were determined as described in Chapter 3, while foetal giraffe ages were determined as described in Chapter 5. Parameters of relative development measured in foetal and early postnatal gonads were the concentration of interstitial cell nuclei and percentage intertubular area. To measure these features a microscope ocular grid was used at 400X magnification. Counts were made of the number of interstitial cell nuclei in 25 squares of the grid for each specimen examined and the results expressed as the concentration of nuclei per unit area (one square). To secure a further quantitative estimate of the cellular composition of the testes samples, but not as detailed as that of Chalkley (1943), the intersections of the cross hairs on the grid

were used as sample points. The cellular composition at each of 1000 points per testis were recorded. Ten fields were sampled for each testis and 100 points per field were taken on a stratified random basis. The results were expressed as percentage intertubular area (i.e. percentage of points lying within seminiferous tubules).

### HORMONE ASSAY

#### Hormone extraction

Steroid hormones were extracted from formalin-fixed testes as the specimens all came from an endemic foot-and-mouth disease zone and neither blood plasma nor frozen tissue could therefore be removed from the area. The methods used were those developed by Short & Mann (1966) and Skinner (1967b) for fresh material. A sample of 25 g of testicular tissue from each animal was homogenised in 100 ml 2,5% sodium hydroxide in a Buhler laboratory homogeniser and an internal isotope standard of  $\Delta^1$ -methyltestosterone (2 ml) added. The homogenate was then extracted with 300 ml diethyl ether and then twice with 100 ml diethyl ether. As emulsions formed readily because of the low ether/water ratio it was necessary to separate the extracts by centrifugation for up to 20 minutes at 1800 rpm (higher ratios resulted in greater concentrations of interfering endogenous material). The pooled ether extracts were washed to neutrality with distilled water and evaporated to dryness. The residue was then redissolved in 3 x 10 ml 40° - 60°C B.P. petroleum ether and extracted with 6 x 10 ml 70% aqueous methanol. The pooled methanolic extracts (2 - 50 µg) were dissolved in 10 µl of chloroform. Samples (4 µl) were purified by liquid chromatography (L.C.) as this procedure is more quantitative (98% recovery) than purification by thin layer chromatography (<90% recovery).

#### Liquid chromatography

A Nester Faust 1200 apparatus was used, the column (3m x 3mm) being packed with a Zipax support coated with 1%  $\beta\beta$  "-Oxydipropionitrile (Dicyanoethylether) and eluted with 5% Di-isopropyl-ether in iso-octane (2 ml/min 1000 psi). Detection was by differential UV absorption at 254 nm. The hormones epitestosterone (e-T) and androstenedione were not separated from testosterone (T) by L.C., therefore quantitative determination of T could not be done on L.C. The marker  $\Delta^1$ -methyltestosterone ( $\Delta^1$ -Me-T) was, however, separated from the other hormones on L.C. The hormone  $\Delta^1$ -testosterone was well separated on L.C. and could be easily estimated when present.

Some extracts were derivatised with 2,4 -Dinitrophenyl hydrazine (Vogel 1961). These derivatised extracts showed the presence of 2,4 DNP hydrazones of the keto-steroids on L.C. and collected fractions gave mass spectra identical with mass spectra of authentic derivatives. Mass spectra on the free hormones themselves collected from L.C. could not be obtained because of the paucity of material and high contamination.

#### Gas chromatography

The apparatus used was a Hewlett-Packard Model 5750 gas-chromatograph equipped with a F.I. Detector. The hydroxy-steroids testosterone, epitestosterone and  $\Delta^1$ -methyltestosterone (internal standard) were chromatographed both as underivatised compounds and as the TMS-ethers, while androstenedione was chromatographed as the underivatised compound only. Details of the preparation of the TMS-ethers are given by Pretorius, Hopkins & van Dyk (1975). Relative retention times ( $R_T$ 's) and gas chromatography (G.C.) conditions are given in Table 33. HMDS silanised 300 cm coiled glass columns, 2 mm in diameter (i.d.) were used.

Calibration curves (Beckett & Rowland 1965a, 1965b) for the authentic compounds T, e-T and androstenedione using 10  $\mu\text{g}$   $\Delta^1$ -Me-T as internal standard were constructed and found to be linear in the region 1-300  $\mu\text{g}$  when 1  $\mu\text{l}$  aliquots of the final extracts were injected. Reference samples were obtained from Fluka AG, Chemische Fabrik. Slopes of the calibration curves were identical to the slopes obtained when 4  $\mu\text{l}$  aliquots of these final extracts were first injected on the L.C.-apparatus, the corresponding fraction (containing  $\Delta^1$ -Me-T, T, e-T, and androstenedione) in each case collected, derivatised and 1  $\mu\text{l}$  aliquots of these fractions injected on G.C. Therefore, no preferential loss occurred during G.C. The standard deviation was  $\pm 3,8\%$  for the TMS-ethers of testosterone,  $\pm 4,05\%$  for e-T and  $\pm 4,7\%$  for androstenedione. No interference from endogenous constituents at the  $R_T$ 's of T and  $\Delta^1$ -M-T and their TMS-ethers were observed on G.C. provided the biological samples were first purified on L.C.

#### Identification of hormones

Presence of the compounds in the biological samples were considered positive when the corresponding fractions collected on L.C. conformed to the following criteria:

1. The relative retention times on G.C. of both the underivatised and

TABLE 33: RELATIVE RETENTION TIMES OF STEROIDS AND THEIR TMS-ETHERS AND G.C. CONDITIONS

Steroid	GC-column			
	I		II	
	Underivatised	TMS-ether	Underivatised	TMS-ether
T	9,4	6,8	4,4	4,7
e-T	8,8	5,9	4,2	4,4
$\Delta^1$ -Me-T	16,5	11,0	5,2	6,4
Androstenedione	20,0	-	4,0	-
$\Delta^1$ -T	11,4	9,0	4,8	5,2

GC-conditions:

Column	Packing	Inlet temp.	Oven temp.	Detector temp.
I	1% SP2401 on Gaschrom Q 100-120	280-300°C	250°C	300°C
II	1% Ov101 on Gaschrom Q 100-120	280-300°C	200°C	300°C

 Gas flow rates: N<sub>2</sub> carrier 15 ml/min, O<sub>2</sub> 200 ml/min, H<sub>2</sub> 20 ml/min.

derivatised fractions were identical to those of the authentic compound on columns I and II (Table 33).

- Molecular ion peaks and fragmentation patterns on a Varian CH7 mass spectrometer of both the underivatised and the 2,4 DNP-hydrazone derivative were identical to those obtained for the authentic compound.

#### Quantification of hormones

T was quantified on G.C. as the TMS-ether on column I and androstenedione as the underivatised compound on column I (Table 33). The TMS-ether of  $\Delta^1$ -Me-T was used as internal standard.  $\Delta^1$ -T was quantified as such on L.C., using  $\Delta^1$ -Me-T as internal standard while e-T was not quantified.

## RESULTS AND DISCUSSION

### ANATOMY

Except for size differences most probably due to individual variability the description of the main features of the male giraffe reproductive tract as given here is similar to that provided by Velhanker *et. al.* (1973).

#### Accessory glands

The testes of the giraffe, which are descended at birth, are contained in a pendulous scrotum which is situated inguinally as in many other mammals. The testis is ovoid being about 10 cm to 14 cm long and 6 cm to 8 cm wide (excluding epididymis) in the middle in mature animals. As in the bovine bull they hang with their long axis vertical. The epididymis has no special features and consists of *caput*, *corpus* and *cauda* as in other mammals. The *vas deferens* is about 60 cm long between the *caput* and the ampulla, the latter organ being up to 10 cm long. Conspicuous paired nonlobulated seminal vesicles are attached to the urethra. The bulbo-urethral glands are ovoid and are situated in a fibrous capsule on the pelvic part of the urethra well covered by bulbo-cavernosus muscle. The arrangement of these organs is illustrated in Plate 3, Fig. 1.

The prostate gland of the giraffe like that of the bovine bull and other ruminants (Trautmann & Fiebiger 1957) consists mostly of a *pars disseminata* which forms a glandular layer in the wall of the pelvic urethra. The lobular *pars disseminata* is wider dorsally than ventrally and the striated urethral muscle is also thicker ventrally.

#### Penis

The penis is of the fibro-elastic type and in mature males it is up to 77 cm long (*post mortem*) and has a marked sigmoid flexure (Plate 3, Fig. 2). The penis retractor muscles are attached to the distal part of the flexure and are about 13 cm long. The *glans penis* is rounded in outline and flattened laterally, it has attached to it a *processus urethrae* (Plate 3, Fig. 2) which is about 7,8 cm long in mature animals and is grooved.

### HISTOLOGY

The major features of the cells comprising the seminiferous epithelium and interstitium were found to correspond closely to published descriptions of these cell types in other mammals (Johnson & Buss 1967a, Onstad 1967,



PLATE 3

Fig. 1. Part of the reproductive tract of a sexually mature male giraffe showing a ventral view of the urethra, right side organs labelled: 1 - testis, 2 - cauda epididymis, 3 - vas deferens, 4 - ampulla, 5 - seminal vesicle, 6 - bulbo-urethral gland.

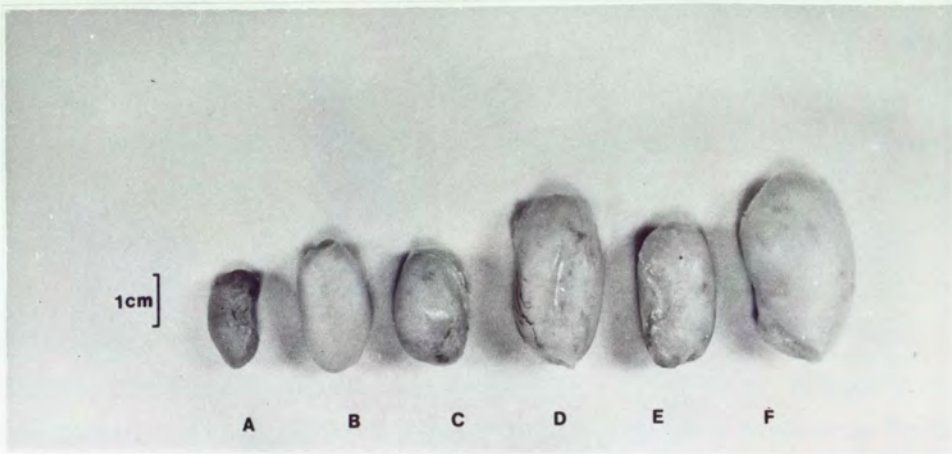
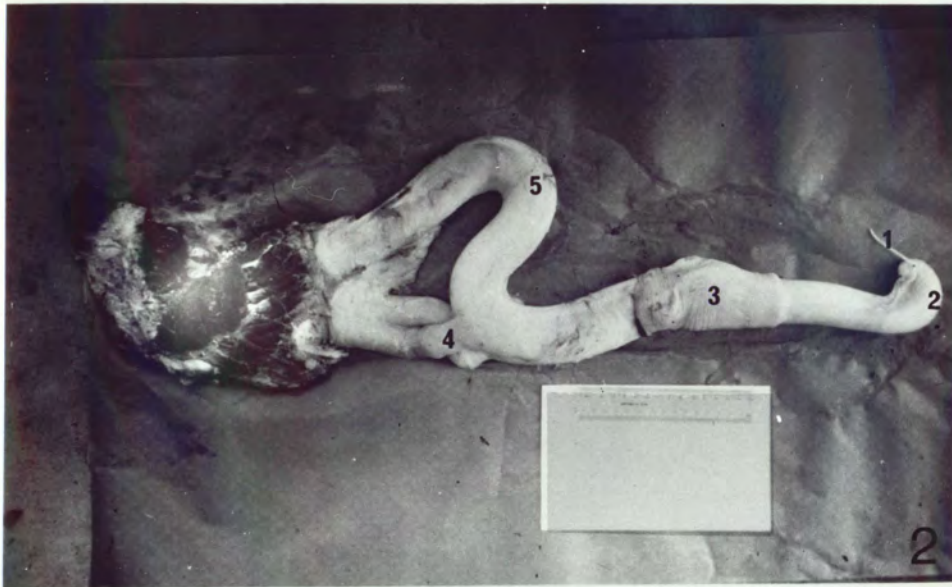
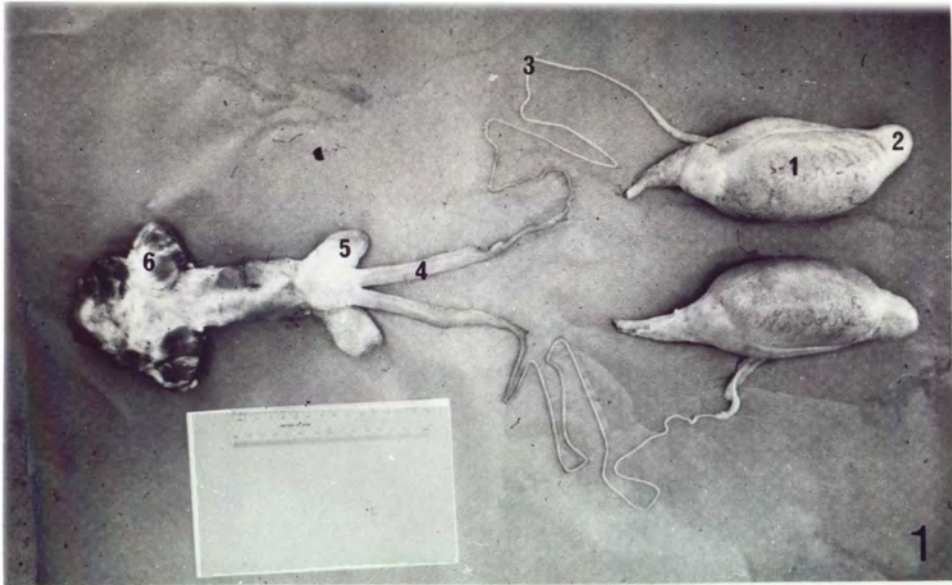
Scale in cm.

Fig. 2. Penis of a sexually mature giraffe viewed from right side. 1 - processus urethrae, 2 - glans penis, 3 - prepuce, 4 - retractor penis muscle, 5 - sigmoid flexure.

Scale in cm.

Fig. 3. Testes of foetal and immature giraffe to show differences in size. Ages are: A - foetus 270d, B - foetus 336d, C - foetus 390d, D - foetus 454d, E - neonate 3d, F - juvenile 6 months.





Ortavant, Courrot & Hocherau 1969). Some of the terms used below (such as chromatin granules) are meant in a purely descriptive way following the usage of the authorities cited.

Two types of cells could be distinguished in the foetal and prepubertal seminiferous tubules. These are the indifferent testicular or supporting cells and gonocytes (Plate 4, Fig. 1). The former give rise to Sertoli cells while the latter divide and give rise to spermatogonia.

### Spermatogonia

Three types of spermatogonia, similar to those described for the mink *Mustela vison* by Onstad (1967) and the domestic mammals by Ortavant *et. al.* (1969), were identified in the mature giraffe testis as type A, type B and Intermediate type and can be described as follows:

1. Type A Spermatogonia (Plate 4, Fig. 3). These are relatively large usually ellipsoid cells ( $9,6 \pm 0,2 \mu\text{m}$  i.d.), usually found attached to the basement membrane of the seminiferous tubule. The nucleus stains poorly, is round to ellipsoid in shape, contains very fine chromatin granules and a large darker staining nucleolus. The nuclear membrane is distinct. Type A spermatogonia were found in two 3y old giraffe and all older animals.
2. Type B Spermatogonia (Plate 4, Fig. 3). These are readily distinguishable from the type A spermatogonia as they are much smaller ( $4,5 \pm 0,1 \mu\text{m}$  i.d.), are rounded and darkly staining. The chromatin material is abundant and coarse and though it tends to adhere to the nuclear membrane forming a 'chromatin crust' it is not as 'beaded' as described for the rat *Rattus norvegicus* by Roosen-Runge & Giesel (1950) and in the elephant by Johnson & Buss (1967a). B type spermatogonia are usually found attached to the basement membrane.
3. Intermediate Spermatogonia (Plate 4, Fig. 5). These cells were intermediate in size between the A and B types ( $6,4 \pm 0,3 \mu\text{m}$  i.d.), had more darkly stained nuclei than type A and were characteristically 'dust-like'. These cells were also usually found attached to the basement membrane.

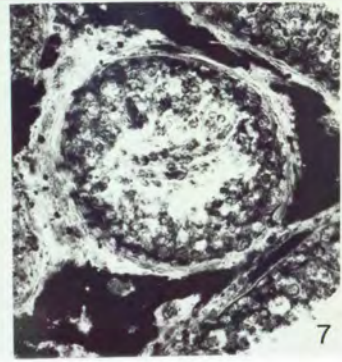
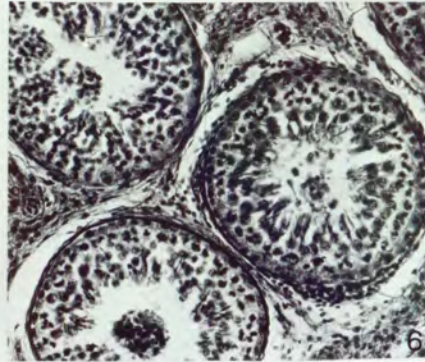
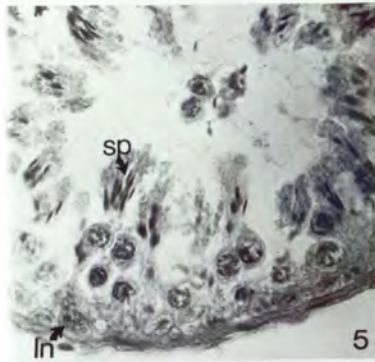
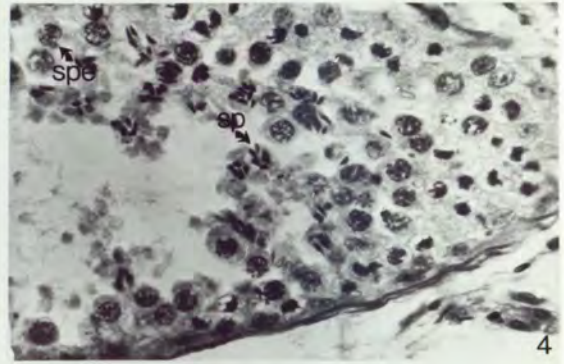
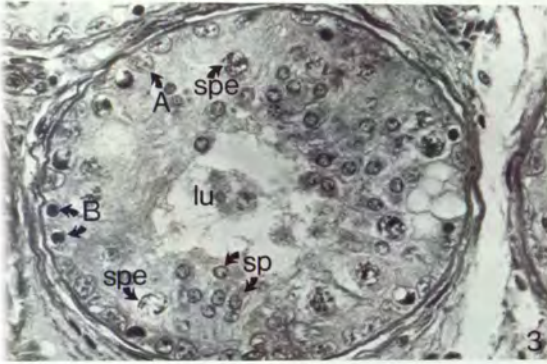
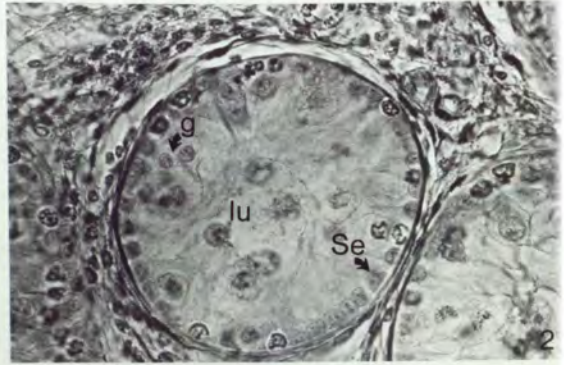
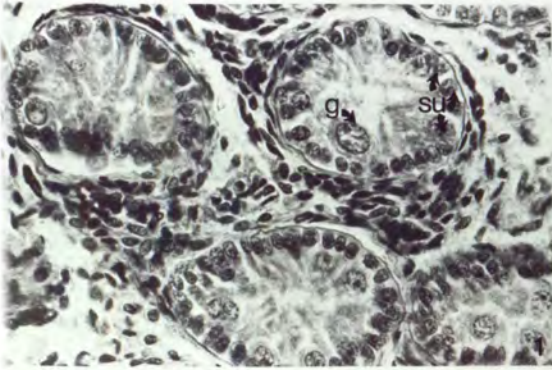
It was not possible to distinguish between the three types in the different stages of division.



PLATE 4

Sections of testes from giraffes at different ages.

- Fig. 1. Testis of a 336-d-old foetus, the tubules contain gonocytes (g) and supporting cells (su) located along the basement membrane. Bouin, 5  $\mu$ m, H & E, X 320.
- Fig. 2. Testis of a 3-y-old immature animal; the tubules are greatly enlarged in comparison with the foetus (Fig. 1), the lumen (lu) is appearing and some supporting cells are still present but others are differentiating into Sertoli cells (Se). A dividing gonocyte (g) which would have given rise to spermatogonia is also shown. Bouin, 5  $\mu$ m, H & E, X 320.
- Fig. 3. Testis of a 3-y-old pubertal animal; the tubules and lumen (lu) are further enlarged and both A type (A) and B type (B) spermatogonia are seen located along the basement membrane. Primary spermatocytes (spe) in different phases of meiosis are seen, two of which are labelled. An earlier generation of spermatocytes has given rise to round spermatids (sp). Bouin, 5  $\mu$ m, H & E, X 320.
- Fig. 4. Testis of a mature animal showing elongating spermatids (sp) and numerous primary spermatocytes (spe) in different phases of meiosis. Bouin, 5  $\mu$ m, H & E, X 320.
- Fig. 5. Testis of a mature animal showing bundle formation of spermatids (sp) and their penetration of the tubule's wall. An intermediate type spermatogonium (In) is also shown. Bouin, 5  $\mu$ m, H & E, X 320.
- Fig. 6. Testis of a mature animal at lower magnification showing large tubules and relatively little interstitial material (*cf.* Fig. 1). Bouin, 5  $\mu$ m, H & E, X 128.
- Fig. 7. Testis of a mature animal showing darkly stained lipid in the interstitial cells. Zenker-formol, 5  $\mu$ m, Sudan black X 128.



### Spermatocytes

The primary spermatocytes are the products of mitosis of the last generation of spermatogonia, the B type spermatogonia. The early spermatocytes are often difficult to distinguish from the B type spermatogonia, however their nuclei are smaller, and are more darkly staining and the nuclear membrane is less distinct. When first recognisable the primary spermatocytes are in the preleptotene stage and are usually close to the basement membrane. Spermatocytes in the leptotene phase can be distinguished by the appearance of chromatin filaments which are gathered together in a ball with loose ends sticking out in all directions. The periphery of the nucleus is almost opaque at this stage. During the next stage of prophase, the zygotene stage, the chromosomes are more contracted and the nucleus is darker with an irregular outline.

By the time the pachytene stage is reached the nucleus has grown to a size of  $9,6 \pm 0,2 \mu\text{m}$  i.d., and the chromatin material forms a characteristic reticulated pattern within the nucleus (Plate 4, Fig. 4). No further stages of meiosis were recognised in the present study. No secondary spermatocytes could be distinguished with confidence.

### Spermatids

The newly formed spermatids in the giraffe have small rounded nuclei ( $5,3 \pm 0,1 \mu\text{m}$  i.d.). The chromatin appears very granular. Spermatid nuclei do not stain as darkly as the nuclear material of the spermatocytes. The nuclear membrane is distinct (Plate 4, Fig. 3). Several stages of spermiogenesis could be distinguished, with various degrees of staining of the nucleus and changes in shape resulting in ovoid and then elongated spermatids (Plate 4, Fig. 4). Bundle formation of the spermatids, migration of the spermatids towards the tubule periphery (Plate 4, Fig. 5) and back to the lumen and a lining up of spermatozoa on the inner surface of the seminiferous epithelium occurs in giraffe much as in other mammals (Roosen-Runge & Giesel 1950, Onstad 1967).

### Sertoli cells

The Sertoli cells are the somatic elements in the seminiferous epithelium. They are generally found as triangular cells attached to the basement membrane with their apex towards the lumen. The cytoplasm is obscure and the nuclei are generally also poorly staining. The Sertoli cell precursors or supporting cells are conspicuous and line the tubules in foetal and immature testes (Plate 4, Fig. 2).

Interstitialium

Leydig cells are easily seen in the interstitium and the presence of lipids in these cells was demonstrated by the Sudan black stain (Plate 4, Fig. 7) in two mature testes.

FOETAL GONADS

Testes of several foetuses and giraffe calves are shown in Plate 3, Fig. 3, while data on testes mass and other parameters of development are given in Table 34. The illustrations indicate a decrease in testis size at birth, and from the table it can be seen that there is a decrease in testes mass which requires some months to be regained. These data, though few, are an indication that foetal hypergonadotrophy occurs in male giraffe.

TABLE 34: INDICES OF TESTICULAR DEVELOPMENT IN FOETAL AND YOUNG GIRAFFE

Specimen	Age	Percentage intertubular area	Conc. of interstitial cell nuclei per square	Seminiferous tubule diameter ( $\mu\text{m}$ )	Testes Mass (g)	Body Mass (kg)
A*	270 d	-	-	-	2,0	16,8
B*	336 d	37,6	3,2	57,0	4,2	36,3
C*	390 d	31,7	2,8	48,2	4,4	60,3
D*	454 d	41,4	3,3	56,1	9,2	101,2
E*	2-3 d (postnatal)	39,4	2,7	57,8	6,4	100,0
F*	6 months	44,1	1,8	58,7	12,6	220,0
Mean adult (n = 16)		75,2	0,6	191,4	539,0	1174,3

\* Specimens illustrated in Plate 3, Fig. 3.

The counts of interstitial cell nuclei per square of the microscope grid showed that the younger foetuses had more interstitial cells per unit area than the calves (Table 34) and in mature testes the concentration of interstitial cell nuclei was only 0,6 per square. These data show that there is an increase of interstitial cell concentration before birth. There was little apparent change in seminiferous tubule diameter or histology from 336 d post conception up to 6 months of age (Table 34) and there was no further increase until the animal was over 1 y old.

The data on intertubular area (Table 34) show very little difference between the foetal and immature testes, but these intertubular areas are much smaller than found in mature animals. These data suggest that there is a change in testicular composition from foetal to early life in the male.

#### MASS CHANGES IN THE REPRODUCTIVE TRACT

The testes mass, epididymes mass and bulbo-urethral mass increased with age following a normal growth curve with asymptotes at about 12y of age. The data on testes mass and epididymes mass are illustrated in Fig. 28. The curves for animals from 2y and older were plotted from polynomial regressions. In the case of testes mass, for which more data are available, the four points below 2y, if plotted, would have resulted in a typical sigmoid curve, with an initial phase of slow increase in mass up to about 3y followed by an exponential phase up to about 12y after which time there was no expected increase in mass, and even an indication of a decrease in mass in old age. These two phases of testicular development are more clearly discerned when testes mass is plotted against the logarithm of body mass (Fig. 29). No data are available on the epididymes mass of calves, the few data shown (Fig. 28) do however, indicate that epididymes development closely follows that of the testes. Though not illustrated, the same situation is found in the case of bulbo-urethral mass.

#### THE SEMINIFEROUS TUBULES

At birth the seminiferous tubules resembled those of the youngest foetus examined (336 d). Supporting cells and gonocytes were present. The numbers of gonocytes increased with age but the mean diameter of the tubules did not increase significantly until the giraffe was about 1y old and testes mass was 24 g to 30 g. The data on seminiferous tubule diameter and age are plotted in Fig. 28, the curve has been drawn in from a polynomial regression calculated from the data. The three giraffe 12y old and older tended to have smaller seminiferous tubule diameters than prime animals 8y to 10y old. The asymptotic diameter was reached at about 9y.

Though the series of young animals available for study was limited it was found that the first spermatogonia and spermatids appeared in two animals both 3y old but having a testes mass of 80 g and 183 g respectively. Small numbers of spermatozoa were found in a few tubules of the latter specimen. The total body mass of these two animals was 513 kg and 510 kg respectively. Supporting cells had apparently differentiated into Sertoli cells by 3y of age, but others appeared to be still unchanged. Some of the stages in spermatogenic



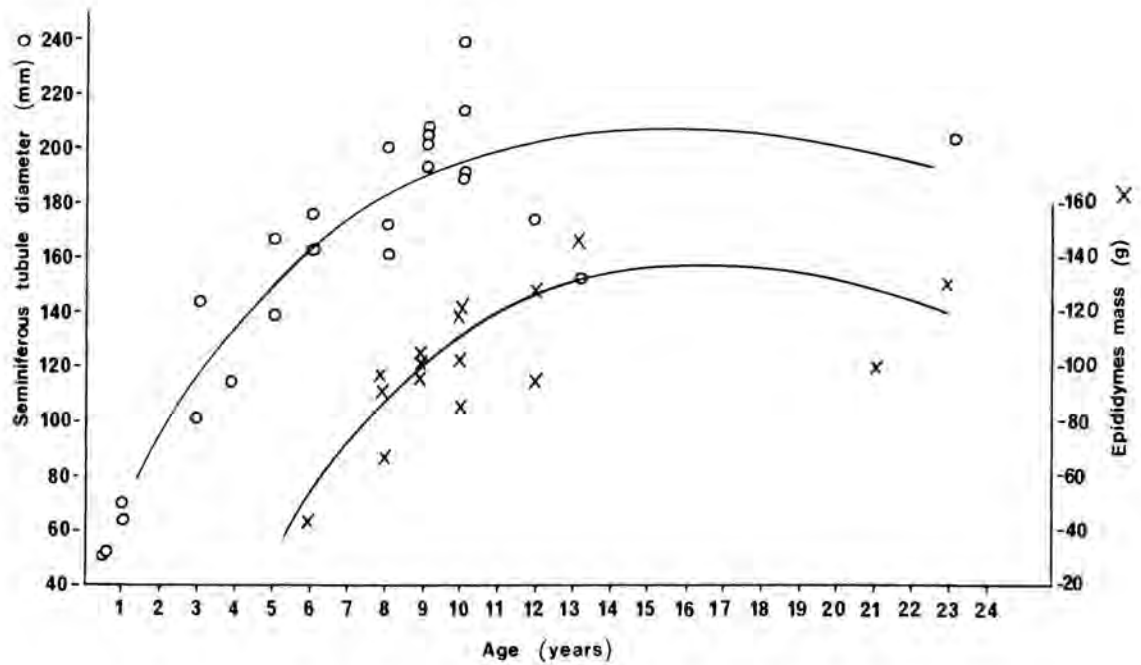
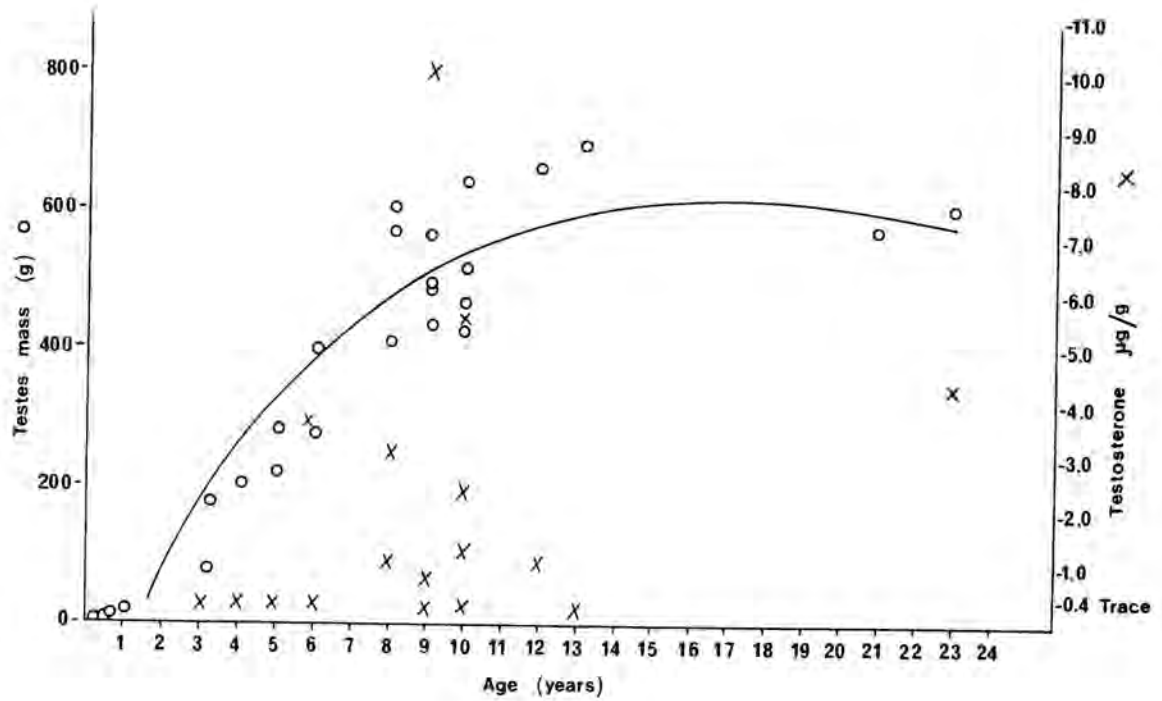


FIG. 28 — Upper: Relationship of testes mass (o) and testicular testosterone concentration (x) to age in giraffe.  
Lower: Relationship of seminiferous tubule diameter (o) and epididymes mass (x) to age in giraffe.

tubule development are illustrated in Plate 4 and several mature tubules are shown in Plate 4, Fig. 6. The relationship of their appearance to testes mass is graphically illustrated in Fig. 29. Due to the paucity of material no individual animals showing primary spermatocytes as the most advanced stage of development were found.

Only three records of the age at first breeding in male giraffe could be traced and these are given in Table 35. The mean age at sexual maturity is 3y 4 months from these records, which however, all refer to captive or tame animals. Because of relatively small body size and behavioural immaturity at this age it is unlikely that giraffe in the wild would normally breed at this age, though they are physiologically capable of doing so.

TABLE 35: AGE AT SEXUAL MATURITY IN MALE GIRAFFE

Date of birth	Date of 1st fertile mating	Age at 1st fertile mating	Locality	Source
November 1966	August 1970	3 y 9 months	Doddieburn Ranch Rhodesia	D. Cowie ( <i>loc. cit.</i> )
1954	December 1957	3 y 6 months	Cleveland Zoological Park, Ohio, U.S.A.	Reuther 1961
3.11.1960	July 1963	2 y 8 months	Honolulu Zoo, Hawaii	Crandall 1964
Mean age	3 y 4 months	3y		

#### HORMONE ASSAY

Testosterone concentrations in adults were found to vary from trace amounts ( $< 0,4 \mu\text{g}$  per g) to  $10,08 \mu\text{g}$  per g of testicular tissue (Table 36). Material was available from 18 males in which spermatogenesis was established. Of these, seven showed only trace amounts of testosterone and one showed none at all (Table 36). Of the seven with trace amounts four were 6y old or younger. The younger spermatogenic animal with higher than trace amounts of testosterone was also 6y old. Testosterone was present in trace amounts in a pooled sample of four fetuses varying in age from 336 d to 454 d; was not present in a pooled sample from a 3d old calf and a 6-month-old calf; and was present in trace amounts in a pooled sample from an

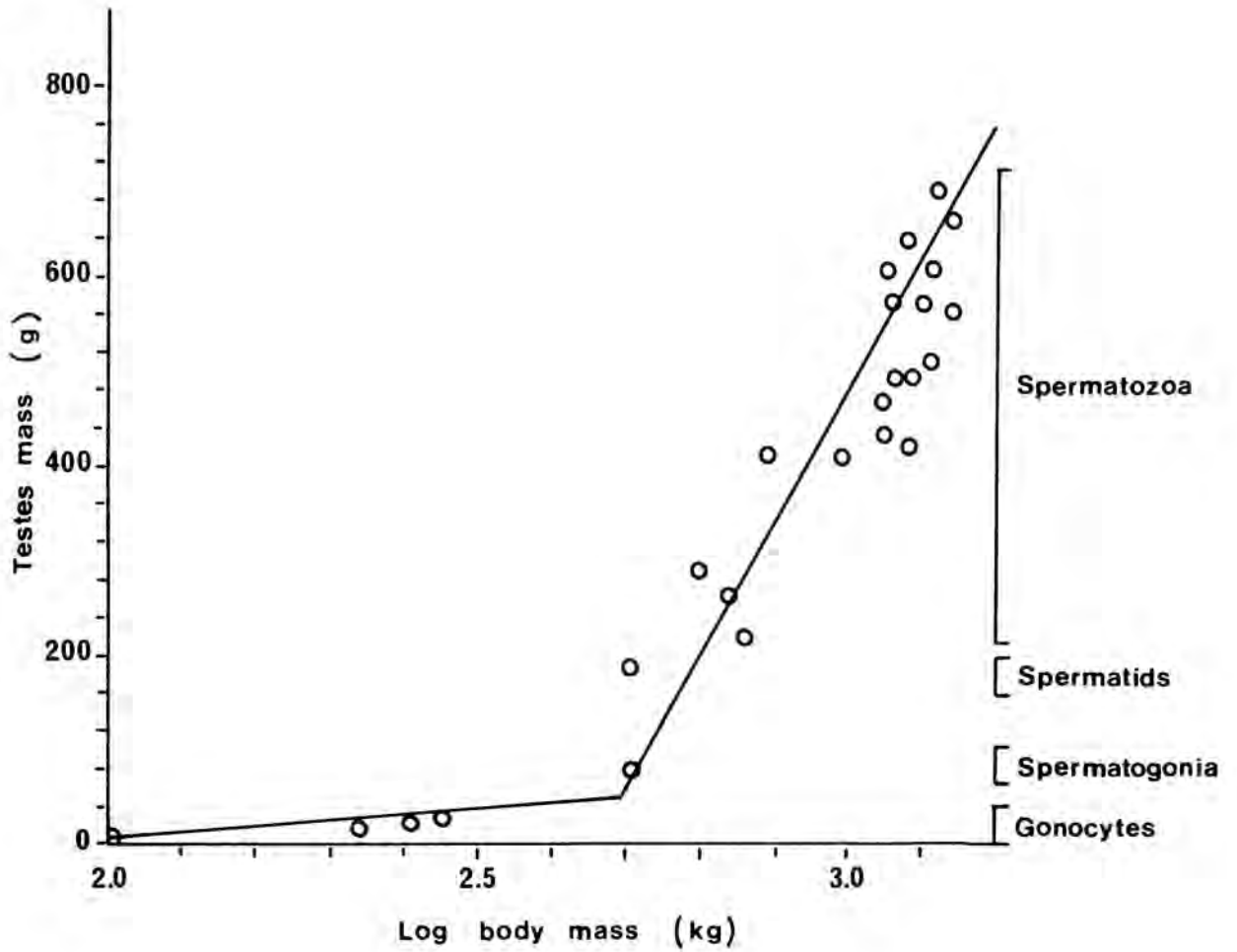


FIG. 29 — Giraffe testes mass plotted against log body mass to show two phases of testicular development.

8-month old calf and two 1 y old animals. These data are illustrated in Fig.28.

TABLE 36: RELATIVE AMOUNTS OF TESTICULAR HORMONES FROM GIRAFFE OF DIFFERENT AGES

Animals in sample	Age	Testosterone	Androstenedione	$\Delta$ 'Testosterone
		Amounts in $\mu\text{g/g}$ of testis		
4 (pooled)	foetuses 270 d - 454 d	+	2,73	-
2 (pooled)	3 d neonate & 6 months	-	-	-
3 (pooled)	8 months - 1 y	+	0,29	-
1	3 y	+	-	-
1	3 y	+	-	-
1	4 y	+	?	+
1	5 y	+	-	-
1	6 y	+	-	-
1	6 y	3,56	1,14	+
1	8 y	3,20	-	-
1	8 y	1,11	-	+
1	9 y	0,84	-	-
1	9 y	10,08	-	?
1	9 y	+	-	-
1	9 y	-	-	-
1	10 y	5,60	-	-
1	10 y	2,48	0,26	-
1	10 y	+	-	-
1	10 y	1,36	0,26	+
1	12 y	1,04	-	?
1	13 y	+	-	-
1	23 y	4,36	-	-

Symbols: + = trace amounts  $< 0,4 \mu\text{g/g}$ , ? = presence questionable,  
 - = no trace found

The presence of androstenedione was confirmed in only four samples, the relevant data for these samples as well as the results for testosterone and  $\Delta$ 'testosterone are presented in Table 36. These data clearly show

that whereas testosterone is present in trace amounts only in foetuses and immature animals it reached high levels in mature males. The converse situation is found for androstenedione which is present in high levels in foetuses and declines or disappears with advancing age (with the exception of the 6y old male).

The presence of  $\Delta^1$ -testosterone in trace amounts was confirmed for 4,6,8 and 10y old bulls, and was questionably present in a 9 and 12y old bull respectively. There was no trace of this androgen in the foetal sample and the calves (Table 36) or the other adults.

As in the bovine *Bos taurus* (Lindner & Mann 1960) but unlike the sheep (Skinner, Booth, Rowson & Karg 1968) androstenedione was the dominant testicular androgen until at least ly *post partum*. The reason why no androstenedione was present in some samples could not be ascertained, nor the significance of the occurrence of  $\Delta^1$ T only in animals 4y old and older. As in other mammals studied (bovine - Mann, Davies & Humphrey 1949; rabbit *Oryctolagus cuniculus*, Skinner 1967c; sheep - Skinner *et. al.* 1968; goat *Capra hircus* - Skinner 1970b and springbok - Skinner & van Zyl 1971) androgenesis preceded spermatogenesis. The endocrinology of the giraffe is thus broadly similar to that reported for other ungulates.

#### SEXUAL DEVELOPMENT

The various features of the reproductive tract measured in this study have already, separately or together, been recognised as parameters for measuring sexual functions in the bovine (Hay, Lindner & Mann 1961), ovine (Skinner *et. al.* 1968), roe deer *Capreolus capreolus* (Short & Mann 1966), springbok (Skinner & van Zyl 1971), kudu (Skinner & Huntley 1971a), blesbok (Skinner & Huntley 1971b), several other species of antelopes (Skinner, van Zyl & Oates 1974) and elephant (Johnson & Buss 1967b, Laws & Parker 1968, Hanks 1972<sup>b</sup>).

Correlation coefficients were therefore computed for some of the data on parameters of sexual development in giraffe based on animals from 3d to 23y old. The significant correlation coefficients are shown in Table 37.

All parameters were significantly correlated with age. Though testosterone concentration was variable (Table 36) it, too, was correlated with age ( $r = 0,683$ ). There was, however, insufficient data on testosterone to form definite conclusions about poor correlations. Epididymes mass, seminiferous tubule diameter and bulbo-urethral mass were all significantly correlated with

TABLE 37: SIGNIFICANT CORRELATION COEFFICIENTS BETWEEN PARAMETERS OF SEXUAL DEVELOPMENT IN MALE GIRAFFE

	Testes mass (g)	Epididymes mass (g)	Seminiferous tubule diameter ( $\mu\text{m}$ )	Bulbo-urethral mass (g)	Testosterone conc. $\mu\text{g/g}$
Age (years)	0,818****	0,509*	0,738***	0,898***	0,683*
Testes mass (g)	-	0,862***	0,805***	0,832***	-
Epididymes mass (g)			-	-	-
Seminiferous tubule diameter ( $\mu\text{m}$ )				0,774**	-
Bulbo-urethral mass (g)					-

Degrees of freedom vary between 6 and 25; - not significant; \*  $0,01 < P > 0,05$ ; \*\*  $0,001 < P > 0,01$ ; \*\*\*\* $P < 0,001$ .

#### SEASONAL EFFECTS

The testes mass, epididymes mass, seminiferous tubule diameter, and testosterone concentration on a seasonal basis for adult male giraffe (animals older than 6 y) from Timbavati are illustrated in Fig. 30. There is no clear indication of any consistent pattern of maxima and minima which could be related to the effects of season. There is a peak in testes mass during the wet season months, but high values are also achieved in June and July. There is also a slight peak in epididymes mass in February but, again, high values are also found in June and July. The seminiferous tubule diameters varied throughout the year and showed minimal values when testes and epididymes mass were at a maximum, and conversely a maximum value in June when testes mass was low. These seemingly conflicting results are most probably due to the small sample size and to the very high correlation between these parameters and age in the giraffe.

Of the four adults which showed only trace amounts of testosterone, two were collected in July, one in August and one in February. The absence of this hormone in quantity could not therefore be directly linked to any seasonal effect.

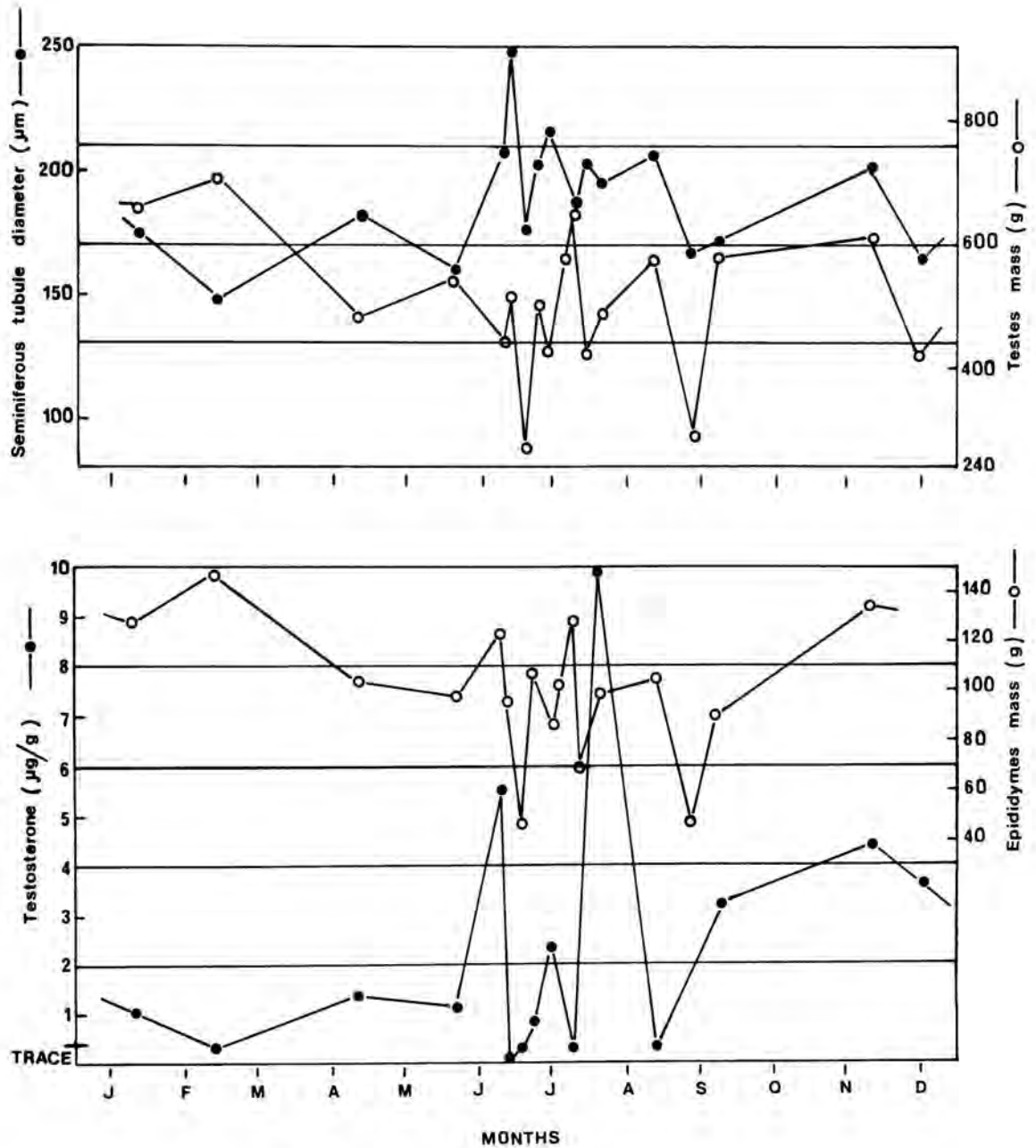


FIG. 30 — Upper: Giraffe seminiferous tubule diameter (—●—) and testes mass (—○—) in different months of the year.  
Lower: Giraffe testicular testosterone concentrations (—●—) and epididymis mass (—○—) in different months of the year.

## CONCLUSIONS

This study, though limited by small sample size, has shown that the reproductive tract of giraffe differs little in morphology, histology and function from that of other ungulates cited and there is no indication of any seasonal sexual cycle, a characteristic of many southern African species. The limited data on testes mass and size in late foetal and early neonatal life suggest that there is a hypergonadotrophic effect in this species.

This study has shown that testes mass, epididymes mass, bulbo-urethral mass, seminiferous tubule diameter, and testicular testosterone concentration are significantly correlated with age, and although there was great variation between animals this could not be explained as being due to seasonal effects on the basis of the available material. Sexual development proceeds slowly from birth to about 3 y of age. The onset of spermatogenesis at 3 y to 4 y of age coincides with a rapid increase in reproductive tract mass and seminiferous tubule diameter. This period in the life of the male giraffe is also characterised by a rapid body growth rate which is a secondary sexual characteristic. (The curves of body growth in Chapter 5 clearly show that sexual differences have already appeared at 3 y of age). The differences in testicular development of two males, both 3 y old having similar body mass and dimensions, indicates that puberty is related to physiological age, rather than chronological age. In the male with the lighter testes (80g) the spermatogenic cycle had only developed to the spermatogonia stage while the animal with the heavier testes (188g) had a more advanced seminiferous epithelium with numerous spermatids and a limited number of spermatozoa present. This supports the reports (Table 35) indicating that male giraffe are capable of breeding from 3 y of age. The data on testosterone concentration are not as adequate as the other parameters as an indicator of sexual function. However, the trend of these results clearly support the definitions of puberty of Marshall (1922), Donovan & van der Werf ten Bosch (1965), and van der Werf ten Bosch (1969). There is also an indication from these results of a decline in androstenedione production after puberty coinciding with increased quantities of testosterone and other testicular hormones being secreted.



## CHAPTER 7

REPRODUCTION IN FEMALE GIRAFFE

## INTRODUCTION

Many aspects of reproduction in female giraffe have been mentioned by other workers, but no comprehensive synthesis of this information has yet appeared other than the short compilation of Dagg (1971). Thus there are several references to the age of sexual maturity in captive giraffe in the literature (Gijzen 1958, Reuther 1961, Crandall 1964) based mostly on approximate dates of birth, first oestrus and first calving. Some records of the duration of oestrus and the periods between oestrus are given by Gijzen (1958), Backhaus (1961), Savoy (1966) and Wilson (1969). Environmental influences on reproduction in giraffe were studied in Kenya by Field & Blankenship (1973) who reported that conception was related to rainfall, biomass of vegetation and crude protein. Giraffe have been recorded as breeding throughout the year in wild populations in various parts of Africa and in captivity (Crandall 1964, Dagg 1971). Wilkinson & de Fremery (1940) reported the presence of gonadotrophic hormones in the urine of pregnant giraffe.

The objectives of this study were, therefore, to relate what was known of reproduction in the female giraffe to what was found during the current investigations; and to assess some aspects in as much detail as the available material would allow.

## MATERIAL AND METHODS

ATTAINMENT OF SEXUAL MATURITY

The date of birth and date of first calving of five females at Taronga Zoological Park, Australia (R. Strahan *loc. cit.*) and a few records from wild giraffe in southern Africa were used to derive the mean age at sexual maturity of female giraffe.

ENVIRONMENT AND OESTRUS

The effect of environment on oestrus was evaluated on the basis of conception dates in different giraffe populations and some environmental features. Some of these data were collected during the course of routine patrols in the Timbavati from May 1971 through to July 1972, when the

incidence of giraffe calves, judged on the basis of size, coat texture and behaviour to be neonates or only a few days old, was recorded. (The presence of an umbilical cord alone is not a reliable criterion of age in giraffe as it can be retained for up to 4 months). The conception dates of foetuses from culled animals, were calculated using the expression of Huggett & Widdas (1951) as described in Chapter 5.

Records of giraffe calving times or calculated conception dates of foetuses from elsewhere in South and East Africa and climatic data from these areas were also included in this study. Thus, 34 records of giraffe births were obtained from the Hans Merensky Nature Reserve (23°39'S, 30°40'E) 70 km northwest of Timbavati (S.M. Zaayman *loc. cit.*). The vegetation and climate of this reserve and the northern part of Timbavati are similar. These records were, therefore, pooled with the Timbavati records for purposes of discussion. Fifteen records (S.M. Hirst pers. comm.)\* of giraffe births from the Langjan Nature Reserve in the northwestern Transvaal (22°52'S, 29°14'E) were included. This reserve is situated in a savanna area where a hot and arid climate prevails. No suitable climatic data were available from the Reserve, therefore 20 y mean rainfall data from Alldays (22°41'S, 29°06'E) and temperature records from Mansefield, adjoining the Reserve, were used (data from Weather Bureau, Pretoria). Sixteen birth records (D. Rowe-Rowe pers. comm.)\*\* from the Umfolozi, Hluhluwe and Mkuzi Game Reserves in Zululand were also included. The habitat occupied by giraffe in these areas is predominantly *Acacia* savanna. Twenty-year mean rainfall from Mkuze town (27°37'S, 32°02'E) and temperature recorded for 1y from Makatini (27°24'S, 32°11'E) were used (data from Weather Bureau, Pretoria). The dates of conception of 20 foetuses from Akira Ranch (01°00'S, 32°22'E) in Kenya were calculated as detailed above from data given by Kayanja & Blankenship (1973). The conception dates given for these foetuses by Field & Blankenship (1973) were not used as the birth mass used by these authors in their calculations is considered to be too low (54,5 kg *cf.* 102 kg, Chapter 5). Giraffe calving records from Nairobi National Park, Kenya (Foster & Dagg, 1972) were also used in this study, long-term mean rainfall and temperature records for Nairobi (01°18'S, 36°45'E) were taken from Griffiths (1972). A total of 64 records of giraffe births at Taronga (R. Strahan *loc. cit.*) were

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\* Dr. S.M. Hirst, Division of Nature Conservation, Transvaal.

\*\* Mr. D. Rowe-Rowe, Natal Parks Board, Pietermaritzburg, Natal.

included for comparative purposes. Long-term mean rainfall and temperature records for Sydney ( $33^{\circ}51'S$ ,  $151^{\circ}13'E$ ) were taken from Gentilli (1971).

Day length for the 17th day of each month at the approximate latitudes of the six areas mentioned above was derived from List (1951).

### PREGNANCY

Notes on placentation and implantation were made during the *post mortem* examinations of giraffe females. Data on the duration of pregnancy were taken from Chapter 5 (Table 27). Mean calving intervals were assessed from published records and from various personal communications as well as from data on pregnant and non-pregnant females. Data on lifetime production and twinning, were also gathered from the literature and personal communications.

Urine was collected from immediate *post mortem* urination, or taken from the bladder following evisceration and frozen. The urine was later tested by the method of Ascheim & Zondek on virgin mice *Mus musculus*, in the laboratory, following detoxification by sulphosalicylic acid (Benesch & Wright 1960). Urine from non-pregnant females, from an immature female and a mature male served as controls.

### CALF MORTALITY

Three methods for estimating calf mortality based on the lactation and pregnancy status of a sample of mature females, and the duration of lactation are discussed by Grimsdell (1973b). These methods were considered in the present investigation, using data on pregnancy and lactation in 26 mature females ( $>6y$ ) that were in either their second or a later pregnancy, and a gestation time of 457 d.

## RESULTS

### ATTAINMENT OF SEXUAL MATURITY

Age at first conception was calculated to the nearest month from age at first calving minus 15 months gestation from the available records (Table 38). It was not possible to determine whether management regimes at the various institutions, availability of mates, possible subspecific differences or the level of nutrition influenced the ages at which calving or oestrus was reported in captive animals. The mean age at first conception for the captive animals was  $3y$  10 months  $\pm$  3 months *cf.*

TABLE 38: AGE AT SEXUAL MATURITY IN FEMALE GIRAFFE

Date of birth	Date of 1st parturition	Age at 1st conception or oestrus*	Locality and source
Captive animals			
ca. Jan. 1948	29.4.1953	4 y	Antwerp, Gijzen 1958
ca. July 1948	5.11.1955	6 y	" " "
29.4.1953	11.3.1958	3 y 8 months	Antwerp, Crandall 1964
-	-	* 3½ y	Copenhagen, Crandall 1964
25.9.1950	16.11.1955	3 y 11 months	Taronga, Dagg 1968
16.11.1955	19.9.1960	3 y 7 months	" " "
20.2.1957	19.11.1961	3½ y	Taronga, R. Strahan <i>loc. cit.</i>
31.8.1958	22.6.1963	3 y 7 months	" " " " "
19.9.1960	2.9.1964	2 y 9 months	" " " " "
8.9. 1958	30.9.1964	4 y 10 months	" " " " "
ca. Oct. 1954	23.3.1959	3 y 2 months	Cleveland, U.S.A., Reuther 1961
		Mean	3 y 10 months ± 3 months
Wild animals			
1959	30.5.1966	ca. 5½ y	S.W.A., J.M. Hofmeyr <i>loc. cit.</i>
28.11.1964	26.6.1970	4 y 3 months	Rhodesia, G.T. Richardson pers. comm. **
-	-	4½ y	Rhodesia, Wilson 1969
Nov. 1968	Dec. 1973	3 y 9 months	Rhodesia, J.H. Grobler <i>loc. cit.</i>
Late 1954	1961	ca. 5 y	Transvaal, S.M. Zaayman <i>loc. cit.</i>
-	-	4½ y	" " " " "
		Mean	4 y 7 months ± 3 months

\*\* Mr. G.T. Richardson, Tods Motel, P.O. West Nicholson, Rhodesia.

4y 7 months  $\pm$  3 months for wild animals ( $P < 0,05$ ) (Table 38). The youngest mature females (pregnant or with a corpus luteum of cycle in their ovaries) collected in the eastern Transvaal were 6y old ( $n = 3$ ). One of these animals (6y) was thought to be in oestrus because of the presence of mucous in the vagina and fluid in the uterine horns. This animal had not been pregnant before, her ovaries were much smaller than any other mature female and contained no large recent corpus albicans, there was a mature follicle 11,2 mm in diameter in one ovary. A 5y-old female did not show signs of having ovulated.

#### ENVIRONMENT AND OESTRUS

##### Conceptions in relation to rainfall and temperature

A total of 89 newly-born calves were recorded at Timbavati during the study period and 20 fetuses were collected. The number of conceptions per month extrapolated from these data are indicated in Fig. 31.

The rainfall and temperature data for the same period are shown as climatograms using the same units of length for 20 mm of rainfall and 10°C respectively. When these climatic data are plotted in this ratio of 1:2 the humid period of the year is represented by that part of the diagram where rainfall exceeds temperature and arid periods where rainfall is below temperature (Gaussen 1955). When rainfall exceeds 100 mm per month the climate is regarded as perhumid.

It can be seen from Fig. 31 that conceptions were recorded in all months of the year, except August. There is a definite peak in conceptions from December 1970 to March 1971, corresponding with the humid period (except for February 1971 when rainfall was low). The sample of conceptions for the 1971/1972 season is small as it is based entirely on the 20 fetuses collected up to the end of July 1972 when the study was terminated. Nevertheless the majority of these occurred during the humid months from November 1971 to March 1972.

The records from the other areas in Africa and Australia were extrapolated back to their months of conception and are presented in Fig. 32 together with their relevant climatograms. Even though the data are few, a distinct relationship between humid months and conception peaks is evident for the combined Timbavati and Hans Merensky data, the Zululand Game Reserves and Akira Ranch. At Nairobi National Park where eight months of the year are humid or perhumid and there is a double peak of rainfall, the conceptions are more evenly distributed with however, a peak in May and June

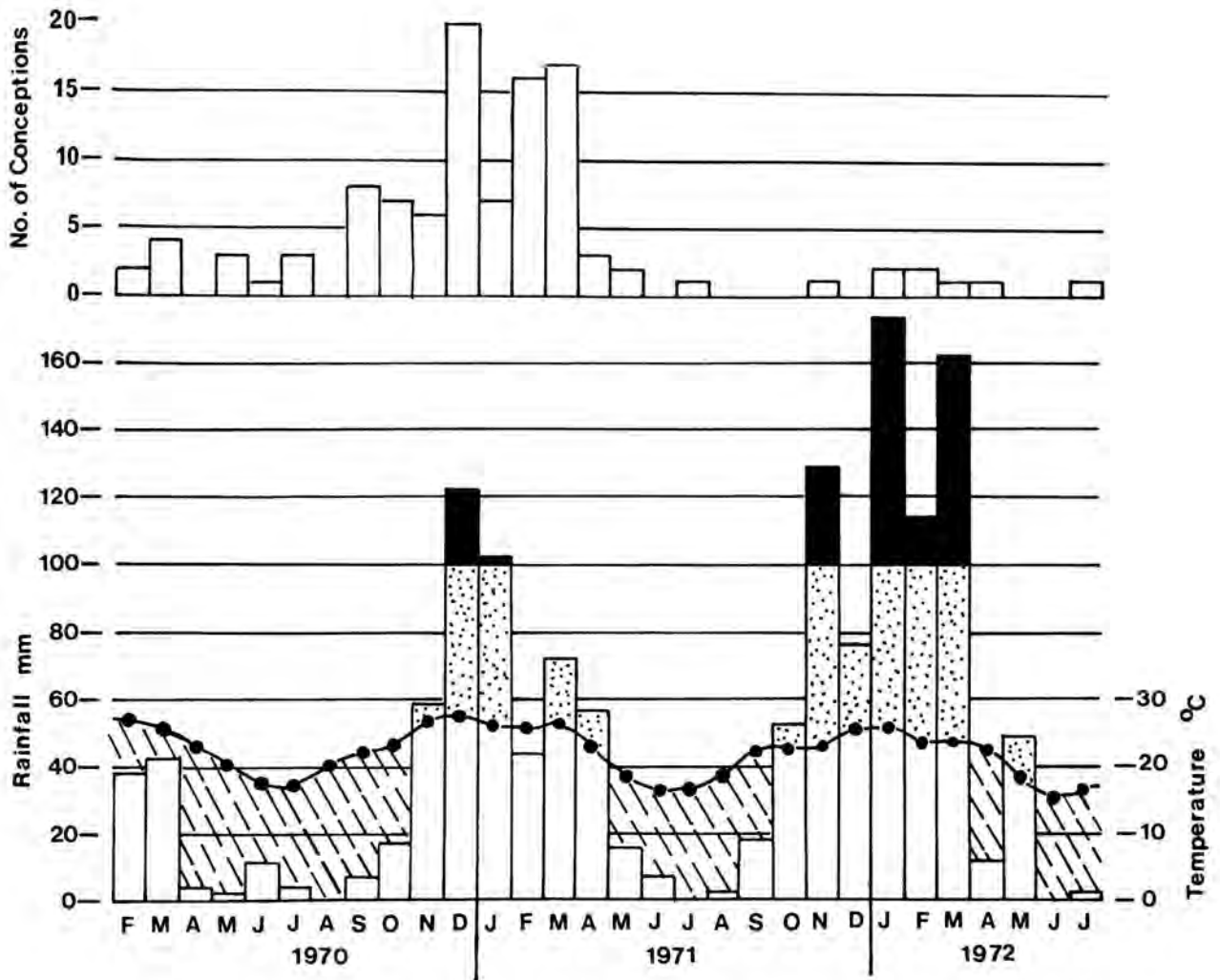


FIG. 31.— Lower: Climatograms showing rainfall (histograms) and temperature (—●—); humid periods — light stippling, perhumid periods — black, arid periods — cross hatching.

Upper: Histograms showing the number of conceptions per month. Data from the Timbavati Private Nature Reserve for the period February 1970 — July 1972.

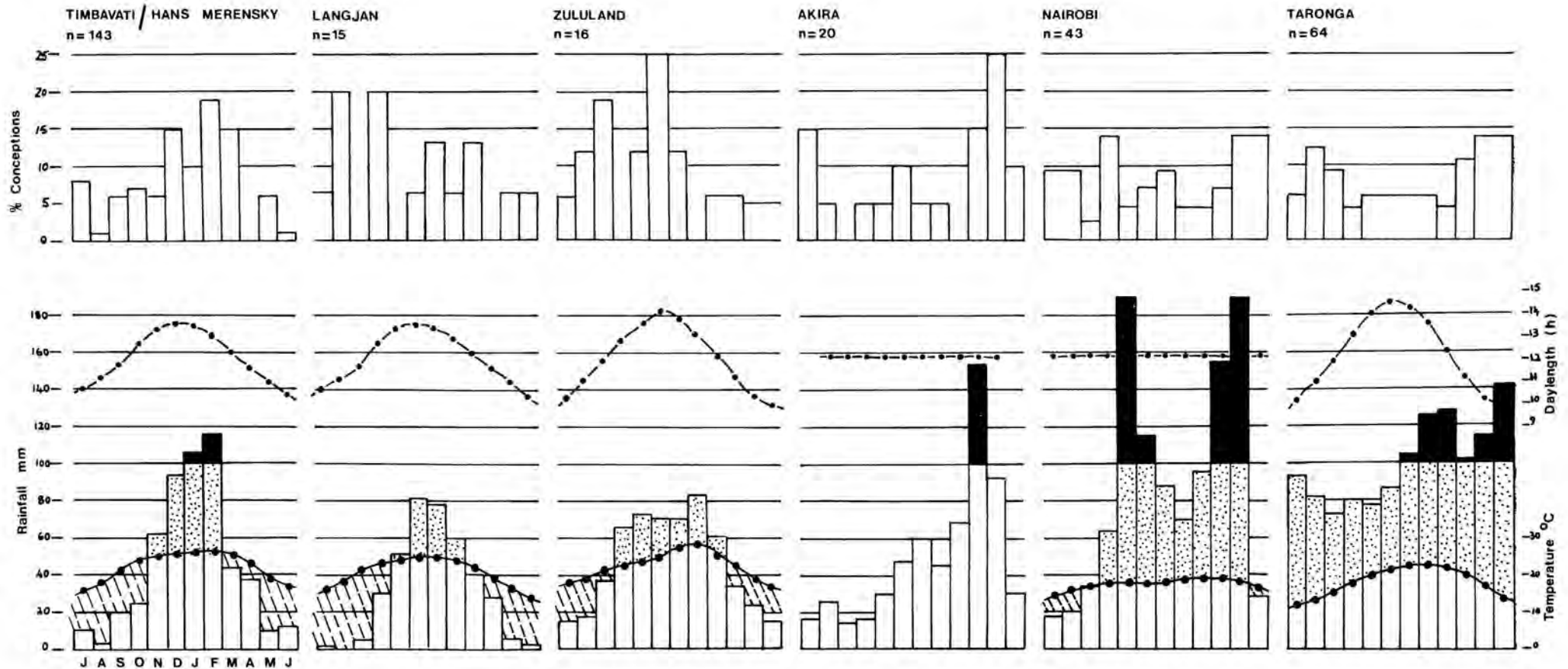


FIG. 32 – Lower: Climatograms showing rainfall (histograms) and temperature (—●—); humid periods – light stippling, perhumid periods – black, arid periods – cross hatching. Day-length curves (—●—) are shown above the climatograms.  
Upper: Histograms showing the percentage conceptions per month (summed).  
Localities and the number of observations are given. Sources are mentioned in the text.

following on the rainfall peak of April and May. The scanty data from the Langjan Nature Reserve show a dissimilar pattern to the Timbavati data in that conception peaks were recorded in August and October. The 64 birth records from captive giraffe at Taronga (R. Strahan *loc. cit.*) show a much more even spread of conceptions throughout the year with more births during winter than during summer.

Correlation coefficients ( $r$ ) and significance probabilities (Simpson *et. al.* 1960) for giraffe conceptions related to total monthly rainfall and mean monthly temperature (Table 39) indicate that there is a significant relationship for those localities with a single rainfall and temperature peak per annual cycle which can probably be explained on the basis of the effect which these environmental factors have on giraffe food sources. This table shows that rainfall during the month preceding conception is highly correlated with conception at Akira ( $r = 0,720$ ;  $P < 0,01$ ), and Timbavati/Hans Merensky ( $r = 0,828$ ;  $P < 0,001$ ), while there is no significant correlation two months before conception. Rainfall during the month of conception is not significantly correlated with conception at Akira, though it is significant at Timbavati/Hans Merensky ( $r = 0,766$ ;  $P < 0,01$ ). This correlation coefficient is, however, smaller than that for the previous month. No significant correlation was found between rainfall and conception at Nairobi. No temperature data were available from Akira, but temperature and conceptions were significantly correlated at Timbavati/Hans Merensky for both the month of conception ( $r = 0,695$ ;  $P < 0,02$ ) and the previous month ( $r = 0,661$ ;  $P < 0,02$ ). There was no significant correlation between temperature and conceptions at Nairobi.

#### Conceptions in relation to latitude

Day length for the 17th d of each month was plotted for the approximate latitudes of the six areas mentioned above (Fig. 32). As could be expected there is no correlation of daylength and conceptions at equatorial latitudes except for the correlation found for the month of conception at Nairobi (Table 39). Highly significant correlations of daylength with conception (Table 39) were found for the Timbavati/Hans Merensky data for both one ( $r = 0,750$ ;  $P < 0,01$ ) and two ( $r = 0,719$ ;  $P < 0,01$ ) months preceding conception. However, the correlation coefficient for the month of conception was only significant at the 5% probability level ( $r = 0,586$ ).



TABLE 39: CORRELATION COEFFICIENTS ( $r$ ) AND SIGNIFICANCE PROBABILITIES FOR GIRAFFE CONCEPTIONS RELATED TO TOTAL MONTHLY RAINFALL, MEAN MONTHLY TEMPERATURE AND PHOTOPERIOD (DAYLIGHT HOURS OF 17TH DAY OF EACH MONTH) FOR THREE LOCALITIES IN AFRICA

	Rainfall			Temperature			Photoperiod		
	*A	B	C	A	B	C	A	B	C
Akira Ranch	0,473	0,720	0,378	No data available			0,187	0,106	0,081
	n.s.	<0,01	n.s.				n.s.	n.s.	n.s.
Nairobi National Park	-0,062	0,347	0,276	-0,194	0,039	0,378	0,637	0,215	-0,048
	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	<0,02	n.s.	n.s.
Timbavati/Hans Merensky	0,766	0,828	0,473	0,695	0,661	0,512	0,586	0,750	0,719
	<0,01	<0,001	n.s.	<0,02	<0,02	n.s.	<0,05	<0,01	<0,01

\* Column A - data for month of conception  
 B - data for one month before conception  
 C - data for two months before conception

## PREGNANCY

### Duration

The relevant data on gestation length have already been given (Chapter 5, Table 27). It was concluded that pregnancy lasts for 457 d in the giraffe.

### Placentation and Implantation

The placenta of the giraffe is polycotyledonary of the syndesmochorial type and the number of cotyledons has been reported to range from about 160 - 180 (Amoroso 1952). In three placentae examined during this study there were 149, 183 and 191 cotyledons respectively. The cotyledons vary greatly in size and Wilson (1969) has reported a large giraffe cotyledon 23 x 5 cm. The largest cotyledons, and in two out of three cases the most cotyledons, were found in the same side as the corpus luteum (CL) of pregnancy. In one case there were more cotyledons on the opposite side but they were, however, all smaller than those on the side of the CL.

There is no evidence of transuterine migration of the blastocyst occurring in giraffe. Out of 20 cases examined the foetus was always found on the same side as the CL of pregnancy, there is no statistical difference between the number of implantations found on the right side (13) and the left side (7) ( $P < 0,50$ ).

### Calving Intervals

As few records of calving intervals in wild giraffe are available, recourse was made to the published records (in months) of Gijzen (1958) from Antwerp; Backhaus (1961) from various institutions in Europe; Crandall (1964) and Savoy (1966) from North America; and these yielded 34 records. A further 36 calving interval records were available from Taronga (R. Strahan *loc. cit.*). Twelve records for wild giraffe from East Africa are listed by Foster & Dagg (1972) and only 11 were found for wild giraffe in southern Africa. These come from giraffe living under very different environmental conditions. Four are from the Daan Viljoen Game Park in South West Africa (J.M. Hofmeyr *loc. cit.*); four from the Jack Scott Nature Reserve, Transvaal (Mason 1973, van Aarde pers. comm.)\* One from the West Nicholson district of Rhodesia (G.T. Richardson *loc. cit.*) and

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\* Mr. R.J. van Aarde, Mammal Research Institute, University of Pretoria, Pretoria, 0002.

three from the Matopos National Park, Rhodesia, one of which is given by Wilson (1969), and two provided by J.H. Grobler (*loc. cit.*). Not all of these 93 records were used, as a cut-off point was set at 27 months. This allowed for a full 12 months for potential breeding plus 15 months gestation. This arbitrary limit was imposed because it is common practice in zoological gardens for males to be separated from females with calves, especially when animals are kept indoors during winter (Gijzen 1958, Crandall 1964) and it could not be assessed to what extent calving intervals from captive animals might have been influenced by this practice. Furthermore, it is unusual for an African ungulate not to conceive within at least one year of parturition (Mentis 1972, Skinner 1973, Dittrich 1974), exceptions being hippopotamus (Laws & Clough 1966), elephant (Laws & Parker 1968, Laws 1969) black rhinoceros and white rhinoceros *Ceratotherium simum* (Mentis 1972). There was only one record from a wild giraffe which had a calving interval longer than 25 months, this was a record from the Matopos National Park (J.H. Grobler *loc. cit.*) of 54 months, but it is possible that this female could have calved in the intervening period and that if the calf died it might have never been recorded. Furthermore, of the 93 records obtained, 83% fell within the 27 month limit.

The mean calving intervals in months for different categories of captive and wild giraffe are given in Table 40. The mean calving interval of wild giraffe is not significantly different from that of captive animals ( $P < 0,5$ ) but the mean calving interval of captives in Australia was significantly shorter than that of captives in Europe ( $P < 0,05$ ).

TABLE 40: MEAN CALVING INTERVALS, IN MONTHS, OF WILD AND CAPTIVE GIRAFFE (DATA FROM VARIOUS SOURCES)

Status	n	Mean	S.D.	S.E.	Range
Wild	23	19,9	2,7	0,6	16,0 - 25,0
Captive - all sources	54	19,4	3,1	0,4	15,7 - 27,0
Captives - Europe	25	20,4	3,3	0,7	16,0 - 27,0
Captives - Australia	26	18,4	2,6	0,5	15,7 - 24,2

The distribution of calving intervals in months is shown in Fig. 33 and it can be seen that most intervals lie in the range of 16 - 18 months. The mean *post partum* reconception interval in wild giraffe is 148 d (mean calving interval in months multiplied by 30,4 to give the product in days minus a gestation period of 457 d). As the frequency of shorter calving intervals was so great (Fig. 33) the reconception interval for all those records for which exact dates were available (mostly captives) were worked out and found to be  $109 \pm 11$  d. The two shortest calving intervals are from one female at Taronga being 481 and 485 d indicating *post partum* reconception intervals of about 23 d and 27 d respectively. Females can therefore come into oestrus after three weeks *post partum*. This is also supported by other observations. For instance a female which gave birth in Zululand came into oestrus one month later (D. Rowe-Rowe *loc. cit.*); similarly a female in the Jack Scott Nature Reserve, Transvaal came into oestrus and mated between 26 d and 40 d *post partum* (R. van Aarde *loc. cit.*).

Several workers (Perry 1953, Buss & Smith 1966, Laws & Parker 1968, Grimsdell 1973b) have calculated mean calving intervals from the distribution of pregnant to non-pregnant adult females in a sample (knowing the gestation period of the species involved). In the present sample of adult female giraffes there are 17 pregnant and 9 non-pregnant giving a calculated interval from parturition to conception of 7,9 months (243 d) and a mean intercalving interval of 22,9 months which is higher than the mean values for wild animals (Table 40) but well within the range.

#### Lifetime production

Few records are available of the lifetime production of calves by a particular individual. The few records to hand are given in Table 41. The oldest female collected at Timbavati was 20 y old and found to be pregnant.

#### Twinning

Though the giraffe is a monotocous species, one case of stillborn twins has been observed in the Timbavati Reserve (J. Downie pers. comm.)\* of which a reconstructed photograph is illustrated (Plate 5). The twins were apparently normally developed.

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PLATE 5

A partly reconstructed photograph of aborted twin giraffes taken in the Timbavati in about 1960. Though unclear, the photograph shows that the twins were contained in the same placenta. This is only the second case of giraffe twins on record.



TABLE 41: LIFETIME PRODUCTION OF CALVES BY INDIVIDUAL GIRAFFE FEMALES

Locality	Age (y)	No. of calves	Mean calving interval (months $\pm$ S.E.)	Source (all <i>loc. cit.</i> )
Hans Merensky Nature Reserve, Transvaal	20	8	19,5	S.M. Zaayman
Daan Viljoen Game Park, S.W.A.	13*	5	20,1 $\pm$ 1,6	J.M. Hofmeyr
Taronga (a)	24	10	28,9 $\pm$ 6,9	R. Strahan
(b)	20	10	20,2 $\pm$ 1,8	" "
(c)	17**	9	18,4 $\pm$ 1,5	" "

\* This female was pregnant when killed and the mean calving interval has been calculated on the assumption that she would have produced her fifth calf had she not been killed, she would also then have reached her 14th birthday.

\*\* This female was still living.

#### Urinary hormones

The Ascheim-Zondeck test gave negative results. As only 5% of the mice died after the injection of purified urine it was concluded that the negative result was not due to incomplete detoxification. As oestrogens are fairly stable it seemed unlikely that the results were due to decomposition of the hormone due to repeated freezing and thawing, though this possibility could not be excluded.

#### CALF MORTALITY

Lactation in Timbavati giraffe could endure for at least 150d (Fig. 38, Chapter 9), and the mean *post partum* reconception interval was estimated to be 7,9 months or 242 d (see above). Therefore it was assumed that lactation could last for at least 150 + 242 = 392 d or 12 to 13 months. This estimate is supported by the finding of milk in the stomach of an animal which was about 1y old ( $M_1$  newly erupted). Furthermore it was reported by Aschaffenburg, Gregory, Rowland & Thompson (1962) that the

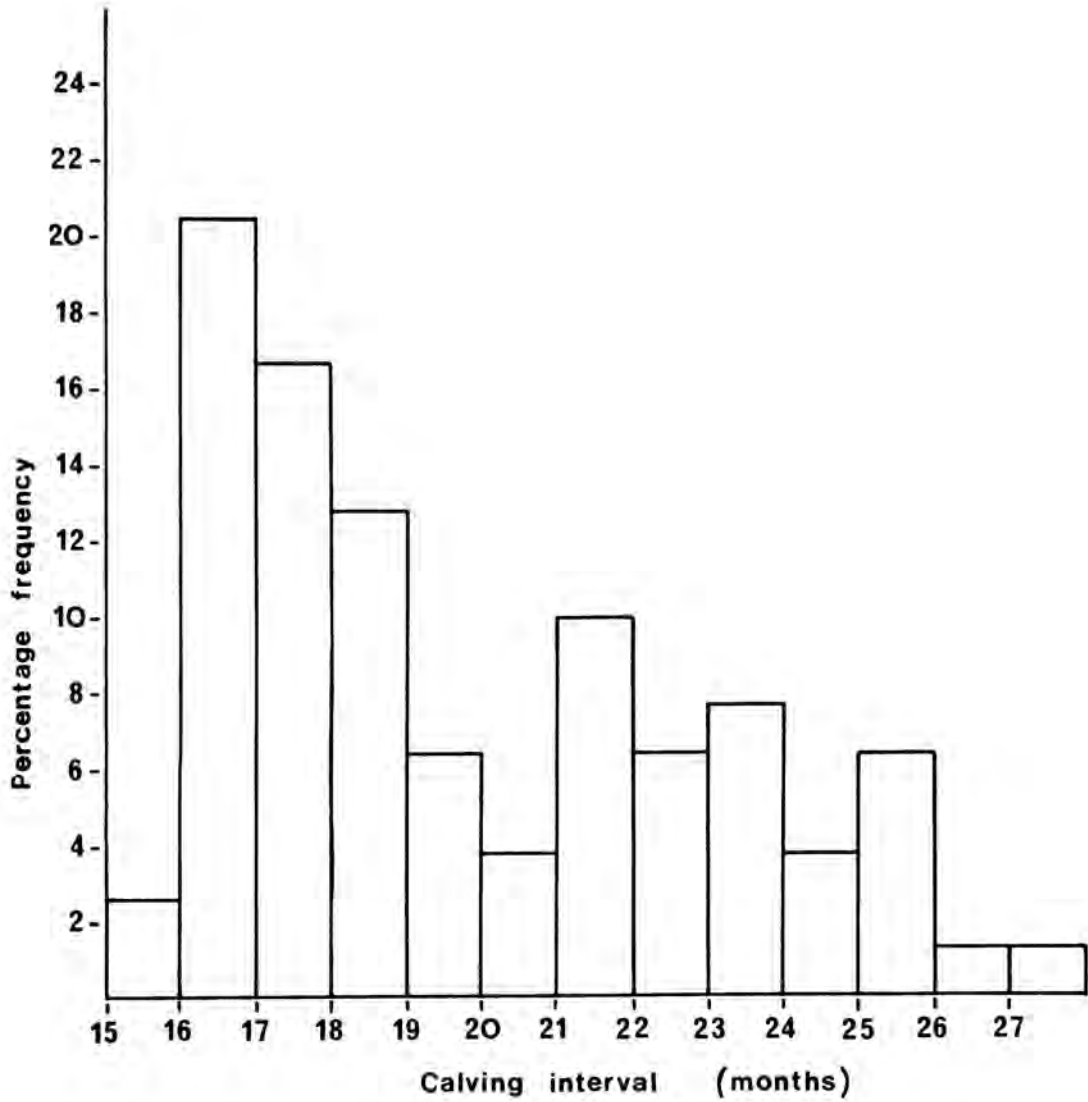


FIG. 33 — The frequency of calving intervals of different lengths (in months) for both wild and captive giraffe. (Data from various sources — see text).



normal duration of lactation in giraffe (presumably captive) is 10 to 12 months, Mason (1973) recorded a wild calf still suckling at 10 months and Dagg (1971) stated that giraffes suckle for more than a year. Based on this information (apart from Mason's record which in any case did not imply that lactation ceased at 10 months) it seems reasonable to assume that lactation does in fact last for 12 to 13 months. For purposes of estimating calf mortality it has been assumed that the udder of a female which lost her calf would soon become inactive, as happens in other species. Data for the estimation of calf mortality were available from 26 parous females (thus they had had an opportunity to lactate) of which 17 (65%) were pregnant; 14 (54%) were lactating; and 5 (19%) were simultaneously pregnant and lactating.

Grimsdell (1973b) describes a method of estimating calf mortality from the difference between normal (expected) and actual (average) lactation time. However for this method to be valid it is necessary to assume, among other things, that the *post partum* reconception interval in females which lose their calves does not differ from those which retain them. It will be argued below (Discussion - Calving interval) that this tenet is invalid in the case of giraffe and so this method cannot be considered. A second method of calculating calf mortality (Grimsdell 1973b) is based on the premise that if there was no calf mortality between succeeding pregnancies then all non-pregnant females would be lactating, because the *post partum* reconception interval (243d) is shorter than the lactation period (392d). The calf mortality could then be inferred from the proportions of non-lactating, non-pregnant to lactating, non-pregnant females. In the present sample there are no non-lactating, non-pregnant parous females therefore indicating no calf mortality. Finally Grimsdell (1973b) estimated calf mortality by comparing the proportion of females simultaneously pregnant and lactating with those which were pregnant but not lactating and which could therefore be assumed to have lost their calves. It could be expected that giraffe in Timbavati would be lactating for at least the first 5 months of pregnancy (based on *post partum* reconception interval of 7,9 months and lactating period of 13 months). In the sample there were six females less than 5 months pregnant. For practical purposes, a seventh female, 158d pregnant was also included. Of these seven animals, five were simultaneously lactating and pregnant while two were pregnant but not lactating, thus the calf mortality which can be inferred is  $(2/7) \times 100 = 28,5\%$ .

From the population composition data derived from the Timbavati sample of

1 007 animals it was found (Chapter 1) that 21% were calves (juveniles) and 11% were immature. These figures indicate a calf mortality of 48%.

## DISCUSSION

### ATTAINMENT OF SEXUAL MATURITY

The apparent early puberty in the majority of the captives is probably due partly to better nutrition and partly to the accurate recording of pertinent dates, and the late maturity of others might have been due to the absence of a male. This could unfortunately not be confirmed. No meaningful conclusions on the age of attainment of sexual maturity of giraffe females in the Timbavati could be reached on the slender evidence in one female of 5 years. It has been suggested, however, (Chapter 2), that Timbavati giraffe are subjected to seasonal nutritional depressions and it is well known that poor nutrition can delay the attainment of puberty in mammals (Sadleir 1969). Whether this is the reason for the apparent late maturity of wild giraffe remains to be shown. Field & Blankenship (1973) have recorded a pregnant female in Kenya which they considered to be less than 3y old (but age criteria are not given).

### THE OESTROUS CYCLE

Crandall (1964) records that a female giraffe in the New York Zoological Park was observed to be in oestrus six successive times at intervals of 19, 16, 14, 16, 17 and 16 d respectively with a mean period of  $16,3 \pm 0,7d$ . On the other hand, Lang (1955) observed a series of oestrous cycles of 12 to 15d and Nouvel (1958) states that non-pregnant giraffe come into oestrus at intervals of 14 d. No observations were made on the occurrence of oestrus in wild giraffe, however, the 46 precisely known mean calving intervals were plotted as histograms and a series of approximately regularly occurring peaks were found. It is interesting to postulate, therefore, that these peaks might be related to the amplitude of the oestrus cycle. The mean time interval between these mean calving interval peaks was  $18,1 \pm 0,9d$  ( $n = 13$  peaks). The duration of oestrus is about 24 hours (Crandall 1964). The observation of Wilson (1969) of a female being mated on two successive days, and a similar observation by J.M. Hofmeyr (*loc. cit.*) confirms that the giraffe's heat lasts for at least 24 hours and possibly a few hours longer.

In seven non-pregnant lactating females one ovary contained a large corpus albicans (presumably from the recent pregnancy) and the opposite ovary contained a regressing corpus luteum (CL) of cycle, presumably resulting from an infertile ovulation. This might have been due to a silent ovulation which could, therefore, be postulated to occur in giraffe. However, there is

also evidence (J.M. Hofmeyr *loc. cit.* ) of observed matings in wild giraffe which were not fertile. Of the wild artiodactyls only the Uganda kob *Adenota kob* has previously been observed not to conceive at oestrus (Morrison & Buechner 1971). Uterine involution usually takes 24 to 28 d in sheep (van Wyk, van Niekerk & Belonje 1972) and 20 to 30 d in Uganda kob, (Morrison & Buechner 1971) and if it can be assumed that giraffe would not take longer than these ungulates for uterine involution to be completed then incomplete involution cannot be invoked as a cause of the infertile matings other than during the immediate *post partum* oestrus. It is unlikely that this issue will be resolved until a study of CL morphology combined with behaviour of the animal is undertaken.

### ENVIRONMENT AND OESTRUS

#### Conceptions in relation to rainfall and temperature

It has been established by several studies that during the humid period the nutritional value of African savanna plants is at its maximum (Groenewald *et al.* 1967; McCullagh 1969; Joubert & Eloff 1971; Myre 1972). Studies on the chemical composition of the stomach contents of giraffe from Timbavati also showed that the protein content of their diet is highest during the humid months (November to March) and lowest during the dry months (September and October); gross energy content (heat of combustion) is also lowest during these two latter months (Table 9, Chapter 2). Many of the shrubs and trees upon which the giraffe feed put out their new leaves before the beginning of the wet season but this is not reflected in the protein values as it has been shown that the leaves of the first flush in several species contain less protein when they first appear than a few weeks later after the rains have commenced (Groenewald *et. al.* 1967, Joubert & Eloff 1971). There is thus a time lag from the commencement of leaf growth in October to the December/January conception peak which is probably due to the poor quality diet and the time required by the giraffe females to recover body condition after having calved during the preceding dry season and endured the physiological drain of lactation. It seems reasonable, therefore, to relate the favourable nutritional status of the vegetation, which is correlated with seasonal maxima of rainfall and temperature, with the conception peaks found in giraffe at this time. Similar conclusions were reached by Field & Blankenship (1973) in their studies on giraffe at Akira in Kenya who likewise found conception rates to be higher when good rains fell, and as a result of which plant production was higher, than during dry years. Similar findings concerning the effect of favourable nutrition on oestrus stimulation have been reported for a variety of species (Laws & Clough 1966; Laws & Parker 1968;

Hanks 1969b; Sadleir 1969; Joubert & Eloff 1971; Grimsdell 1973b).

The somewhat contradictory data from the Langjan Nature Reserve could be ascribed to opportunism on the part of the animals in an arid environment in response to the effect of early showers on the vegetation. However the sample size was small, the animals were only recently reintroduced to the area, and these data should therefore be treated with caution. The even spread of conceptions in the Taronga population could be expected as the level of nutrition of these animals is not subject to fluctuations as found in the wild. However this herd is intensively managed and these procedures may also affect breeding. Where numbers of giraffe births in captivity in other localities have been available for comparison such as Europe (Backhaus 1961), London and Taronga (Strahan, Newman & Mitchell 1973) and where nutrition is also constant there are no indications of seasonal peaks in calving comparable to that found in wild giraffe. Though the latter compilation shows more births occur in London between March and September. However captive animals are often separated and kept indoors during inclement weather and this and other aspects of their care and management (Gijzen 1958; Crandall 1964) may affect breeding. The temperature correlations for the Nairobi data have to be interpreted with caution as the range of mean monthly temperature fluctuations is only 3°C *cf.* 10°C for Timbavati/Hans Merensky. In both areas, however, the mean temperature of the month preceding conception is significantly correlated with conception. In the absence of experimental data the high correlation between conception and temperature at Timbavati/Hans Merensky is difficult to explain other than through its effect on plants. The data from Langjan and Zululand are too few for any meaningful statistical interpretation while those from Taronga do not come from a normal population.

#### Conceptions in relation to latitude

It is known that photoperiod is one of the factors that influences the appearance of new leaves and flowers (Kozlowski 1971, Longman & Jenik 1974). In a study on African savanna vegetation Hall-Martin & Fuller (1975) showed a peak leaf flush in trees and shrubs following the September equinox and giraffe make intensive use of these new leaves. However these new leaves contain less protein than a few weeks later after the rains have commenced as mentioned above and there is thus a time lag before the giraffe respond by improved body condition and oestrus. Thus it can be concluded that there is an indirect photoperiodic stimulus acting on female giraffe via the nutritional status of the vegetation and this agrees with the correlations

shown in Table 39, for Timbavati at least, for both one and two months before conception. It is difficult however to explain the correlation at Nairobi, except on spurious grounds, as seasonal variation in day length does not exceed 3 minutes. Moreover, at Timbavati, despite a correlation between photoperiod and conception there is no seasonal effect on male fertility.

#### Calving season

It is apparent from the literature reviewed by Ansell (1960a) and Mentis (1972) as well as from the data presented above that giraffe breed throughout the year. Other authors have made similar observations although several have reported seasonal peaks in calving. Berry (1973) confirms Ansell's reports (1960a, 1960b) that giraffe in the Luangwa Valley calve throughout the year, but he states that there is a peak calving period during or near the end of the rains. This would be approximately from January to about March or April (Dodds & Patton, 1968). Smithers (1971) reports that giraffe calve throughout the year, perhaps with a peak towards the end of the rains about May to June in Botswana. In the Kruger National Park where calving occurs throughout the year reports have been conflicting regarding peak calving periods. For instance, Stevenson-Hamilton (1947) indicates a peak from October to January. Pienaar (1963) cites peak periods during September to October and again in February to April; Fairall (1968) also reports two peak periods, one during February to March and the other from August to October.

The observation that African ungulates tend to produce their young at the most favourable time of the year for survival of the offspring (e.g. du Plessis 1972; Skinner, van Zyl & van Heerden 1973; Skinner 1973) is not apparently applicable to giraffe as oestrus is related to body condition in the adult female. Any selective disadvantage which might be expected to be exercised upon the young giraffe being born during the dry season might be mitigated to some extent by a long lactation period in this species.

#### PREGNANCY

##### Placentation and implantation

The placenta of the giraffe is similar to that found in most ruminants (Amoroso 1952). Although Dagg (1971) states that implantation occurs without delay, J.M. Hofmeyr (*loc. cit.*) found a 30-day old foetus not yet implanted. Kayanja & Blankenship (1973) also found several preimplantation foetuses in their sample of giraffe collected in Kenya. Ipsilateral implantation similar to that found in giraffe has also been reported in Sharpe's grysbok

*Aphicercus sharpei* (Kerr & Wilson 1967), blue wildebeest (Watson 1969) and tsessebe (Child, Robbel & Hepburn 1972). This contrasts with the commonly found right horn unilateral implantation of some other African ungulates such as the dikdik *Madoqua kirkii* (Kellas 1954), Uganda kob (Buechner 1961), lechwe *Kobus leche* (Robinette & Child 1964), impala (Mossman & Mossman 1962, Hofmeyr & Skinner 1969) and Defassa waterbuck (Spinage 1969) where transuterine migration occurs.

#### Calving intervals

The *post partum* reconception interval in giraffe as extrapolated from the data in Table 40 (4,4 to 5,4 months) and estimated from the proportions of pregnant to non-pregnant adults (7,9 months) is lower than that generally found among the other larger African mammals such as buffalo 7 to 13 months (Grimsdell 1973b), elephant 26 to 86 months (Laws 1969), white rhinoceros 7 to 12 months and black rhinoceros 9 to 15 months (Mentis 1972) and hippopotamus 9½ to 24 months (Laws & Clough 1966). If the pattern of peak conceptions in giraffe during the humid months (December to March) followed by a peak in births 15 months later (March to June) is a true reflection of the long-term pattern then it can be inferred that the mean *post partum* reconception interval would be 9 months resulting in a mean calving interval of 24 months. The difference between this estimate and the mean estimate of 19,9 months (Table 40) is most likely due to the influence of calf mortality resulting in an earlier return to oestrus, and thus a shortened calving interval. Evidence that this occurs in giraffe has been presented by Foster & Dagg (1972) who found that the calving interval is short (17 months, n = 5) if the calf was lost during the first month after birth, a little longer (21 to 22 months, n = 4) if the calf lived for about 3 months and longer still (22, 23 & 24 months respectively, n = 3) if the young survived. If body condition of the female, which is significantly influenced by lactation, (Smith 1959) is a partial determinant of whether oestrus and conception occurs, then these results are to be expected.

#### Lifetime production

A 20 y old pregnant female collected in Timbavati confirms the report of giraffe females breeding to at least 20 y of age (Dagg 1971) and the data in Table 41 raises the upper limit to 24 y, at least for captives. There is thus no suggestion of any cessation of reproductive activity in old female giraffe as found in elephants (Laws, Parker & Johnstone 1970).

## Twinning

The only other positive record of twinning in giraffe is cited by Dagg (1971) and refers to stillborn twins, having a combined mass of only 41kg, born in San Francisco in 1943. Other reports in the literature of females with twins (Shortridge 1934, Innis 1958, Dorst & Dandelot 1970) are most likely due to the nursery system of giraffe whereby a single female accompanies several young of the herd.

## Urinary hormones

The negative results obtained during this study do not confirm the findings of Wilkinson & de Fremery (1940). Short (pers. comm.)\* also recently examined urine from a near-term giraffe but was unable to demonstrate any gonadotrophic activity in it.

## CALF MORTALITY

When applied to a reasonably large sample Grimsdell (1973b) found his methods of estimating calf mortality to give reasonably consistent results. In the present case it would seem that the sample was far too small to give any meaningful estimate of calf mortality. In addition the calculated *post partum* reconception interval of 7,9 months is also based on scanty data and if very different would significantly influence any estimate of calf mortality derived from the abovementioned methods.

It would be most unusual to find a population of African ungulates in which there is no calf mortality (apart from the known predation losses) and even the estimate of 28,5% is low compared with the mortality rate derived differently (48%). Foster & Dagg (1972) estimated a calf mortality of up to 73% in the Nairobi National Park. From the proportion of calves to immatures in the Akira giraffe population given by Field & Blankenship (1973) a calf mortality of 46% can be calculated (26,5% calves, 14,3% immature). This figure agrees well with the 48% found for Timbavati calves. This latter figure is therefore regarded as being a reasonably close approximation to the actual mortality of giraffe calves in Timbavati. The data on calf carcasses recovered during the study period (Chapter 1) indicated that 90% of these deaths were due to predation.

A 48% calf mortality rate falls within the range found for some other African ungulates such as 30 to 60% in buffalo (Grimsdell 1973b), up to 80% in blue wildebeest (Talbot & Talbot 1963) and 40 to 80% in zebra (Smuts 1974).

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## CHAPTER 8

STRUCTURE AND FUNCTION OF THE OVARIES

## INTRODUCTION

Until the publication of reports by Kayanja & Blankenship (1973) and Gombe & Kayanja (1974) little information was available on the structure or function of the giraffe ovary. Kellas *et al.* (1958) had discussed the structure and possible function of ovaries in some foetal and prepubertal giraffes. Of particular interest was their finding of luteinized follicles and apparently normal "corpus luteum-like structures" in the late gestation foetus and in neonates. These features were discussed also by Perry & Rowlands (1962), Eckstein (1962) and Amoroso & Finn (1962). Mossman & Duke (1973) could report no further information on the ovaries of the giraffe.

The purpose of this study was, therefore, to investigate briefly the structure and function of the ovaries and to compare the findings with the literature on giraffe and other mammals.

## MATERIAL AND METHODS

Material was available from 29 mature parous females collected in the eastern Transvaal Lowveld, the Loskop Dam Nature Reserve in the southern Transvaal and the Daan Viljoen Game Park, South West Africa. In addition, the ovaries of four foetuses of different ages; one neonate; two calves <6-months-old; two immature animals, one 1-y-old and one 5-y-old; and one young sexually mature but non-parous female 6-y-old. Of the parous animals 21 were pregnant, six were not pregnant and the status of the remaining two was not known. The ages of only 22 of these females were determined. All of the non-pregnant adults were lactating.



The ovaries were removed as soon as the animals were eviscerated. Formalin (10%), Bouin's fluid or AFA fluid (Mosby, Cowan & Karstad 1969) were routinely used for fixation and specimens were stored in 10% formalin or 70% alcohol. The mass and dimensions of the ovaries were measured on returning to the field laboratory. They were later cut into slices 2 mm thick and the corpora lutea (CL), corpora albicantia (CA) - (brown, orange, orange-brown or bright yellow regressing CL) and follicles were counted. All bodies having at least one diameter of 2 mm or more were measured in three dimensions at right angles. In the case of CL and large follicles this was easily done on the sliced ovaries alone while in the case of smaller bodies some of the measurements were made on thinner sections with the aid of a micrometer eyepiece. As the follicles appeared distinctly spherical their volume was obtained by the method of Rowlands (1956) for measuring the volume of the CL of the guinea pig *Cavia porcellus*. This was based on the formula for the volume of a sphere ( $\frac{1}{6}\pi d^3$ ) and was calculated from the product of the three diameters X 0,523. In the cases where difficulty was experienced in obtaining a third diameter, an average diameter was obtained from measurements of two diameters at right angles as described by Rowlands & Heap (1966). Although the CL in giraffe is sometimes ovoid rather than spherical and the CA are usually irregular in shape the formula for a sphere was used for convenience or else only an average diameter was used. This latter measurement was calculated for all CL, follicles and CA and was obtained from measurements of two diameters (the greatest diameter, and the least diameter, taken at right angles to the greatest) as described by Rowlands & Heap (1966) and Mossman & Duke (1973). Slices from mature and prepubertal ovaries were routinely dehydrated, embedded in paraffin wax, sectioned at 5  $\mu$ m on a rotary microtome and stained with Delafield's haematoxylin and eosin, or with the trichrome stain (MSB) of Lendrum, Fraser, Slidders & Henderson

(1962) for subsequent histological examination. Entire foetal and calf ovaries were embedded and serially sectioned, every 10th or 20th section being mounted and stained as outlined above.

## RESULTS

### OVARY LOCATION, SIZE AND SHAPE

The position of the ovaries within the abdominal cavity varied with age and pregnancy. Thus in the immature animal they lay in the pelvic cavity. In adults they were found at the level of the pelvic brim but during early pregnancy they had moved forward and downwards as a result of the enlarging uterus to a position a few centimeters cranial to the pelvic brim, (opposite the junction of the third and fourth lumbar vertebrae) and in later pregnancy they were pulled a little deeper into the abdominal cavity. The uterine horns were helically coiled so that the tubal ends, and therefore the oviducts and ovaries were situated more caudally than much of the main portion of each horn. There was a partial ovarian bursa.

The quiescent ovaries were amygdaloidal in shape with a smooth, non-lobulated, non-fissured surface, and except for functional changes right and left ovaries were the same size (Plate 6). During pregnancy the ovary containing the corpus luteum of pregnancy was greatly enlarged and could be almost rounded in shape, when quiescent the ovaries were somewhat flattened. The total ovarian mass and dimensions (measured at right angles) at different ages and different stages of pregnancy are shown in Table 42. Large corpora lutea and mature follicles were usually easily discernible through the surface epithelium, and ovulation stigmata were conspicuous.

PLATE 6

Sliced ovaries from a giraffe in early pregnancy (145 d). Note the large numbers of vesicular follicles in the left ovary, especially in the other regions of the cortex (as in slices 1 & 5), a large vesicular follicle (vf) is labelled in slice 2 and a corpus albicans (ca) is indicated in slice 3. The right ovary contains the corpus luteum of pregnancy (cl in slice 4) which has a connective tissue core (ct in slice 7), Vesicular follicles are fewer than in the left ovary, some are indicated (vf) in slice 8. A corpus albicans (ca) is also present as shown in slice 5. Bouin, slices 2 mm thick, scale in cm.

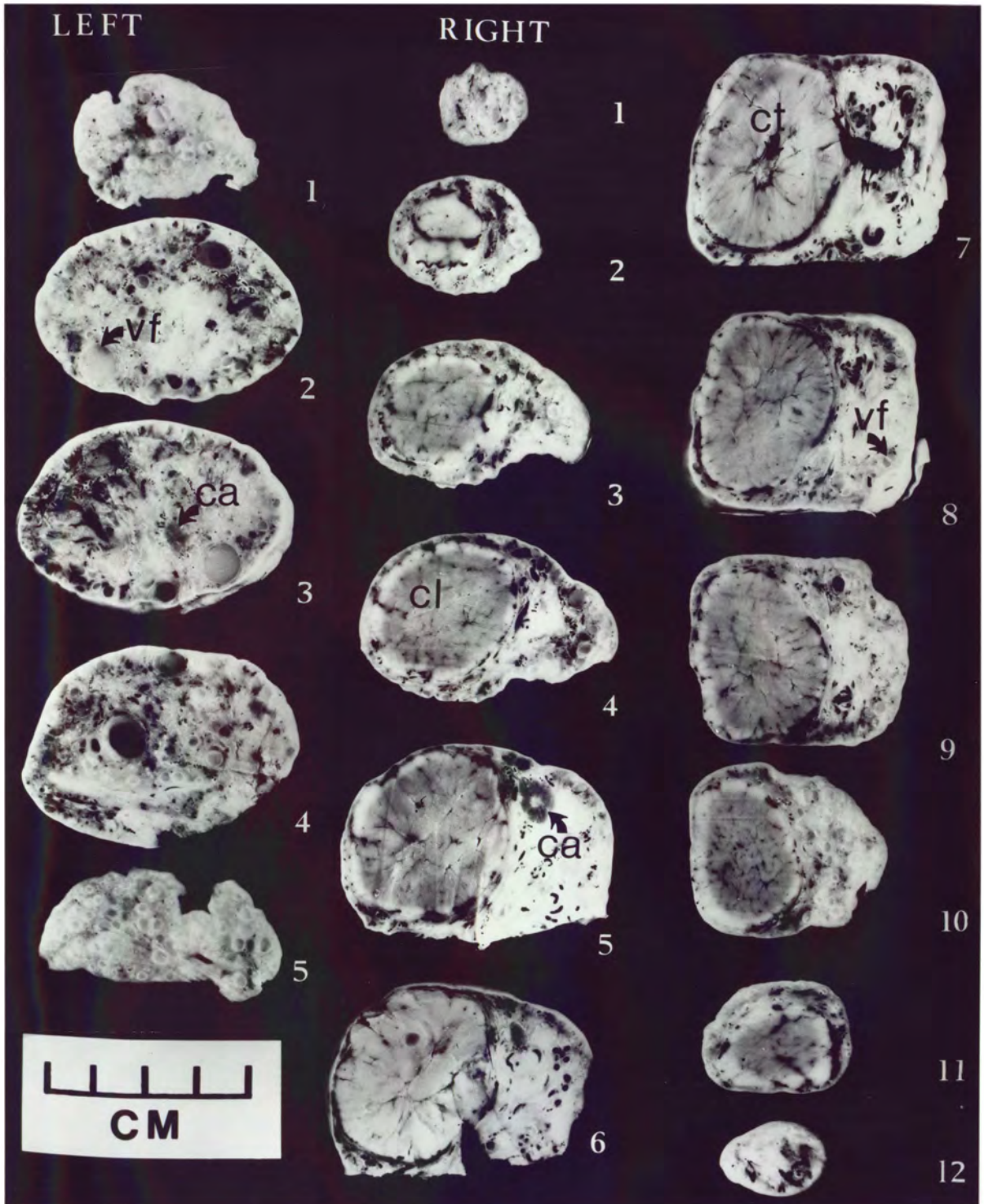


TABLE 42: MEAN DIMENSIONS AND MEAN MASS OF GIRAFFE OVARIES

Class	n	Dimensions (cm)	Mean mass (g) <sub>±</sub> S.E.
Foetuses (273 d, 274 d)	2	1,2 x 1,4 x 0,5	1,0
Foetuses (405 d, 414 d)	2	2,1 x 1,5 x 1,3	2,8
Calf (2 weeks)	1	2,2 x 1,5 x 1,0	2,4
Calf (2 months)	1	2,4 x 1,9 x 1,1	3,1
Immature (5 y)	1	3,3 x 2,2 x 1,6	8,0
Mature non-parous (7 y)	1	3,6 x 2,2 x 2,0	10,4
Adult non-pregnant	7	4,9 x 3,7 x 2,2	46,1 ± 3,0
Adult pregnant	22	5,4 x 4,0 x 2,7	75,5 ± 4,3

### OVARIAN STRUCTURE AND DYNAMICS

#### Regions of the ovary

The giraffe ovary, like that of other mammals (Mossman & Duke 1973), is divided into an outer cortex and an inner medulla. The surface germinal epithelium, a tunica albuginea of varying width and a broad zone of stroma containing oocytes, follicles, corpora lutea, corpora albicantia constitutes the ovarian cortex. The inner region is known as the medulla and contains the larger blood and lymph vessels and some interstitial gland tissue in a more fibrous stroma.

#### The prenatal ovary

The four pairs of foetal ovaries available for study were 273 d, 274 d, 405 d and 414 d old respectively. The two younger foetuses had features

in common and they are discussed together, as are the two older ones. Terminology follows Mossman & Duke (1973).

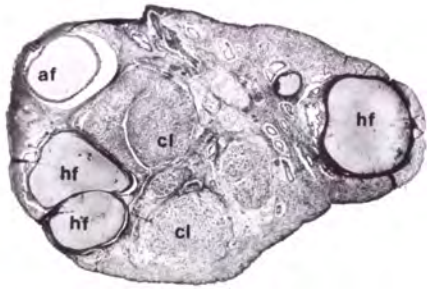
#### The 273/274-d-old foetal ovary

The giraffe ovary, like that of other mammals, is covered by a single layered surface germinal epithelium consisting of cuboidal cells resting on a basal lamina. In foetuses of this age the cells were 5,4- 6,5  $\mu\text{m}$  high. Subsurface crypts or invaginations of the surface epithelium commonly found in carnivores, some primates and rodents (Mossman & Duke 1973) and also reported as occurring in impala (Kayanja 1972) were not found in giraffe. The germinal epithelium did, however, have shallow indentations often associated with 'egg nests' of naked ova.

The tunica albuginea was clearly distinguishable in giraffe ovaries and in the present foetal material it was 28 - 50  $\mu\text{m}$  wide. It is chiefly composed of reticular fibrin and collagen fibres and stained very clearly with the MSB stain as a predominantly blue (collagen) zone. Primary oocytes were commonly found in the tunica albuginea of these foetal ovaries; though they were concentrated in the cortex. The cortex was clearly demarcated from the medulla (Plate 7, Fig. 3) and was divided into three zones. The outer zone of the cortex, contiguous to the tunica albuginea was packed with masses of mostly naked primary oocytes which were from 20 - 27  $\mu\text{m}$  in diameter (Plate 8, Fig. 1). In many cases the first cells of the developing epithelial envelope were present. Deeper to this zone was an intermediate zone where most oocytes had been surrounded by a single layer of follicular epithelium to form primordial follicles. These squamous epithelial cells were  $< 4 \mu\text{m}$  in their greatest diameter at this early stage of their development. The next zone (further into the cortex) contained more stromal tissue with fewer oocytes, most of which were in

PLATE 7

- Fig. 1. Section through an ovary of a 273-d-old giraffe foetus showing a large atretic vesicular follicle (af), large haemorrhagic follicles (hf). Several corpora lutea (cl) can be seen in the medulla. Bouin, 5  $\mu$ m, H & E, X 7.
- Fig. 2. Section through an ovary of a 2-week-old giraffe showing numerous corpora lutea (cl) and characteristically compressed vesicular follicles (arrowed). Bouin, 5  $\mu$ m, H & E, X 8.
- Fig. 3. Section through an ovary of a 6-month-old giraffe showing clear division between cortex (C) and medulla (M) and medullary follicles and corpora lutea. Bouin, 5  $\mu$ m, H & E, X 5.
- Fig. 4. Section through an ovary of a 6-y-old giraffe showing large corpora albicantia (ca) which are the remains of the corpora lutea of the prepubertal period with their characteristic wide collagen capsule. Several large follicles are also present (e.g. lower left). Bouin, 5  $\mu$ m, H & E, X 5.
- Fig. 5. Section through an ovary of a 7-y-old adult giraffe showing the complete disappearance of the corpora lutea of the prepubertal period and many large vesicular follicles. The cortex and medulla are distinct. Formalin, 5  $\mu$ m, H & E, X 4.



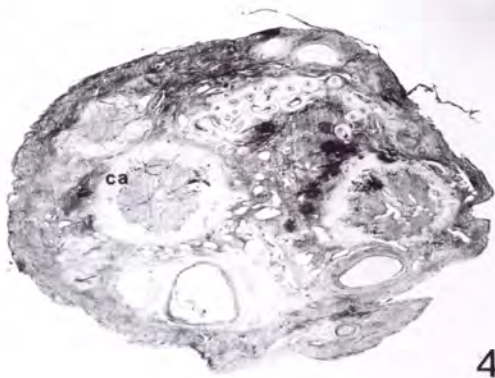
1



2



3



4



5



primordial follicles or the epithelial cells were simple low and columnar thus forming primary follicles. The first secondary follicles were also found here. The medulla at this stage was crowded with primary, secondary and vesicular or Graafian follicles. The secondary and vesicular follicles were surrounded by a well differentiated theca interna of glandular cells but the theca externa was rather poorly differentiated. Most of the vesicular follicles were in various stages of atresia demonstrated by pyknotic nuclei in the membrana granulosa cells (follicular epithelium) sloughing and folding of the granulosa layer, granulosa cells and cellular debris in the liquor folliculi. Well developed rete ovarii tubules were found in the region of the hilus (Plate 8, Fig. 8). The tubules were 40 - 83  $\mu\text{m}$  in diameter and no glandular tissue was found associated with the rete.

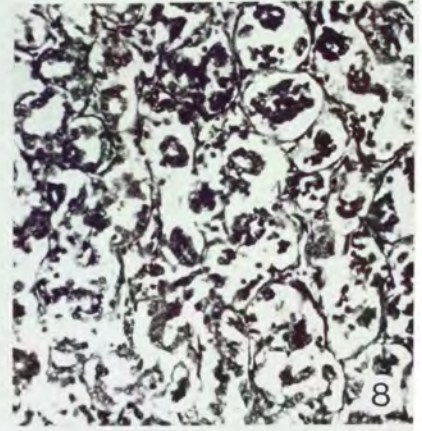
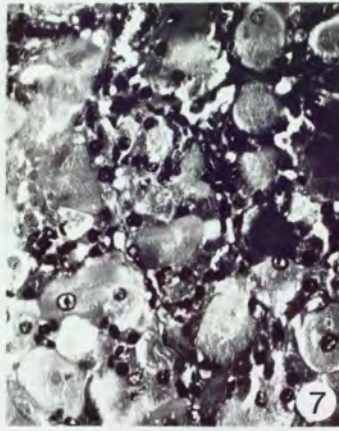
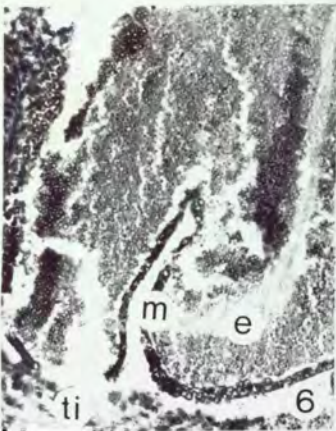
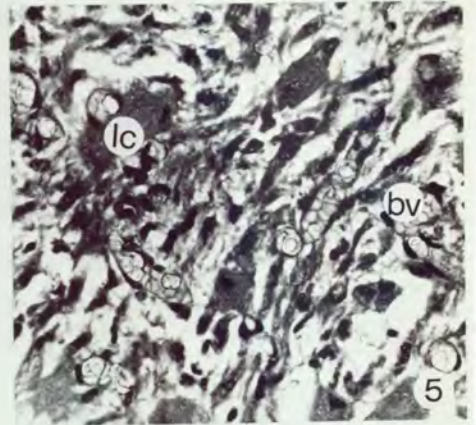
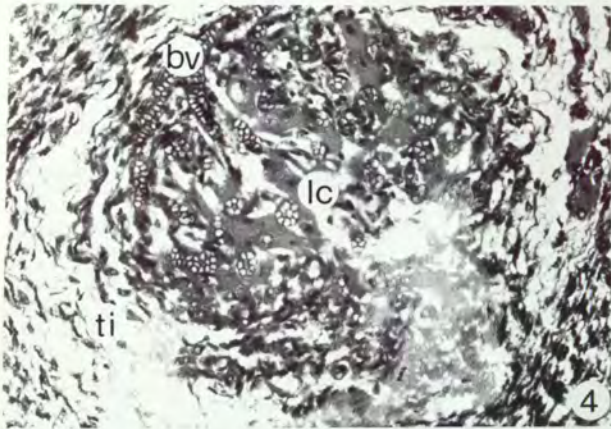
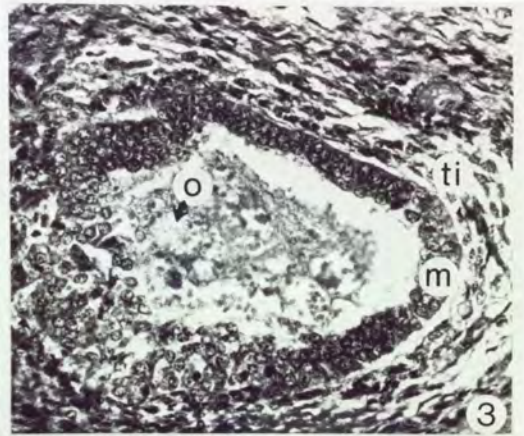
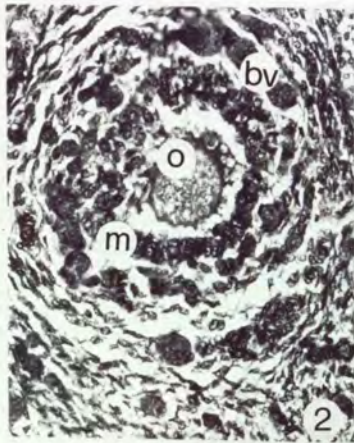
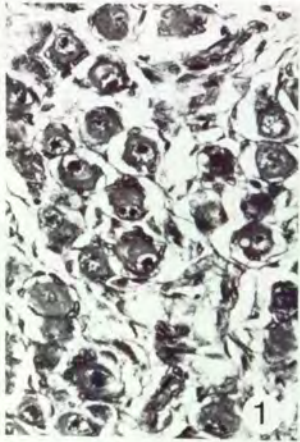
A prominent feature of both these pairs of ovaries was the presence of several large haemorrhagic follicles in each ovary (Plate 7, Fig. 1). The largest of these was 3,1 mm in diameter. The corpora lutea which are a feature of foetal and prepubertal giraffe ovaries (Kellas, *et al.* 1958, Kayanja & Blankenship 1973) were not found in the older of these foetuses, but the younger had four CL in the medulla of one ovary. These glands contained large polyhedral lutein cells like those of adult CL. The lutein cells were much smaller than those found in CL of pregnancy and were from 12 - 20  $\mu\text{m}$  in diameter while their nuclei varied from 4,1 - 5,7  $\mu\text{m}$  in diameter. Large amounts of interstitial cells and reticular fibres were also found and the glands were richly supplied with blood vessels. As these were true CL (Gombe & Kayanja 1974) there was no thecal gland but a distinct fibrous thecal capsule was developed, probably from the theca externa. Septation was not as conspicuous in these foetal CL as in adult CL. However there were masses of interstitial



PLATE 8

Sections of foetal and immature giraffe ovaries.

- Fig. 1. The outer zone of the cortex of a foetal (273 d) ovary showing numerous naked oocytes and developing primordial follicles. Bouin, 5  $\mu\text{m}$ , H & E, X 240.
- Fig. 2. A follicle in the cortex of a foetal (414 d) ovary in which antrum formation is advanced. The theca interna is occupied by hyperaemic blood vessels (bv), the membrana granulosa (m) has pushed into the antrum (upper left) and the oocyte (o) is degenerating. This is thought to be a stage in the development of a foetal corpus luteum. Bouin, 5  $\mu\text{m}$ , H & E, X 240.
- Fig. 3. A follicle in the cortex of a foetal ovary (414 d) showing invasion of the antrum (left) by cells from the membrana granulosa (m). An oocyte (o) is still present but regressing and the theca interna (ti) is apparently intact. Bouin, 5  $\mu\text{m}$ , H & E, X 240.
- Fig. 4. A later stage in the luteinization of a follicle in a foetal (414 d) ovary. The blood vessel network (bv) has ramified into the antrum which is by now occluded by cells apparently of thecal as well as granulosal origin. Many of their cells are luteinized (lc) and the theca interna (ti) is no longer intact. Bouin, 5  $\mu\text{m}$ , H & E, X 240.
- Fig. 5. Same section as Fig. 4 showing detail of luteal cells (lc), blood vessels (bv) packed with erythrocytes and other cells in the developing corpus luteum of the foetal ovary. Bouin, 5  $\mu\text{m}$ , H & E, X 384.
- Fig. 6. Section through the wall of a large follicle in a foetal (273 d) ovary. The theca interna (ti) is still intact but the membrana granulosa has broken away and has become folded into the antrum which is filled with blood (e). It is thought that this represents a stage in the development of a haemorrhagic follicle. Bouin, 5  $\mu\text{m}$ , H & E, X 153.
- Fig. 7. Detail of a corpus luteum in a 2-week-old calf, large primary luteal cells with rounded nuclei as well as other cells can be seen. Bouin, 5  $\mu\text{m}$ , H & E, X 240.
- Fig. 8. Section through the hilus of a foetal (273 d) ovary showing rete ovarii tubules. Bouin, 5  $\mu\text{m}$ , H & E, X 153.



tissue which formed a network ramifying throughout the body.

Another conspicuous feature of these ovaries and older ones was the great development of hyperaemic blood vessels mainly in the theca interna of secondary and vesicular follicles (Plate 8, Figs. 2 & 4) also reported by Kayanja & Blankenship 1973. There was evidence from many follicles of these blood vessels rupturing the membrana propria (Plate 8, Fig. 4) particularly in secondary follicles. Many examples were seen of vesicular follicles with the antrum invaded and occluded by masses of granulosa cells and blood vessels (Plate 8, Figs 2 & 3 & 5); the remains of the liquor folliculi were still present confirming the identity of the follicle in some cases. It seems reasonable to postulate that this condition could lead to the development of a corpus luteum. The haemorrhagic follicles showed no trace of a granulosa cell layer and this is probably due to the separation of this layer from the theca (Plate 8, Fig. 6) during the period when the antrum is filled by blood. In other cases the loss of the granulosa layer has apparently resulted in a cystic follicle. Interstitial gland tissue was not positively identified.

#### The 405/414-d-old foetal ovary

These ovaries had several characteristic features. One of the most conspicuous of these was the marked decrease in the numbers of primary oocytes in the cortex. In addition, many oocytes were shrivelled and degenerate. With fewer oocytes present the reticular fibre network was most conspicuous. The fibres lay parallel to the ovarian surface in the tunica albuginea but were orientated at right angles to the surface deeper in the cortex. This arrangement influenced the orientation of the naked ova and the primordial follicles. Those lying superficially in the tunica al-

buginea were orientated parallel to the ovarian surface and those deeper in the cortex were orientated at right angles to the surface. In general the indentations of the surface germinal epithelium were deeper and more numerous than found in the earlier foetuses.

In these ovaries, in contrast to the earlier two, primary and secondary follicles were almost entirely absent. As in the earlier material most of the few vesicular follicles were atretic. The largest vesicular follicle was 6,2 mm in diameter. These large follicles contained apparently normal liquor folliculi and the membrana granulosa was mostly narrow, but a few had a glandular theca interna like that found in the younger material.

Corpora lutea were more common in these ovaries, each one containing at least four with a maximum of nine, the largest of which having a diameter of 3,4 mm. Many of the CL were compressed and flattened. The primary lutein cells fell into the same size range as those of CL of pregnancy. Individual cells within the same CL varied from active looking to regressed, though most of the CL could be classified as regressing. Active cells had a uniform cytoplasm, round nucleus and one or two clearly distinguished nucleoli. Regressing cells had vacuolated cytoplasm with shrunken and pyknotic nuclei. Septation in these CL as in the younger foetuses was not as distinct as in adults. Most CL had a fairly large central core of connective tissue and large blood vessels. These blood vessels and the network interspersed among the cells were much more conspicuous than those of adults. The bore of these vessels commonly exceeded 60  $\mu$ m. Some of the CL had a network of hyperaemic blood vessels in the thecal capsule, similar to that observed in secondary and vesicular follicles of the younger material. No corpora albicantia were recognised in any of the foetal ovaries examined.

The prepubertal ovary

Calves 2-weeks / 6-months-old

The ovaries of a 2-week-old calf, a 6-week-old calf and a 6-month-old calf were sufficiently similar to each other, and different from older immature animals to justify being described together.

The surface germinal epithelium was not as conspicuous as in the foetal material and was already apparently becoming attenuated. The tunica albuginea was conspicuous. The numbers of oocytes in the cortex apparently even further reduced as also were the numbers of primordial follicles present. Well developed secondary and vesicular follicles with wide thecae interna were found once more in the cortex but many were compressed (Plate 7, Fig. 2). Masses of thecal type interstitial gland tissue were also present (Plate 9, Fig. 8) and rete ovarii tubules were conspicuous. The largest vesicular follicles were 4,8 mm, 1,9 mm, and 0,8 mm in diameter from the youngest to oldest animals respectively. Biovular follicles were found in the two older animals.

All these ovaries contained corpora lutea (e.g. Plate 7, Figs. 2 & 3), the most numerous being 16, but most were small and the largest (in the oldest calf) was 9,0 mm in diameter. The CL, especially of the older animals, had distinct septae as found in adults (Plate 7, Fig. 2). Luteal cells varied from 26 - 33  $\mu\text{m}$  in diameter with nuclei from 10,1 - 11,9  $\mu\text{m}$  in diameter and were histologically similar to those of adults (Plate 8, Fig. 7). No corpora atretica were found. The centre of the medulla, especially in the older animal (Plate 7, Fig. 3), was a mass of blood vessels with only a few scattered CL and masses of thecal type

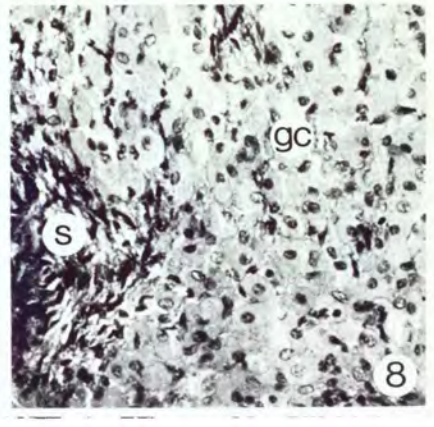
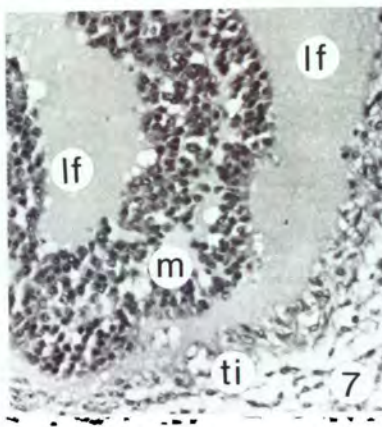
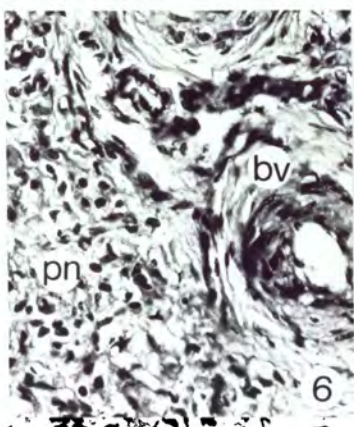
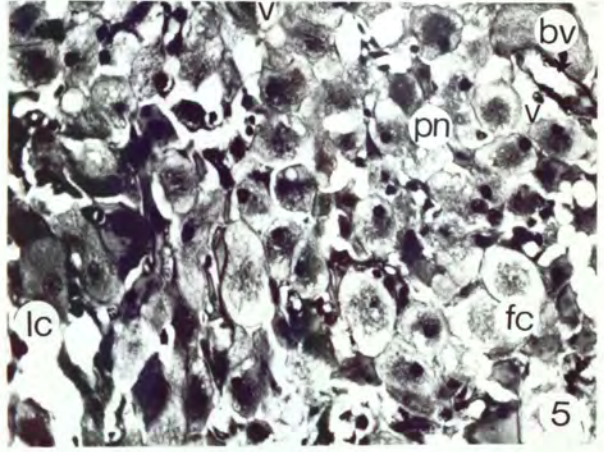
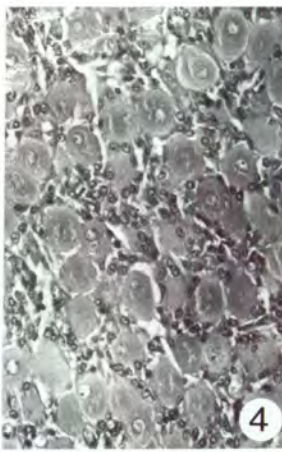
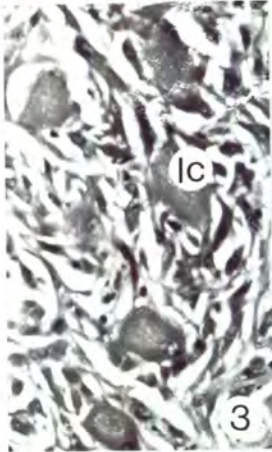
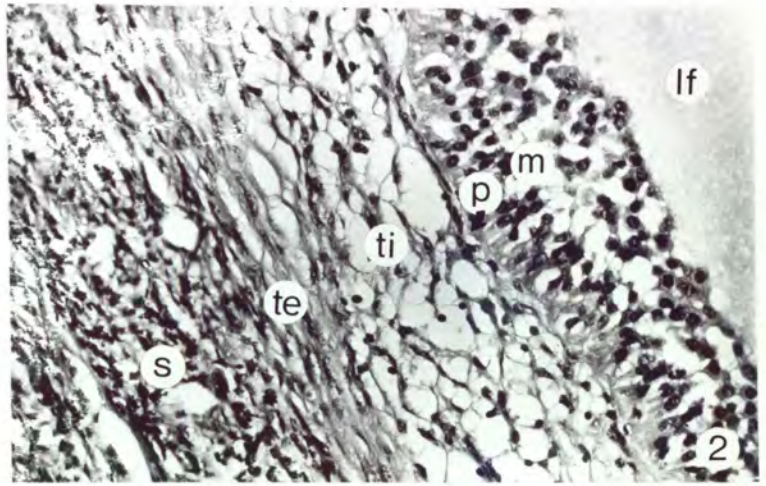




PLATE 9

Sections of adult giraffe ovaries

- Fig. 1. Section through outer zone of adult ovary to show reticular fibres in tunica albuginea (ta) and outer zone of cortex (c) with no primordial follicles. The surface germinal epithelium (sge) is also shown. Bouin, 5  $\mu$ m, H & E, X 270.
- Fig. 2. Section through wall of vesicular follicle undergoing atresia in adult ovary. Section passes through liquor folliculi (lf), membrana granulosa (m) with many vacuolated cells, membrana propria (p), vacuolated theca interna (ti), theca externa (te) and ströma (s). Bouin, 5  $\mu$ m, H & E, X 270.
- Fig. 3. Early corpus luteum of pregnancy, Class A, showing irregular shaped primary luteal cells (lc) Bouin, 5  $\mu$ m, H & E X 270.
- Fig. 4. Corpus luteum of cycle showing well differentiated luteal cells with active nuclei and supporting cells. Bouin, 5  $\mu$ m, H & E, X 154.
- Fig. 5. Late corpus luteum, Class D, showing mostly degenerating luteal cells with pyknotic nuclei (pn), frothy cytoplasm (fc), and large vacuoles (v). A degenerating blood vessel (bv) is also shown and a single luteal cell with an active nucleus (lc). Bouin, 5  $\mu$ m, H & E, X 270.
- Fig. 6. Early corpus albicans with shrivelled, degenerated luteal cells containing the dark staining remains of nuclei (pn) and hypertrophied blood vessels (bv). Bouin, 5  $\mu$ m, H & E, X 270.
- Fig. 7. Wall of vesicular follicle in atresia. The membrana granulosa has been sloughed off from the theca interna (ti) and follicular liquor (fl) has penetrated between the membrana and theca. Bouin, 5  $\mu$ m, H & E, X 154.
- Fig. 8. Interstitial gland cells (gc) in the medullary stroma (s) of the ovary of a 6-month-old calf. Bouin, 5  $\mu$ m, H & E, X 246.



interstitial gland tissue. The few medullary follicles found were atretic.

#### Immature animals 1-y to 5-y-old

The surface germinal epithelium cells were even more attenuated than those of the younger animals. The surface of the ovary in the 5-y-old animal was deeply indented. Few oocytes were in evidence, and most were degenerating. A few small atretic vesicular follicles were found in the younger animal, but the ovaries of the older animal contained many vesicular follicles which were mostly compressed and elongated, atretic but with conspicuously wide and well developed thecal glands. Although many CL were found, most of the luteal cells in both animals were regressing and most were extensively vacuolated. The largest CL present was 3,9 mm, in diameter (in the younger animal) and the largest vesicular follicle was 7,4 mm (in the older animal). Several small corpora albicantia were found in the ovaries of the older animal.

The ovaries of the 5-y-old animal were smaller than those of mature animals and there was no indication that ovulation had yet occurred. It was therefore concluded that this animal was not yet sexually mature.

The mature ovary

#### Animals 6-y-old

The ovaries of three animals in this age class differed conspicuously from all other ovaries, prepubertal or mature, in possessing a broad band of fibrous material surrounding all the degenerating multiple CL of the earlier period (Plate 7, Fig. 4). This fibrous zone was predominantly collagenic and was characterized by thick-walled blood vessels. The luteal cells were all in an advanced stage of regression

as evidenced by pyknotic nuclei, a cytoplasm which no longer stains well; empty, thick-walled blood vessels and extravasated erythrocytes; numerous vacuoles in CL cells, and the matrix of the corpus was dominated by fibrous connective tissue. These bodies were therefore corpora albicantia.

In all other respects the ovaries of these animals were similar to those of other parous adults. In the case of pregnant 6-y-old females the CL of pregnancy was the same as of older animals.

#### Parous adults

The adult giraffe ovary differed little from that of other artiodactyls as discussed by Mossman & Duke (1973). The main features found were:

##### 1. Surface germinal epithelium and tunica albuginea

The surface germinal epithelium was attenuated (Plate 9, Fig. 1) and in some cases appeared to have been torn off during processing. There were few indentations. The tunica albuginea was prominent and characterized by its composition of mostly reticular fibrous tissue, orientated parallel to the ovarian surface (Plate 9, Fig. 1).

Oocytes were found only rarely in the adult tunica. The outer zone of the cortex, just below the tunica albuginea was clearly differentiated. The matrix consisted predominantly of reticular fibres orientated at right angles to the ovarian surface. The shrivelled remains of oocytes and primordial follicles could be clearly seen in this outer zone (Plate 9, Fig. 1). Deeper into the cortex primordial and primary follicles were present, but not in quantity. The deepest zone of the cortex contained mostly developing or atretic vesicular follicles

(Plate 7, Fig. 5). Where vesicular follicles were close to the surface the deflection of reticular fibres around them resulted in the formation of thecal cones similar to those described in the impala ovary by Kayanja (1972).

## 2. The Follicles

The structure of the vesicular follicle was similar to that in other mammals. The oocyte had a zona pellucida and a *cumulus oophorus*. The oocyte and cumulus was eccentrically located within the follicle and was in contact with the membrana granulosa. The membrana granulosa was several cell layers thick and the basement membrane was distinguishable. A well developed thecal layer was present with a glandular theca interna and fibrous theca externa. A section through the wall of an atretic vesicular follicle is shown in Plate 9, Fig. 2. Anovular follicles were occasionally found, but were usually atretic. Haemorrhagic follicles, common in foetal ovaries were not found in mature ovaries.

Atresia occurs in giraffe ovaries much as in other mammals (Mossman & Duke 1973). Granulosa cells have been found having sloughed off and drifted into the liquor folliculi; or a lifting and folding of the intact membrana granulosa can occur, as shown in Plate 9, Fig. 7. Pyknotic nuclei in granulosa cells are generally indicative of atresia as are degenerating oocytes.

The number of visible vesicular follicles increased after 6 y and declined steadily after the age of 10 y as shown by those animals whose ages were determined (Fig. 34a). The oldest animal in the series (20 y), having the least number (24) of visible ovarian follicles present. More follicles were found in pregnant females than in non-pregnant females

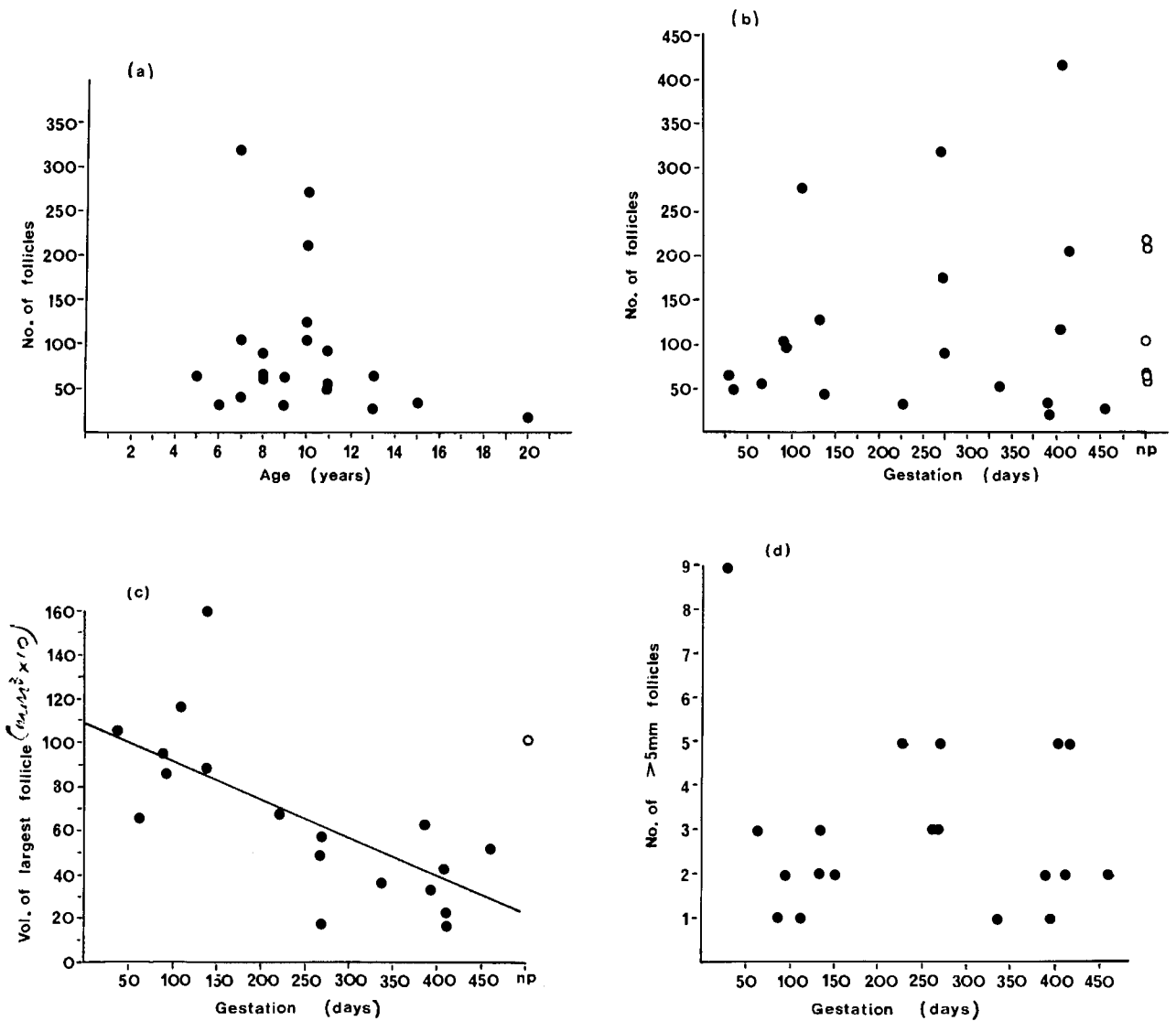


FIG. 34 — Number and size of vesicular follicles in relation to age of the female and gestation age. (a) No. of follicles at age of female, (b) No. of follicles at gestation age, (c) volume of largest follicle at gestation age, (d) No. of >5 mm follicles at gestation age. Number and mean volume of largest follicle, in non-pregnant (np) females also indicated (o).

(mean of  $134,3 \pm 26,7$  *cf.*  $108,1 \pm 29,5$ ) but this difference is not significant ( $P < 0,50$ ). Follicles were present at a reasonably constant rate throughout gestation (Fig. 34b), the apparent increase close to term is not statistically significant. The mean number of follicles per pair of ovaries for five females with a gestation age of 390 - 414 d was compared with five females with a gestation age of 87 - 135 d and no significant difference was found. ( $129,6 \pm 39,8$  and  $159,2 \pm 72,5$  follicles respectively,  $P < 0,05$ ). The small number of follicles (27) in the 454 d pregnant female was perhaps related to the age of the animal (13 y). With advancing gestation the volume of the largest follicle (Fig. 34c) decreased significantly, but the number of follicles  $\leq 5$  mm did not change (Fig. 34d). The volume of the largest vesicular follicle found was  $1600 \text{ mm}^3$ , having a mean diameter of 14,8 mm. The regression equations for the volume of largest follicle in  $\text{mm}^3$  (Y) against gestation age in days (X), is  $Y = -1,757 X + 1078,2$  ( $r = -0,703$ ;  $P < 0,001$ ). The regression equation for the largest follicle diameter in mm (Y) against gestation age in days (X) is  $Y = 0,110 X + 133,4$  ( $r = -0,761$ ;  $P < 0,001$ ).

### 3. The Corpus Luteum

The corpora lutea of the ovarian cycle in the giraffe were significantly smaller than the CL of pregnancy. *viz.*  $20,0 \pm 2,0$  mm *cf.*  $37,0 \pm 1,2$  mm in diameter ( $t = 6,906$ ; d.f. = 18;  $P < 0,001$ ). A section of a CL of cycle is illustrated in Plate 9, Fig. 4. Corpora haemorrhagica (CL with central blood clot) were not found in the present study. Accessory corpora (CL developed from luteinization of unruptured follicles) were common and no evidence for secondary CL (CL produced from ovulation during pregnancy) in this species was found. The CL in the giraffe was confined within the

ovary and the whole ovarian surface enlarged around it, thus retaining a smooth outline (Plate 6). The CL had a connective tissue core (Plate 6) in its early stages enclosing a small cavity which was later filled by lutein cells. The typical mature CL was a solid structure (Plate 6). Septa of connective tissue of varying size and composed of collagenous fibres and stromal fibroblasts radiated from the periphery to the centre of the CL. Blood vessels and lymph capillaries were typically associated with these septa. Kayanja & Blankenship (1973) who also described septation in the giraffe CL suggested that the septa indicated the original invasion path of the thecal tissue during CL formation.

There are two types of luteal cells in the mature giraffe CL (Kellas *et al.* 1958) similar to those found in other artiodactyls (Mossman & Duke 1973). These are the typical large primary luteal cells which are usually spheroidal and the smaller, usually irregularly shaped secondary luteal cells. Several workers (some reviewed by Morrison 1971) have investigated the changes in the morphology and size of luteal cells which accompany growth and regression of the CL. Such detailed investigation is beyond the scope of the present study and instead, a classification based on the criteria of Weir (1967) has been prepared. This classification is not definitive but merely serves to group together those CL which have similar features. Four types of CL of pregnancy have been recognized and are described below, the dimensions of the primary luteal cells and nuclei and other details are given in Table 43.

#### Class A

The primary luteal cells were mostly irregular in shape and sparsely scattered among supporting cells and differentiating granulosa cells



which were not closely apposed (Plate 9, Fig. 3). The supporting cells were spindle shaped or irregular with eccentric nuclei. The cytoplasm was finely granular, homogenous and not vacuolated. Nuclei were mainly situated eccentrically but could also be central, they contained one or more nucleoli, the chromatin was usually finely granular and dispersed to the nuclear membrane. Many blood and lymph vessels were present throughout. Primary luteal cell dimensions and the age of the CL described are given in Table 43. Class A CL were present during the phase of luteal cell proliferation and the rapid increase in CL size. These CL were equivalent to the Type I and Type II CL of Weir (1967).

TABLE 43: DIMENSIONS OF PRIMARY LUTEAL CELLS FROM CL OF PREGNANCY IN GIRAFFE

Class	Conception age (d)	n	Cell diameter (µm)	Nucleus diameter (µm)	Nucleus to cytoplasm ratio	Significant size differences	
						Cell size	Nucleus size
A	30-98	3	27,2 ± 0,4	7,8 ± 0,2	3,5	—	—
B	116-150	4	27,3 ± 0,5	8,1 ± 0,2	3,4	—	>A P < 0,02
C	226-274	4	30,1 ± 0,6	8,3 ± 0,2	3,6	>B P < 0,001	n.s.
D	390-454	5	35,9 ± 0,6	8,4 ± 0,2	4,3	>C P < 0,001	n.s.

#### Class B

The primary luteal cells in this category of CL were usually well formed and spheroidal in outline. The first signs of vacuolation of the cytoplasm were seen and in some cells there were so many vacuoles forming that the cytoplasm had a frothy appearance. Lipid droplets were common in the cytoplasm. Cells were closely apposed and blood and lymph vessels and septa were less conspicuous. Nuclei appeared largely active, rounded, but occasionally pyknotic. Nuclear chromatin was partly dispersed from

the membrane. The nuclei of the luteal cells were significantly larger than those of Class A but the cells were not (Table 43). This is difficult to explain as the CL at this stage were smaller in size than earlier (this aspect is discussed further below). This category of CL seems equivalent to Type IIIa of Weir (1967).

#### Class C

Primary luteal cells were still spheroidal with distinct margins. The small vacuoles and lipid droplets could still be seen in the cytoplasm and larger vacuoles (larger than 10  $\mu\text{m}$  in diameter) were occasionally found. The nuclei were beginning to lose their rounded outline and were frequently irregular, the chromatin material was reticulately distributed throughout the nucleus. Many primary luteal cells with darkly staining cytoplasm and pyknotic nuclei were found. This category included Type IIIb CL of Weir (1967).

#### Class D

The primary and secondary luteal cells and supporting cells were no longer all regularly shaped and many were extremely irregular with wrinkled, partly disintegrated walls. The cytoplasm was extensively vacuolated and in most cells was distinctly granular in appearance and reduced to strands around the abundant vacuoles. Nuclei were mostly pyknotic, shrunken and often amygdaloidal, if not so then the chromatin was distinctly reticulate. Most nuclei stained darkly. Blood vessels showed evidence of thickening and even occlusion in the older CL, extravasated erythrocytes were also found. A section through a 405-d-old CL in which most of these features are present including some active luteal cells and some with frothy cytoplasm is shown in Plate 9, Fig. 5. The primary luteal cells had reached

their maximum size prior to their regression (Table 43). The CL in this category corresponded to Type IV of Weir (1967).

The limited data available indicated very rapid development of the CL following ovulation. The lumen was completely occluded by granulosa and luteanized cells by 30 d post-conception and the CL increased in size to about 50 d. Then followed a steady decrease in size over the next 100 d. At about mid-gestation the CL again increased in size reaching a maximum at term. This interpretation of CL growth is somewhat speculative in view of the small sample size but is supported by the changes in CL mean diameter (Fig. 35a), CL volume (Fig. 35b) and mass of the ovary containing the CL of pregnancy (Fig. 35c), but individual luteal cells did not decrease in size when the total CL size was decreasing (Table 43). Two linear regression equations for CL diameter from 50 - 150 d and 200 - 454 d were computed and these are shown in Fig. 35a. The equation of the line (1) showing decreasing CL size from 50 - 150 d is:

$$Y = -0,174 X + 56,3 \quad (r = -0,869; P < 0,05)$$

where Y is CL mean diameter and X is gestation time. The ascending phase of CL development from 200 - 454 d is described by a line (2) where  $Y = 0,049 X + 20,5$  ( $r = 0,729; P < 0,02$ ). The regression lines intersect at about 160 d of gestation. The distribution of the points representing CL volume and ovary mass were not as clearly linearly distributed. Polynomial regressions were therefore calculated up to the fourth degree and are plotted in Fig. 35b & c.

Degeneration of the CL occurred rapidly after parturition. The relative size of a regressing CL (strictly CA) in an early *post partum* female is also indicated in Fig. 35<sup>a</sup> & b.

Multiple CL were common but more frequently found in young females (Fig. 36). These accessory CL were usually small, having a diameter

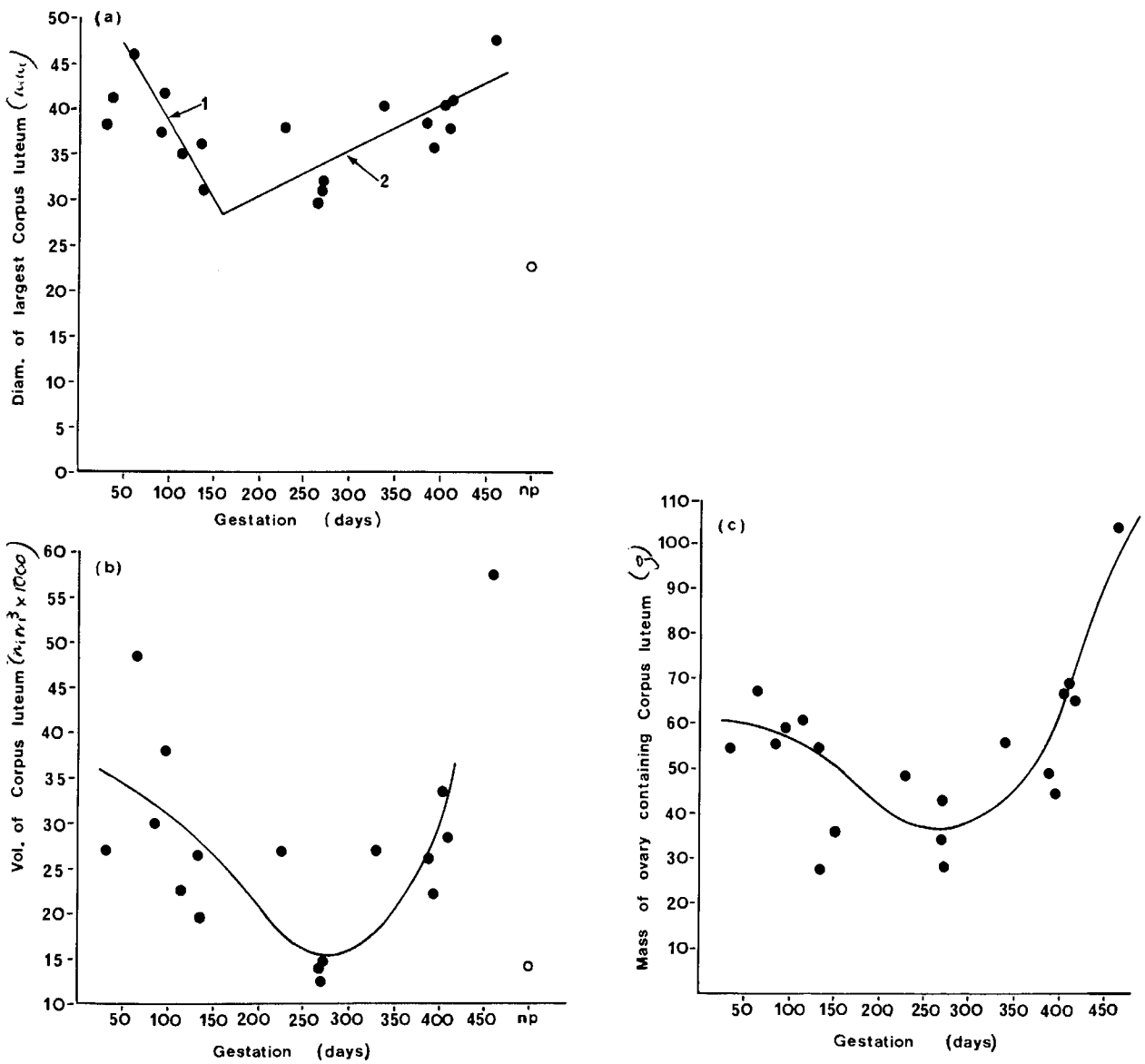


FIG. 35 — Size of corpus luteum and mass of ovary in relation to gestation age. (a) diameter of largest corpus luteum at gestation age, (b) volume of largest corpus luteum at gestation age, (c) mass of ovary containing largest corpus luteum at gestation age. Mean size of largest corpus luteum in non-pregnant (np) females also shown (o).

$< 5$  mm and were found as commonly in non-pregnant as in pregnant females ( $P < 0,50$ ). The mean number of CL in pregnant and non-pregnant giraffe combined decreased with age (Table 44). A 13-y-old pregnant giraffe 3 d *pre partum* which had 24 CL in her ovaries was not included in this table as this condition seemed to be unusual.

TABLE 44: MEAN NUMBER OF CORPORA LUTEA IN PREGNANT AND NON-PREGNANT GIRAFFE OF VARIOUS AGES

Age group (y)	n	Mean no. of CL/giraffe $\pm$ S.E.
5 - 7	7	21,3 $\pm$ 11,3
8 - 9	6	4,5 $\pm$ 1,5
10 - 11	7	2,1 $\pm$ 0,8
13 - 20	4	1,0 $\pm$ 0,0

#### 4. The Corpus Albicans

In the CA cell degeneration was highly advanced. It was no longer possible to identify cell remains as the size and shape were extremely irregular and cell walls were disintegrated or were present only as wrinkled fragments. The remains of the cytoplasm was contracted into dark staining masses. Nuclei were wrinkled, irregular and hyperchromatic or had disintegrated. It was no longer possible to measure cell size accurately. Blood vessels were occluded or hypertrophied. The much wrinkled walls contained abundant pyknotic nuclei, few if any erythrocytes were found. The collagenous remains of the septa could be demonstrated with the MSB stain. A section through a CA is shown in Plate 9, Fig. 6.

Corpora albicantia were present in all but one of the post-pubertal ovaries examined. The female in which they were absent was a 6-y-old

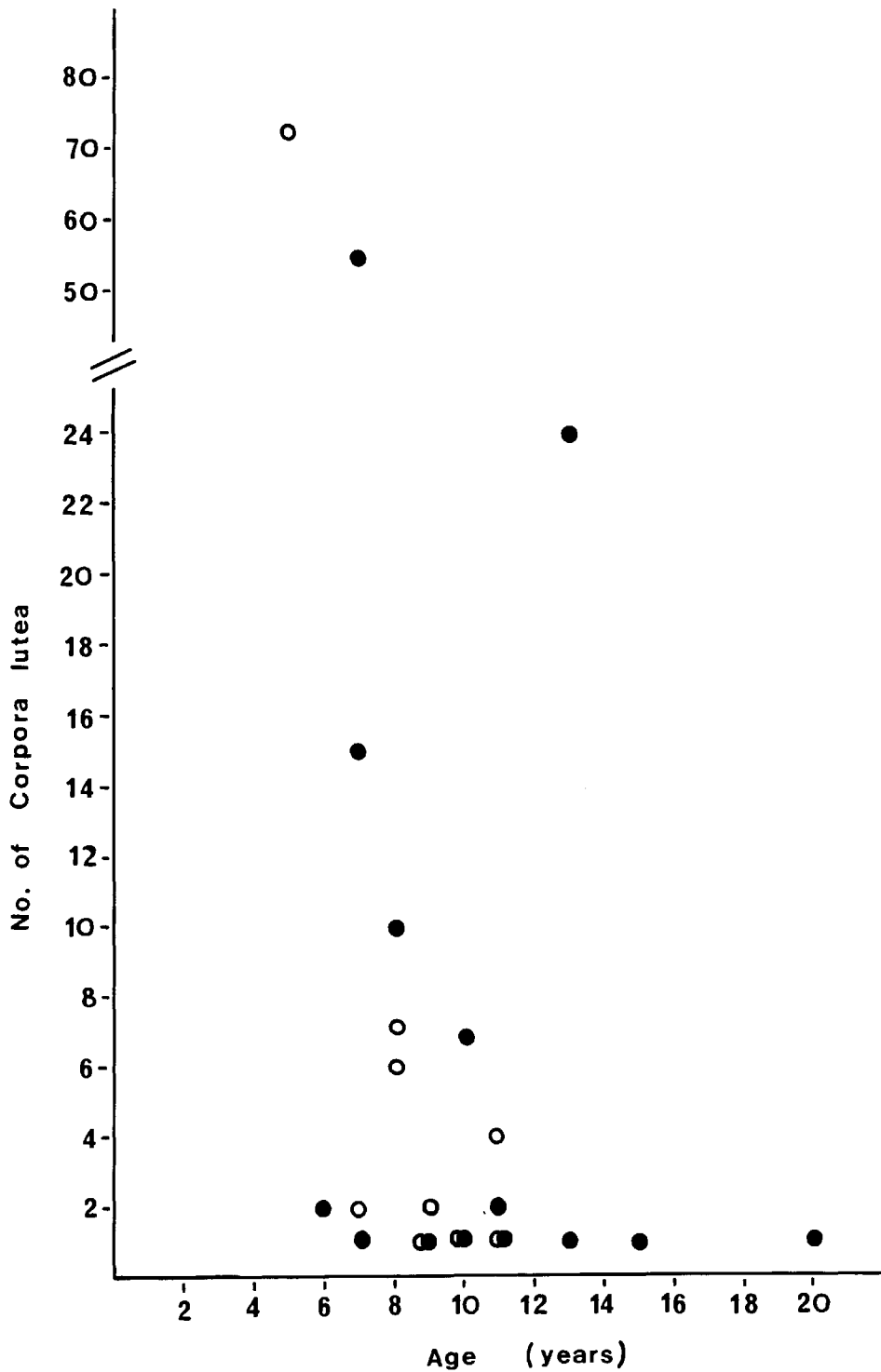


FIG. 36 — Number of corpora lutea at age in female giraffe.  
o = non-pregnant, ● = pregnant.

presumably primiparous animal whose ovaries contained 55 corpora lutea. The maximum number of CA found was 24, also in a 6-y-old animal and these were presumably due to regressing CL of the prepubertal period. With the exception of this individual the number of CA showed an increase with age (Fig. 37a). As could be expected there was no significant difference between the number of CA found in pregnant and non-pregnant giraffe ( $P < 0,50$ ). The decrease in mean diameter of CA during gestation is linear (Fig. 37b) and can be described by the regression equation  $Y = -0,010 X + 8,9$  ( $r = -0,696$ ;  $P < 0,01$ ) where  $X$  is gestation time in days and  $Y$  is the diameter of the CA. The size of CA in non-pregnant and early *post partum* animals is also shown in Fig. 37b. When the volume of the largest CA is plotted against gestation time a similar distribution of points is seen (Fig. 37c).

If it can be assumed that pregnancy does not accelerate the rate of regression of CA then by extending the regression line one will find the endurance of the CA from its mean size at conception to where it disappears, theoretically at the point where the regression line cuts the  $Y$  axis. One can also continue this line to the left of the  $Y$  axis until it reaches a point equivalent to the mean size of the CA *post partum*. The CA is then found to endure for about 1630 d or about  $4\frac{1}{2}$  y.

##### 5. Ovarian activity

Both ovaries were equally active, out of 28 pairs of adult ovaries examined the largest CL occurred 13 times in the left ovary *cf.* 15 times in the right ovary. There were 76 CL in the left ovary and 75 in the right; there were 74 CA in the left and 83 in the right ovary. There is evidence of a statistically significant alternation of function between right and left ovaries. Thus, the largest vesicular follicle occurred in the op-

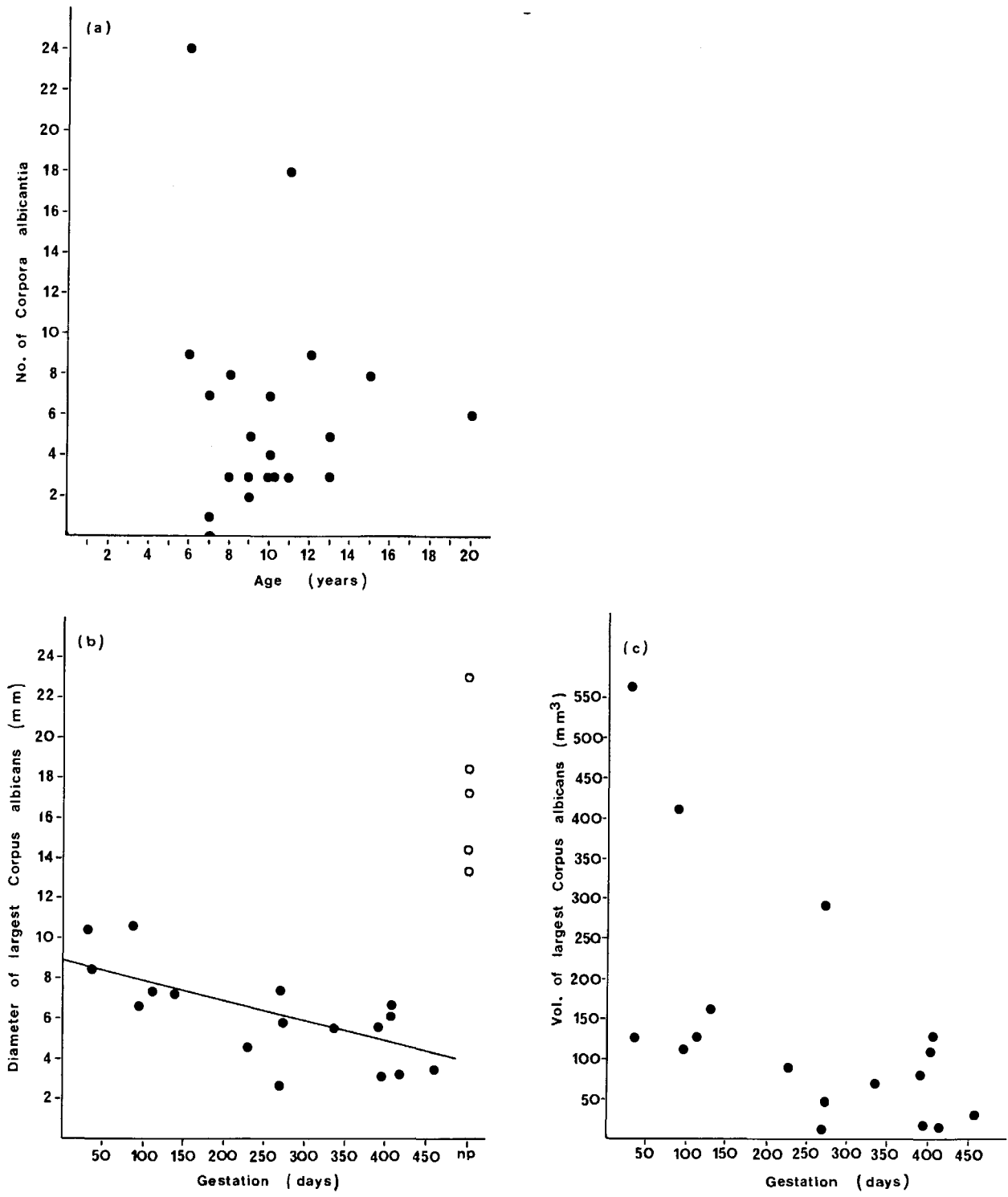


FIG. 37. — Number and size of corpora albicantia in relation to age of the female and gestation age. (a) No. of corpora albicantia at age, (b) diameter of largest corpus albicans at gestation age, (c) volume of largest corpus albicans at gestation age. Diameter of largest corpus albicans in non-pregnant (np) females also shown (o).



posite ovary from the one having the largest CL in 26 out of the 28 pairs of adult ovaries examined ( $P < 0,001$ ), and the largest CA occurred in the opposite ovary in 21 out of the 28 cases ( $P < 0,025$ ).

## DISCUSSION

### OVARY LOCATION, SIZE AND SHAPE

The ovaries of the giraffe are situated in a similar position to that in the ruminating artiodactyls and is correlated with the type of uterus or posture, or both (Mossman & Duke 1973).

Though limited, the data on ovarian mass and dimensions available from foetal and juvenile giraffes indicate that near-term foetal ovaries are larger than those of small calves (Table 42) a similar situation to that found in the male gonads (Chapter 6). Hypertrophy of foetal gonads has been reported in the horse *Equus caballus* (Amoroso & Rowlands 1951), some Pinnipedia (Amoroso, Harrison, Matthews & Rowlands 1951). The African elephant (Perry 1953, Hanks 1973) and Burchell's zebra (Smuts 1974). In all cases this condition was ascribed to an enormous development of interstitial cells, which subsides during late foetal life in the equids, and soon after parturition in the seals and African elephant. In the case of the giraffe, however, if the material examined is representative, then hypertrophy cannot be ascribed to interstitial cell development. It is probably due to the multiple CL which are present especially in the medullary stroma in the foetal ovaries. The medulla has fewer CL in the calves examined, where most active follicles and CL were in the cortex.

The size of foetal ovaries 'shortly before birth' (2 x 1 x 0,8 cm with a mass of 1,6 g) given by Kayanja & Blankenship (1973) are much smaller

than the ovaries of the largest foetuses in the present study (2,1 x 1,5 x 1,3 cm with a mass of 2,8 g). However this is probably due to Kayanja & Blankenship (1973) ascribing an older age to the foetuses than was the case. This point has been mentioned earlier (Chapter 5) and is discussed further below.

#### OVARIAN STRUCTURE AND DYNAMICS

The prenatal ovary

It is clear from the descriptions provided above as well as those in the literature (Kellas *et al.* 1958; Kayanja & Blankenship 1973) that the ovaries of the foetal giraffe exhibit several adult mammalian features. These are the development of vesicular follicles and corpora lutea during foetal life. Concomitantly there are typically embryonic features such as masses of naked oocytes, primordial follicles and distinctive cuboidal surface germinal epithelium cells. Development of vesicular follicles and widespread luteanization of these elements has been previously reported in the human full-term foetus (Amoroso & Finn 1962). Mossman & Duke (1973) consider these vesicular follicles to be derived from medullary cords, although there is no direct proof of this. Development of follicles up to the stage of antrum formation is also a feature of foetal ovaries in cattle and sheep (Perry & Rowlands 1962).

Mossman & Duke (1973) doubt that the corpora lutea of foetuses are true luteal glands and argue that they are thecal type interstitial bodies (corpora atretica). However, it is clear from the material studied and the figures presented (Plate 8, Fig. 7) that the CL of giraffe foetal and juvenile ovaries contain adult type luteal cells. Even though Kayanja & Blankenship (1973) found that in their material the luteal tissue of

the foetal CL was sometimes continuous with the theca interna of vesicular follicles, this does not, however, prove that the origin of these CL is from thecal tissue, though they regarded the theca interna as being "most vital" to the process of CL formation. Their histological and ultra-structural investigations confirmed the identity of the CL cells. In addition, later work by Gombe & Kayanja (1974) confirmed that these CL are endocrinologically active and similar in function to the CL of adult female giraffes.

In their description of foetal ovaries Kellas *et al.* (1958) mention discrete spherical masses of granulosa like cells surrounding an oocyte. These structures were penetrated by large sinusoidal capillary vessels and contained a conspicuous network of reticular fibres. Mossman & Duke (1973) suggested that these bodies are derived from medullary cords. However, Kellas *et al.* 1958 do not mention medullary cords, and none were found during this study. Also if they are cords it could be expected that they would be found in different transects and not only transverse. In the present study these structures are interpreted as being follicles usually secondary but some contain material which stains like follicular liquor and they are therefore regarded as vesicular follicles. The membrana propria has usually been ruptured and a theca is distinguishable. It is suggested that this leads to the formation of a CL and the oocyte degenerates. In other cases the hyperaemic vessels burst and a haemorrhagic follicle is formed, the cellular debris being phagocytosed.

The data suggest that there is at least one wave of follicular growth and proliferation followed by a cessation of this activity in foetal life. Evidence for this is the large number of developing follicles found in the early foetal ovaries and their relative sparseness in the two which are close to term. This situation is common in mammals (Perry & Rowlands 1962).

### The prepubertal ovary

These are similar to foetal ovaries in that they contain large vesicular follicles and CL. The luteal cells are however larger than in the foetal ovaries. The appearance of masses of interstitial gland tissue is noteworthy. This is usually a feature of foetal ovaries but was not found to be so in giraffe. The data also suggest that CL regression takes place and that by the time puberty is reached the CL of the prepubertal period have all become corpora albicantia. There is no evidence to support Gombe & Kayanja's (1974) statement that these CL are maintained cyclically until puberty is reached.

### The mature ovary

The description provided indicates that the giraffe ovary is in most aspects similar to other mammals but differs markedly in the growth and regression features of the CL. Also the presence of multiple CL in pregnant adults is notable, as Kayanja & Blankenship (1973) regarded it as remarkable that there were no accessory CL during pregnancy.

### The corpus luteum of pregnancy

The interpretation of the growth of the corpus luteum of pregnancy has been cautious because of the small number of animals sampled and because this pattern of a decline to mid-term followed by an increase in the last third of gestation is unusual among mammals. A similar course of events has so far only been described in the pregnant rat, the corpora lutea of which cease to grow, or even regress a little in size after the first week of pregnancy and then rapidly double their volume to be followed by an equally rapid decline well before the end of gestation.

This "sudden increase in size nearly two thirds of the way through pregnancy is difficult to relate to any embryological event or endocrinological crisis" - Perry (1971).

Kayanja & Blankenship (1973) observed that the CL of pregnancy in their material was usually largest during the first third of pregnancy. They do not give any measurements of these CL so it is difficult to compare their material with that derived from the present study. If the foetal ages of their material are calculated by the same formula used in Chapter 5, then it is clear that most of their material comes from animals early in pregnancy. It seems valid to use the same formula ( $W^{1/3} = 0,114 [t - 45,7]$ ) as the growth of the Kenya foetuses was not found to differ significantly from the growth of the Transvaal foetuses when the regressions of foetal length (crown/rump - L.H. Blankenship pers. comm.)\* up to a length of ~~56~~<sup>4</sup> cm (after which this measurement becomes unreliable) against foetal mass were compared (Chapter 5). It seems reasonable to speculate therefore that when these workers mentioned that the ovarian mass and CL diameter tended to drop "towards the end of gestation" — they were in fact observing the decline in CL size from about day 100 to day 250 as postulated here. They did not have sufficient material from late gestation females to detect the subsequent rise in CL size.

Wilkinson & de Fremery (1940) found that gonadotrophic hormones were excreted in the urine by pregnant giraffe. The urine that they examined by the method of Ascheim and Zondek on day 243 gave a negative result, but on days 322 and 337 the result was positive. This report suggests that some endocrinological event did occur sometime between the 243rd

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and 322nd day of pregnancy which could conceivably be related to the changed status of the CL. However, it must be borne in mind that these findings have not been confirmed. Gombe & Kayanja (1974) have shown that luteal progesterone increased with the duration of gestation. They also found high levels of  $20\beta$ -hydroxyprogesterone in immature giraffes, low levels in early pregnancy and none in later pregnancy or in a *post partum* CA. The levels of  $17\alpha$ -hydroxyprogesterone were lower than those of the other two and were found in juvenile giraffe and in early pregnancy but not at all in later pregnancy or *post partum*. These data, though scanty, do lend some credence to the suggestion that there is some endocrinological event occurring during gestation which results in an inversion of the relative concentrations of progestins in the CL. Though it may well be totally unrelated to this phenomenon it is perhaps worth noting that, as shown in Fig. 38, the ending of one lactation cycle and the first appearance of pre-lactation secretion of the next cycle occurs between day 150 and day 336 of pregnancy.

Perry (1971) has commented on the phenomenon that in mammals where the CL remains large and active in the later stages of gestation it regresses suddenly just before term. African examples are seen in the defassa waterbuck (Spinage 1969) and the impala (Kayanja 1969). This is apparently not the case in the giraffe as shown above (Fig. 35) where the CL increases in the later stages of gestation nor in the guinea pig where the CL of pregnancy maintains its size until after parturition (Heap, Perry & Rowlands 1967).

#### Ovarian activity

The evidence available from this study does not confirm the statement of Kayanja & Blankenship (1973) that ovulation appears to occur at random in

the left and right ovaries of the giraffe. On the contrary, it appears that there is a highly significant alternation of function between the left and right ovary. In this respect the giraffe differs from, for example, the Uganda kob (Buechner, Morrison & Leuthold 1966), the impala (Mossman & Mossman 1962, Kayanja 1969) and the lechwe (Robinette & Child 1964). Both ovaries are not equally active in all mammals. Thus, for example, right ovaries are more active than left in the Peruvian mountain viscacha *Lagidium peruanum* (Pearson 1949) and in the chinchilla *Chinchilla laniger* (Weir 1967). The left ovary is more active than the right in the defassa waterbuck (Spinage 1969). Equal activity in both ovaries, as in the giraffe, is also found in the rock hyrax *Procavia habessinica*, (Kayanja & Sale 1973).

## LACTATION AND MILK COMPOSITION

### INTRODUCTION

The composition of giraffe's milk has been described by Greed (1961) and Aschaffenburg *et. al.* 1962 whose reports refer to the same sample, and a further report was that of Ben Shaul (1962). No further investigations of giraffe milk are known to have been undertaken. Subsequent reviews refer only to the abovementioned data (Jenness & Sloan 1970, Smith 1970, Guèguen 1971).

Milk samples were available from females taken at different stages of pregnancy and lactation. It was possible therefore to investigate changes in the composition of the milk during lactation to compare giraffe's milk with that of other species, both domestic and wild. Data available on stomach fill (Chapter 4) was re-evaluated in relation to the physiology of lactation

### MATERIAL AND METHODS

#### COLLECTION OF MILK

Milk or *pre-partum* secretion was routinely collected by manual expression from all four teats immediately *post mortem* until no further milk could be obtained, and frozen as soon as possible. After excising the udder the procedure was repeated and this usually resulted in more milk being collected. The mass of the excised udder was then measured on a spring balance.

#### CHEMICAL ANALYSIS

Analysis of the milk was carried out using conventional procedures (Horwitz 1970). Thus fat was measured by the Babcock method and total protein was determined by Kjeldahl analysis for nitrogen and multiplication by the factor 6,38. Casein and whey proteins were not measured in the present analysis, though small aliquots were prepared for examination by zone electrophoretic techniques described fully by Osterhoff (1968). Total solids (T.S.) were determined by air drying over a water bath and then drying in an oven at 100°C until constant mass was reached. Ash was determined from samples incinerated overnight at 600°C. Lactose was estimated from the difference between T.S. and the sum of fat, protein and ash. Minerals were determined by atomic absorption spectrometry.



## RESULTS

UDDER MASS AND ACTIVITY

The mammary gland is situated inguinally and has two pairs of teats, not one pair as quoted incorrectly by several authors (Shortridge 1934, Roberts 1951, Ansell 1960b, Walker 1964). The heaviest udder (7,32 kg) was that of a lactating female 14 y old, while the lightest (1,81 kg) was that of a pregnant non-lactating female, 10 y old. The udder mass as a percentage of total body mass of 18 females at different stages of lactation and pregnancy is shown in Fig. 38 and summarised in Table 45. Inactive mammary glands have the lowest mass, while udders from cows in the last third of pregnancy are also small. Lactating udders have a greater relative mass than others, even though no correction has been made for the mass of the milk extracted. The rapid development of the gland during the last 50 d of gestation is also apparent (Fig. 38).

TABLE 45: UDDER SIZE IN PREGNANT AND NON-PREGNANT GIRAFFE

Status	n	Mean mass of udder (kg) + S.E.	Mass of udder as % of total body mass (mean) + S.E.
Pregnant, lactating	4	3,68 ± 0,23	0,49 ± 0,03
Pregnant (< 400 d) not lactating *	6	2,24 ± 0,12	0,27 ± 0,01
Near term (454 d) pre-lactation secretion	1	6,80	0,72
Early <i>post partum</i>	1	7,26	0,82
Non-pregnant, lactating	5	4,99 ± 0,28	0,65 ± 0,04

\* Pre-lactation secretion in two animals

Out of a total sample of 26 postpubertal females for which the lactation status was recorded it was found that all non-pregnant females were lactating and pregnant females lactated until 150 d gestation ( n = 4). Pre-lactation secretion could be expressed from the teats of pregnant females as early as 231 d *pre-partum* and was present in all females from 60 d *pre-partum*. This secretion, which was cream coloured varied in consistency from a jelly-like substance when first present to a less viscous fluid closer to term. The udders of five females ranging from 131 d to 390 d gestation were dry. Calves were seen suckling up to at

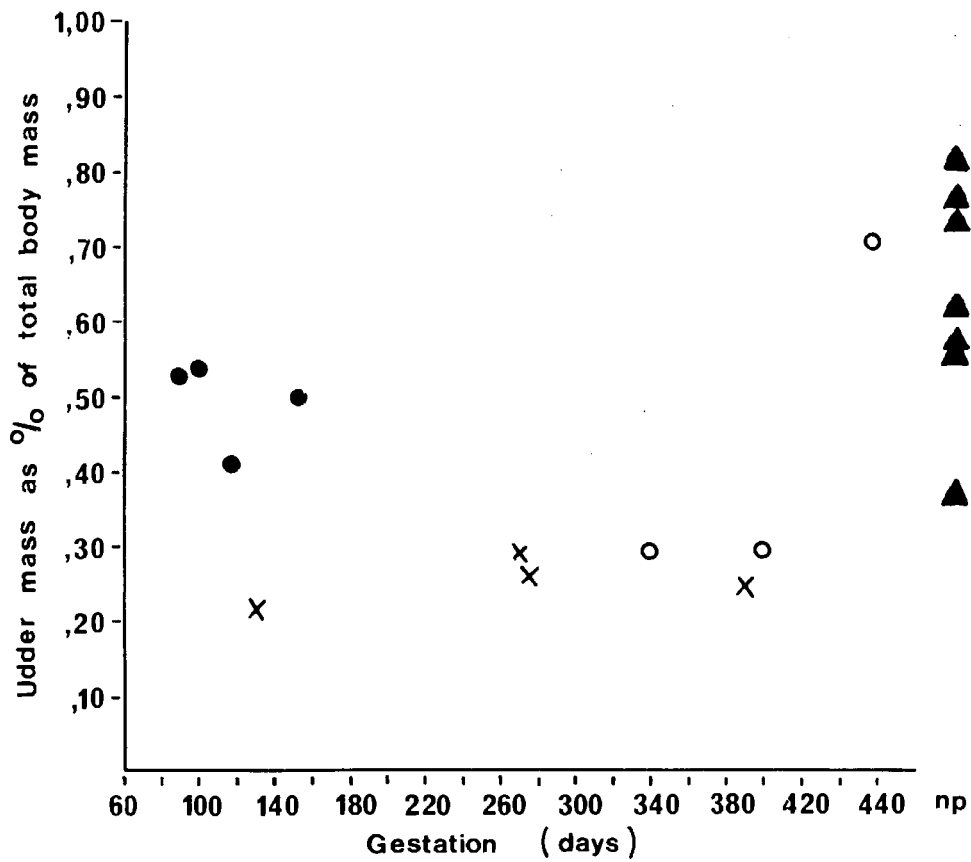


FIG. 38 — Udder mass as a percentage of total body mass in giraffe at different stages of pregnancy and lactation. Pregnant and lactating (●); pregnant but not lactating (x); pre-lactation secretion (o); non-pregnant (np) but lactating (▲).

least 10 months of age (see also Mason 1973) though they may suckle for up to 1 y (Aschaffenburg *et. al.* 1962, Dagg 1971). It has been estimated (Chapter 7) that lactation lasts for 13 months. Most females will however conceive before lactation has ceased (mean *post partum* reconception interval being shorter than the lactation period).

#### STOMACH FILL

The mass of the stomach fill expressed as a percentage of total body mass of 23 females at different stages of pregnancy and lactation is summarised in Table 46, together with the t values for comparisons of the different categories. The mean mass of the stomach contents of pregnant giraffe was significantly lower than that of non-pregnant animals ( $P < 0,05$ ) while lactating females had more food in their stomachs than non-lactating females ( $P < 0,01$ ). As could be expected from the above results the mean mass of stomach fill of lactating pregnant females was greater than that of pregnant non-lactating females and the difference was almost statistically significant at the 5% level. Within the lactating group there was no significant difference between pregnant and non-pregnant animals, as a lactating pregnant female is unlikely to be carrying a large enough foetus to seriously decrease the abdominal space available for stomach contents. It can be seen from Fig. 39, that stomach fill decreased with advancing gestation. The regression line for this relationship was calculated and found to be  $Y = - 0,018 X + 13,87$  where Y is stomach fill as percentage of total body mass and X is gestation time in days. The decrease in stomach mass is significantly correlated with gestation as shown by the value of r which is  $- 0,733$  ( $P < 0,01$ ). The percentage of stomach contents of females in the second half of gestation, and that of females in the last third was significantly less than that of the middle third ( $P < 0,05$ ). As mentioned above, females in early pregnancy are usually still lactating and their stomach fill most probably reflects lactational demands. It is only later in pregnancy that the effect of the pregnant tract becomes important by decreasing abdominal space. Therefore, the regression equation relating stomach fill to gestation was calculated for those females more than 100 d pregnant. The correlation coefficient was much higher,  $r = - 0,832$  ( $P < 0,001$ ) as could be expected and the equation is  $Y = - 0,023 X + 15,5$  where Y and X are as defined above.

#### MILK COMPOSITION

##### Gross Composition

The results of the chemical analysis of the gross composition of 12 samples

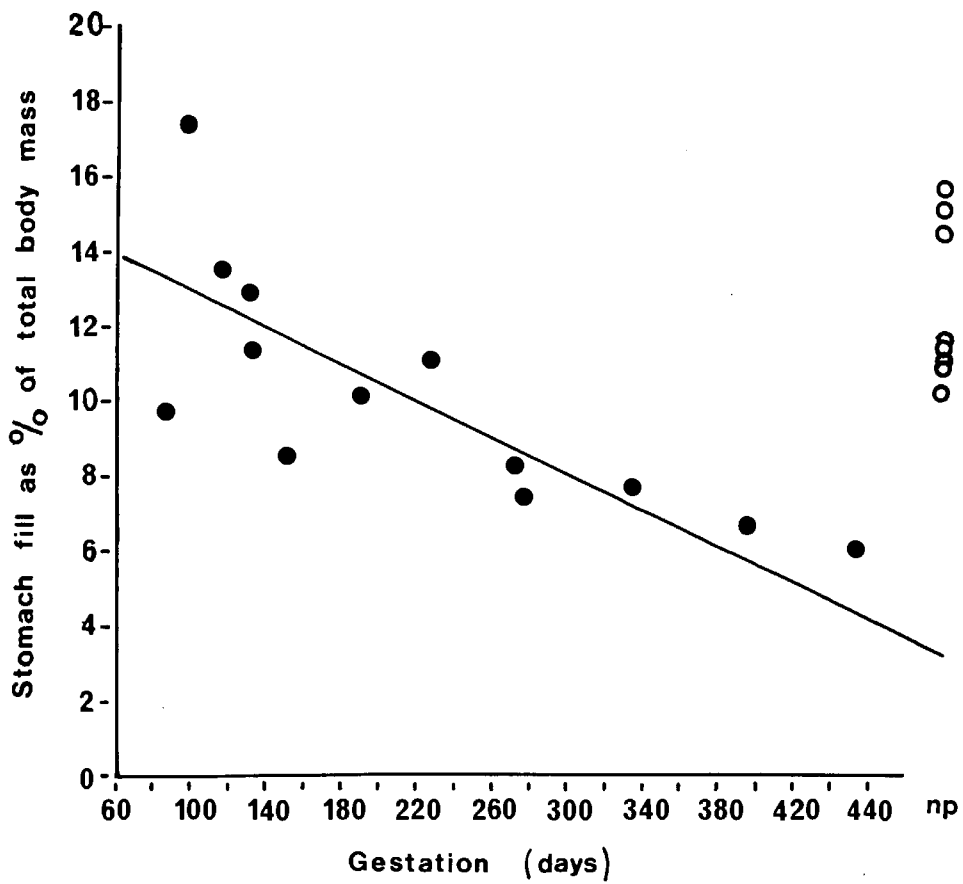


FIG. 39 — Stomach fill of adult female giraffe as a percentage of total body mass at gestation time. Pregnant (●), non-pregnant (np) (o). Equation of regression line in text.

TABLE 46: STOMACH FILL OF ADULT FEMALE GIRAFFE

Status	n	Mean stomach fill as % of total body mass	S.D.	S.E.	Range	Student's t
All females	22	10,9	3,0	0,6	6,2-17,5	
Pregnant	14	9,9	3,0	0,8	6,2-17,5	-2,134 P < 0,05
Non-pregnant	8	12,6	2,0	0,8	10,3-15,7	
Pregnant, lactating	4	12,4	3,5	2,0	8,6-17,5	2,058 n.s.
Pregnant, non-lactating	10	9,0	2,1	0,7	6,2-13,0	
Lactating	11	12,7	2,7	0,8	8,6-17,5	3,247 P < 0,01
Non-lactating	11	9,2	2,1	0,7	6,2-13,0	
Lactating, pregnant	4	12,4	3,5	2,0	8,6-17,5	-0,248 n.s.
Lactating, non-pregnant	7	12,8	2,1	0,8	10,3-15,7	

samples of giraffe's milk from different stages of lactation are shown in Table 47. As it is well known that the *pre-partum* secretion and colostrum differ in composition from milk of established lactation (Ling, Kon & Porter 1961) the composition of these are shown separately. The earliest *pre-partum* secretion, (referred to as sample 1 in Table 47) was from a female 409 d pregnant and was cream coloured with a jelly-like consistency. Samples no. 2 and 3 were from females 405 d and 414 d pregnant respectively and were a cream coloured liquid. Samples 4 and 5 have been referred to as early milk rather than colostrum as it is not known how soon *post partum* they were collected, these and the other samples were white. Evidence from the degree of uterine involution, presence and condition of cotyledons and ovaries indicated that the females had recently calved. The remaining samples have been arranged in order of the relative udder size (udder mass as % of total mass) as it has been shown (Fig. 38) that udder size decreases with time, at least during early pregnancy. It is assumed that there is little individual variation in udder size and that none of these females had lost their calves. Of the latter seven animals numbers 9 and 10 were 98d and 116d pregnant respectively.

TABLE 47 : THE MAJOR CONSTITUENTS OF GIRAFFE'S MILK FROM THE EASTERN TRANSVAAL LOWVELD

Sample No.	Composition in g per 100 g				
	Fat	Protein (N x 6,38)	Total Solids	Ash	Lactose (by difference)
Pre-lactation secretion (jelly)					
1	11,5	3,9	19,9	0,8	3,7
Pre-lactation secretion (fluid)					
2	15,6	10,4	28,8	0,7	2,1
3	17,8	15,4	34,6	1,0	0,4
Mean	16,7	12,9	31,7	0,8	1,2
Early lactation					
4	12,8	10,4	25,6	1,4	1,0
5	17,5	16,3	38,8	1,2	3,8
Mean	15,1	13,3	32,2	1,3	2,4
Established lactation					
6	7,5	3,6	18,6	0,9	6,6
7	3,4	4,2	12,3	0,7	4,0
8	3,6	4,1	12,5	0,8	4,0
9	10,0	4,2	18,0	0,9	2,9
10	10,8	9,8	22,5	0,8	1,1
11	5,5	13,4	19,9	0,7	0,3
12	9,5	4,8	17,1	1,2	2,4
Mean	7,2	6,3	17,3	0,9	3,0
+ S.E.	1,1	1,4	1,4	0,06	0,8

#### Variation with stage of lactation

The data in Table 47 indicate an increase in fat, protein, T.S. and ash in the pre-lactation secretion which declines following parturition. Lactose is high in the pre-lactation jelly secretion, falls in the later pre-lactation

liquid secretions, rises again during early lactation remaining fairly constant for a while and then declines towards the end of lactation. Despite the small sample size it was found that the composition of early milk was significantly different from milk of established lactation ( $P < 0,01$  -  $P < 0,02$ ) except for lactose which did not differ significantly. However, samples are small and in these calculations the very high protein value of no. 11 (Table 47) when included, made the difference in protein values only just not significant at the 5% level of probability. When comparing the first three samples from the early part of established lactation (nos. 6, 7 & 8) with the samples from late lactation it seems clear that there is a fall to minimum values of fat, protein and T.S. followed by a recovery in later lactation, though this cannot be statistically substantiated due to the small sample size. There is little apparent trend in the values for ash except for high values following parturition and in sample 12.

#### Characteristics of protein fraction

The pattern of migration of the casein, lactalbumin and lactoglobulin fractions of the milk proteins in starch gel were examined and found to be very similar to those obtained for bovine milk.

#### Minerals and trace elements

Table 48 shows the mineral and trace element composition of milk from eight females (identified by the same numbers as in Table 47) at different stages of lactation. No clear trends could be discerned (as seen in the ash composition of the samples). The level of potassium in the early milk was however higher than that of later milk.

#### Milk yield

The maximum volume of milk obtained from a single female was 2 250 ml during established lactation. Most samples varied between 100 - 800 ml while the volumes of pre-lactation secretion collected were less than 100 ml. The time elapsed from last suckling to death was not known nor could the amount of milk present in the udder after milking be determined.

#### DISCUSSION

#### METHODS OF ANALYSIS

The method used for determining total protein is subject to some error, as pointed out by Jenness & Sloan (1970) in that the nitrogen content of

TABLE 48 : MINERAL AND TRACE ELEMENT CONSTITUENTS OF GIRAFFE'S MILK FROM THE EASTERN TRANSVAAL LOWVELD

Sample No.	Minerals in g per 100 g					Trace elements in ppm			
	Ca	Mg	K	Na	P	Fe	Mn	Cn	Zn
Early milk									
5	0,08	0,006	0,134	0,031	0,099	0,08	0,2	0,28	5,7
Established lactation									
6	0,07	0,005	0,102	0,030	0,106	0,20	0,2	0,36	4,9
7	0,08	0,006	0,102	0,038	0,110	1,80	0,2	0,32	5,3
8	0,07	0,005	0,039	0,024	0,108	4,40	0,2	0,48	6,4
9	0,003	0,004	0,099	0,025	0,055	0,04	0,2	0,24	4,4
10	0,08	0,005	0,129	0,030	0,092	1,60	0,2	0,20	6,0
11	0,07	0,005	0,122	0,034	0,085	0,80	0,2	0,24	6,5
12	0,10	0,006	0,042	0,083	0,160	2,00	0,2	0,64	7,2
Mean	0,07	0,005	0,091	0,038	0,102	1,55	0,2	0,35	5,8
+ S.E.	0,01	0,0003	0,014	0,008	0,012	0,56	0	0,06	0,4

proteins has not been determined precisely for the milk of any species other than the bovine *Bos taurus*, goat and human *Homo sapiens*. More important is the fact that the non-protein nitrogen is also expressed as protein when using this method. Non-protein nitrogen amounts to about 5% and 17% of the total in the milk of bovines and humans respectively, however, in the case of giraffe's milk it is only of minor importance as Aschaffenburg *et. al.* (1962) found only 0,023 g per 100 g non-protein nitrogen in the sample they analysed, and this amounted to only 0,4% of the total proteins.

The estimation of lactose by difference is also subject to error and according to Jenness & Sloan (1970) it is likely to err on the high side of the actual value for several reasons, the most important of which is the loss of organic salts, such as citrate in the determination of ash. Thus ash, as expressed here, represents the mass of the mineral residue and does not precisely represent the quantity of salts in the milk.



## LACTATION

From Fig. 38 it can clearly be seen that the relative mass of the udder in lactating pregnant females is less than that of lactating non-pregnant females. This is a further indication that pregnancy usually occurs late in the lactation cycle. The lower relative udder mass of the non-lactating animal at 131d gestation could possibly be due to this female having lost her calf, in which case lactation would probably have ceased earlier than normal as found in other mammals (Grimsdell 1973b, Smuts 1974).

The results of the investigation of stomach fill in females at different stages of pregnancy and lactation are much the same as found by other workers in that there is an increase in food intake in lactating females. Thus Penzhorn & Meintjés (1972) found that in Africander cattle *Bos indicus* there was a reduction in feed consumption prior to calving which they suggested was due to physical limitation of abdominal capacity. They found an increased consumption after calving probably explained by a combination of the increased abdominal and ruminal capacity and an accelerated metabolic requirement due to lactation. A similar situation has been reported in the hippopotamus by Laws & Clough (1966) who found that lactating females fed more intensively than other classes of female. In the African buffalo (Grimsdell 1973b) the rumen contents of lactating females were 15% heavier than other mature females, but those in the last 2 months of pregnancy had a lower rumen content mass than those in earlier stages of gestation. Arman, Kay, Goodall & Sharman (1974) also found increased food intake in lactating red deer.

It seems reasonable to conclude that in the giraffe, as in other ruminants studied (Laws & Clough 1966, Forbes 1970, Penzhorn & Meintjés 1972, Grimsdell 1973b) abdominal capacity was reduced with growth of the foetus. Furthermore, the giraffe foetus is much larger in relation to the size of its mother than in other very large African mammals. (Table 29, Chapter 5).

Grimsdell (1973b) has pointed out that the limited rumen capacity in late pregnancy would result in there being a premium on an intake of high quality food. In the buffalo populations studied by him in Uganda it was found that most births occurred when nutrition conditions were near optimal, implying a rising quality of food as gestation neared completion. This was not found to be the case in giraffe where most births occurred when nutrition conditions were poor.

## MILK COMPOSITION

The method of collection of the milk samples could have resulted in the samples being unrepresentative or even misleading (Arman *et. al.* 1974). However, the clear trends in the major constituents from milk at different stages of lactation, and the general similarity of milk of the same category indicates that the samples probably were representative of the milk in the udders despite possible artefacts due to the methods of collection and handling. Such artefact might be invoked to explain the apparently anomalous relationships among the salts and ions as indicated in some samples (e.g. low ash and low lactose in sample 11, Table 47).

The early milk was found to be much richer than the colostrum analysed by Ben Shaul (1962). She also analysed milk after the first lactation and found that the fat, protein and ash content were lower while the value for carbohydrates was higher. Unfortunately she gives no indication of how many samples were analysed, or whether the values she presents are mean values. It is well known that colostrum or early milk is richer than milk of established lactation in bovines, and that the pre-lactation secretion is even richer than the colostrum (in terms of those constituents normally high in colostrum i.e. T.S., fat, non-fatty solids and ash) as discussed by Ling *et. al.* (1961). In this respect the giraffe is similar to the bovine and the eland (Treus & Kravchenko 1968, Van Zyl & Wehmeyer 1970) though it is difficult to explain why total solids were found to be lower in the jelly than in the fluids (Table 47, No. 1,2,3). Once the colostrum stage is past in cattle the lactational effects follow fairly well-defined trends with fat, non-fatty solids, protein and casein falling to low values during early lactation and thereafter increasing (Ling *et. al.* 1961). In this respect too, the apparent trend is the same in giraffe (Table 47) as in bovines and eland (Treus & Kravchenko 1968).

The mean of the seven samples taken during established lactation (Table 48) is considered to be fairly representative of giraffes milk for purposes of discussion. These data differ from that of Aschaffenburg *et. al.* (1962) mainly in that values are lower than those found in their sample from a captive giraffe. When compared with bovine milk the main features are that the fat, total protein and ash content of giraffe's milk is higher while, on average, lactose is lower. When compared with eland milk (Posselt 1963, Treus & Kravchenko 1968, Van Zyl & Wehmeyer 1970) the giraffe's milk has a lower percentage of all major components.

The ash content of giraffe's milk tends to be less than that found in the milk of the domestic species listed by Ling *et. al.* (1961). The ash content in the present giraffe samples is also lower than that found in eland by Treus & Kravchenko (1968) and Van Zyl & Wehmeyer (1970), and in red deer by Arman *et. al.* (1974). The mean values for mineral components in wild giraffe milk are also lower than the values found by Aschaffenburg *et. al.* (1962), though their phosphorous and potassium values of 0,104 and 0,100 g/100 g fall within the range of the wild giraffe values, as does their value for iron (0,00016 g/100 g). In a comparison with the mineral content of the milk of red deer given by Arman *et. al.* (1974) it can be seen that only in its composition of sodium is the giraffe's milk richer than red deer, some individual values of potassium fall within the red deer range but the others are all markedly lower.

For those major trace elements which were measured (Table 48) it was found that giraffe's milk had higher concentrations of iron and zinc while the manganese and copper values were close to the higher end of the range found in bovine milk (Ling *et. al.* 1961).

As a result of their paper electrophoresis studies of the soluble protein fraction of their sample of giraffe's milk, Aschaffenburg *et. al.* (1962) found it to be of a complex nature with both globulins and albumins present. The present work confirmed their findings. However as only a small subsample was examined the effect of globulins on total solids could not be ascertained.

The most noteworthy features of the results of this study are the confirmation of the changing composition of pre-lactation secretion and milk produced at different stages of lactation, roughly in accordance with the trends well known in cattle (Ling *et al.* 1961), sheep (Corbett 1968) and Dall sheep *Ovis dalli* (Cook, Pearson, Simmons & Baker 1970). This trend was not described by Arman *et. al.* (1974) in the red deer, but it is clear from their figures that a similar train of events does occur. Changes in the composition of milk with stage of lactation in elephants as tabled by Peters, Maier, Hawthorne & Stowick (1972) are not as easily interpreted, though there does seem to be a gradual increase in most components with time. However, these authors include data from both Indian elephants *Elephas maximus* and African elephants in their table which may not be justifiable, even though the composition of the milk of

the two genera is similar (Jenness & Sloan 1970).

The difference in composition of giraffe's milk could not be explained on the basis of seasonal nutritional deficiencies. Only one sample (no. 11 in Table 47) was collected in the dry season (19th July) and had a particularly low lactose content and high protein. Whether this was due to a seasonal effect of diet or a diseased udder could not be determined. Abnormally low lactose and high protein values are indicative of mastitic infections in dairy cattle (Ling *et. al.* 1961). Sample 3, (Table 48) also showed these characteristics. Age of the females was also not obviously related to milk composition, the youngest female (no. 5) was 7 y old and the two oldest (nos. 9 & 12) were both 11 y old. There are, however, indications of individual differences such as in an animal 9 y old (no. 9, Table 48) which was particularly low in most minerals and trace elements.

Though little data was collected on milk yield the largest sample collected (2 250 ml) was greater than the estimated 600 ml udder contents of a captive giraffe on the 150th day of lactation (Aschaffenburg *et. al.* 1962). It seems likely that giraffe milk production might be within the range of that of other wild species e.g. Yazan & Knorre (1964) reported yields of 2 to 6 litres per day in handmilked domesticated elk *Alces alces* in Russia, while Treus & Kravchenko (1968) obtained 0,9 - 7,0 kg/day from domesticated eland also in Russia.

The increased food intake of lactating giraffe females is presumably necessary to sustain lactation and provide for their maintenance needs. The decreasing demands towards the end of lactation (evidenced by decreasing udder size) was accompanied by a decrease in food intake. These trends are also found in red deer (Arman *et. al.* 1974).

The peak in births in the dry season comes at the time when food quality and availability are decreasing. Therefore when females are having to cope with the demands of lactation only relatively poor food (Chapter 2 & 7) is available. This may additionally ensure that the conception peak only occurs late in the rainy season (Chapter 7) when the demands of lactation are apparently declining and the female has had an opportunity to recover condition.

## SUMMARY

This study on various aspects of giraffe biology, was based on material derived from 39 culled animals and 54 natural deaths. As the availability of material was usually due to considerations other than research priorities adequate samples and observations were not always secured.

The main study area was the Timbavati Private Nature Reserve and its environs in the eastern Transvaal Lowveld. The climate is tropical with a unimodal temperature, radiation and rainfall peak per annual cycle. This results in a hot humid season (November to March) during which plants are actively growing, a cool dry season (April to July) during which growth ceases and deciduousness sets in, and a hot dry season (August to October) during which most deciduous plants are bare and towards the end of which a flush of new leaves appears. The vegetation is predominantly tree savanna with riverine thicket and termitarium thickets. There have been widespread vegetation changes over the past few decades resulting in an increased woody plant density which has contributed to an increase in the giraffe population to a crude density of 2,6 per km<sup>2</sup>, the highest yet recorded. Several large scale die-offs have been associated with starvation and malnutrition. Patterns of lion predation on giraffe have not changed significantly over the past 10 y, and the relative proportions of different age classes taken are, calves (41%), immature (11%) and adults (48%). The adult sex ratio which departs significantly from unity in favour of females (1:1,3) has also not changed significantly.

Food selection was studied by identifying plant fragments from stomach contents. Large fragments were randomly taken from the material while small fragments were taken from a 50 ml sample. Plant identifications

were based on diagnostic keys and over 8 000 fragments were classified. The validity of the samples was tested and found to be satisfactory. Giraffe were found to subsist mainly on leaves of trees and shrubs. In addition, fruit, flowers, twigs and grass were utilised seasonally. There was a marked seasonal change in the plant species selected. During the wet season and the cool dry season deciduous species were mostly taken such as *Combretum apiculatum*, *Acacia nigrescens*, and *Colophospermum mopane*, during the hot dry season the giraffe subsisted mainly on evergreen species such as *Euclea undulata* and *Maytenus senegalensis*. Seasonal changes in diet were apparently influenced by availability of plant species.

Rumen contents were also analysed for their chemical composition. Variations in crude protein, ash and gross energy content of the diet could be related to the plant species utilised by the giraffe and to seasonal phenological changes of the vegetation, nutritional conditions being poorest during the hot dry season. There was no evident correlation for crude fibre or fat, but this could have been masked by digestive processes.

There was a marked seasonal utilisation of different vegetation types by giraffe which was related to the availability of preferred deciduous food sources. Riverine thickets, containing mostly evergreen food sources were intensively used only when the preferred predominantly savanna tree species were no longer available. Multivariate statistical analysis confirmed the interpretations of the data by more conventional means. The analyses also indicated that measurements of relative percentage surface area and relative percentage mass of plant species in the two categories of stomach contents was closely correlated with their relative percentage frequency of occurrence in the stomach contents.

Various criteria of age were investigated and it was found that the age of a giraffe could be reasonably accurately determined for practical purposes. Thirteen stages of tooth eruption with their relevant chronological ages were described with reference to which, the age of an animal with erupting teeth could be determined. Good correlations were found between the lingual crown height ( $r = 0,957$ ;  $P < 0,001$ ) and lingual occlusal surface width ( $r = 0,959$ ;  $P < 0,001$ ) of  $M^1$  and the number of dark staining cementum lines counted in thin sections of the same tooth. Age of an animal could therefore be found by solving the relevant regression equations presented. A composite plate showing the  $M^1$  wear pattern was also prepared, and teeth could be compared with these standards. Thin sections of undecalcified teeth were found unsuitable for age determination purposes. Teeth were decalcified using EDTA or trichloroacetic acid and sections ( $5 \mu\text{m}$ ) stained successfully with Ehrlich's haematoxylin and eosin. In these sections darkly staining incremental lines were discerned in the cementum. Some difficulties were associated with this technique, among them being the variation in intensity and clarity of staining, split bands and double bands in some sections. The latter phenomenon was found to occur only in sexually mature animals but was not a sex-linked feature ( $\chi^2 = 0,485$ ,  $P < 0,05$ ) and was therefore thought likely to be related to the endocrinology of reproduction. Mandible measurements and other measurements of tooth wear as well as eye lens mass were also investigated and found unsuitable for use in age determination. The eye lens dry mass might have been of use in determining the ages of young animals ( $< 5$  y) but insufficient material was available to conclusively show this.

All culled giraffe were dissected into standard cuts as far as possible and their mass was determined. Carcass composition and an index of meat

quality were also investigated by means of buttock dissections and muscle fibre diameter measurements. It was found that mean total body mass was  $1174,3 \pm 31,5$  kg and  $791,8 \pm 17,6$  kg for adult males and females respectively. There were significant seasonal differences in total body mass and amount of fat present in the carcass, indicative of a decline in body condition during the hot dry season (August to October). This loss of condition could be related to the lower nutritional levels demonstrated for the same period. Giraffe carcasses dressed out at 61,9% (males) and 56,6% (females) with a fairly good conformation yielding a high proportion of buttock, but the low fat and high bone content are disadvantages. The late maturity of giraffe carcasses is also a disadvantage but should be weighed against the fact that muscle fibre diameter increases in older animals to probably unacceptable levels for the sophisticated consumer. The total body mass and total carcass mass of both sexes could be predicted with a high level of accuracy from either buttock or foreleg mass, regardless of age, season or pregnancy.

Gestation period was calculated as 457 d being the mean of 48 observations of other workers. Birthmass from full term foetuses and neonates was found to be 102 kg which is almost twice as great as some published figures. However, wild and captive animals differ and there might also be subspecies differences. Foetal increase in mass with age followed a typical 'J' shaped curve as plotted from data on 24 foetuses. The increase in vertebral column length followed a straight line. Crown/rump length could not be accurately measured on older foetuses due to unavoidable *post mortem* movement. The growth rate of giraffe foetuses from East Africa did not differ significantly from those in Southern Africa up to a crown/rump length of 54 cm ( $t = 0,556$ ; d.f. = 16;  $P < 0,5$ ), thus indicating greater difficulties in reconciling the very different re-



ported birth masses. Postnatal growth in mass, height, length and chest girth followed typical growth curves with asymptotes for males at 12 y, 12 y, 11 y and 12 y respectively and 11 y, 11 y, 11 y and 10 y for females. The measure of chest girth was probably influenced by seasonal subdermal fat deposits. The data on body measurements and body mass yielded highly significant correlation coefficients (0,938 - 0,993) and prediction equations which could be used with confidence. Logarithmic and semi-logarithmic transformations gave much better correlations (0,950 - 0,997) especially when measures of volume of the animal such as length X girth<sup>2</sup> were used. A single prediction equation could be confidently used for predicting body mass of a giraffe, regardless of age, sex or time of collection.

The reproductive tract of the male giraffe was investigated and found to be much the same as that of other ruminants. Testes are scrotal and ovoid with a mean adult mass of 539,0 g, the prostate is disseminate and the penis is of the fibro-elastic type up to 77 cm long.

The histology of the testes and the spermatogenic cycle was much the same as found in other mammals. Evidence from foetal and young material indicates that hypertrophy of the foetal testis occurs. Increase in testis mass, epididymis mass, bulbo-urethral mass and seminiferous tubule diameter followed well-known trends as found in other ungulates and their development was significantly correlated with age ( $r = 0,509$  -  $r = 0,898$ ). Spermatogenesis was found to commence at about 3 y of age when testes mass was 188,0 g, but was dependant on physiological status, not chronological age. Hormones were assayed from formalin-fixed testes and it was found that androstenedione was the dominant hormone in the foetus (2,73  $\mu\text{g/g}$  of testis). In mature animals

testosterone was dominant ( $< 10,08 \mu\text{g/g}$  of testes), though also present in foetal life in small quantities ( $< 0,4 \mu\text{g/g}$  of testis), and  $\Delta$  Testosterone was also found in some mature animals. No regular seasonal fluctuation was found in any of the parameters of sexual function measured.

The age of sexual maturity in female giraffe was found from various sources to be about 3 y 10 months in captives and 4 y 7 months in wild animals, the youngest mature animals collected were, however, 6 y old. This difference was possibly due to nutrition but this could not be confirmed. Environmental influences on oestrus were investigated by calculating conception dates of neonates and foetuses and comparing these with rainfall, temperature and photoperiod. Data were from the study area and elsewhere. It was found that in those areas with a unimodal peak in temperature and rainfall that most conceptions occurred during the humid period of the year when nutrition was optimal. The role of photoperiod, which was significantly correlated with reproduction was regarded as influencing giraffe only through its indirect effect on plants and their nutritional value. Giraffe do however breed throughout the year and they are polyoestrus and monotocous, one record of twins from the study area is cited. The placenta is polycotyledonous of the syndesmochorial type, implantation occurs on the same side as the corpus luteum of pregnancy, and reproductive activity does not cease in females in old age. The mean calving interval of wild animals calculated from various sources was found to be 19,9 months, and when estimated from the proportion of pregnant to non-pregnant females in the sample was found to be 22,9 months. *Post partum* reconception intervals as short as 23 d and 27 d were also recorded. Urine of pregnant females was examined by the method of Ascheim and Zondek but no gonado-

trophic activity was demonstrated. Calf mortality was estimated to be about 48% in the first year of life.

The histology of a sample of ovaries of different ages from foetal life onwards was examined. The presence of vesicular and haemorrhagic follicles as well as corpora lutea (CL) in foetal ovaries was confirmed. The latter bodies did not differ greatly in morphology from those of adults. Numbers of CL were also a feature of immature females and these degenerated at puberty. Pregnancy in adults was often accompanied by accessory corpora lutea. Evidence was presented that the CL underwent a decrease in size during the early part of gestation followed by a gradual increase till term. In other respects the adult giraffe ovary differed little from those of other artiodactyls. Both ovaries were found to be equally active.

Lactation and milk composition was also investigated and it was found that lactation endured for about 13 months. There was a reduction in stomach fill in late gestation probably due to decreased abdominal space and a significant increase in stomach fill in lactating females over non-lactating females, probably due to the increased metabolic requirements of lactation. It was found that early milk was richer than milk of established lactation and that the pre-lactation secretion was even richer than the colostrum (as measured by total solids, fat, protein and lactose). When compared with bovine milk it was found that giraffe's milk contained much more fat, total protein and some minerals and trace elements but lactose was lower. Milk yield was of the order of that of other wild ungulates.

## SAMEVATTING

Hierdie studie, wat handel oor verskillende aspekte van die biologie van die kameelperd, is gebaseer op materiaal afkomstig van 34 diere wat geskiet is en 54 wat 'n natuurlike dood gesterf het. Aangesien die materiaal primêr nie vir navorsing bestem was nie, was voldoende monsters en waarnemings nie altyd verseker nie.

Die Timbavati Privaatnatuureservaat en omstreke, in die Oos-Transvaalse Laeveld was die hoofstudiegebied. Die klimaat is tropies met 'n enkele jaarlikse temperatuurs-, stralings- en reënvalspiek. Gevolglik heers daar 'n warm vogtige seisoen (November tot Maart) waartydens die plante aktief groei; 'n koel droë seisoen (April tot Julie) waartydens die plante in 'n rusperiode oorgaan en bladwisselende soorte hulle blare afstoot gevolg deur 'n warm droë seisoen (Augustus tot Oktober), waartydens die meeste bladwisselende plantsoorte blaarloos is, maar teen die einde van hierdie periode begin die meeste plantsoorte weer te bot. Die plantegroei is hoofsaaklik 'n boomsavanne afgewissel deur rivieroewerbos van termitaria. Oor die afgelope paar dekades het uitgebreide plantegroei patroonsveranderinge voorgekom wat daartoe gelei het dat houtagtige plantsoorte vinnig vermeerder het. Dit het bygedra tot die toename in die kameelperdbevolking tot 2,6 individue per km<sup>2</sup>, die hoogste bekende digtheidswaarde. Verskeie grootskaalse afsterwings kan toegeskryf word aan ondervoeding en uithongering. Die aantal kameelperde wat deur leeus gevang is, het oor die afgelope 10 jaar nie betekenisvol verander nie en die verhoudings van die verskillende ouderdomsklasse wat gevang is, is soos volg: kalwers (41%), onvolwassenes (11%) en volwassenes (48%). Alhoewel daar meer volwasse vroulike as manlike diere (1,3:1) voorkom en hierdie geslagsverhouding betekenisvol verskil van die verwagte verhouding het daar geen betekenisvolle verandering ingetree nie.

Die voedselvoorkeure van die kameelperk is bestudeer deur plantdele afkomstig van maaginhoud te identifiseer. Die groter plantdele is ewekansig uit die materiaal geneem, terwyl die kleiner fragmente in 50 ml monsters geïdentifiseer is. In totaal is daar meer as 8 000 plantstukkies met behulp van sleutels geklassifiseer. Die geldigheid van die monsters is aan betekenisvolheidstoetse onderwerp en bevredigend gevind. Daar is gevind dat kameelperde hoofsaaklik blare van bome en struike vreet, terwyl blomme, vrugte, takkies en grasse ook seisoenaal ingeneem word. Die dieet van kameelperde wissel van seisoen tot seisoen en word blykbaar bepaal deur die beskikbaarheid van die plantspesies. Gedurende die warm vogtige en koel droë periodes selekteer kameelperde hoofsaaklik bladwisselende spesies soos *Combretum apiculatum*, *Acacia nigrescens* en *Colophospermum mopane*, terwyl hulle tydens die warm droë periode meesal immergroen spesies soos *Euclea undulata* en *Maytenus senegalensis* vreet.

Chemiese ontledings van die rumeninhoud is gedoen en daar is 'n laagtepunt in die voedingswaarde van die plante tydens die warm droë periode gevind. Seisoenale verskille in ruproteïene, as- en bruto energie-inhoud van die dieet kan gekoppel word aan die plantspesies wat die kameelperd selekteer asook seisoenale fenologiese veranderinge. Geen korrelasie met ruwesels en vet is gevind nie, waarskynlik as gevolg van die werking van verteringsprosesse.

Daar is 'n duidelike verskil in die seisoenale benutting van verskillende plantegroeitipes deur kameelperde en dit word gekorreleer met die beskikbaarheid van bladwisselende spesies waaraan hulle voorkeur verleen. Rivieroewerbos wat hoofsaaklik uit immergroen soorte bestaan, word alleenlik intensief benut wanneer die spesies waaraan voorkeur

gegee word, hoofsaaklik boomsavanna spesies, nie meer beskikbaar is nie. Meervoudige statistiese analises het nie slegs die afleidings waartoe op 'n meer konvensionele wyse gekom is, bevestig nie, maar het aangetoon dat die relatiewe oppervlak- en -massapersentasie van die plantsoorte in die twee kategorieë wat in die maaginhoud onderskei word, nou gekorreleer is met die relatiewe frekwensie teenwoordigheid van hierdie spesie in die maaginhoud.

Nadat verskeie kriteria van ouderdomsbepaling ondersoek is, is gevind dat die ouderdom van 'n kameelperd redelik akkuraat vasgestel kon word. Dertien stadia van tandsnyding met hul toepaslike chronologiese ouderdomme is beskryf. Hierna kan verwys word om die ouderdom van diere wat tande sny, te bepaal. Betekenisvolle korrelasies is gevind tussen, linguale kroonhoogte ( $r = 0,957$ ;  $P < 0,001$ ) en linguale okklusale oppervlak breedte van  $M^1$  ( $r = 0,959$ ;  $P < 0,001$ ) en die aantal donker gekleurde sementumlae wat sigbaar is in dun <sup>snylê</sup>sneë van een en dieselfde tand. Die ouderdom van 'n kameelperd kan dus aan die hand van die toepaslike gegewe regressies bepaal word. 'n Saamgestelde figuur waarin die  $M^1$  slytasiepatroon aangetoon word, kan as standaard gebruik word om ander tande mee te vergelyk. Dun <sup>snylê</sup>sneë van nie-ontkalkte tande is ongeskik gevind vir ouderdomsbepalings. Tande is gevolglik ontkalk deur middel van EDTA of trichloorasynsuur en die <sup>snylê</sup>sneë (5  $\mu\text{m}$ ) kon suksesvol gekleur word met Ehrlich se haematoxylien en eosien. In hierdie <sup>snylê</sup>sneë kon donkergekleurde inkrementale strepe in die sement onderskei word. 'n Aantal probleme is met hierdie tegniek ondervind, onder andere die variasie in intensiteit en helderheid van kleuring, asook gesplete en dubbele bande. Die voorkoms van laasgenoemde kenmerk is slegs by geslagtelik volwasse diere aangetref maar is nie geslagsgekoppel nie

$\chi^2 = 0,485; P < 0,05$ ) en kan moontlik toegeskryf word aan die endokrinologie van voortplanting. Afmetings van die mandibel en ander afmetings van die slytasie van die tande, sowel as die massa van die oog-lens is nagegaan en ongeskik gevind vir die ouderdomsbepaling van kameelperde. Die droë massa van die ooglens van jong diere (< 5 jaar) kan moontlik gebruik word om die ouderdom van 'n jong kameelperd vas te stel, maar weens onvoldoende beskikbare materiaal kon dit nie bevestig word nie.

Alle kameelperde is sover moontlik opgesny in erkende snitte waarvan die massas bepaal is. Die samestelling van die karkas en 'n kwaliteitsindeks van die vleis is nagegaan aan die hand van bouddisseksies en die deursnee van spiervesels. Die gemiddelde totale liggaamsmassa van volwasse manlike en vroulike diere was  $1174,3 \pm 31,5$  kg en  $791,8 \pm 17,6$  kg onderskeidelik. Die totale liggaamsmassa en die hoeveelheid vet per karkas het betekenisvol oor die seisoene verskil wat dui op 'n afname in die kondisie van die diere gedurende die warm droë periode (Augustus tot Oktober). Hierdie afname in die kondisie van die diere kan toegeskryf word aan die vermindering in die voedingswaarde van die plante gedurende dieselfde periode. Manlike en vroulike diere het onderskeidelik 61,9% en 56,6% uitgeslag. 'n Karkas lewer 'n groot hoeveelheid boud, maar die lae vet- en hoë beeninhoud is nadelige kenmerke. 'n Verdere nadeel is dat die karkas van 'n kameelperd eers laat volwassenheid bereik en dit moet opgeweeg word teen die feit dat die deursnee<sup>te</sup> van spiervesels in ouer diere toeneem tot 'n vlak wat moontlik onaanvaarbaar is vir die gesofistikeerde verbruiker. Die totale liggaam- en karkasmasse van beide geslagte onafhanklik van ouderdom, seisoen of dragtigheid, kan met 'n redelike mate van akkuraatheid geskat word aan die hand van die massa van die boud of blad.

Die gemiddelde dragtigheidsperiode, bereken uit 48 waarnemings van ander navorsers, is 457 dae. Daar is gevind dat die geboortemassa van die kameelperd 102 kg is (gebaseer op die massa van 'n volontwikkelde fetus en 'n pasgebore kalf), wat twee maal so groot is as sommige gepubliseerde syfers. Wilde diere en diere in gevangenskap verskil egter van mekaar, terwyl daar ook tussen subspecies verskille mag voorkom. Volgens gegewens wat verkry is van 24 fetusse volg die toename in massa van die fetus met ouderdom 'n tipiese "J"-kromme. Die toename in die lengte van die werwelkolom beskryf 'n reguit lyn. In ouer fetusse kon die kop/kruis lengte nie akkuraat bepaal word nie as gevolg van *post mortem* verskuiwings. Daar is gevind dat die groeitempo van 'n kameelperdfetus tot op 'n kop/kruis lengte van 54 cm ( $t = 0,556$ ; d.f. = 16;  $P < 0,5$ ) afkomstig van Oos-Afrika, nie betekenisvol verskil van dié van Suidelike Afrika nie. Dit maak dit nog moeiliker om die groot verskille in die geboortemassas wat bekend is, te verklaar. Die toename in die gewig, hoogte, lengte en borsmate van kameelperde na geboorte volg tipiese groeikrommes met asimptote vir manlike diere op 12 jaar, 12 jaar, 11 jaar en 12 jaar en vir vroulike diere op 11 jaar, 11 jaar, 11 jaar en 10 jaar onderskeidelik. Borsmates was moontlik beïnvloed deur seisoenale hipodermale vetlae. Gegewens oor liggaamsafmetings en -massa is hoogsbetekenisvol gekorreleer (0,938 — 0,993) en lewer voorspellingsvergelykings wat met vertroue gebruik kan word. Logaritmiëse en semilogaritmiëse transformasies het selfs nog beter korrelasies opgelewer (0,950 - 0,997) veral in gevalle waar volumebepalings soos lengte X omtrek<sup>2</sup> gebruik is. 'n Enkele voorspellingsvergelyking om die liggaamsmassa van 'n kameelperd, ongeag ouderdom, geslag of seisoen, te bepaal, kan met vrymoedigheid gebruik word.



Die manlike voortplantingstelsel is ondersoek en toon baie ooreenstemming met dié van ander herkouers. Die testes is ovaalvormig, kom in 'n skrotum voor en het 'n gemiddelde massa van 539,0 g by volwasse diere. Die prostaat is gedissemineerd en die penis is van die fibro-elastiese tipe met 'n lengte van 77 cm.

Die histologie van die testes en die spermatogeniese siklus stem baie ooreen met dié van ander soogdiere. Hipertrofie van die testis is by fetusse waargeneem. Toename in die massa van die testes, epididymes, bulbo-uretrale en die deursnee van die seminale buise volg dieselfde patroon as by ander hoefdiere en hul ontwikkeling is betekenisvol gekorreleer met ouderdom ( $r = 0,509$  -  $r = 0,898$ ). Daar is gevind dat spermatogenese op 'n ouderdom van ongeveer 3<sup>1</sup>/<sub>2</sub> jaar, wanneer die testes 'n massa van 188,0 g het, 'n aanvang neem en is afhanklik van die fisiologiese status van die dier en nie die chronologiese ouderdom nie. Hormoonbepalings is gedoen op testise wat in formalien gefikseer was. Androstenedioon is die dominante hormoon in die fetus (2,73  $\mu\text{g/g}$  testis). In die volwasse kameelperd is testosteroon oorheersend (<10,08  $\mu\text{g/g}$  testis) maar dit kom wel in klein hoeveelhede in die fetus voor. By sommige volwasse diere is daar ook  $\Delta^1$  testosteroon gevind. Geen reëlmatige seisoenale skommelings kon in enige van die seksuele parameters wat ondersoek is, waargeneem word nie.

Volgens verskeie bronne bereik vroulike diere in gevangenskap geslagsrypheid op 'n ouderdom van ongeveer 3 jaar 10 maande en diere in die natuur eers op 'n ouderdom van 4 jaar 7 maande, terwyl die jongste geslagsrype vroulike dier wat met hierdie studie versamel was, 6 jaar oud was. Hierdie verskille kan moontlik aan voeding toegeskryf word, alhoewel dit nie bevestig kon word nie. Die invloed van die omgewing op estrus is nagegaan deur te bereken wanneer bevrugting van die fetusse

en pasgebore kalwers plaasgevind het en dit met die reënval, temperatuur en daglengte van die spesifieke tydperk te vergelyk. Gegewens is van die studiegebied asook ander dele versamel. In gebiede met 'n eenmalige temperatuurs- en reënvalspiek het bevrugting in die meeste gevalle gedurende die warm vogtige periode, wanneer optimale voedings-toestande heers, voorgekom. Daar word aangeneem dat daglengte, wat betekenisvol gekorreleer is met voortplanting, kameelperde slegs indirek beïnvloed deur die invloed van daglengte op plante en hul voedingswaarde. Kameelperde teel egter dwarsdeur die jaar, is poli-oestrus en eenlinge word voortgebring alhoewel een tweeling in die studiegebied waargeneem is. Die plasenta is meerlobbig en van die sindesmochoriale tipe. Inplantasie kom aan dieselfde kant voor as waar die corpus luteum tydens dragtigheid gevorm word. Reproductiewe aktiwiteit van die vroulike diere neem nie met ouderdom af nie. Die gemiddelde interval tussen opeenvolgende kalwers, bereken uit verskeie bronne, word vasgestel op 19,9 maande. Wanneer die verhouding van dragtige tot nie-dragtige diere in aanmerking geneem word, kom hierdie interval op 22,9 maande te staan. Herbevrugting na geboorte intervalle van 23 en 27 dae is aangeteken. Die urine van dragtige kameelperde is volgens die metode van Asheim en Zondek ondersoek, maar geen gonadotrofiese aktiwiteit is waargeneem nie. Die mortaliteit van kalwers tot op eenjarige ouderdom word op ongeveer 48% geskat.

Monsters van ovaria op verskillende ouderdomme is vanaf die fetale stadium histologies nagegaan. Die teenwoordigheid van vesikulêre en haemorrhagiese follikels sowel as corpora lutea (CL) in fetale ovaria is bevestig. Morfologies het die CL in die fetus nie veel verskil van die in volwasse diere nie. Die voorkoms van 'n hele aantal CL is ook 'n kenmerk van onvolwasse vroulike diere, maar hulle degenereer tydens

puberteit. Addisionele corpora lutea word dikwels by dragtige diere gevind. Dit is bewys dat die CL tydens die vroeë stadia van dragtigheid kleiner word, waarna hul weer geleidelik toeneem in grootte tot en met geboorte. Andersins verskil die ovaria van volwasse kameelperde min van ander Artiodactyla. Albei ovaria skyn ewe aktief te wees.

Laktasie en die samestelling van die melk is ondersoek en daar is vasgestel dat laktasie ongeveer 13 maande duur. Teen die einde van die draagtyd is daar 'n afname in die maaginhoud van die diere, waarskynlik as gevolg van minder beskikbare ruimte in die abdominale holte. Daarteenoor is die maaginhoud van sogende diere baie hoër as dié van nie-sogende diere, wat moontlik toegeskryf kan word aan die verhoogde metaboliese behoeftes van soging. Die melk van sogende diere is net na geboorte ryker as later tydens soging terwyl die voor-laktasie sekresies selfs ryker as die kolostrum is (uitgedruk as totale vaste stowwe, vette, proteïene en laktose). In vergelyking met beesmelk bevat die melk van kameelperde meervette, totale proteïene, sekere minerale en sporelemente maar die laktose-inhoud is laer. Die melkopbrengs van die kameelperd is in dieselfde orde as dié van ander wilde hoefdiere.

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