

T REPRODUCTION AND POPULATION ECOLOGY

OF THE

BLUE WILDEBEEST ✓ CONNOCHAETES TAURINUS TAURINUS

✓  
IN ZULULAND

SR by

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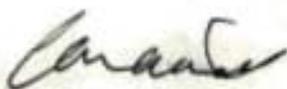
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This thesis, unless specifically indicated to the contrary in the text, is my own original work. It has not been submitted for a degree to any other university.

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ABSTRACT

A two-year study was made of the blue wildebeest Connochaetes taurinus taurinus in Zululand, Natal. Aspects investigated included age determination methods, growth and condition, reproductive physiology, habitat interactions, and population dynamics. Findings were related to suggested management of the species.

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## CHAPTER 1

### INTRODUCTION

#### 1.1.

##### JUSTIFICATION FOR CONSERVATION AND WILDLIFE RESEARCH

In the light of increasing human population pressures, conservation of wild animal species requires justification. The aesthetic and cultural grounds for maintaining wildlife sanctuaries have been eloquently expressed (Darling, 1960, 1970; Huxley, 1961; and Ratcliffe, 1976), but the realities of exponential human population growth demand that such considerations become increasingly irrelevant (Hanks, 1976).

#### 1.1.1.

##### ECONOMIC CONSIDERATIONS

The necessity for the economic justification of conservation no longer requires emphasis: in Africa south of the Sahara only about 10% of the land is suitable for continuous crop production, yet 80% of the people are directly dependent upon agriculture for their livelihood. By the year 2000 the soil will have to support at least twice as many people (Swank and Casebeer, 1972). Protein-hungry people demand practical evidence that proper management of

wildlife stocks results in the provision of protein-rich foods from land otherwise unsuitable for food production, and in the provision of a foreign currency from tourism.

Babich (1973) lists facets of the wildlife industry, and concludes that wildlife utilisation is economically viable. One aspect of tourism is simple game viewing: this has world-wide appeal, and, for example, contributed \$ 27 million to Kenya's Gross National Product in 1968 (Mitchell, 1968).

Game farming may provide recreational hunting and supply wildlife products at the same time. The ecological justification for this form of land use has been argued at length (Kyle, 1972). However, there has been little factual information on the meat production potential in South Africa (Joubert, 1969), and some authors have even doubted the value of game ranching as a competitive form of land use (Parker and Graham, 1971). Subsequent to these papers, Johnstone (1974) has provided an exposition of a Rhodesian game ranch where the meat yield was in excess of the production when the same area was utilised by cattle. Deane and Feely (1974) also reported confidence in satisfactory returns from capital invested in a Zululand game farm.

Bigalke (1974) states that in South Africa, wildebeest have become important on large holdings where extensive pastoral farming is practised. Elsewhere in Africa, utilisation of the species has reached the stage where domestication programmes have been initiated (Field, 1973). A species such as the wildebeest Connochaetes taurinus constitutes a replenishable resource, although it may become non-renewable under certain conditions of population instability (Tisdell, 1972). The high reproductive rate of the wildebeest implies that populations could be managed for high sustained yields. This situation is as yet not strictly applicable to Natal, because populations open to utilisation are (with the exception of

the Zululand reserves), small and isolated. In contrast, Child (1971) estimates that in Botswana some 60% of all meat eaten by humans is from an undomesticated source.

Utilisation of blue wildebeest populations is not without problems. Watson (1966) expressed concern that the Serengeti population would act as a reservoir for a non-virulent strain of rinderpest, and Plowright (1965) described the transmission of malignant catarrh from wildebeest calves to domestic stock. In the Kruger National Park, Young, Wagener and Bronkhorst (1969) recorded seventeen parasites in the blue wildebeest, six of which might significantly affect the commercial value of the carcasses.

#### 1.1.2.

#### ECOLOGICAL CONSIDERATIONS

The ability of ecosystems which support human life to persist and perform their functions in the face of inevitable environmental change is related to the complexity of these systems (Ehrlich and Holdren, 1975). Many ecologists maintain that preservation of extensive natural communities should be undertaken so as to serve as buffers and reservoirs of diversity.

Maintenance of such communities generally requires management to maintain biological systems at some reasonably constant composition; effective management is aided by a research program that provides information which is interpreted in the light of management aims.

It has been deplored on occasion that ecological work in Africa has been so centred on the larger vertebrates (Watson, 1966), but no other continent has such a diversity and abundance of large land mammals, and they are the only part of the fauna amenable to management and utilisation. Short (1977) maintains that wild animals are a virtually untapped source of information, and that

research findings may be relevant to the problems confronting mankind, especially in the field of population regulation. In view of the rate at which African ecosystems are being modified, field studies under natural conditions while opportunities exist become of importance.

## 1.2.

### HISTORICAL PERSPECTIVES IN ZULULAND: BACKGROUND TO THE PROBLEM

The history of wildebeest populations in Zululand, and in particular the Umfolozi Game Reserve (Fig. 2.3.), is essential for the understanding of present management problems. Probably no other African wild life sanctuary has suffered so markedly in the past from human impact. This impact took the form of measures to eradicate the tsetse fly Glossina spp..

Archaeological evidence suggests that human activity took place in the Umfolozi area over half a million years ago (Parnell and Penner, 1973). Vincent (1970) has outlined the more recent history of Zulu tribal occupation, and the subsequent historical developments summarised below are based on his paper. By 1840, European hunters had arrived in the area: depletion of wild life resources continued until the proclamation of Umfolozi Game Reserve in 1897. A further proclamation of 1907 extended the reserve, but deproclamation in 1915 opened the entire area south of the White Umfolozi to hunting (refer to Fig. 2.3.). With increasing farming activity bordering the reserve, the problem of transmission of nagana (trypanosomiasis) from game to domestic stock arose, with resultant pressurisation from farmers to eradicate the food reservoir of the tsetse fly within the reserve. Special Shooting Areas were established adjacent to the reserve to act as Buffer Zones, and the status of the reserve itself was uncertain until the Division of Veterinary Services assumed full control in 1940. In 1942 the nagana campaign was initiated - an attempt to

eradicate game (excluding the Square-Lipped Rhinoceros Ceratotherium simum) in Umfolozi Game Reserve.

Up until this stage, various species formerly prolific in the area had already been eliminated by hunting. Larger species eliminated included eland Taurotragus oryx, elephant Loxodonta africana, wild dog Lycaon pictus, hippopotamus Hippopotamus amphibius, brown hyaena Hyaena brunnea, oribi Ourebia ourebi, lion Panthera leo, giraffe Giraffa camelopardalis, and cheetah Acinonyx jubatus. The last three species have been re-established in the reserve in recent years, the lion independently of man. The wildebeest status was relatively unaffected, and Hobley (1926) estimated between 400 and 500 animals in Umfolozi, and 400 in Hluhluwe Game Reserve. By 1938 an estimate of 600 in Umfolozi and 400 in Hluhluwe was given by Jeannin (1951).

Prior to the start of the nagana campaign, Mentis (1970) estimated Umfolozi had a population of 300 wildebeest. Between 1942 and 1950 some 70000 animals were shot (Vincent, 1970), which included 1025 wildebeest (721 were shot within the reserve, and the remainder in the Special Shooting Areas). The campaign is described in detail by Mentis (*ibid.*); the relevant fact emerging is that by the end of the campaign, wildebeest, zebra Equus burchelli and impala Aepyceros melampus had been exterminated.

In 1952 the Division of Veterinary Services relinquished control of the area to the Natal Parks Board. Control of poaching was instigated both in Umfolozi Reserve and in the State land north of the Black Umfolozi (the Corridor: see Fig. 2.3.). Game dispersed from Hluhluwe Reserve into Umfolozi, and by 1959 concentrations of wildebeest and zebra were such that it was considered that they would compete for grazing with the square-lipped rhinoceros. Consequently a policy was instigated to exclude these species from Umfolozi, but this remained in force for only a short while, and by 1960 wildebeest were again permanently resident in the area south of the White

Umfolozi. Human population disturbance (and, later, fencing) prevented migration westwards out of the reserve.

Smuts (1972) has shown that migration allows for the rotational use of summer and winter ranges. Relatively sedentary populations with no predatory checks must ultimately result in habitat degradation, and stage 3 of Savory's (1963) ecological regression scale (Fig. 1.1.) was achieved around 1959. Deterioration in veld conditions was noted east of Dengezi and the Matshemnyama Hills, and in the Meva, Mpekwa and Mfulumkulu areas along the White Umfolozi River. This was attributed to the influx of zebra, wildebeest, warthog Phacochoerus aethiopicus, square-lipped rhinoceros and waterbuck Kobus ellipsiprymnus from the Corridor. Mentis (1970) used the kill figures from the nagana campaign to derive estimates of past and present biomasses, and his tentative conclusion was that the post-nagana stocking rates in 1967 were excessive.

Although the first culling programme was undertaken in Hluhluwe Game Reserve in 1954 (729 wildebeest were shot), removal of wildebeest in Umfolozi began only in 1959. Table 1.1. shows the extent of removal by culling or capture from the Complex ("Complex" hereafter refers to the Hluhluwe - Corridor - Umfolozi areas regarded as a unit). Although culling programmes were aimed chiefly at wildebeest and warthog, other species which have been subject to control include impala, zebra, waterbuck and nyala Tragelaphus angasi.

Table 1.2. provides a breakdown of some census data. The relative percentages of the total population are displayed graphically in Fig. 1.2. to illustrate major changes in distribution in the Complex. The relative percentages of the population in the Corridor and Umfolozi follow an inverse pattern, implying that the major movement patterns are between these two areas. High removal rates in 1970, 1971 and 1972 may have caused a drop in the relative distribution in Umfolozi. Despite these fluctuations, Umfolozi has experienced a

TABLE 1.1. : The numbers of wildebeest removed (by culling and capture) from the Central Complex, Zululand. Data from Natal Parks Board files. Figures should be taken as approximate, as there are numerous cases of conflicting totals in the files. Hence, results are not in complete agreement with those published by Vincent (1974).

(HGR = Hluhluwe Game Reserve

UGR = Umfolosi Game Reserve)

YEAR	HGR and N. CORRIDOR		UGR and S. CORRIDOR		COMPLEX TOTAL
	SHOT	CAPTURED	SHOT	CAPTURED	
1954	278	0	0	0	278
1955	451	0	0	0	451
1956	NO DATA	0	0	0	NO DATA
1957	309	0	0	0	309
1958	199	0	0	0	199
1959	1300	0	25	0	1325
1960	462	0	270	0	732
1961	382	0	359	0	741
1962	348	0	546	0	894
1963	418	0	526	0	944
1964	326	0	509	0	835
1965	427	0	782	0	1209
1966	546	15	451	0	1012
1967	386	44	308	63	801
1968	145	31	187	479	842
1969	146	130	159	417	852
1970	226	1037	41	0	1304
1971	99	207	183	1030	1519
1972	132	51	69	1430	1682
1973	0	0	127	164	291
1974	0	0	50	341	391
1975	0	0	0	0	0

TABLE 1.2. : Census figures for wildebeest in Umfolosi Reserve, the Corridor, and Hluhluwe Reserve, showing relative percentages of the total Complex populations.

Data derived from NPB files (except for 1944, 1949 and 1951, which are estimates of Sidney (1966)). As in Table 1.1., the files contained conflicting data e.g. the HGR subtotal for 1967 has been adjusted to agree with the grand total for that year. The 1969 figures must be regarded as highly suspect: they are so far below the 1970 figures as to suggest an impossible rate of increase.

YEAR	U.G.R.	% TOTAL	CORRIDOR	% TOTAL	H.G.R.	% TOTAL	COMPLEX TOTAL
1944		NO DATA	AVAILABLE		650		
1949		" "	" "		1000		
1951		" "	" "		1000		
1962			5793				
1965	1042	13,3	3755	47,9	3027	38,6	7824
1967	1062	28,2	2037	54,1	667	17,7	3766
1968		NO DATA	AVAILABLE		1646	38,2	4305
1969	1507	40,0	1598	42,4	661	17,5	3766
1970	3367	52,9	1972	31,0	1024	16,1	6363
1971	2182	42,9	2067	40,6	835	16,4	5084
1972	1454	41,4	1292	36,8	763	21,7	3509
1973	1950	56,9	812	23,7	667	19,4	3429
1974	1364	50,8	764	28,4	559	20,8	2687
1975	1358		520*		NO CENSUS		
1976	1347	50,1	751	27,9	591	21,9	2689

\* S. Corridor only.

Fig. 1.1. : Theoretical succession of stages of ecological regression under unmanaged conditions.

Stage 0 : Numerous animal species live in apparent stability on a range exhibiting high plant diversity.

Stage 1 : Mammals begin to approach potential rates of increase.

Stage 2 : Adverse habitat changes lead to reduction in unadaptable animal species (e.g. reed-buck). Habitat is however closer to optimum for some species (e.g. impala), leading to higher rates of increase, with concomitant boost in biomass.

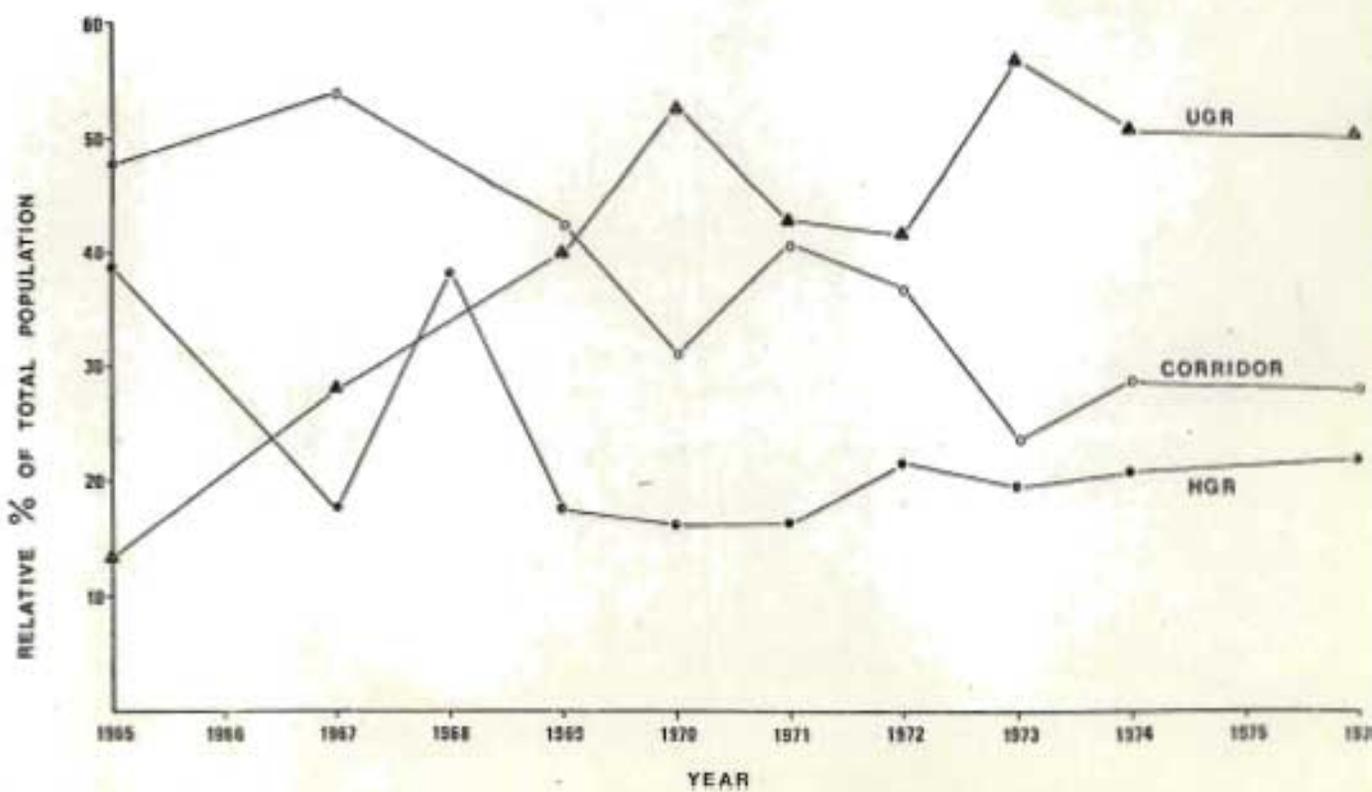
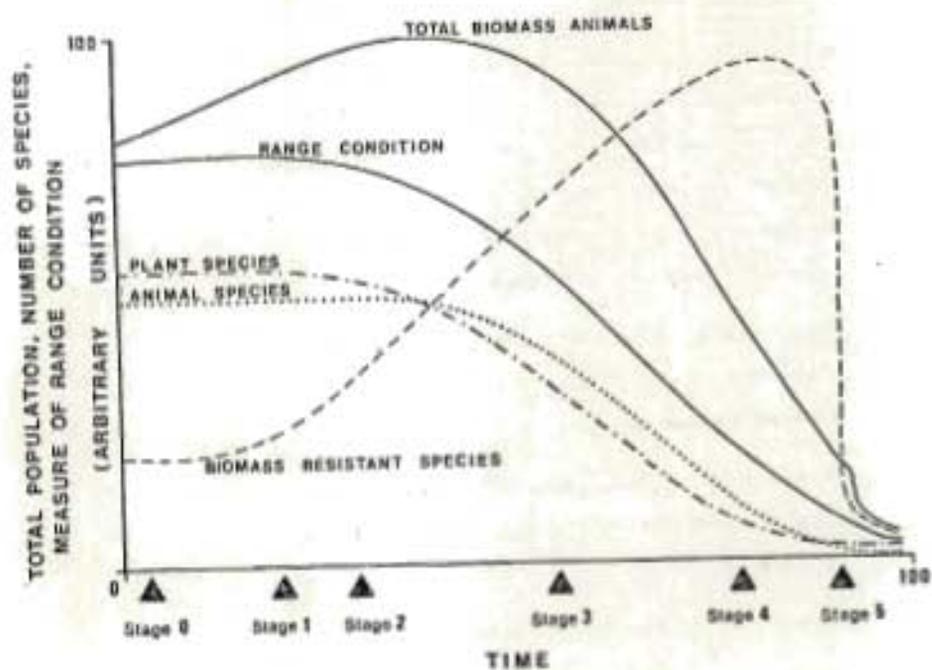
Stage 3 : Bare ground marked; decline in number of palatable shrubs. Trees show a pronounced browse line.

Stage 4 : Animal species decline accelerated. Ground cover almost limited to unpalatable species.

Stage 5 : Desert conditions approximate.

(Adapted from Savary, 1963).

Fig. 1.2. : Changes in the relative percentages of census figures for the three major subdivisions of the Complex.



steady rise in relative distribution, with a corresponding fall in the Corridor. Latterly, the Hluhluwe relative distribution has remained fairly constant, possibly indicating the limited desirable habitat in that reserve.

Fig. 1.3. indicates the effects of game removal programmes on the Complex population. The accuracy of counts varies from year to year; the discrepancy between the 1969 and 1970 figures is far beyond that attributable to the annual increment, and reflects the major differences in ground counts (1969) and aerial counts (1970). These differences would not however cause marked errors in the relative distribution between the Complex subdivisions (Fig. 1.2.).

### 1.3.

#### TAXONOMY AND DISTRIBUTION

##### 1.3.1.

#### TAXONOMIC STATUS

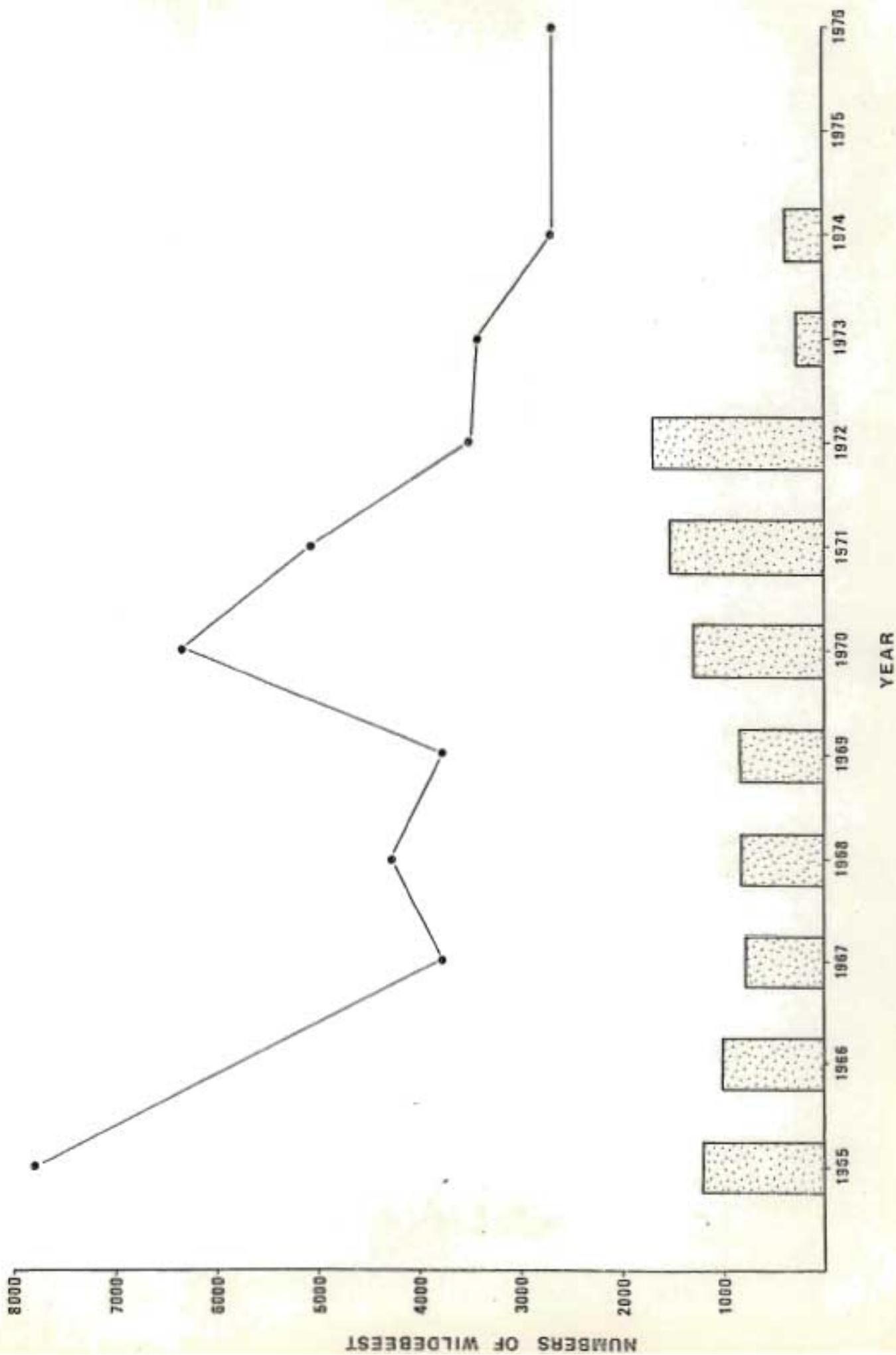
The genus Connochaetes (Lichtenstein, 1812) is classified as follows (Von Richter, 1974):

Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Hippotraginae, Tribe Alcelaphini, Genus Connochaetes.

Ansell (1971) places it in the subfamily as Alcelaphini and the Tribe Connochaetini. Leaky (quoted in Ansell, 1971) placed the genus with the Bovini on osteological grounds, and based on the fact that wildebeest share some diseases with cattle. However, features such as pedal and preorbital glands, a single pair of mammae, and seasonal calving are all Alcelaphine. There are, moreover, behavioural grounds for associating wildebeest with hartebeest (Estes, In: Ansell, 1971).

Roberts (1951) recognised two separate genera: Gorgon taurinus (Blue Wildebeest) and Connochaetes gnou (Black Wildebeest), but the presence of fertile hybrids (Van Ee, 1962; Zukowsky, 1959) negates

Fig. 1.3. :: Change in wildebeest numbers in the Complex from 1965. Points are census figures; histograms indicate the number of wildebeest removed in any particular year. Census values prior to 1970 are questionable (see captions to Tables 1.1. and 1.2.).



separation at genus level, and Connochaetes is now the accepted generic name, with the species names remaining as above. Historical developments in taxonomic nomenclature are traced by Ansell (ibid.), Sidney (1966) and Talbot and Talbot (1963). Alternatives in subspecies nomenclature, as with most taxonomic treatments, appear in the literature. For example, Allen (1939) recognised the Angola wildebeest as a subspecies Connochaetes taurinus mattosi, which was later regarded (Ellerman, et al 1953) as synonymous with C.t. taurinus. Talbot and Talbot (1963) may have been in error in designating the Western White-bearded wildebeest as C.t. hecki, as both Sidney (1966) and Ansell (1971) agree on C.t. mearnsi as the subspecies name.

I have accepted Ansell's (ibid.) division into five subspecies, viz.:

<u>C.t. taurinus</u>	(Burchell, 1823)	Blue Wildebeest
<u>C.t. cooksoni</u>	(Blaine, 1914)	Cookson's Wildebeest
<u>C.t. johnstoni</u>	(Sclater, 1896)	
<u>C.t. albojubatus</u>	(Thomas, 1892)	Eastern white-bearded wildebeest
<u>C.t. mearnsi</u>	(Heller, 1913)	Western white-bearded wildebeest

It is with C.t. taurinus that this study is concerned.

### 1.3.2.

#### DISTRIBUTION OF CONNOCHAETES TAURINUS

Fig. 1.4. shows the limits of distribution of the species in Africa. The past and present Southern African distribution has been described in detail by du Plessis (1969), from which source maps have been drawn (Figs. 1.5. and 1.6.).

In South Africa, the populations originally extended north of the Orange River in the Cape and Orange Free State, over most of the Transvaal, and into northern Natal. The species occurred in South West Africa, except in the subdesert of the south and west. The

Fig. 1.4. : The limits of distribution of Connochaetes taurinus  
in Africa. (After Sidney, 1966).



Fig. 1.5. : Past distribution of C. taurus in Southern Africa.  
(After du Plessis, 1969).

Fig. 1.6. : Present distribution of C. taurus in Southern  
Africa. (After du Plessis, 1969).



original range outside South Africa is documented by Ansell (1971). There is evidence that the extent of the species from Tanzania southwards has not been continuous in historical times.

With regard to the present distribution, the species in the Cape is limited to the extreme north (Kalahari Gemsbok National Park). After extinction in the Orange Free State, reintroductions took place (Van Ee, 1962). Kettlitz (1962) reports that the animal is no longer found in the central and southern Transvaal, and that, outside the Kruger National Park, the status is most secure in the Pilgrim's Rest area. Originally confined to the northern game reserves and surrounding farms in Natal (Vincent, 1962), reintroduction has occurred in other physiographic regions in central, southern and north-western Natal (Mentis, 1974).

In South-West Africa, the wildebeest favours the north-east (Sidney, 1966). The species is widespread in Botswana, except in the south-east (Smithers, 1968). In Angola, it is confined to the south, central and eastern areas. Child and Savory (1964) record the species mainly along the southern and western borders for Rhodesia, but not in the Zambesi Valley. Rock paintings from the Matopos and Marandellas of C. taurinus suggest an earlier more widespread distribution (Cooke, 1964), and indeed reintroduction has taken place in the Matopos.

The above present distribution patterns refer to C.t. taurinus. Zambia contains both this subspecies (in the south-west, west of the Kafue river), and a relict population of C.t. cooksoni in the Luangwa Valley in the east. This latter subspecies may have extended into Malawi (Sidney, 1966). C.t. johnstoni, now extinct in Malawi, is found in Mozambique, north of the Zambesi. This subspecies now occurs with C.t. taurinus (Tello, 1975), although the latter tends to occur south of the Zambesi. C.t. johnstoni extends into southern Tanzania, where it intergrades with C.t. albojubatus (Sidney, 1966). In Kenya and Tanzania, the Rift Valley divides C.t. albojubatus

from C.t. mearnsi, the former occurring in north-eastern Tanzania and southern Kenya, east of the Rift Valley, and the latter west of the Rift Valley, including the Serengeti plains (Ansell, 1971).

Sidney (1966), after a detailed analysis of the distribution of the Blue Wildebeest, concluded that the range had not altered appreciably over the last fifty years.

#### 1.4.

##### THE PURPOSE OF THIS STUDY

There have been three major works on C. taurinus, all from East Africa. The earliest work was done by Talbot and Talbot (1963) in western Masailand, and included data on growth, parasitology, behaviour, migration and population characteristics.

Estes (1966, 1969, 1974) provided a detailed account of the behaviour of the species, based on work in the Ngorongoro crater. His emphasis was on territoriality, and the differences between sedentary and nomadic populations, outlining the ethologically adaptive features of reproduction.

The third investigation of note was carried out by Watson (1966, 1969, 1970) in the Serengeti, and was chiefly concerned with population dynamics and reproductive physiology.

A more detailed review of the literature follows in the relevant Chapters. In general, one cannot assume that the data on reproductive physiology from East Africa are directly applicable to Southern African populations, as major differences exist in factors like photoperiodicity, rainfall and nutritional planes. For similar reasons, methods of age determination in Southern Africa require independent study. Further, little information is available on population dynamics and predictions, condition, and the multiplicity of factors contained in feeding and habitat selection.

Section 1.2. emphasised the necessity for management of the wildebeest in the Central Complex. To base management policies on scientific grounds, it was found that there were considerable gaps in the knowledge of the species in Zululand. With this in mind, the study included the following objectives:

- a) Age criteria: these were a prerequisite to evaluating growth rates, age at sexual maturity and reproductive senescence, and the age structure of populations.
- b) Reproduction: data on ages at sexual maturity and on the seasonality of calving were required to investigate rates of increase.
- c) Range utilisation: as populations were being controlled in order to prevent overutilisation of the available food supply, information was required on the extent to which wildebeest were responsible for the production or utilisation of overgrazed areas.
- d) Population Dynamics: to determine whether a population is increasing, decreasing or stable, it is necessary to examine natality, mortality and the factors governing these parameters. Data of this nature provide a framework for population trend prediction.

It was envisaged that data of this nature could (in addition to its application to management), be incorporated into a Land Capability Analysis for South Africa, where accurate information on all natural resources could be pooled. Knowledge of ungulate species ecology, particularly of those species which may flourish in marginal habitats, is essential if Land Capability Planning is to be effective.

With the above objectives as a framework, fieldwork was begun in 1973, and continued for two years.

## CHAPTER 2

### STUDY AREAS

#### 2.1.

##### INTRODUCTION

The major portion of the fieldwork was undertaken in Umfolosi Game Reserve. Data collection on habitat interactions and feeding behaviour was centred in this reserve, as it was chiefly in this area where herbivore populations were exerting considerable impact on the habitat. Material from culled animals was also collected from Umfolosi.

Data from the other areas (the Corridor and Hluhluwe Game Reserve), making up the Complex, were derived mainly from population and distribution analyses only. For these reasons the bulk of the study area description below concerns Umfolosi Game Reserve.

Culling material from Umfolosi was supplemented by data from additional animals culled or captured in Mkuzi Game Reserve. Apart from occasional herd classifications, no other data were collected from Mkuzi. It is considered that the Complex and Mkuzi wildebeest populations are, in zoogeographical terms, so similar that the Mkuzi culling data are directly applicable to those of the Complex. Clearly, this assumes that the two populations have similar nutritional

status, and that social factors (including population density) are not significantly different. Of necessity, this assumption was made, and in broad terms is probably valid. Again, because of the absence of data on habitat relationships in this study from Mkuzi, I have limited the Study Area description for that reserve in favour of Umfolosi.

## 2.2.

### LOCALITIES

#### 2.2.1.

##### THE COMPLEX

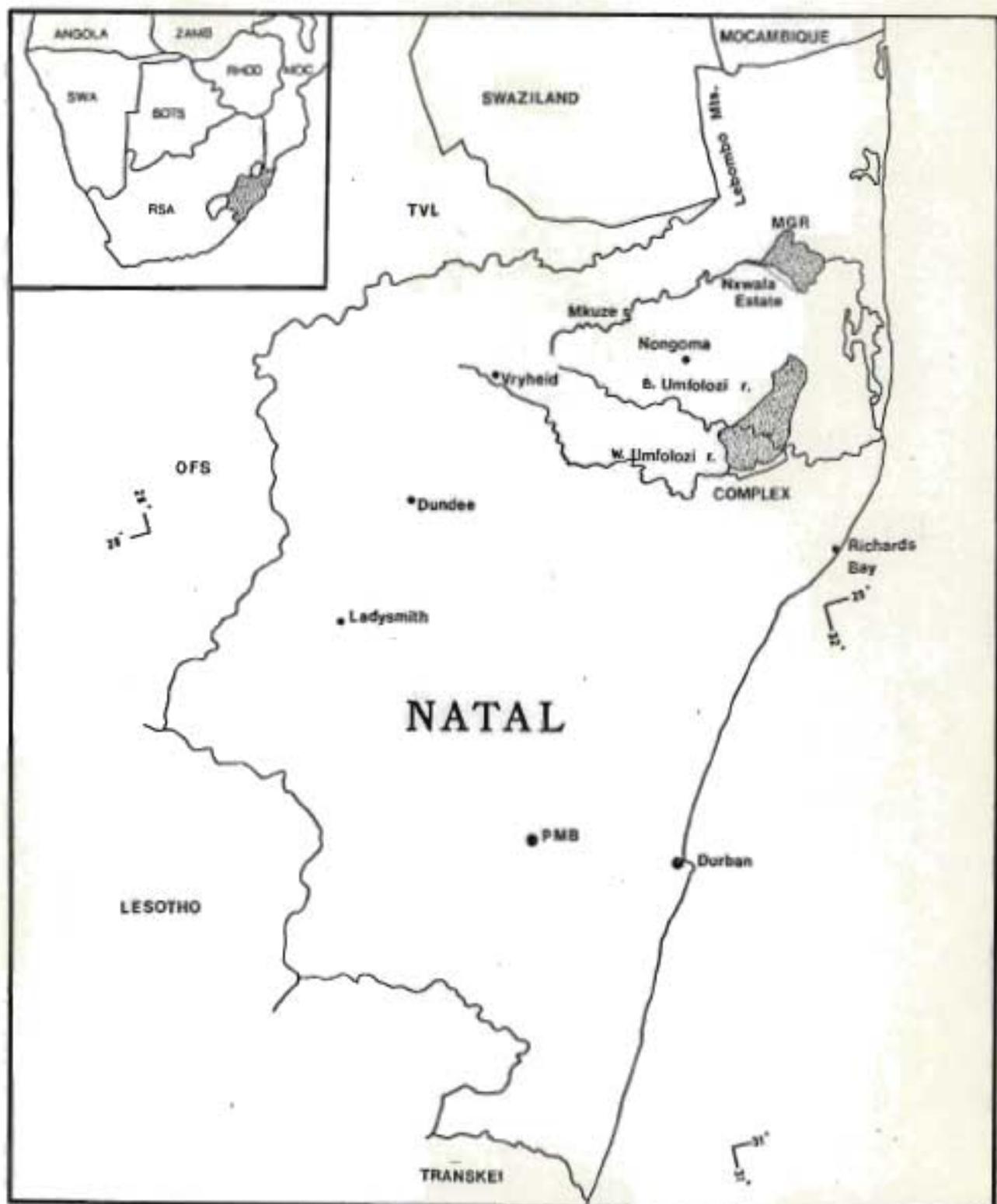
The Complex is situated in central Zululand, Natal. Geographic relationships to Natal and the rest of Africa are shown in Fig. 2.1.. It is some 94 000 hectare in extent, and comprises Hluhluwe Game Reserve (14 250 ha), the Corridor (32 000 ha) and Umfolosi Game Reserve (47 753 ha). The interconnecting Corridor (Fig. 2.3.) is in fact unallocated State Land, but ecologically and in the context of land-use has functions identical with those found in the legally proclaimed reserves bounding it. The Complex thus forms a single unit, virtually entirely contained by game-proof fencing, and surrounded by relatively primitive Zulu agricultural development. In many respects the Complex corresponds to an 'island ecosystem' (Plate 2.1.). Subsequent references to the three Complex subdivisions will be made as HGR, the Corridor, and UGR.

#### 2.2.2.

##### MKUZI GAME RESERVE

This area (approx. 24 300 ha) is situated east of the Lebombo Mountains on the Mozambique Plains (Fig. 2.1.). An ecological extension of the reserve to the south is formed by State Land (Nxwala Estates),

Fig. 2.1 : Geographic relationships of the Complex and Mkuzi Game Reserve to Natal and Southern Africa.



which makes an additional 8000 ha available.

## 2.3

### TOPOGRAPHY

#### 2.3.1.

##### THE COMPLEX

In UGR, the topographic features have largely resulted from a series of upheavals, each followed by an erosional cycle (Downing, 1972). This interplay between tectonics and pedimentation resulted in the present-day occurrence of three land surfaces within the reserve: Miocene, Pliocene and Quaternary. The oldest Miocene surfaces are found on the summits of the higher features. The Pliocene surface is represented by gently undulating topography, and forms the major part of the reserve. Quaternary components form the more recent valley plain terraces, which are alluvial in origin. The reserve extends westwards from the confluence of two major rivers, the Black and White Umfolozi, from an elevation at this point of 45m, to 579m at the summit of the Zintunzini Hills on the western boundary.

The Corridor is a tract of generally hilly country, at a higher elevation than UGR, interspersed by narrow valleys and occasional plains.

Maximum altitude in the Complex is attained in HGR (650m). The hills in this reserve have a more pronounced slope than in the Corridor, and descend relatively steeply into the catchments of the Hluhluwe and Nzimane Rivers.

#### 2.3.2.

##### MKUZI TOPOGRAPHY

Essentially flat topographically, the reserve is elevated only in the west by the Lebombo foothills.

Plate 2.1. : Satellite Image of the Complex (Earth Resources Technology Satellite, 29.1.73). Habitat degradation outside the Complex is so marked that the Complex appears demarcated even in a black-and-white image (with infra-red photography the effect would be far more pronounced). Boundaries of the Complex lie within (not on) the dashes.

b = Black Umfolosi River

w = White Umfolosi River

L = Lake St. Lucia

O = Indian Ocean



PLATE 2.1

## 2.4.

GEOLOGY AND SOIL ASSOCIATIONS

Adequate geological and soil descriptions are found only for UGR (Downing, 1972).

## 2.4.1.

UMFOLOSI GAME RESERVE

As described by Downing (ibid.), the sedimentary rocks are composed of five series. The Table Mountain Sandstone series is very localised, and is represented only by the Mhlolokazana Cliffs. The Dwyka series is found chiefly along the western boundary. The lower Ecca series comprises shales which may be exposed on Pliocene surfaces. Overlying this series is the Middle Ecca, prominent in the hills in the wilderness area in the south of the reserve. Differential weathering of this series has resulted in a terraced topography displayed on hillslopes. The final series of sedimentary rocks is the youngest Stormberg sediments, represented by exposures along the eastern boundary.

The igneous geological component is represented mainly by dolerites which intrude through the sedimentary strata in the form of dykes and sills. Other volcanics, in the form of basalts and rhyolites, are fairly localised.

Inasmuch as the nutrient content of vegetation reflects the mineral status of the soil on which it was grown, the soil-wildlife relationship is important. In East Africa, Anderson and Talbot (1965) have indicated that game distribution patterns are at least partially dictated by soil types, probably mediated through vegetation species composition. The derived soils of the reserve are readily correlated with woodland communities and topography, such that Downing (ibid.) was able to describe three major associations: Upland, Bottomland and Riverine soils. The Upland soils are shallow, suffering from rapid

drainage and consequent leaching. They have a characteristically low water storage capacity, resulting in soil moisture stress for associated vegetation during the dry season. From the Pliocene surfaces five Upland soil series have been identified: Williamson, Arcadia, Springfield, Mispah, and Kiaora.

The Bottomland soils are of transported origin, reflected by accumulations several metres deep on alluvial terraces and valley bottoms. The presence of Carbonate nodules, revealed by erosion, indicates a degree of illuviation, and accounts for the high fertility of these soils. A higher moisture storage capacity is found, although these soils will seasonally dry out, resulting in the precipitation of dissolved carbonate salts as nodules. Eight soil series have been defined in the Bottomland Association: Weldene, Uitvlugt, Bonheim, Rensburg, Sun Valley, Doveton, Makatini and Sturrocks. The last three series are exceptionally fertile.

Unconsolidated, unstable alluvia up to 5 m deep constitute the Riverine Association. The major components of these alluvia are sands and silts in the beds and banks of the Black and White Umfolozi rivers. Coarse alluvium extends some way upstream of tributaries entering these two rivers. This Association clearly has a perennial availability of soil moisture.

#### 2.4.2.

##### MKUZI GEOLOGY AND PEDOLOGY

During the Cretaceous, the flatter parts of this reserve constituted part of the sea bed (Vincent, 1972). The marine deposits were subsequently overlaid by sands and volcanic derivatives from the Lebombo mountains. Consequently, rhyolitic-derived soils predominate in the western foothills which merge into quaternary sand-derived soils towards the east.

## 2.5.

CLIMATE AND WATER RESOURCES

## 2.5.1.

THE COMPLEX

A general pattern of hot wet summers (October to March inclusive) and mild dry winters (April to September inclusive) applies to the Complex as a whole. The details below pertain chiefly to UGR, and may be taken as applying to the Complex, with the exceptions of rainfall and temperature. HGR has a mean annual rainfall figure of 985mm over 35 years, compared to 668mm for UGR over a 15-year period.

## 2.5.1.1.

TEMPERATURE AND INSOLATION

Downing (1972) has detailed the differences in intensity of insolation for slopes of different aspect. In general, south aspect slopes receive less insolation than north aspect, and east aspect slopes receive less than west.

Temperatures recorded over a seven-year period at Mpilo, UGR (Altitude 290m) are given in Table 2.1.. Mean monthly temperatures range from 23,3°C to 27,2°C during summer (October to March inclusive), and from 19,3°C to 22,5°C in winter (April to September). The maxima recorded in the Table have been exceeded at other lower-lying places in the reserve. Temperature inversions may occur during the dry season. Frost does occur, but rarely (Vincent, 1970).

## 2.5.1.2.

WIND

Wind strength is generally from light to moderate in the Complex. Southerly winds occur during the dry season, but will only produce rain if cool and overcast conditions persist for several days.

TABLE 2.1. : Air temperatures ( °C ) recorded at Mpila, Umfolozi Game Reserve, from April 1960 to March 1963, and from September 1966 to September 1970 (After Downing, 1972).

MONTH →		OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	ANNUAL
M A X	Absolute	39,4	40,0	40,0	43,3	40,0	40,0	36,7	34,4	31,7	33,3	40,6	38,9	43,3
	Mean	28,4	29,4	30,7	32,6	32,9	29,9	27,6	26,7	25,3	25,3	26,8	26,8	28,7
M I N	Absolute	10,6	10,0	13,3	16,7	8,3	6,7	10,6	8,9	7,2	6,7	8,9	10,0	6,7
	Mean	18,2	18,5	19,9	21,8	21,6	20,3	17,4	15,7	13,2	13,2	14,8	17,3	17,6
MEAN		23,3	23,9	25,3	27,2	27,2	25,1	22,5	21,2	19,3	19,3	20,8	22,1	23,2
MEAN DAILY RANGE		10,2	10,9	10,8	10,8	11,3	9,6	10,2	11,0	12,1	12,1	12,0	9,5	11,1

This uncommon winter precipitation takes the form of a light drizzle. Towards the end of the dry season hot and dry northerly and north-westerly winds predominate. With the onset of summer, southerly winds account for most of the rainfall, often accompanied by a drop in temperature of up to 10°C (Downing, 1972).

### 2.5.1.3.

#### PRECIPITATION AND WATER RESOURCES

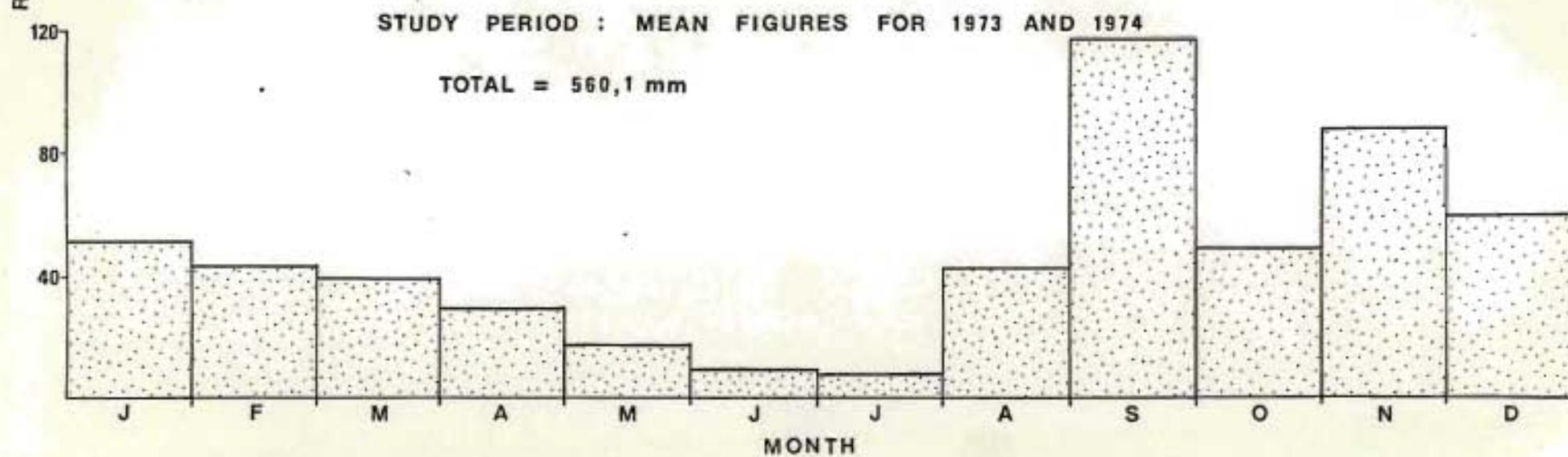
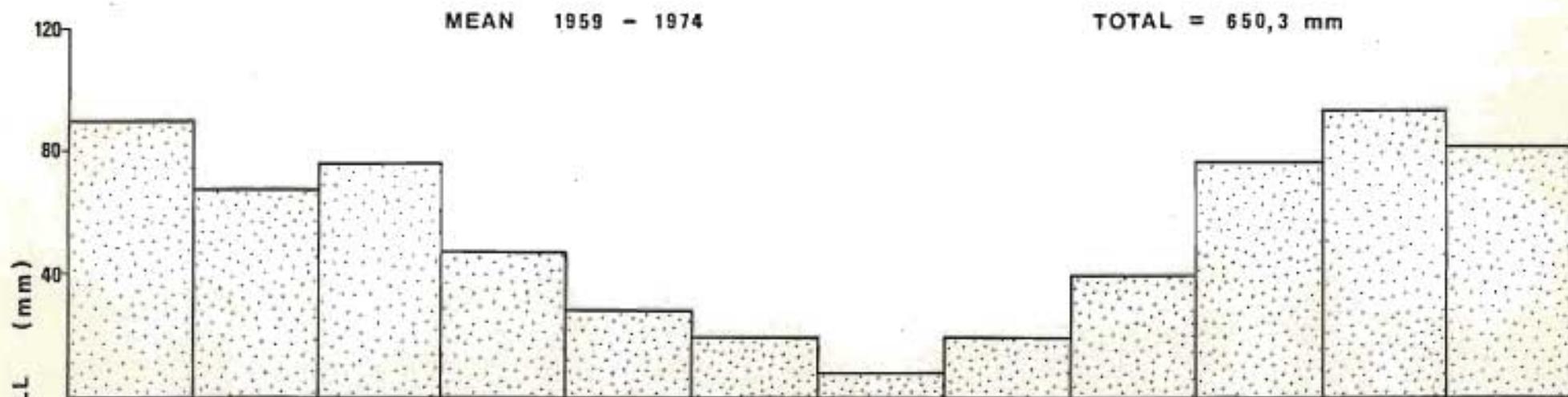
Table 2.2. shows the rainfall in mm recorded at Mpila from 1959 to 1974. The mean annual rainfall is 676,7mm, including the 1963 total. This year was unique in living memory, in that 352,5mm were recorded for July alone, with 281,5mm on one specific day (Downing, *ibid.*). The anomaly is so marked that inclusion of this July figure lends marked bias to the mean figures. In the table, I have bracketed the mean figure for July when the 1963 figure is excluded. Excluding the 1963 annual total from the mean total, a figure of 650,3mm results. This is about 66% of the mean annual total for HGR. About 72% of the mean annual rainfall in UGR falls during the summer rainy season, from October to March inclusive. Monthly rainfall decreases from the end of March, and occasionally no rain may fall from May to August inclusive, with June and July normally the driest months.

Inspection of Table 2.2. will show the marked monthly and annual variation. To demonstrate departure from the norm during the study period, Fig. 2.2. was prepared. Total rainfall during the study period was some 14% below average. Monthly patterns appeared to correspond to the norm, except for unusually early rains which fell in August and September 1973. Both these months received the highest rainfall ever recorded for them; indeed the September total formed the maximum monthly contribution for that year. Of major significance to vegetation was that the following month, October 1973, received the least rain ever recorded for that month. Annual

TABLE 2.2. : Rainfall figures (mm) from 1959 to 1974, for Mpila, Umfolozi Game Reserve. See text for explanation of July mean. (Data from NPB files.)

MONTH	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	MEAN
JAN	109,1	19,5	72,7	61,9	91,6	178,7	29,3	219,8	32,7	49,5	29,9	83,5	224,9	131,0	25,7	79,0	89,9
FEB	12,7	134,8	72,0	10,3	198,3	26,7	28,0	51,6	147,4	28,7	19,3	21,0	28,2	226,5	77,1	12,0	68,4
MAR	12,0	67,4	133,6	134,5	114,0	15,4	15,0	79,8	46,6	127,3	222,5	83,3	68,3	37,7	20,4	60,7	77,4
APR	18,2	92,5	68,0	47,1	40,0	74,9	44,4	34,5	118,6	9,5	37,9	29,5	75,2	10,2	32,1	28,8	47,6
MAY	76,0	7,9	26,1	5,0	0,0	9,0	11,0	12,0	11,5	0,0	25,2	64,3	114,0	73,4	2,4	34,2	29,5
JUN	0,0	6,6	75,3	0,0	86,5	12,5	67,1	27,5	0,0	2,4	4,0	10,9	0,1	6,9	2,0	19,5	20,1
JUL	2,4	1,9	4,5	0,5	352,5	3,2	19,5	0,0	10,0	3,1	20,8	0,0	24,2	23,1	18,8	0,0	(8,8) 30,3
AUG	38,7	6,1	6,5	33,5	1,8	7,7	58,0	19,0	7,0	31,9	0,0	4,2	16,0	7,4	78,2	7,9	20,2
SEP	18,5	48,7	66,0	9,6	6,1	9,5	40,5	18,9	22,0	24,9	58,0	47,9	20,0	9,0	200,1	35,3	39,7
OCT	80,5	32,4	61,3	62,7	68,6	196,8	78,6	28,4	92,4	68,8	130,1	95,1	86,4	60,9	22,1	63,7	76,8
NOV	48,5	204,4	123,8	87,3	77,3	59,5	109,7	75,6	194,4	59,8	45,6	133,2	37,1	70,4	78,9	98,6	94,0
DEC	62,9	321,8	46,9	117,3	35,9	85,5	23,0	78,1	53,8	143,5	33,5	24,6	94,4	70,2	31,0	91,5	82,1
ANNUAL TOTAL	479,5	944,0	756,7	569,7	1072,6	679,4	524,1	655,2	736,4	549,4	626,8	597,5	788,8	726,7	588,8	531,4	676,7

Fig. 2.2. : Comparison of rainfall patterns during study period with mean patterns (data for Mpila, UGR).



cycles in plant physiology were thus initiated earlier than usual, and then halted or retarded as a result of an abrupt change in rainfall. The effect of such stresses on vegetation that has evolved with a dry season/wet season climate is unknown.

Some field observations may serve to illustrate the climatic stresses sub-tropical vegetation are subject to. A period of relatively little rain in February 1974 was followed by a sudden increase in March. The low rainfall period presumably induced a "winter response" in some of the woody plants, for several species (Acacia nigrescens and A. grandicornuta) responded to the March rainfall by producing a flush of new leaf buds, essentially a "spring response". Further, seasonal growth cycles between monocotyledons and dicotyledons appear to be initiated by different factors. For example, by the end of July 1973, rainfall had contributed to the formation of green growth in short grass swards, but had had no visible effect on trees. Conversely, towards the end of September 1974 most of the Acacia species had come into leaf (presumably the proximate factors were daylength and increased temperature), but the rainfall had been insufficient to change the appearance of the grasses. The result was a marked visual disparity between the green of the Acacias (particularly A. nigrescens) standing in the dry, yellow grasses.

An additional obvious effect of variation in rainfall pattern is that peak vegetation productivity will tend not to occur at similar times every year. Again, this was well illustrated during the study period in UGR. Observations made in mid-February 1974 showed vegetation to have already assumed the characteristic dry winter appearance. By contrast, observations at the end of February 1975 gave the subjective impression that the vegetation had attained peak greenness and biomass.

Non-measurable precipitation occurs as fog, mist and dew. During the dry season these phenomena may contribute significantly to the

moisture available to plants. Fog occurs particularly in winter, when it is confined to valley systems. It is marked at dawn, but usually dissipates by 0900 hrs (Downing, ibid.) Mists are frequent in summer in higher lying areas, particularly in HGR. Dense dew may occur on winter nights. Lightning and thunderstorms are frequent in summer, but hailstorms are rare. Observations of lightning starting veld fires have been made in the Complex by Natal Parks Board staff (Downing, ibid.), and one can consequently assume that fire has been an ecological factor in the area before the arrival of man.

The availability of water to animal populations is a major factor influencing their distribution. Precipitation is clearly the main source of water, but the availability is governed by topography, pedology and evaporation. In UGR, the Black Umfolosi is perennial, but agricultural malpractices in the catchment area have led to a decrease in the flow during winter, and to an increased frequency of summer floods. Vincent (1970) noted that the severe floods of July 1963 had markedly altered the nature of the bed of the river, leading to a predominantly sandy substrate as opposed to the previously rocky make-up. Reduced flow and depth have had important consequences on animal movement, in that the river is now fordable for a longer period of the year.

The White Umfolosi river suffers from even more severe siltation, and surface flow during winter months now ceases entirely. Water is however available in the form of scattered pools which tend to occur beneath the banks where evaporation is limited. These pools tend to be maintained by the digging behaviour of species such as warthog, Phacochoerus aethiopicus.

All tributaries of these two main rivers have temporary flows, carrying water for only a few days after heavy rain. Permanent springs in the reserve have a very limited saline flow: recorded

situations include points in the Nyonikazana stream (a tributary of the Madlozi), in the Thobothi and Ntshiyana streams in the west, and on the slopes of Ngqolothi Hill. Fig. 2.3. illustrates the sources of permanent water in UGR and the Corridor at the end of the dry seasons in 1974 and 1975.

Numerous pans occur throughout the Complex, formed chiefly by the wallowing action of the square-lipped rhinoceros, Ceratotherium simum. These are temporary in nature, and persist for several weeks only after heavy rainfall. In UGR, an artificially maintained pan is situated near Gqoyini, and serves as a tourist hide. Two small semi-permanent lakes are found in the east. Dadethu Pan will dry out in a particularly dry winter, but Mggizweni Pan is more reliable, and there are only two records of it drying out (Vincent, 1970). I consider Mggizweni to possibly form an ox-bow lake of the White Umfolozi. The shape of the pan is similar to that of a classic ox-bow, and it is surmised that, when the ox-bow was cut off from the river, siltation continued in the river and ceased in the ox-bow. The end result is that the bed of the White Umfolozi is now elevated with respect to the bed of the pan, and thus allows the water table to be exposed in the pan when the adjacent river is dry.

The availability of water secondary to the two main rivers is not of marked significance to the more mobile animals, because no point in UGR is further than 8 km from either river.

The Corridor, with an annual rainfall of about 762mm, has the Nyalazi river as its chief water source. Although flow is maintained only after heavy rains, pools do persist throughout the winter. Northern sectors of the Corridor embrace the perennial Hluhluwe river. The absence of water on the higher features of the Corridor during winter results in relative underutilisation of grazing during this period, and the provision of water in such areas has been considered as a

Fig. 2.3. : Distribution of permanent water at the end of the dry seasons in 1974 and 1975. Data collected by NPB staff, and collated by C. J. Forrest.



management tool.

HGR is served by the perennial Hluhluwe river, which is interspersed with deep pools and rocky stretches. The two main tributaries the Nzimane and the Manzibomvu, both have year-round water available, but the latter's flow terminates in winter to leave isolated pools. An artificial pan is maintained at Munywaneni.

#### 2.5.1.4.

##### EVAPORATION AND HUMIDITY

Monthly evaporation figures from Hluhluwe Dam are presented in Table 2.3.. The mean evaporation for summer (October to March inclusive) is 1039,6mm and 679,2mm for winter (April to September inclusive). The maxima of 236 and 204mm were recorded for January and February, which are the warmest months in the Complex. The ratio of evaporation to rainfall at the Dam is 2,7 : 1. The effects of evaporation are most noticeable on water in the pans. Magunda Pan, a substantial reservoir relative to most pans, was full in late August 1974. Three weeks later, despite sporadic rainfall, the pan was seen to be dry.

By constructing a climatic diagram, Downing (1972) portrayed the duration and intensity of humid and arid periods. His classification of UGR into a dry, sub-humid to nearly semi-arid climate is reflected by the predominantly deciduous woodlands, composed mostly of Acacia spp.. The arid winter period limits plant development. The most arid conditions prevail on west and north-west aspects as a result of strong afternoon insolation. South and east aspects, exposed to the path of the rain-bearing winds, are cool and moist in comparison to northern aspects.

TABLE 2.3. : Monthly evaporation (mm) at Hluhluwe Dam from 1st October 1963 to 31st December 1970.  
(After Downing, 1972.)

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	YEAR
MAXIMUM	236,5	204,5	192,8	140,0	122,7	102,6	115,3	132,6	175,5	177,0	185,7	214,6	236,5
MINIMUM	168,4	128,0	125,2	108,0	88,4	78,2	84,6	101,1	131,3	143,0	124,5	175,5	78,2
MEAN	201,2	170,2	163,3	119,9	103,4	92,2	96,5	120,4	146,8	154,9	156,2	193,8	1718,8

## 2.5.2.

MKUZI CLIMATE AND WATER RESOURCES

The average annual rainfall for the reserve is about 700mm. Rain-bearing winds are, as in the Complex, southerly and produce erratic rainfall, largely in the form of thunderstorms. Data from nearby weather stations suggest a mean summer temperature of 24,5°C and a mean winter temperature of 19,5°C (Vincent, 1972).

The Mkuzi river is not perennial, and the numerous pans are ephemeral as a water source, as described for the Complex. Two pans in the centre of the reserve are artificially maintained.

## 2.6.

VEGETATION

## 2.6.1.

UMFOLOSI GAME RESERVE

The reserve lies within one major veld type as defined by Acocks (1953): the Zululand Thornveld of the Coastal Tropical Forest type. The thornveld is divided into two subtypes - a low and a high altitudinal form. The low altitude form is the major veld type occurring within the reserve (Porter, 1975). UGR is predominantly wooded grassland or savanna, with Acacia spp. as the dominant trees.

The vegetation has been described in detail by Downing (1972). Essentially, he recognised three woody associations containing ten communities, using normal association analysis. The associations were distributed according to soil associations. His grouping was as follows:

Acacia - Combretum open woodland association

- a) Acacia caffra community
- b) Acacia tortilis community

- c) Acacia nigrescens community
- d) Acacia burkei community
- e) Combretum apiculatum community

Acacia - Spirostachys closed woodland association

- a) Acacia nilotica community
- b) Acacia grandicornuta community
- c) Spirostachys africana community

Acacia - Ficus riverine woodland association

- a) Phoenix reclinata community
- b) Acacia robusta community

With reference to these communities, Downing (ibid.) discussed the effects of soil factors, fire and the biota on physiognomy, notably secondary thicket encroachment. Further descriptions of some of these communities in relation to wildebeest habitat selection are found in Chapter 7 .

Downing (ibid.) described nine grass communities in UGR:

- a) Cynodon community
- b) Themeda-Aristida community
- c) Trichoneura community
- d) Bothriochloa community
- e) Panicum maximum community
- f) Panicum coloratum community
- g) Themeda-Urochloa community
- h) Themeda-Panicum community
- i) Themeda community

The grasses in the Closed Woodland association are more heavily grazed than those in the Open Woodland association, as a result of a higher soil fertility in the Closed Woodland. Although these soils have a high fertility they are susceptible to erosion if the grass cover or topsoil is adversely affected. Downing's work on

the grass communities showed a retrogression whereby climax grasses were being replaced by mid-seral and pioneer grasses. The retrogression was ascribed to selective grazing by an increasingly large herbivore biomass.

Downing's (ibid.) work deemed further vegetation analysis unnecessary for this study. Some broad-based ecological comments on the vegetation of UGR can however be included. The general appearance of the vegetation is that of an unstable ecosystem, possibly in a low successional stage. Under-tree grasses and open grasses are not radically different, as they would be in a more stable ecosystem (I. MacDonald, pers. comm.). The preponderance of broad-leaved grasses (characteristic of a low successional stage) lends an unnaturally lush appearance during the summer. Further support to my hypothesis of instability is shown by the relative absence of regeneration of species like Acacia nigrescens, possibly on account of an overabundance of browsers like impala and nyala.

### 2.6.2.

#### THE CORRIDOR

The high-altitude Zululand Thornveld is represented in this area. Previously, extensive areas of Themeda triandra grassland dominated the hills, but many of these expanses have been invaded by thicket in the form of Acacia karoo and Dichrostachys cinerea. The reasons for this invasion have been outlined by Deane (1966).

### 2.6.3.

#### HLUHLUWE GAME RESERVE

A detailed vegetation map for this reserve was compiled by Whateley in 1975. He recognised six physiognomic divisions containing sixteen communities:

Forest

- a) Celtis africana - Harpephyllum caffrum community
- b) Celtis africana - Euclea schimperi community

Riverine Forest

- a) Acacia robusta - Ficus sycamorus community
- b) Spirostachys africana - Euclea schimperi community

Woodland

- a) Spirostachys africana community
- b) Combretum molle community
- c) Acacia burkei community
- d) Acacia nilotica community
- e) Acacia karoo community

Thicket

- a) Euclea divinorum community
- b) Acacia karoo community
- c) Acacia caffra community
- d) Acacia davyi community

Induced Thicket

- a) Dichrostachys cinerea - Acacia karoo community

Grassland

- a) Panicum maximum - Cyperus textilis community
- b) Themeda triandra community

To the north-west of HGR, high forested hills are dominated by Celtis africana, particularly on the wetter south-east facing slopes. Many of the south-eastern hills are however unforested, and are characterised by Themeda triandra grassland subject to Acacia karoo invasion. The lower-lying south-western regions display typical Acacia woodland, similar to that occurring in UGR. An undesirable vegetation trend is reflected by large tracts of Euclea divinorum thicket in the south and central areas.

Grass cover is negligible in the forested areas. The Themeda triandra on hill slopes shows a characteristic progressive reduction in height from tall stands at the bases to relatively short stands on the ridges. In closed woodland of Spirostochys africana and Euclea divinorum thickets, the grass Dactyloctenium australe predominates. A little-utilised grass, Sporobolus pyramidalis, grows extensively in low-lying reaches, presumably old flood plains. Grass-covered hills are not all dominated by Themeda triandra; relatively unpalatable species like Hyperthelia dissoluta may be found in restricted elevated areas e.g. Mashiyo.

#### 2.6.4.

##### MKUZU GAME RESERVE

This reserve is unique in Zululand with respect to the mosaic of vegetation types which occurs. Moll (1968) recognised six major types:

- 1.) The Tall Tree Savanna, in the Lebombo area, has Combretum apiculatum and Dombeya rotundifolia as its dominant trees.
- 2.) The Riverine Woodland is dominated by Ficus sycamorus and Acacia xanthophloea.
- 3.) The Tongaland Sand Forest contains the following main canopy trees: Newtonia hildebrandtii, Cleistanthus schlechteri, Pteleopsis myrtifolia and Dalium schlechteri.
- 4.) Short Tree Savanna is found on the plains adjacent to the Lebombo range. Acacia nilotica and Acacia tortilis dominate a grass understory of Themeda triandra, Bothriochloa insculpta and Aristida barbicollis.
- 5.) Tall Tree Savanna, on red loam soils, is dominated by Acacia nigrescens, Ozoroa paniculosa and Themeda triandra.

- 6.) Short Tree Savanna intergrading with Thicket lies adjacent to the Mkuze river. Important plant species are Acacio luderitzi and Euclea divinorum.

## 2.7

### LARGE MAMMAL STATUS

#### 2.7.1.

##### THE COMPLEX

Bourquin, Vincent and Hitchins (1971) listed 48 mammalian species in the Complex. Important contributors to the biomass are 14 Bovid species, two species of the Family Rhinocerotidae, zebra (Equidae) and warthog (Suidae).

Downing (1972) tabulated estimates of biomass for UGR, and concluded that a threefold increase in the biomass had occurred between 1942 and 1972. By comparing the relative biomasses of grazers, mixed feeders and browsers, he showed that the biomass increase was caused chiefly by the grazers. This implied that the grazing demand for climax grass species had declined whilst that for mid-seral and pioneer grasses had increased.

Table 2.4. tabulates the numbers of larger species counted in the Complex during a helicopter census (Whateley and Brooks, 1974). An incomplete census was made the following year: figures for UGR only are displayed, and these are bracketed. The Complex totals are for the complete 1974 census.

Brooks (1972) has pointed out that differences in body size affect the visibility from a helicopter of different species, and has suggested a method of establishing accuracy limits for specific species based on subjective considerations of the relative visibilities of different species under suitable counting conditions.

**TABLE 2.4.** : Numbers of some large mammals in the Complex, 1974. Data from helicopter census. Figures for the first five species can be regarded as being reliable; species below the line have figures which should be taken as indicators only. The bracketed UGR figures are for 1975. (Whateley and Brooks, 1974; Brooks, Whateley, Forrest and Densham, 1975.)

	HGR	CORRIDOR	UGR	COMPLEX
Buffalo ( <u>Syncerus caffer</u> )	730	809	956 (908)	2495
Giraffe ( <u>Giraffa camelopardalis</u> )	26	10	14 (36)	50
White Rhino ( <u>Ceratotherium simum</u> )	143	363	836 (1022)	1342
Wildebeest ( <u>C. taurinus</u> )	559	764	1364 (1358)	2687
Zebra ( <u>Equus burchelli</u> )	417	582	657 (686)	1656
Impala ( <u>Aepyceros melampus</u> )	2077	1641	1986 (1224)	5704
Kudu ( <u>Trogelaphus strepsiceros</u> )	54	264	702 (651)	1020
Common Reedbuck ( <u>Redunca arundinum</u> )	0	9	70 (41)	79
Mountain Reedbuck ( <u>Redunca fulvorufula</u> )	4	10	71 (33)	85
Waterbuck ( <u>Kobus ellipsiprymnus</u> )	13	84	527 (494)	624

Many important species are grossly under-represented by an aerial census, on account of their crepuscular, fossorial or nocturnal behaviour, and are consequently not included in the Table. Estimates of the status of some of these species follow. Of the Carnivores, lion (Panthera leo) have been estimated by Anderson (1974) to number at least 128. The first lion re-appeared in the Complex in 1958 (Steele, 1970), and an unofficial reintroduction of several females took place in 1965. Since 1966, 40 cheetah (Acinonyx jubatus) have been reintroduced. Present numbers are unknown. Leopard (Panthera pardus) are seldom seen but can be assumed to be fairly common. The spotted hyaena (Crocuta crocuta) is very numerous.

Nyala (Tragelaphus angasi) is a very common species, but the related bushbuck (T. scriptus) is believed to have declined, and is now uncommon. Warthog are prolific but estimates of density are very hard to arrive at. Primates are well represented by baboons (Papio ursinus) and two species of monkeys. Of the smaller antelope, the klipspringer (Oreotragus oreotragus) is now a rare species, but steenbuck (Raphicerus campestris) and grey duiker (Sylvicapra grimmia) are common.

The black rhino (Diceros bicornis) was estimated by Hitchins (1975) to number over 300 in the Complex. The status of this species is assured, and populations are increasing.

### 2.7.2.

#### MKUZI

Dixon (1964) presented a preliminary check list of the mammalian fauna. He suggested that the high numbers of smaller Carnivora (Canis mesomelas, the black-backed jackal, in particular) may account for the poor Rodent and Soricid representation. Apart from the spotted hyaena, there are however no large carnivores to control

herbivore populations. Constant management has thus become necessary, aimed primarily at the prolific impala (Aepyceros melampus) populations. Table 2.5. contains some of the results of the 1975 helicopter census. Species contributing significantly to the biomass which are not shown in the Table include warthog and nyala. In comparison to the Complex large mammal populations, the following points arise:

- a) The absence of buffalo (Syncerus caffer) may detract from the utilisation of long-grass areas by other species.
- b) The habitat appears eminently suitable for impalo.
- c) The wildebeest in Mkuzi do not have to compete for grazing with a large white rhino population (the grazing requirements of the two species are very similar).

## 2.8.

### MANAGEMENT PRACTICES

The following management practices are common to both the Complex and Mkuzi Game Reserve:

- a) the use of game-proof fences on the boundaries;
- b) the removal of game;
- c) the implementation of anti-poaching patrols;
- d) the use of fire-breaks to control undesired burning;
- e) the introduction of measures to combat soil erosion;
- f) the burning of selected areas.

The historical developments leading up to, and the necessity for game removal have been discussed in Chapter 1. Mass removal of game has been facilitated by the Oelofse capture method (Densham, 1974). Removal was initially aimed at the overall reduction of the biomass of grazers, but since 1972 removal in the Complex has been designated to specific areas based on the degree of veld deterioration.

TABLE 2.5. : Numbers of some larger mammals in Mkuzi Game Reserve and Nxwala Estate, resulting from the 1975 helicopter census. Species are grouped according to the reliability of the results, as for Table 2.4..  
(Data from Brooks, Whateley, Forrest and Densham, 1975.)

SPECIES	MKUZI GAME RESERVE + NXWALA ESTATE
Giraffe	35
White Rhino	4
Wildebeest	1064
Zebra	167
Impala	8209
Kudu	306
Common Reedbuck	27
Mountain Reedbuck	31

Vincent (1970) records the use of fire in UGR for management purposes between 1911 and 1932. In the 1930's burning was discouraged owing to the presence of numerous wooden-framed Harris tsetse fly traps in the reserve. This period may have been important in the establishment of thicket nuclei. The more recent history of fire use in UGR has been outlined by Porter (1975). Controlled burning and the annual construction of boundary firebreaks have been instituted since 1959. This aspect of management was originally aimed at the prevention of bush encroachment which was considered as a threat to white rhino habitat. Porter (*ibid.*) cites the present objectives in the use of fire:

- a) to remove excess litter, and stimulate plant growth;
- b) to attract game away from deteriorating veld onto fresh growth produced by burns;
- c) to control bush encroachment.

Since 1965, controlled burning has been started soon after the first spring rains in August or September. This not only simulates the effects of lightning but coincides with a stage in grass growth whereby detrimental effects of burning are minimised. Upland parts of UGR are burnt once in every three to six years, but the Bottomland areas are seldom if ever burnt on account of the relative absence of litter.

Soil erosion results from over-utilisation, selective grazing, the effects of trampling and the misuse of fire. It is characterized by a reduced aerial or basal grass cover, by soil movement and by increase in unpalatable or pioneer grass species. In conjunction with removal of game from areas thus affected, anti-erosion structures (chiefly gabions) have been constructed since 1964.

The general principles and techniques of management have evolved chiefly in the Complex, but are similarly practised in Mkuzi Game Reserve.

## CHAPTER 3

### AGE DETERMINATION

#### 3.1.

##### INTRODUCTION

##### 3.1.1.

##### RELEVANCE OF AGE DETERMINATION

The determination of age is fundamental to most major studies on large wild mammals. The following aspects of study into an animal's life history depend upon division of the population into age classes for their investigation:

- a) the attainment of puberty;
- b) the measurement of body growth rates;
- c) the peaks in fertility;
- d) the estimation of senescence and longevity;
- e) the interpretation of social behaviour;
- f) the variation with age of any other physiological process.

The above aspects fall largely within the field of population dynamics. It is a knowledge of this field which is vital to the management of mammals, and this fact may account for the prolific literature on age determination, which is the basis of population dynamics. A review

of mammalian age determination methods was compiled by Morris (1972); a more specific review relating to dentition alone with relevance to African mammals has been prepared by Spinage (1973).

### 3.1.2.

#### REVIEW OF AGE DETERMINATION TECHNIQUES APPLICABLE TO WILDEBEEST

Most age determination techniques suffer from limitations, and it is thus advisable to use a combination of techniques where possible. Common to all techniques is one essential requirement: the availability of animals of known age on which to base or deduce absolute ages for any specific technique. Without known-age material it is only possible to group animals of similar ages into age classes, and these classes must of necessity be arbitrary.

#### a) Increase in mass or linear dimensions.

Growth studies are concerned in part with changes in mass, height and length of the whole animal with age. These changes are usually represented as growth curves; the reliability of such curves is clearly dependant on the accuracy of the age determination techniques used to derive them.

Ansell (1965) listed the more common parameters which are measured in wild life studies. These parameters may show a linear (isometric) relation with age, but more commonly the relation is non-linear (allometric). In the latter case complexity arises in the fitting of curves to such data. Some workers have fitted these curves by eye (Child, 1964; Rothe, 1965; Pienaar, 1969; Flux, 1970; Blood, Flook and Wishart, 1970). Work by Beverton and Holt (1957), based on Von Bertalanffy (1938), has led to the fitting of theoretical growth equations. The Von Bertalanffy equation is discussed further in Chapter 4, and has been used on elephant (Hanks, 1972), impala (Howells and Hanks, 1975), and zebra (Smuts, 1975a). The use of this

method in impala demonstrated that some measurements (e.g. hindfoot length, ear length, and tail length) were relatively valueless in age determination, on account of the early attainment of the asymptote (Howells and Hanks, *ibid.*). A similar shortcoming was found by Smuts (*ibid.*) for zebra, for he considered that after two years of age it was almost impossible to estimate age using shoulder height.

Other types of theoretical growth equations have been used on elephant (Laws and Parker, 1968; and Laws, Parker and Johnstone, 1970); on hippopotamus (Laws, 1968); and on the cottontail rabbit Sylvilagus floridanus (Bothma, Teer and Gates, 1972).

Growth equations in this study are considered in Chapter 4.

b) The use of eye lens mass.

The eye lens is an ectodermal structure, and consequently displays apparent growth throughout life. The relation between age and lens mass was first demonstrated by Lord (1959) on the cottontail rabbit, and has subsequently been used for a variety of larger mammals, including elephant (Laws, 1967) and hippopotamus (Laws, 1968). The lens/age relationship can be extended to cover foetal development as well (Nellis, 1966).

Artiodactyl families for which eye lens mass has been determined include North American Cervidae (Longhurst, 1964; Connolly, Dudziński and Longhurst, 1969) and Antilocapridae (Kolenosky and Miller, 1962). African studies have used the technique on impala (Fairall, 1969; Rautenbach, 1971); kudu (Simpson and Elder, 1968); and warthog (Child, Sowls and Richardson, 1965).

In all cases, there was an initial growth spurt, followed by rectilinear growth in which considerable overlap of age classes occurred. It would thus appear that the technique is of

limited use in large mammals; it appears more successful with medium-sized mammals. Martinson, Holten and Brakhage (1961), for example, found no overlap in swamp rabbits (Sylvilagus aquaticus).

c) Biochemical Methods.

The biochemistry of the lens alters with age, chiefly in the increasing proportions of insoluble proteins. Colorimetric analysis of protein composition, using tyrosine as an index, leads to accurate differentiation between animals of different ages. The procedure is described by Otero and Dapson (1972). The method is highly accurate for small mammals, where reference can be made to a laboratory-reared population of exact known age. The method has as yet received little attention in large mammals, possibly on account of the microchemical or biochemical techniques involved.

d) Tooth eruption sequence, attrition, and growth rings.

In mammalian diphyodont dentition, the deciduous teeth are succeeded by permanent teeth in a fairly fixed sequence. The sequence of eruption appears to be constant within a species, but eruption times may be altered by genetic or environmental factors.

This method, applicable only to young animals, has been used for age determination of domestic stock for well over a century (Spinage, 1973). In wild animal species, some of which may breed throughout the year, the designation of age classes is hampered by the lack of known-age material.

Tooth eruption schedules have been documented for many African ungulates, including springbok, Antidorcas marsupialis (Routenbach, 1971); waterbuck (Spinage, 1967); impala (Child, 1964; Roettcher and Hoffman, 1970); tsessebe, Damaliscus

lunatus (Huntley, 1973); buffalo (Grimsdell, 1973); kudu (Simpson, 1966); and bushbuck, Tragelaphus scriptus (Simpson, 1973).

The complete original dentition of placental mammals is believed to have consisted of three incisors, one canine, four premolars, and three molars in each jaw half (Hyman, 1942). The first premolar (P<sub>1</sub>) has been lost in Artiodactyl evolution (but retained in Suidae); for this reason the most anterior premolar is termed P<sub>2</sub>. This tooth is found in both upper and lower jaws of most ungulates, except in the case of wildebeest, where P<sub>2</sub> is lost in adults, leaving only two premolars (P<sub>3</sub> and P<sub>4</sub>) in the lower jaw. One may tentatively conclude from this that the wildebeest shows the most advanced stage in the evolution of ungulate dentition, if one accepts that progressive premolar loss is an evolutionary trend.

The formula for wildebeest deciduous teeth is: \*

$$i \frac{\dots}{123}, c \frac{\cdot}{1}, p \frac{\cdot 234}{\cdot 234} = 20; \text{ and for adult dentition:}$$

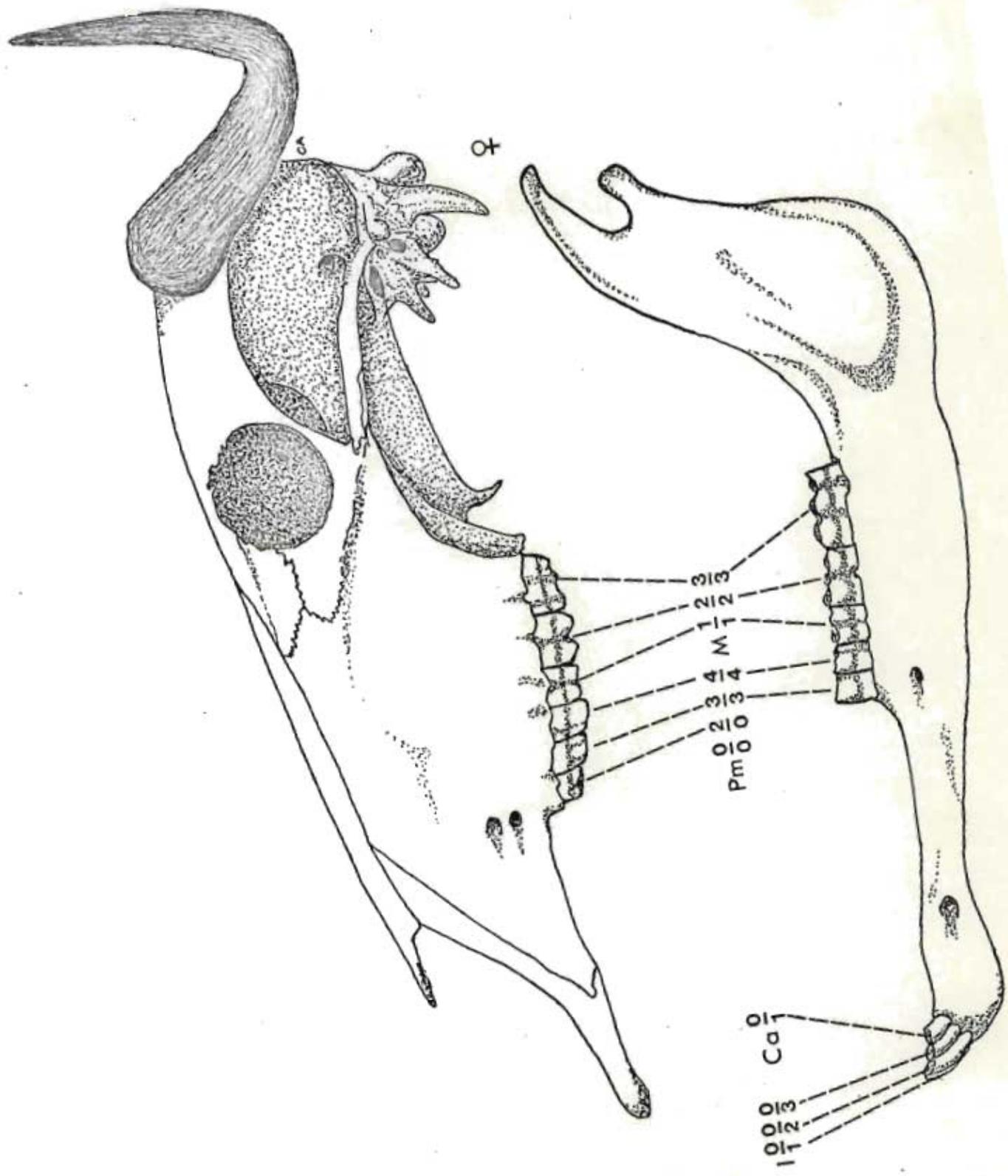
$$I \frac{\dots}{123}, C \frac{\cdot}{1}, P \frac{\cdot 234}{\cdot \cdot 34}, M \frac{123}{123} = 30$$

The positions of the adult teeth are shown in Fig. 3.1.. As with other Bovids, the molars have no deciduous predecessors, and maxillary incisors are absent. As in all true ruminants, the third mandibular molar has an additional third cusp. The canines are incisiform in both form and function.

Progressive wear in teeth results in loss of enamel and exposure of dentine. This process causes marked changes in the appearance of teeth. Within the cusp is a characteristic "pocket", termed the infundibulum, which extends towards the roots. With increasing wear the shape of the infundibulum changes, and eventually disappears in some teeth. The change in shape

\* in the above formulae, and hereafter, the lower case refers to deciduous dentition.

Fig. 3.1. : Relative positions of adult teeth in mandible  
and maxilla of adult female wildebeest.



♀

3/3  
2/2  
1/1  
M  
4/4  
3/3  
2/0  
Pm 0

0/1  
0/2  
1/1  
Cal

may be used as an index of age. The tooth-wear approach to age determination must be used with caution, because wear varies not only with diet but also with genetic factors within a species.

Mechanical attrition of teeth begins at eruption, and results from the properties of food and ingested gritty bodies. The first work of note in this field was published on white-tailed deer (Severinghaus, 1949), in which criteria were described for age determination based on tooth wear in the mandible. Subsequently this technique allowed age estimation for that species up to  $16\frac{1}{2}$  years (Severinghaus and Tanck, 1950). Designation of age-wear classes has occurred only comparatively recently in wild African bovids. Rautenbach (1971) used attrition in this way for impala, as did Roettcher and Hoffman (1970). Spinage (1967) described attritional changes in waterbuck up to 10 years, and Grimsdell (1973) based his buffalo tooth-wear classes on cementum annuli counts.

Age determination in bovids originally centred on tooth eruption in animals with immature dentition, and on attrition in adults. More recent approaches have involved the use of incremental growth rings in dental histology. This approach is very important because it facilitates the assignment of absolute ages, provided that it can be established that a specific number of growth rings are laid down within a defined period. Dentine and cementum are the tissues commonly investigated. Dentine is laid down in incremental lines within the pulp cavity, but occlusion of the cavity may occur within a few years. Cementum, however, is deposited in annular layers throughout life, external to the tooth. Cementum is first formed as uncalcified cementoid tissue (composed of collagen and mucopolysaccharides), which is then later calcified. Spinage (1973) differentiated between two types of cementum: the first-formed acellular cementum adjacent to the dentine, and the

cellular secondary cementum which is laid down when the tooth begins to erupt. Cementum is laid down on the roots of all teeth in an uneven layer, favouring the ends of the roots and the cavity at the base of the tooth between the roots. As layers are laid down throughout life, the process may serve to continue eruption and consequently compensate for loss of crown height resulting from tooth wear. The alternating broad, translucent layers and the narrower dark layers are caused by differences in the rate and nature of calcification.

The application of the cementum layer technique in age determination was initially developed by Laws (1952) on marine mammals. The work of Low and Cowan (1963) on mule deer, Odocoileus hemionus, introduced what is now a well-established technique to North America. Klezeval and Kleinenberg (1967) listed 16 mammalian families displaying cemental layering. Among African ungulates for which the technique has been used are waterbuck (Spinage, 1967); kudu (Simpson and Elder, 1969); springbok (Rautenbach, 1971); bushbuck (Simpson, 1973); buffalo (Grimsdell, 1973); and Thomson's gazelle, Gazella thomsoni (Robinette and Archer, 1971).

e) The fusion of epiphyses.

Growth in the long bones of young mammals takes place in terminal cartilaginous epiphyses. Towards adulthood, this zone ossifies to become solidly fused to the bone shaft. The degree of fusion may thus serve as a guide to age (Weinmann and Sicher, 1955). Examination of the ends of long bones for epiphyseal cartilage will provide a guide to age. An alternative approach which can be used with living animals is to employ the use of X-Rays, for epiphyseal cartilage is readily apparent on radiographs. The technique in general is possibly applicable to estimating ages of bone remnants from, for example, a kill. The method is limited, for it serves only to separate juveniles from adults.

It has been applied in the age determination of jackal, Canis mesomelas, by Lombaard (1971).

f) Appearance of external features.

Use of these features is approximate, for they serve only to differentiate between more obvious age classes using factors like horn growth and pelage appearance. The latter may serve only to differentiate between adults, juveniles and subadults, but horns and their growth checks have been used successfully as criteria of age in some North American and European bovids (Couturier, 1961; Geist, 1966). Simpson (1971) listed nine African antelopes for which horn shape has been used as an index to age. Seasonal fluctuations in horn growth may result in the formation of growth "checks", which appear as bands or grooves around the horn. Simpson (ibid.) found these checks in nine African antelope.

Horn shape differs markedly in adult Tragelaphines of different ages, but in adult wildebeest no clear divisions into adult age classes can be made with any accuracy. Growth checks do occur in wildebeest, but are highly compressed at the periphery of the base of the boss, and are consequently not clearly distinguishable.

### 3.1.3.

#### CHOICE OF METHODS

Some limitations of the above methods have been already discussed. The epiphyseal cartilage method was discarded as it was considered that tooth eruption or even bone size would serve to distinguish between juveniles and adult kill remains. Complexity of biochemical methods precluded their use when dealing with a large sample. The eye lens technique was chosen to see if adult age class overlap occurred as in other ungulates. Trial sectioning of teeth showed

the clarity of cementum annuli, which justified the use of incremental layers. Tooth eruption sequence is a classic, simple and accurate method of subadult age determination, and its choice was obvious. With the clarity of cementum annuli, it was clear that a tooth-wear pattern could be established on this basis.

A further consideration in choice of methods lies in the fact that some methods are applicable only to a shot sample, whereas others (tooth wear and eruption) can be used on living animals. Measurements or mass of a restrained animal can be related to growth curves, and tooth impressions can be taken (Spinage, 1967).

#### 3.1.4.

##### PREVIOUS WORK ON *C. taurinus*.

Talbot and Talbot (1963) arrived at an eruption calendar for *C.t. hecki*, based on the eruption sequence of molariform teeth. This calendar, with seven age classes of sub-adult dentition, is reproduced in Table 3.1.. For animals with adult dentition, progressive wear of incisors and canines enabled them to draw up a further table (Table 3.2.) with four mature age classes. This method also included nine sub-adult age classes.

Watson (1969) used a dentine layer count from sections of the third maxillary molar for his work on *C.t. albojubatus* in the Serengeti. Details of the preparation of sections and of the reliability and accuracy of his method are contained in his thesis, which was unfortunately not available to me.

In analysing age structures of wildebeest killed by lion in the Serengeti, Schaller (1972) arrived at five adult wear classes. This schedule of wear (Table 3.3.) was based on descriptions of changes in infundibular patterns: it provided only an arbitrary chronological sequence, and did not attempt to attribute absolute ages, except for

TABLE 3.1. : Eruption and replacement of molariform teeth in wildebeest from East Africa (C. taurinus hecki)

M = milk  
A = adult

(Superscribed numeral indicates number of cusps.  
Circle indicates period when tooth first erupts.  
(After Talbot and Talbot, 1963)).

<u>C. taurinus hecki</u>												
AGE	LOWER JAW						UPPER JAW					
	PREMOLARS			MOLARS			PREMOLARS			MOLARS		
	2	3	4	1	2	3	2	3	4	1	2	3
Birth	(M <sup>1</sup> )						(M <sup>1</sup> )					
1 - 7 days	(M <sup>1</sup> )	(M <sup>1</sup> )	(M <sup>3</sup> )				M <sup>1</sup>	(M <sup>2</sup> )	(M <sup>2</sup> )			
6 months	M <sup>1</sup>	M <sup>1</sup>	M <sup>3</sup>	(A <sup>2</sup> )			M <sup>1</sup>	M <sup>2</sup>	M <sup>2</sup>	(A <sup>2</sup> )		
15 months	M <sup>1</sup>	M <sup>1</sup>	M <sup>3</sup>	A <sup>2</sup>	(A <sup>2</sup> )		M <sup>1</sup>	M <sup>2</sup>	M <sup>2</sup>	A <sup>2</sup>	(A <sup>2</sup> )	
26 - 28 months	M <sup>1</sup>	M <sup>1</sup>	M <sup>3</sup>	A <sup>2</sup>	A <sup>2</sup>	(A <sup>3</sup> )	M <sup>1</sup>	(A <sup>1</sup> )	M <sup>2</sup>	A <sup>2</sup>	A <sup>2</sup>	
30 - 33 months	M <sup>1</sup>	M <sup>1</sup>	(A <sup>1</sup> )	A <sup>2</sup>	A <sup>2</sup>	A <sup>3</sup>	M <sup>1</sup>	A <sup>1</sup>	(A <sup>1</sup> )	A <sup>2</sup>	A <sup>2</sup>	(A <sup>2</sup> )
37 - 40 months		(A <sup>1</sup> )	A <sup>1</sup>	A <sup>2</sup>	A <sup>2</sup>	A <sup>3</sup>	A <sup>1</sup>	A <sup>1</sup>	A <sup>1</sup>	A <sup>2</sup>	A <sup>2</sup>	A <sup>2</sup>

**TABLE 3.2.** : Method for determining age of wildebeest, *C. taurinus hecki* from East Africa based on incisors and canines. Explanation for symbols as for Table 3.1.. 0 = tooth absent. (After Talbot and Talbot, 1963.)

AGE OR AGE CLASS	INCISOR			CANINE
	1	2	3	1
1 - 7 days	(M)			
2 weeks	M	(M)	(M)	(M)
8 - 10 months	M	M	M	M
12 - 14 months	M	M	M	M
15 - 20 months	M	M	M	M
20 - 26 months	(A)	M	M	M
26 - 33 months	A	(A)	M	M
33 - 37 months	A	A	(A)	M
37 - 44 months	A	A	A	(A)
Mature Class I	A	A	A	A
Mature Class II	A	A	A	A
Old	A	A	A	A
Very old	A-0	A-0	A-0	A-0

Wearing rapidly to gums heaviest wear shown by I<sub>1</sub> and I<sub>2</sub>.

Worn low, widely spaced.

All high, relatively even, no wear shows on C<sub>1</sub>.

Wearing towards gums, but not into nerve canal.

Worn into nerve canals, gaps between teeth.

Worn into tooth roots, some or all teeth missing.

TABLE 3.3.

Age classes for mature C.t. albojubatus from Serengeti, based on changes in infundibular patterns. The preceding classes not included in the Table (Classes I - V) contain those animals displaying immature dentition, for which age ranges were estimated as follows:

<u>AGE CLASS</u>	<u>AGE</u>
I	0 - 2 months
II	2 - 6 months
III	6 - 12 months
IV	12 - 24 months
V	24 - 42 months

(After Schaller, 1972.) Note that Schaller ascribes infundibula to P<sup>2</sup>. I did not consider this tooth to show true infundibula in C.t. taurinus.

ARBITRARYAGECLASS

- VI      Mandible: Full permanent dentition. Infundibulum on P<sub>3</sub> usually open; posterior infundibulum on P<sub>4</sub> present and usually open or just closed; incisor length is greater than 2 X the width.
- Maxilla: M<sup>1</sup> accessory infundibulum usually present; M<sup>2</sup> accessory infundibulum present, and M<sup>3</sup> one present or not yet formed. Posterior infundibulum on P<sup>4</sup> usually present.
- VII     Mandible: Anterior infundibulum on M<sub>1</sub> chevron or U-shaped; infundibulum on P<sub>3</sub> often closed; posterior infundibulum of P<sub>4</sub> present or absent, and, if present, closed at posterior end; incisors oval, often touching, with length less 2 X the width.
- Maxilla: At least one accessory infundibulum present on M<sup>3</sup>, and usually one on M<sup>2</sup>. Accessory infundibulum absent on M<sup>1</sup>. Usually no posterior infundibulum on P<sup>2</sup> and P<sup>3</sup>.
- VIII    Mandible: Infundibulum on anterior part of M<sub>1</sub> small, round or oval; on posterior part chevron or U-shaped; posterior infundibulum on P<sub>4</sub> absent; incisors oval or rectangular, often not touching.
- Maxilla: Infundibulum on anterior part of M<sup>1</sup> oval or chevron-shaped, on posterior part U-shaped; accessory infundibulum on M<sup>3</sup> present or absent; anterior infundibulum on P<sup>4</sup> present.
- IX      Mandible: Infundibulum worn off anterior part of M<sub>1</sub> and posterior part has small round or oval infundibulum. Usually one or both infundibula worn off P<sub>4</sub>; incisors some non-functional, worn to gums, others round, not touching.
- Maxilla: Infundibulum worn off anterior part of M<sup>1</sup>, or rarely a small remnant left; posterior surface has small infundibulum. Anterior infundibulum of P<sup>4</sup> present or absent.
- X        Mandible: Both infundibula worn off M<sub>1</sub>, sometimes off M<sub>2</sub>; most incisors non-functional.
- Maxilla: Both infundibula worn off M<sup>1</sup>, except for occasional remnant on posterior part; infundibula

an estimate for Age Class VI (3,5 - 5,5 years).

Braack (1973) applied Talbot and Talbot's (ibid.) methods directly to C.t. taurinus in the Kruger National Park, and did not attempt to draw up a separate eruption calendar. He did however section canines and first lower molars in order to compare ages determined from cementum annuli counts with those derived from Talbot and Talbot's wear schedule. His finding was that the latter method overestimated ages of Kruger Park wildebeest, particularly in the 4 year-old age class, where the overestimation was as much as two and a half years. This is ample justification for the need to establish separate criteria for age determination in separate areas, particularly where differences in nutrition and soil types are marked. (Soil type is an important variable when considering rates of tooth attrition.)

Hitchins (pers. comm.) drew up an approximate eruption calendar for wildebeest in the Complex, but this was found to be inadequate for this study.

Methods of field age determination for the species have been discussed by Estes (1969) and Petersen and Cosebeer (1972) for East Africa. In South West Africa, a photographic record of horn development related to age was compiled by zur Strassen (1969).

### 3.2.

#### MATERIALS AND METHODS

In this section I have separated eruption and attrition, as the methods pertaining to the latter are dependent on the cementum layer technique.

#### 3.2.1.

##### TOOTH ERUPTION

In species having an annual period of parturition which is short and

distinct, it is relatively simple to assign immature dentition to specific age classes, because the young born in any one year constitute a uniform and easily recognizable group within the population. Eighty-two skulls of immature dentition were available for the determination of the eruption sequence. This number included skulls collected from culling operations prior to the start of this study. Immature skulls are readily characterized by horn growth, incomplete eruption of permanent teeth, and the presence of milk or deciduous teeth. Horn conformation in calves is straight or slightly bowed. In yearlings the boss of the horns is still underdeveloped. Development of the boss conforms more to the adult pattern in 2 - 3 year olds, but lacks the gnarled or pitted appearance of adults. Deciduous teeth may be distinguished by the number of cusps (Tables 3.1. and 3.4.) when molariform, and by their characteristic spatuliform shape when incisiform.

For each skull, the eruption phase for each tooth was recorded by placing a tick mark in the appropriate box on an eruption/wear sheet, reproduced in Fig. 3.2.. Horn growth usually indicated whether the animal had died in the first, second or third year of life. If any doubt was apparent, reference was made to Talbot and Talbot's (1963) calendars (Tables 3.1. and 3.2.). An age was then ascribed to a specific skull by estimating the interval from the date of death back to the assumed birth period. This period was defined as six weeks, from mid-November until the end of December, and was based on observation and extrapolation of foetal weights (Chapter 5). For convenience, the central point of this period, i.e. the end of the first week in December, was taken as an arbitrary birth date. Results were expressed with reference to this central point, but with the understanding that the error would be of the order of one month. To arrive at the eruption calendar, those sheets with the same or closely similar ages were grouped. The predominant eruption

Fig. 3.2. : Form or sheet used to record stages of eruption of teeth and patterns of infundibula. The number of cementum layers for any specific molar extracted and sectioned was recorded against that tooth at the top of the form. The stage of eruption of sub-adult dentition was recorded to the left of the double vertical line, by placing a cross in the appropriate "box". To the right of the line, the actual patterns of infundibula were drawn in the appropriate square. For incisiform teeth, crosses were placed in appropriate "boxes", and measurements of  $I_1$  recorded.



pattern from each group was then taken as being characteristic of that group or age class. Sheets within a group which showed marked deviations from the relatively consistent eruption phase of that group were discarded on the grounds that these related to out-of-season births. The rarity of discarded sheets lent support to the supposition that they did indeed relate to aseasonal parturition.

### 3.2.2.

#### ADULT DENTITION

##### 3.2.2.1.

#### CEMENTUM ANNULI

The first molar (M1) and third molar (M3) were extracted from either the mandible or the maxilla. The different eruption times of these teeth were taken into account, and are discussed in Section 3.3.2..

The positions of the extracted teeth were recorded at the top of the tooth sheet (Fig. 3.2.). Teeth were sectioned dorso-ventrally along the long axis, using a lapidary saw with a 0,5mm diamond blade. As there was no method whereby the blade could be made to pass un-faillingly through that section of the tooth displaying the broadest "pad" of cementum, no attempt was made to relate the thickness of the pad to age. Some cementum layers were clearly visible after this initial sectioning, but the majority required further processing by polishing on a geological Cut Rock Lapping Machine. A progression of increasingly finer grain Corundum powder (from 220 to 600) ensured a smooth finish. The final highly polished state was achieved by using 'Brasso' on a soft rag.

Various authors have reported on the necessity of preparing stained, decalcified sections (Low and Cowan, 1963; Spingale, 1967; Simpson and Elder, 1969). Histological methods have been discussed by

Steenkamp (1975). Cementum layers in wildebeest teeth were considered sufficiently clear not to warrant decalcification and staining. Instead, I followed the method of Mitchell (1967) by which facial sections were viewed by reflected light under a low-power binocular dissecting microscope. Sections were examined under a power of 25X, but sometimes 12X power was used in order to see if the continuity of a particular band persisted along the entire depositional layer.

Both light and dark bands were counted, but those lines lying on or close to the dentino-cement border were discounted, as they were considered to correspond to 'eruption lines' (Spinage, 1967). An 'eruption line' is considered to be laid down as a result of heightened physiological processes relating to eruption, and thus bears no relation to season. These lines were also discounted by Grimsdell (1973).

Klezeval and Kleinenberg (1967) postulated that the thin dark lines corresponded to periods of arrested growth and the broader light bands to periods of optimal nutrition. Consequently, most workers have assumed that a biannual season would result in a dark line and a light band for each year. Spinage (1976) has, however, shown that the annual correlation may be spurious, and it was thus considered essential to validate the "two layers per year" theory for the age determination to be meaningful. This study was marked by the absence of known-age adult material. Co-workers in this field were unable to assist, and the following institutions proved unsuccessful as a source of known-age material: The British Museum of Natural History, the National Museum of Rhodesia, the National Museum of Zambia, the Transvaal Museum, and the Veterinary Investigation Centre of the Kruger National Park. As a result I had to rely on permanent molariform teeth from sub-adult (for which eruption age could be fairly accurately determined) as being "known-age." Consequently a sample of first and third molars was also extracted and sectioned from sub-adult animals. As the approximate age at eruption of a

particular tooth was known, the number of annuli on eruption allowed the determination of an adjustment factor to compensate for those annuli laid down prior to eruption.

### 3.2.2.2.

#### EYE LENS MASS

Consistent methods appear to have been used by most authors, and this study followed the established pattern. The left eyeball was excised as soon after death as possible, and was injected with 10% formalin into the vitreous humor. The organ was left to fix in formalin for at least two weeks. A superficial circular incision was then made through the cornea, and the lens carefully expelled into 10% formalin until such time as it could be dried. Before drying, the lenses were washed in white methylated spirits and freed of any remaining attached ciliary muscle. One hundred and thirty-eight lenses from animals of all ages were used; this figure excluded those which appeared damaged or had obvious cataracts. Drying took place in an oven at 98° C. Lenses were weighed to  $10^{-3}$ g on a Mettler electrical balance: the first weighing was performed two days after placing lenses in the oven, and lenses were only judged to be fully desiccated when no further mass loss occurred.

Lens mass was plotted against eruption or cementum age, and computer-fitted curves were applied to the graphs thus obtained. A non-linear regression line was fitted according to the method of Nelder and Mead (1965). A second curve-fitting program for the Von Bertalanffy growth equation (Hanks, 1972) was also applied. Both programs were run on an IBM 1130 Computer of the University of Natal. The latter curve was used in some cases to determine the age of animals for which skulls had been lost during the study.

### 3.2.2.3.

#### AGE DETERMINATION BASED ON TOOTH ATTRITION

Each molariform tooth from 175 adult skulls was considered in this study. The infundibular pattern was drawn in the relevant box (Fig. 3.2.). The right tooth row was chosen in the maxilla, and the left in the mandible. This was considered to be a more efficient alternative to "averaging" infundibular patterns between, for example, the two maxillary rows.

Animals containing the same or closely similar cementum ages were then grouped, and an attempt was made to assign a characteristic infundibular pattern for each tooth to a specific cementum age. It was considered that relating cementum age to wear would only be of value if the rate of wear was shown to be reasonably uniform with age. Thus, to give a measure of the reliability of the age-wear chart produced, the percentage dissimilar infundibular patterns which were "excluded" from the final characteristic patterns, was assigned for each tooth. Found skulls were collected by field staff after termination of the field study, and their age was determined from the age-wear chart. In addition, the chart was used to estimate ages for those specimens in which cementum layers appeared indistinct or unreliable.

Quantitative estimates of tooth wear may be arrived at by measuring a designated zone on any particular tooth, provided that the measurement obtained varies with age. Watson (1967) measured the height of M3 in wildebeest, while Grimsdell (1973) measured the height of cusps and the width of the occlusal surface in M1 from buffalo. I chose to relate incisor heights and widths to wear and age. The height of the first left incisor was measured from the tip of the tooth to the gum line. Measurements were taken as soon after death as possible to obviate errors resulting from gum shrinkage. The greatest width of the same tooth was measured across the occlusal

surface. All measurements were made with a Vernier caliper to  $10^{-2}$  mm, and transcribed onto the tooth sheet (Fig. 3.2.). These measurements were then related graphically to cementum or eruption.

### 3.2.3.

#### FIELD AGE DETERMINATION

As the calf crop of any specific year is uniformly distinguishable, characteristics of that crop may be followed through into succeeding years. When observing a herd in the field, it was borne in mind that representatives of each age class would be present, allowance being made for the differences in age structure between different social groupings. In this way, notes were taken of the diagnostic field characteristics whereby age groups might be separated.

### 3.3.

#### RESULTS AND DISCUSSION

#### 3.3.1.

##### TOOTH ERUPTION

Table 3.4. contains 11 eruption classes arrived at for C.t. taurinus in this study. Adult dentition can be taken as complete at about 38 months, but the great variability in canine eruption may prolong the attainment of adult dentition, if the criterion for the latter status is taken as uniformity in the level of the incisiform teeth. Spingale (1973) also noted this variation in canine eruption. The first two classes were poorly represented: eruption at birth was based on Talbot and Talbot (1963), and the next class was based on only two specimens. The succeeding classes could however be established with some confidence.

Some departure from the calendar occurs, which is explained by

TABLE 3.4. Eruption calendar for C.t. taurinus based on specimens from Zululand.

Explanation of symbols:

Superscripts show number of cusps present

M = milk tooth

A = adult tooth

CA = canine

- a) □ : tip of erupting tooth just visible, level with or below the bone line. If the erupting tooth is preceded by a deciduous tooth, then this stage may sometimes only be discernible on removal of the deciduous tooth.
- b) ■ : tip of tooth now projecting above bone line. In adult premolar or adult incisor eruption, the overlying deciduous tooth is often still in situ.
- c) Δ : intermediate between c) and d)
- d) ▲ : eruption nearly complete; tooth is almost level with other fully-erupted teeth in the tooth row.
- $\bar{M}$  - indicates heavy wear on a milk tooth, with smooth surfaces and no dentine/enamel ridges.

AGE CLASS MONTHS	M A X I L L A						M A N D I B L E						SAMPLE SIZE USED				
	PREMOLARS			MOLARS			INCISORS			CA	PREMOLARS			MOLARS			
	2	3	4	1	2	3	1	2	3	1	2	3		4	1	2	3
BIRTH	M <sub>■</sub> <sup>1</sup>						M <sub>■</sub> <sup>1</sup>				M <sub>■</sub> <sup>1</sup>						0
0,5 - 0,75	M	M <sub>Δ</sub> <sup>2</sup>	M <sub>□</sub> <sup>2</sup>				M	M <sub>▲</sub>	M <sub>▲</sub>	M <sub>▲</sub>	M	M <sup>1</sup>	M <sub>Δ</sub> <sup>3</sup>				2
5 - <6	M̄	M	M	A <sub>Δ</sub> <sup>2</sup>			M	M	M	M	M	M	M	A <sub>Δ</sub> <sup>2</sup>			5
6 - 8	M̄	M	M	A <sub>Δ</sub>			M	M	M	M	M	M	M	A <sub>▲</sub>	A <sub>■</sub> <sup>2</sup>		6
12 - <16	M̄	M	M	A	A <sub>Δ</sub> <sup>2</sup>		A <sub>□</sub>	M	M	M	M	M	M	A	A <sub>Δ</sub>		5
16 - <18	M̄	M	M	A	A <sub>Δ</sub>		A <sub>Δ</sub>	M	M	M	M	M	M	A	A <sub>▲</sub>	A <sub>■</sub> <sup>3</sup>	6
18 - 20	M̄	M̄	M	A	A <sub>▲</sub>	A <sub>□</sub> <sup>2</sup>	A	M	M	M	M	M̄	M̄	A	A	A <sub>Δ</sub>	9
21 - 24	M̄	A <sub>□</sub> <sup>1</sup>	M̄	A	A	A <sub>Δ</sub>	A	A <sub>■</sub>	M̄	M̄	M̄	A <sub>□</sub> <sup>1</sup>	A <sub>□</sub> <sup>1</sup>	A	A	A <sub>Δ</sub>	7
25 - <28	A <sub>■</sub> <sup>1</sup>	A <sub>■</sub>	A <sub>□</sub> <sup>1</sup>	A	A	A <sub>Δ</sub>	A	A	M̄	M̄	M̄	A <sub>■</sub>	A <sub>■</sub>	A	A	A <sub>Δ</sub>	10
28 - 32	A <sub>Δ</sub>	A <sub>Δ</sub>	A <sub>Δ</sub>	A	A	A <sub>Δ</sub>	A	A	A <sub>■</sub>	M̄		A <sub>Δ</sub>	A <sub>Δ</sub>	A	A	A <sub>▲</sub>	11
33 - <38	A <sub>▲</sub>	A <sub>▲</sub>	A <sub>▲</sub>	A	A	A	A	A	A <sub>▲</sub>	A <sub>Δ</sub>		A <sub>▲</sub>	A <sub>▲</sub>	A	A	A	10
38 - 46	A	A	A	A	A	A	A	A	A	A <sub>▲</sub>		A	A	A	A	A	11

individual variation, and not by aseasonal births. The more consistent deviations are listed below:

1. The second and fourth maxillary milk premolars may persist through into the 28 - 32 month age class. Of the eleven specimens in this age class, three (27,3%) showed this variation.
2. The second mandibular milk premolar may persist beyond the 25 - 28 month age class. It was recorded twice (18,2%) in the 28 - 32 month age class, and once in the 38 - 46 month age class (9%). It is also maintained in some adult animals: of 178 adult mandibles examined, 6 (3,4%) showed the persistence of this tooth. The maximum age of an animal with this deviation was 13 years.
3. The adult maxillary premolars may not be fully erupted in the 38 - 46 month age class. This occurred in 2 out of 11 specimens (18,2%).

Both Caughley (1965) and Steenkamp (1969) found that the age at which a tooth erupted was dependent upon the age at eruption of the preceding one, and variability in eruption increased the later the tooth appeared. Consequently the probability of placing an animal in the wrong class increases with the age of the animal.

It is clear from radiographs, (Plate 3.1.), that at the age of about two to three weeks there is no sign of development of the second and third molars within the mandible. The same situation (absence of macroscopic signs of the second and third molars at this age) holds for the maxilla. Some eruption stages are shown in Plates 3.2. to 3.5.. The mandibular eruption calendar is similar to that of the black wildebeest (Table 3.5.). Von Richter (1971) has also recorded the persistence of second mandibular premolars in this species. Comparison of the blue wildebeest eruption calendar from Zululand

TABLE 3.5. : Mandibular eruption calendar for the Black Wildebeest, Connochaetes gnou.

○ : period when tooth first erupts.  
(Modified from Von Richter, 1971.)

AGE CLASS	PREMOLARS			MOLARS		
	2	3	4	1	2	3
Birth		○ M	○ M			
1 month	○ M	M	M			
6 months	M	M	M	○ A		
13 - 17 months	M	M	M	A	○ A	
20 - 30 months	M	M	M	A	A	○ A
27 - 30 months	M	○ A	M	A	A	A
28 - 30 months		A	○ A	A	A	A
36 months		A	A	A	A	A

AGE CLASS	INCISORS			CA
	1	2	3	1
Birth	○ M		○ M	○ M
1 month	M	○ M	M	M
12 - 16 months	○ A	M	M	M
17 - 24 months	A	○ A	M	M
27 - 31 months	A	A	○ A	M
29 - 32 months	A	A	A	○ M
36 months	A	A	A	A

with Talbot and Talbot's (*ibid.*) calendar for East Africa shows that, in general, the Zululand subspecies has earlier eruption times, with eruption proceeding over a longer period. Talbot and Talbot did not differentiate between different stages of eruption for each tooth; consequently I assume that their stage ○ corresponds to my stage ▲ (Tables 3.1. and 3.4.). On this basis, the major differences in eruption patterns between the two subspecies are summarised in Table 3.6..

A similar deviation in eruption between two populations of the same species has been noted for impala. Roettcher and Hoffman (1970) found much later eruption of the first molar in Kenyan impala, when compared to the Rhodesian chronology of eruption given by Child (1964).

Variation in eruption and replacement times between geographically separate populations occurs as a result of different nutritional planes. Steenkamp (1970) has shown that the age at which eruption occurs in cattle is accelerated by a high plane of nutrition. His work on different breeds of cattle showed a further relationship between early tooth eruption and slow maturation. This finding appears to be applicable to wildebeest as well. For example, East African wildebeest ovulate first as yearlings whereas the majority of Zululand females attain puberty only a year later.

Differences in eruption times may have functional or adaptational significance. Steenkamp (1969) maintained that the early loss of deciduous teeth might influence the pattern of wear of the permanent teeth, resulting in reduced food intake and delayed growth in later life.

It can however be assumed with some confidence that replacement within the same population will be consistent, for Hemming (1969) has shown consistency over 16 years in a study on dall sheep, Ovis dalli.

TABLE 3.6. : Comparison of eruption patterns between *C.t. taurinus* and *C.t. hecki* (Based on Tables 3.1., 3.2., and 3.4.)

\* denotes insufficient data.

DECIDUOUS DENTITION		MINIMUM AGE AT WHICH MILK TOOTH IS LOST (MONTHS)		DIFFERENCE
		<i>C.t. taurinus</i>	<i>C.t. hecki</i>	
M	$i_1$	8	20	12
A	$i_2$	20	26	6
N	$i_3$	28	33	5
D	c	32	37	5
I	$p_2$	28	33	5
B	$p_3$	20	33	13
L	$p_4$	20	28	8
E				
M	$p^2$	24	33	9
A				
X	$p^3$	24	*	*
I				
L	$p^4$	28	28	0
L				
A				

PERMANENT DENTITION		MINIMUM AGE AT ERUPTION OF PERMANENT TOOTH (MONTHS)		DIFFERENCE
		<i>C.t. taurinus</i>	<i>C.t. hecki</i>	
M	$I_1$	12	20	8
A	$I_2$	21	26	5
N	$I_3$	28	33	5
D	C	33	37	4
I	$M_1$	5	6	1
B	$M_2$	6	15	9
L	$M_3$	16	26	10
E				
M	$M^1$	5	6	1
A				
X	$M^2$	12	15	3
I				
L	$M^3$	18	30	12
L				
A				

Plate 3.1. : Radiograph of mandible of wildebeest calf, estimated to be about three weeks old.  $M_1$  is below the gum line; there is no sign of  $M_2$  or  $M_3$ . (Radiograph : Ms B. Taylor).

Plate 3.2. : Mandibular left tooth row of female calf, estimated to be about six months old. Neither  $M_2$  nor  $M_3$  have begun to erupt. Note that  $p_4$  has three cusps, and  $M_1$  two.

Plate 3.3. : Maxillary left tooth row of a yearling female, estimated to be about twenty months old. Note heavy wear on deciduous premolars.

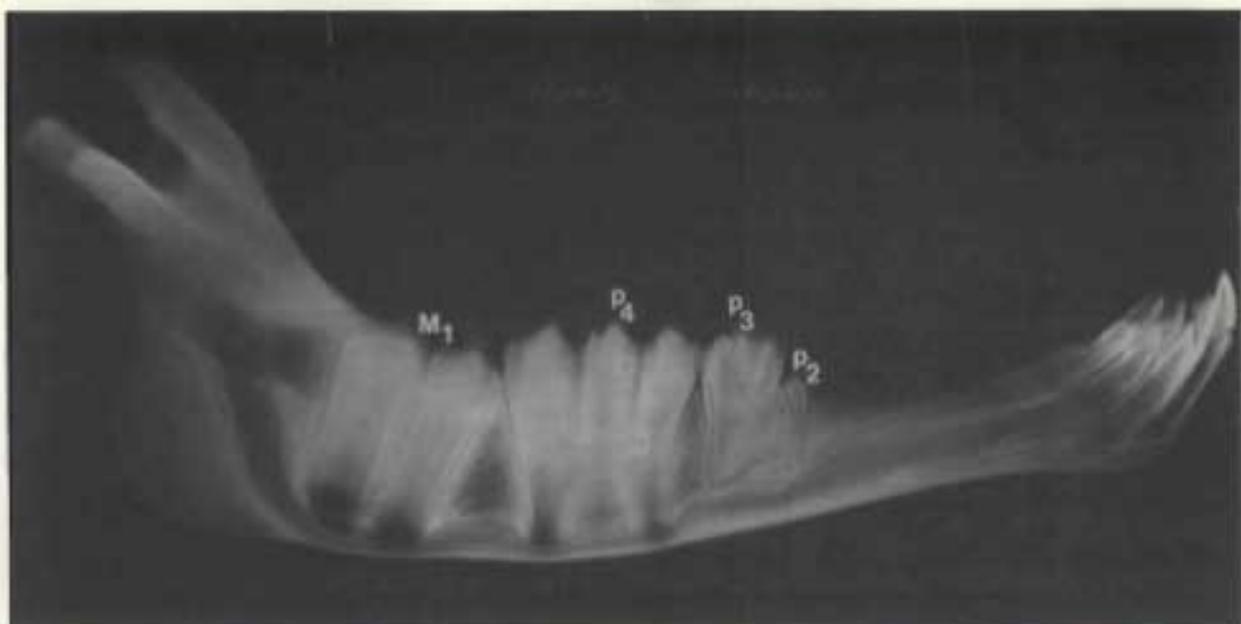


PLATE 3.1



PLATE 3.2



PLATE 3.3

## 3.3.2.

CEMENTUM ANNULI

The first molar was found to be consistently preferable in distinguishing cementum annuli owing to the degree of development of the cementum "pad" between the roots. In contrast, the mandibular third molar almost invariably showed a relatively thin accretion with annuli ill-defined. In cases where the accretion was uniformly distributed around the roots and within the between-roots concavity, the annuli were better defined within the concavity or "pad." In some teeth there was a distinct break between annuli in the pad and those displayed on the inner lateral aspects of the roots. Although counts from the two regions may be the same, the annuli are in these cases not confluent from one region to the other. This suggests that accretion of cementum occurs simultaneously in different zones, but that there is a possible physiological mechanism preventing continuity between the zones. This phenomenon has not been described by other workers.

Usually the first layer laid down tends to be thicker than subsequent layers, in some cases up to 5X thicker. The rates of accretion were found to vary between teeth of the same animal, and within the same tooth. In general, the annuli appeared to be compressed with increasing age, apparently because growth of the cementum slows and more annuli must be accommodated within a narrower layer. In cases of exceptional wear in a molar tooth, attrition of the dentine may result in exposure of the cementum pad at the tooth cusp (Plate 3. 6.). This does not detract from the possibility of counting annuli, as teeth of this age have pronounced accretion at the roots which can be used instead.

The 30 molars and permanent premolars from sub-adult "known-age" animals were tabulated in terms of increasing age (derived from the eruption calendar), with the numbers of light and dark annuli recorded

opposite each tooth. In the summary of results below, I have used "band" to represent one light annulus and one dark annulus combined.

For  $M_1$  :

15 months (  1 year) had  $\frac{1}{2}$  band.

30 months (   $2\frac{1}{2}$  years) had  $1\frac{1}{2}$  bands.

40 months (   $3\frac{1}{2}$  years) had  $2\frac{1}{2}$  bands.

46 months (  4 years) had 3 bands.

This clear pattern did not hold for all teeth; variation from the pattern in a minority of first molars was discounted in arriving at the above sequence. Those teeth not conforming to the pattern were assumed to either represent deviation from the eruption calendar, or to exhibit anomalous accretion. This latter phenomenon is discussed below.

The results show a sequence from which it can be concluded that one band is in fact laid down per year. For  $M_1$ , one year must be added to the number of bands to arrive at the true age. This formula must also apply to  $M^1$ , as this tooth shows the same age at eruption. The  $\frac{1}{2}$  band shown by  $M_1$  from 15 month old animals consisted of a single broad light annulus, and thus the light annulus must be laid down first.

The formula for  $M_1$  was then :

$$\text{Age in years} = \frac{\text{number of light annuli} + \text{number dark annuli}}{2} + 1$$

In a similar way, correction factors for third molars were determined. It was found that an addition of  $2\frac{1}{2}$  years was required to compensate for the later eruption of these teeth. If any difference in age resulted between estimates based on the first and third molars, the mean was taken as representing the true age.

If the deposition of cementum around a tooth exhibits layering, and if the layers are laid down in all teeth at the same time of the year,

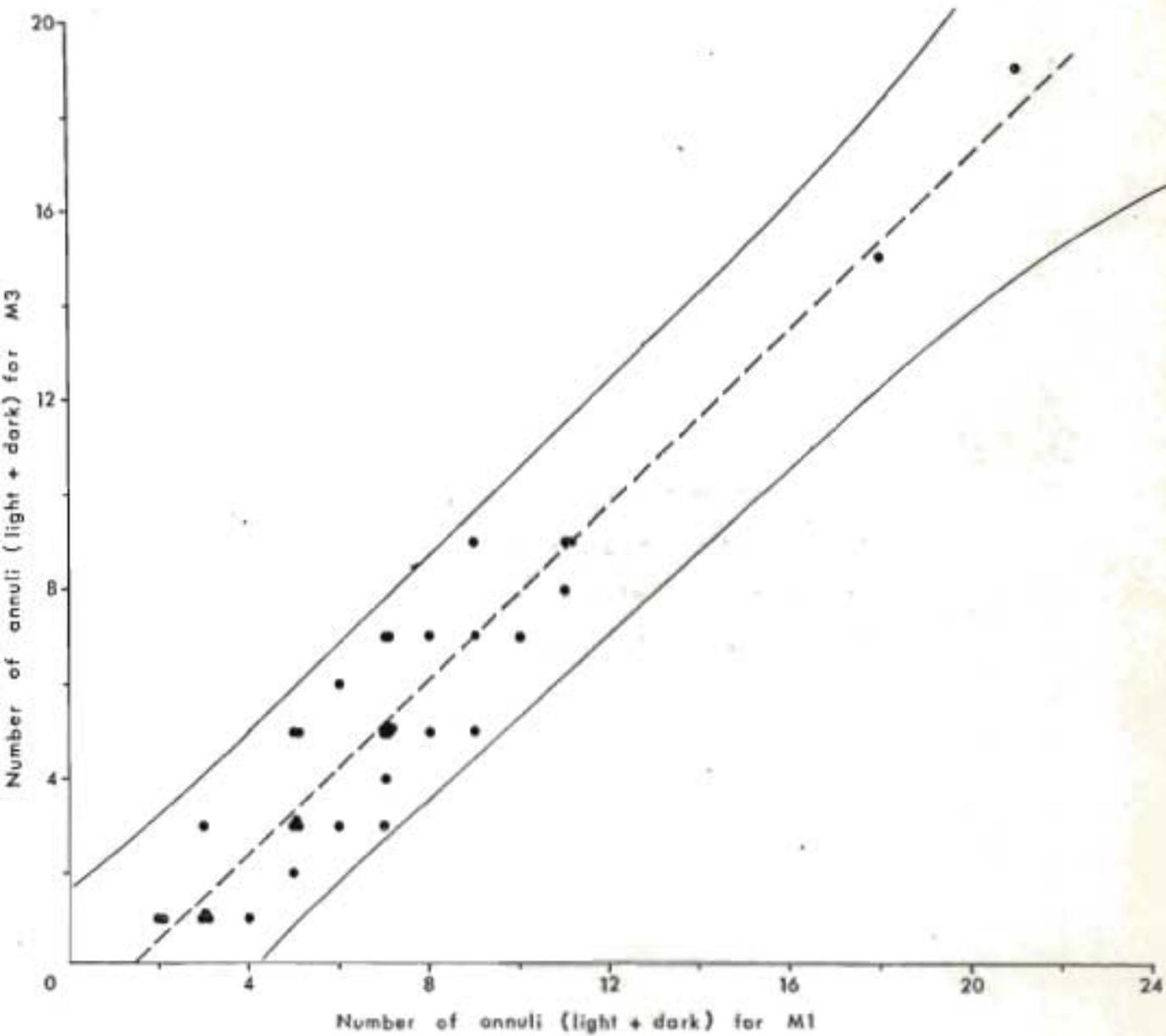
there should be a consistent difference in the number of these annuli in teeth that erupt at different ages. Anderson (pers. comm.) plotted the number of annuli on M1 against the number on M3 for nyala; the regression showed a high positive significant correlation. A similar plot was made with my data (Fig. 3.3.). The number of points plotted is limited, because

- a) only teeth with distinct annuli were used,
- b) sometimes M1 was extracted from both mandible and maxilla in place of both M1 and M3, and
- c) I tended to discard one of the M1/M3 pair if the results from the other tooth were completely satisfactory.

Despite the few M1/M3 combinations, some deductions may be made. The regression equation for the points is  $y = 0,924x - 1,315$  ( $r = 0,956$ ;  $p < 0,001$ ). All the points fall within the 95% confidence limits to this regression. The "fitted" line is between 1,5 and 2,5 annuli away from the bisector. M1 shows a mean value of 1,86 annuli more than M3. With an interval of about 13 months between the eruption times of M1 and M3, one would expect (if two annuli are laid down per annum) the difference to approximate 2 annuli. The departure from expectation may be explained in part by individual variation in eruption times, or possibly by misinterpretation of annuli. Closer agreement with the expected value would probably have resulted had stained, decalcified sections been used instead of the macroscopic preparations.

Discrete and obvious layering is clearly visible macroscopically in Plate 3.7.. Few teeth however show such obvious, well-defined layering. Of 194 animals, 35 (18%) had both molars unsatisfactory for age determination based on cementum annuli. Some teeth gave unusually high or low counts which were clearly unrelated to the wear of the tooth. In others, no annulation could be distinguished in facial sections; presumably these would have been apparent in thin, stained

Fig. 3.3. : Plot of number of cementum annuli counted in the first molar against number counted in the third molar. Regression line is dashed (equation in text); unbroken lines indicate 95% confidence intervals.



sections. The section might not have passed through the region of maximum discernible number of annuli and consequently some teeth displaying no macroscopic annulation were re-sectioned in different planes. The results indicated that if annuli were not immediately apparent in one section, then further sections in other planes were unlikely to reveal any change in detectability.

Errors in the technique are manifest. Faint "accessory" lines may be present between "true" annuli. These can be recognised with experience, and disregarded; subjectivity cannot be avoided however, because it is sometimes difficult to decide on what constitutes a true annulus. Any suspect annulus should be disregarded if it is not continuous. Accessory or "background" annuli may stain well in histological preparations (Spinage, 1976); in this respect facial sections may be superior, for in these annuli are not readily apparent.

"Double" lines or "twinning" of annuli have been reported by various authors (Mitchell, 1967; Simpson and Elder, 1969; Simpson, 1973). This phenomenon is caused presumably by the accretion of limited translucent cementum during the period of accretion of opaque cementum. To detect and compensate for "twinning" it is necessary to examine the entire length of the cementum layer.

Resorption of cementum is a further complication. This occurs in old animals, and commences at the root apex. Resorption has been recorded in buffalo (Grimsdell, 1973), and waterbuck (Spinage, 1967). Thus the technique can be considered to provide only a minimum age, and will decrease in accuracy with increasing age (Sergeant and Pimlott, 1959; Simpson and Elder, 1969; Lockard, 1972).

There is some controversy as to the factors governing spurts and retardation in cementum accretion, which result in the annuli. Grimsdell (1973) was able to discount photoperiodism. Spinage (1976) concluded from buffalo teeth that a single dark-staining line per year

Plate 3.4. : Incisiform teeth from male wildebeest, estimated to be about thirty-one months old. The third permanent incisor is erupting, with the left third deciduous incisor still in situ. The tips of the permanent canines are just visible, but where the bone has been chipped away.

Plate 3.5. : Mandibular tooth row of male wildebeest, judged to be about thirty-eight months old. The eruption sequence is slightly anomalous: all permanent teeth are fully erupted, yet  $p_4$  still overlies the erupting  $P_4$  (arrowed).

Plate 3.6. : Section through mandibular first molar ( $M_1$ ) of male wildebeest of about sixteen years of age. The tooth has worn right down to expose the cementum pad at the occlusal surface.

C = cementum

B = part of **mandible** bone forming socket.



resulted from an annual unimodal rainfall pattern, compared to two lines in equatorial bimodal rainfall areas. The findings south of the equatorial zone suggest an inherent rhythm approximating to two lines per year, irrespective of seasonal changes, and not the result of nutritional variation (Grimsdell, 1973; Simpson, 1973). Simpson and Elder (1969) reported two lines per year from kudu in Rhodesia (a unimodal rainfall pattern area), which they attributed to "hormonal balance on the one hand and nutritional stress on the other." Smuts (1974) assumes nutritional changes to be the causal factor of regular bold cementum line formation, for he maintains that annuli in South African mammals are clearer than those in the same species from the tropics, where green vegetation may be available throughout the year. The evidence appears inconclusive as yet. The nutritional variation hypothesis is further confused by the presence of annuli in carnivores which are not subject to marked seasonal nutritional changes. The greatest cementum age derived from this study was 20 years, in a female. Consideration of the errors in the technique preclude acceptance of this figure as ecological longevity. Table 3.7. shows a breakdown of cementum ages of skulls older than four years. As the sources of these skulls are diverse (found skulls, culling operations prior to this study and during this study), the Table does not purport to show age structure, but rather to indicate ecological longevity. The 14 - 15 year old age class would appear to be the maximum age attained by most animals. Talbot and Talbot (1963) suggest maximal ecological longevity for C.t. hecki as eighteen years. Physiological longevity records from zoos have been listed by Mentis (1972). These ranged from 12,7 years to 20,1 years, with a mean of 16,75 ( $n = 5$ ). This cannot be taken to indicate ecological longevity in the wild, because zoo animals receive a less fibrous and abrasive diet, which would lessen the rate of tooth wear.

TABLE 3.7. : Cementum ages of skulls more than four years old from Zululand. This table relates to longevity and should not be taken to represent a true age structure.

AGE CLASS	♂	♀	TOTAL
4 - < 5	30	10	40
5 - < 6	22	6	28
6 - < 7	8	5	13
7 - < 8	5	5	10
8 - < 9	9	4	13
9 - < 10	3	3	6
10 - < 11	3	4	7
11 - < 12	3	4	7
12 - < 13	3	3	6
13 - < 14	2	4	6
14 - < 15	2	6	8
15 - < 16	0	1	1
16 - < 17	1	1	2
17 - < 18	0	0	0
18 - < 19	0	1	1
19 - < 20	0	0	0
20 - < 21	0	1	1

## 3.3.3.

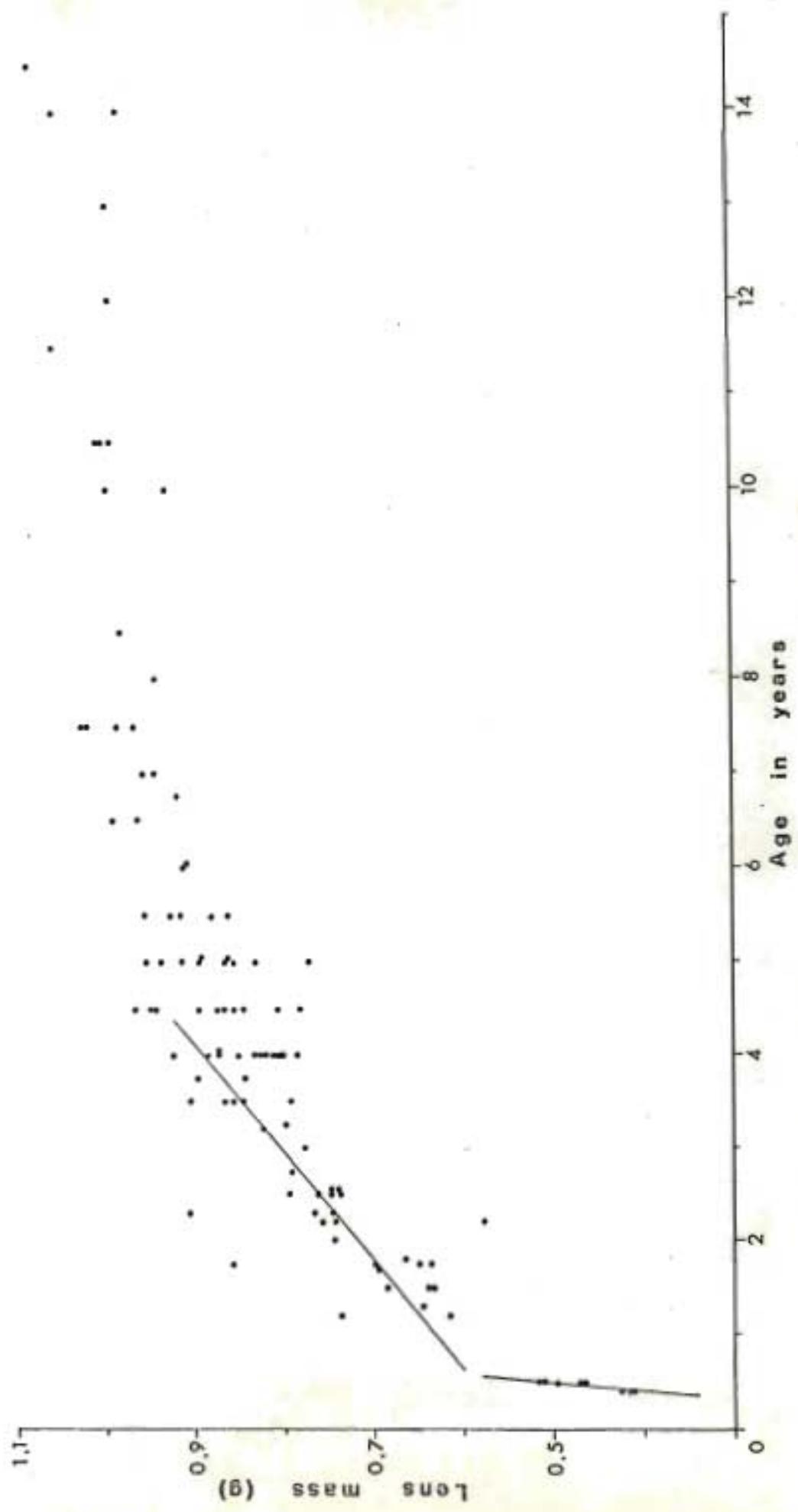
EYE LENS MASS

No distinction was made between sexes when considering eye lens mass. The correlation coefficient between cementum or eruption age against lens mass was 0,767 ( $p < 0,001$ ), indicating increasing mass with age (Fig. 3.4.). The Nelder and Mead (1965) method of fitting a curve proved unsatisfactory, in that the curve tended not to include the youngest age classes. Inclusion of these classes may be considered in an alternate approach, by plotting two straight line regressions. For animals less than one year old the equation is  $y = -0,048 + 1,106x$  ( $r = 0,76$ ;  $p < 0,001$ ). For animals between one and four years old, the regression equation is  $y = 0,5496 + 0,085x$ ; ( $r = 0,89$ ;  $p < 0,01$ ). The pattern of growth is fairly rapid up to about four years, followed by a rectilinear relationship. This agrees with results on pronghorn antelope (Kolenosky and Miller, 1962), impala (Fairall, 1969; Rautenbach, 1971), elephant (Laws, 1967), and zebra (Smuts, 1974). The break in the curve has been interpreted by Smuts (1972) to correspond with the attainment of sexual maturity. Cowley (1975) found that in impala, lens mass followed a positively skewed rectangular growth curve.

To illustrate the reliability with which age classes could be separated from lens mass data, a further computer-based curve was plotted (Fig. 3.5.). This curve was based on the Von Bertalanffy growth equation (method described in Chapter 4), and shows mean  $\pm$  one Standard Error for various ages. Clear differentiation occurs only between animals below one year old and the older age classes. Nevertheless this curve was used to estimate ages of those animals for which skulls had been lost, in conjunction with the regressions. Twenty-three animals from the culling programme had ages determined by this method.

The general conclusion is that the technique is of little value for age determination of wildebeest. Because the rate of growth of the lens

Fig. 3.4. : Straight-line regressions of lens mass against  
age for animals under four years of age. Regression  
equations in text.



is not constant, only the very young age classes are distinguishable with any confidence. Ages of these classes are more easily and more accurately determined from the tooth eruption calendar. These findings parallel those from other medium-sized to large mammals (Child et al., 1965; Rautenbach, 1971; and Smuts, 1974).

Errors in determining lens mass may have occurred in this study. No attempt was made to distinguish between left and right lenses. Although Lord (1959), Simpson and Elder (1969), and Rautenbach (1971) found no significant difference between the mass of left and right lenses, this may have been a source of error in wildebeest. Further, both Longhurst (1964) and Cowley (1975) found significant differences between the lens mass of males and females. This was not taken into account in this study. A further error may result from the fact that fixation times in formalin were not standardised. Friend (1967) has shown that considerable inaccuracies can be introduced by varying fixation time before drying and weighing the lenses.

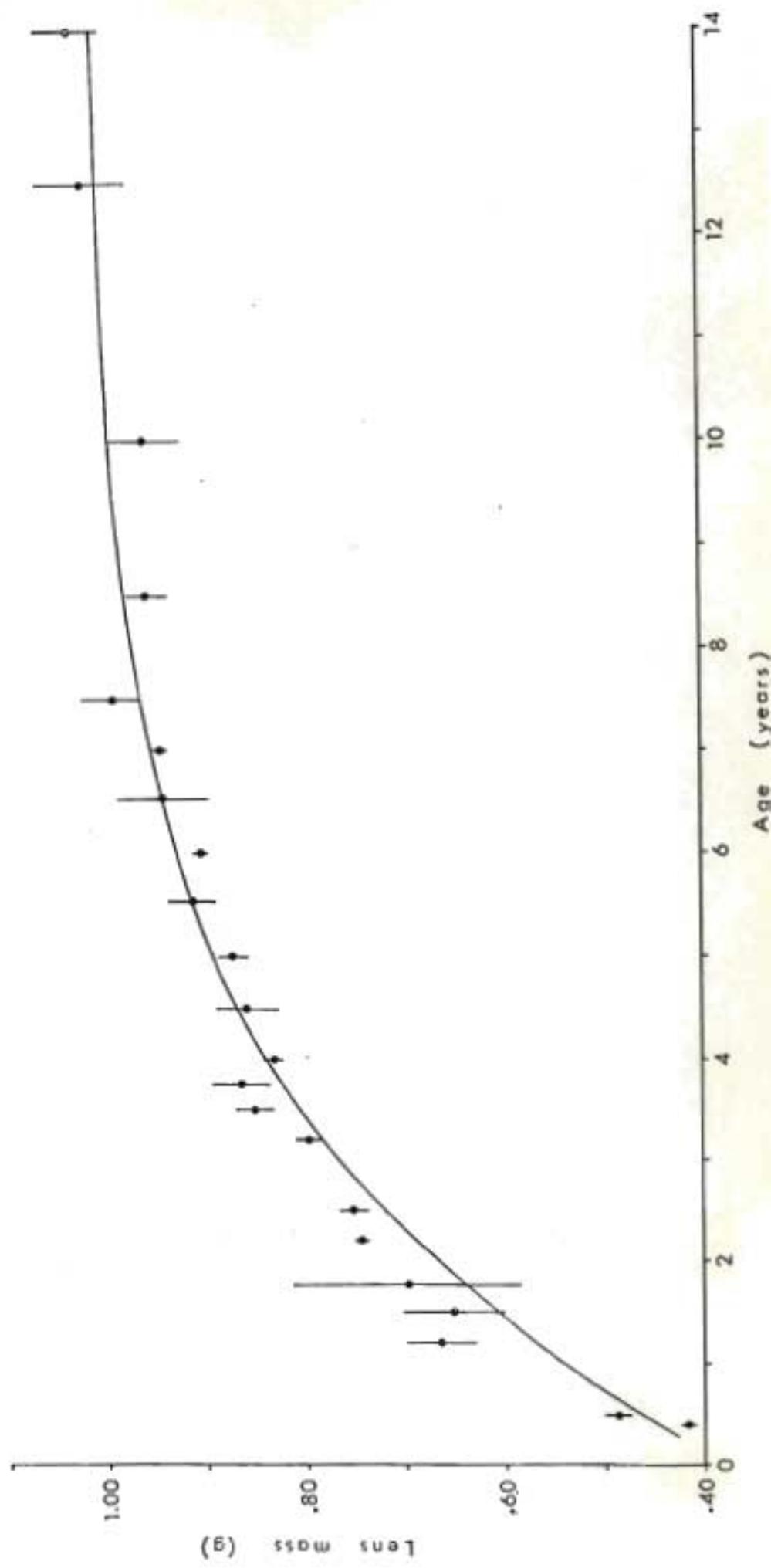
Variation may also occur due to factors in the life of the animal. Myers and Gilbert (1968), for example, found that stress affected the lens/age relationship in Australian rabbits. Nutrition has also been demonstrated to be a factor governing variation in lens mass in deer (Friend and Severinghaus, 1967).

These inherent or experimental errors cannot wholly account for the overlap between age classes. I suggest that if workers wish to persevere with the use of eye lenses in age determination of larger mammals, then attention should be diverted to biochemical methods rather than lens mass. Only increased accuracy would minimise the overlap in older age classes. Otero and Dapson (1972) consider the biochemical assay of eye lens proteins to be "the most accurate method known to date for estimating age of wild vertebrates."

Fig. 3.5. : Von Bertalanffy growth curve for wildebeest eye lens mass. Circles indicate mean values, and vertical lines extend for one standard error either side of the mean. Equation:

$$m_t = 1,0194 (1 - e^{-0,3781 (t + 3,3936)})^3 ,$$

where  $m_t$  is mass at age  $t$ . Further discussion of the form of the Von Bertalanffy equation is given in Section 4.3.1..



## 3.3.4.

TOOTH ATTRITION

Attrition results from mechanical abrasion and from the chemical action of the food during mastication. Baker, Jones and Wardrop (1959) suggested that the constituents of actively metabolising herbage like proteinase enzymes and acids could predispose a sheep's teeth to excessive wear. Cutress and Healy (1966) however considered these effects insignificant in the wear of sheep's teeth in comparison to mechanical wear. This was further borne out by the work of Healy and Ludwig (1965), who found a relationship between dental wear and ingested soil. Spingale (1973) was reluctant to draw inferences from this work to wild herbivores, because the teeth of domestic stock are not selected for hardness. Nevertheless, the effects of ingested soil have been clearly demonstrated in white-tailed deer Odocoileus virginianus by Severinghaus and Cheatum (1956). They showed that the rate of wear from sandy ranges in Massachusetts and Texas was almost double that found in New York state. This is significant in the present study, for the results presented below are based on specimens from both the Complex and Mkuzi. The latter reserve has large tracts of sandy soil, and this fact may well be a source of error.

## 3.3.4.1.

MOLARIFORM ATTRITION : CHANGES IN INFUNDIBULAR PATTERNS

Fig. 3.6. shows the changes in infundibular patterns in each molariform tooth with age. Fourteen adult age classes are distinguished. I have dispensed with the more conventional approach of drawing the entire tooth row, by considering each tooth separately. It is envisaged that the chart could be used for rapid age estimation of skulls found in the field; a characteristic feature of such skulls in Zululand is that the full toothrow is rarely present, particularly in young animals. Anterior portions of both mandible and maxilla are often

Fig. 3.6. : Tooth wear chart for adult wildebeest, based on change in molariform infundilular patterns. Where more than one pattern occurs for a specific tooth in any age class, these patterns are alternatives for that age class.

Age class (years)	Maxilla					Mandible				
	PM <sup>3</sup>	PM <sup>4</sup>	M <sup>1</sup>	M <sup>2</sup>	M <sup>3</sup>	PM <sub>3</sub>	PM <sub>4</sub>	M <sub>1</sub>	M <sub>2</sub>	M <sub>3</sub>
3 - <4										
4 - <5										
5 - <6										
6 - <7										
7 - <8										
8 - <9										
9 - <10										
10 - <11										
11 - <12										
12 - <13										
13 - <14										
14 - <15										
15 - <18										
18 - <21										

consumed by hyaena, leaving only the more posterior molariform teeth. Skulls which have been in the field for some time often lose teeth, which fall from the sockets with increasing decomposition of bone.

The orientation of teeth on the chart has been arranged so that maxillary and mandibular toothrows can be examined side by side. The maxilla must clearly be viewed from a ventral aspect, and the mandible dorsally. Because the right tooth row is considered in the maxilla, and the left in the mandible, the drawings for both maxillary and mandibular teeth show lingual aspects on the left, and buccal on the right. Teeth were drawn with the anterior aspects towards the bottom of the chart.

Photographs of some stages of tooth wear are given in Plates 3.8. to 3.10..

The reliability of tooth wear charts is open to question. Firstly it is naïve to assume that the same degree of wear represents the same age. Roettcher and Hoffman (1970) considered the possibility of individual variation in impala, and further postulated that behavioural differences during the rut may result in sex differences in wear. Ransom (1966) found that in older white-tailed deer tooth-wear criteria had severe limitations; he accounted for the variation by assuming the amounts of ingested abrasive material to be the causal factor. In Defassa waterbuck, Spingé (1967) found marked differences in the molar wear in ten year old animals. Further limitations in the wear-age technique were described by Kerwin and Mitchell (1971) for pronghorn antelope, Antilocapra americana. Anderson (pers. comm.) maintained that in nyala the change in number and shape of the infundibula was unreliable over nine years of age.

Some idea of "confidence limits" in the use of the chart was arrived at by comparing the number of tooth wear categories for each tooth which was used in compilation of the chart with the number of those

Plate 3.7. : Pronounced cemental layering in molariform tooth of an adult female wildebeest. Based on cemental layers (and employing the correction factor explained in the text), this animal was estimated to be about nine and a half years old.

E = Enamel; I = Infundibulum; D = Dentine;  
C = Cementum. The dashed lines indicate the cementum pad which shows maximum definition of annuli.

Plate 3.8. : Infundibular patterns of left maxillary tooth row from a male wildebeest which has just achieved adult dentition. Note that the central circular infundibulum in M<sup>3</sup> is yet to form.



PLATE 3.7



PLATE 3.8

categories discarded i.e. those categories which fell outside the final wear pattern for the chart, in adjacent classes. Results are shown in Table 3.8.. The results indicate that  $M^3$  and  $M^2$  are the most "reliable" teeth: they show least variation in wear patterns at the same age. When all teeth are considered together, only 68,2% will show the same wear pattern at the same age.

A more detailed interpretation of the reliability of the chart may be achieved by referring to Table 3.9., where each age class is considered separately. The conclusion is that the chart is consistently "reliable" (over 60% reliability) up to 12 years. Thereafter the reliability drops rapidly to 37,7% in the 14 - <15 years age class. Both the 15 - <18 and 18 - <21 years age classes must be regarded as extremely unreliable, as these classes were based on minimal numbers of specimens, and because wear patterns are by now very diverse for the same cementum age.

Despite these limitations, I consider the chart to provide a rapid field age determination technique, without resorting to the laborious preparation of sections. Any particular specimen will allow an estimate of age, with the range in which that estimate will lie. The range will vary with the age of the animal, and with the number of teeth that can be examined. In some cases a skull can be assigned to a specific age class, without inclusion of the range of "adjacent" classes.

Future work pertaining to the chart should aim at quantifying the agreement of cementum-age of skulls with age determined from the chart.

#### 3.3.4.2.

##### INCISOR ATTRITION

The results of incisor height and width measurements are presented graphically in Figs. 3.7. and 3.8.. The height relationship (Fig. 3.7.)

Plate 3.9. : Infundibular patterns of right maxillary tooth row from a male wildebeest. This animal was estimated to be about ten years old, based on cementum annuli. No sign remains of the central circular infundibula on the molars, and the anterior infundibulum on M<sup>1</sup> has worn away completely.

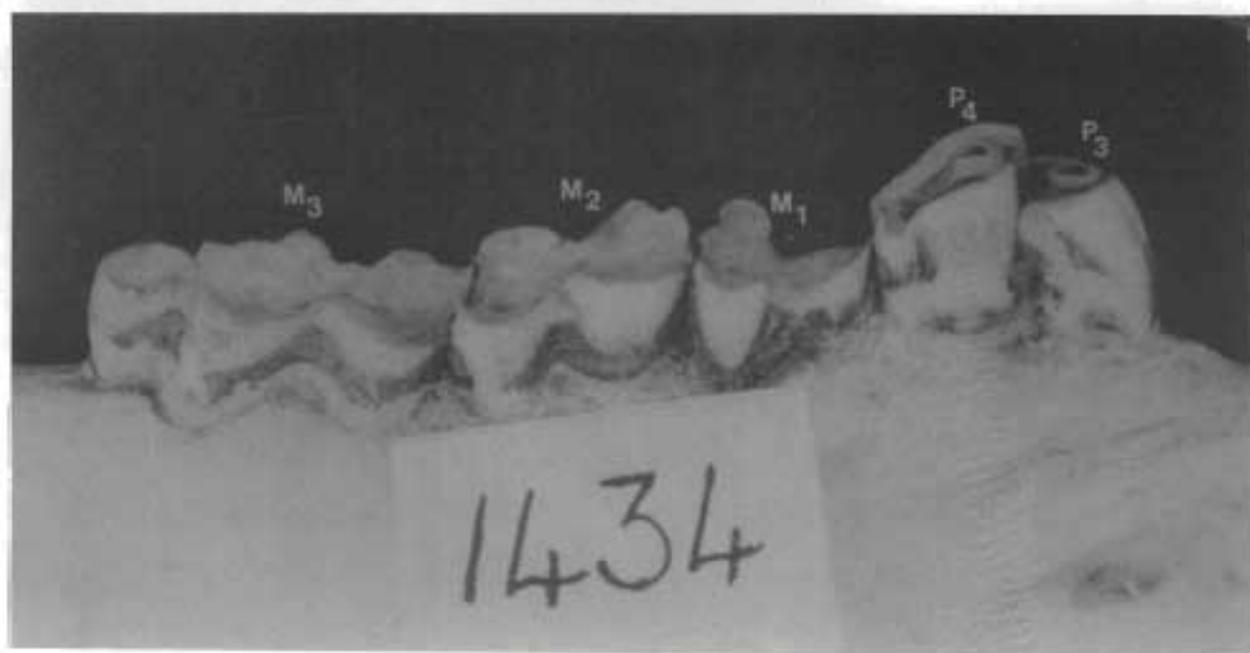
Plate 3.10. : Right mandibular tooth row of adult male (estimated cementum age of sixteen years), and incisiform teeth showing excessive wear. All infundibula have been worn off the molars; differential wear has allowed infundibula to remain on the premolars. M<sup>3</sup> in this animal was split completely in half.



PLATE 3.9



PLATE 3.10



**TABLE 3.8.** : Comparison of numbers of tooth wear categories used in the compilation of age-wear chart, with numbers of categories discarded.

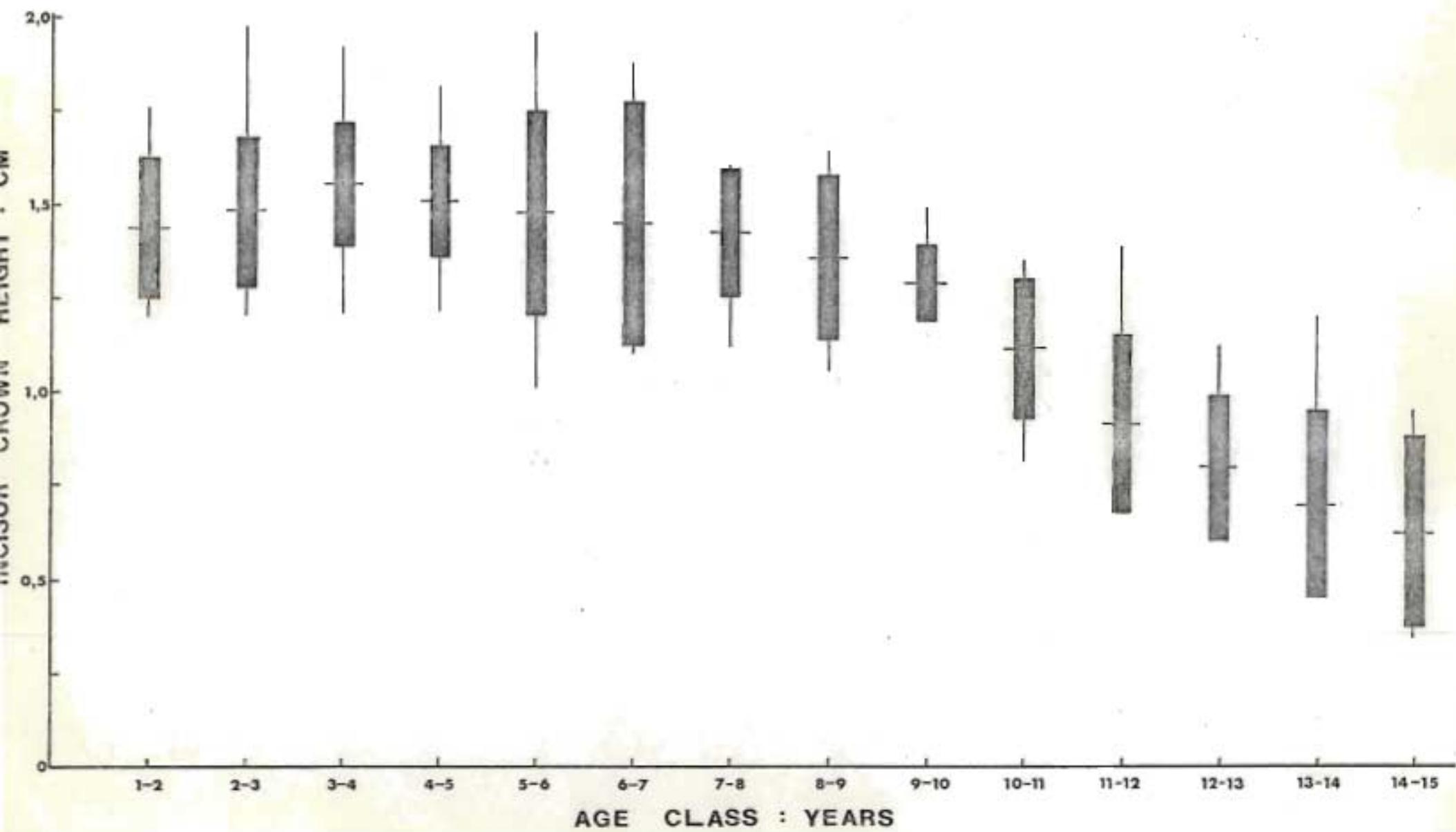
TOOTH		NUMBER OF WEAR CATEGORIES CONFORMING TO CHART	NUMBER OF WEAR CATEGORIES FALLING IN "ADJACENT" WEAR CLASSES	TOTAL	% CONFORMING TO CHART
M A X I L L A	P <sup>2</sup>	NO INFUNDIBULAR CHANGE : PATTERN CONSISTENT.			100
	P <sup>3</sup>	91	26	117	77
	P <sup>4</sup>	80	46	126	63,5
	M <sup>1</sup>	84	46	130	64,6
	M <sup>2</sup>	106	31	137	77,4
	M <sup>3</sup>	86	47	133	64,7
M A N D I B L E	P <sub>3</sub>	65	43	108	60,2
	P <sub>4</sub>	74	46	120	61,7
	M <sub>1</sub>	86	30	116	74,1
	M <sub>2</sub>	74	42	116	63,8
	M <sub>3</sub>	86	31	117	73,5
TOTAL		832	388	1220	68,2

**TABLE 3.9.** : Estimates of "reliability" of wear chart, considering each age class.

- NOTES:**
- ① : The maximum numbers of conforming patterns were used as the final definitive pattern for that age class.
  - ② : 10 patterns are possible for each skull (Total number of adult teeth is 11, but  $P^2$  was not used as no infundibular pattern was apparent). The third column is not, however, merely 10 X the second column, because teeth, mandibles or even maxillae were sometimes missing.
  - ③ : The sample size in the 3 - <4 year age is small because the majority of these skulls had their ages determined by eruption.

Cementum age class (Years)	Number of specimens used (Both sexes)	Total number of teeth for which infundibular patterns were recorded ②	Maximum number of infundibular patterns the same ①	% of total number of patterns: "variability" or "reliability"
3 - <4	9 ③	78	47	60,3
4 - <5	37	340	243	71,5
5 - <6	25	235	143	60,8
6 - <7	11	105	72	68,6
7 - <8	9	87	60	70,0
8 - <9	7	58	42	72,4
9 - <10	6	40	26	65,0
10 - <11	6	47	34	72,3
11 - <12	7	63	53	84,0
12 - <13	5	51	30	58,8
13 - <14	6	54	25	46,3
14 - <15	8	61	23	37,7
15 - <18	2	} 41	} 9	} 22
18 - <21	2			

Fig. 3.7. : Mean values (horizontal lines) of incisor crown height above gum line plotted against age. Bars extend for 1 X Standard Deviation either side of the mean; ranges are denoted by vertical lines.



during the first three years of life is not a true reflection of wear. Although wear is taking place during this period (confirmed by Fig. 3.8.), the rate of eruption of the tooth exceeds the downward wear. The incisor is a wedge-shaped tooth, the broad dorsal edge tapering ventrally towards the roots. Consequently, as an animal ages, the occlusal width will become narrower and downward wear (decrease in incisor height) will become more rapid. This is clearly apparent from Fig. 3.7. after about nine years.

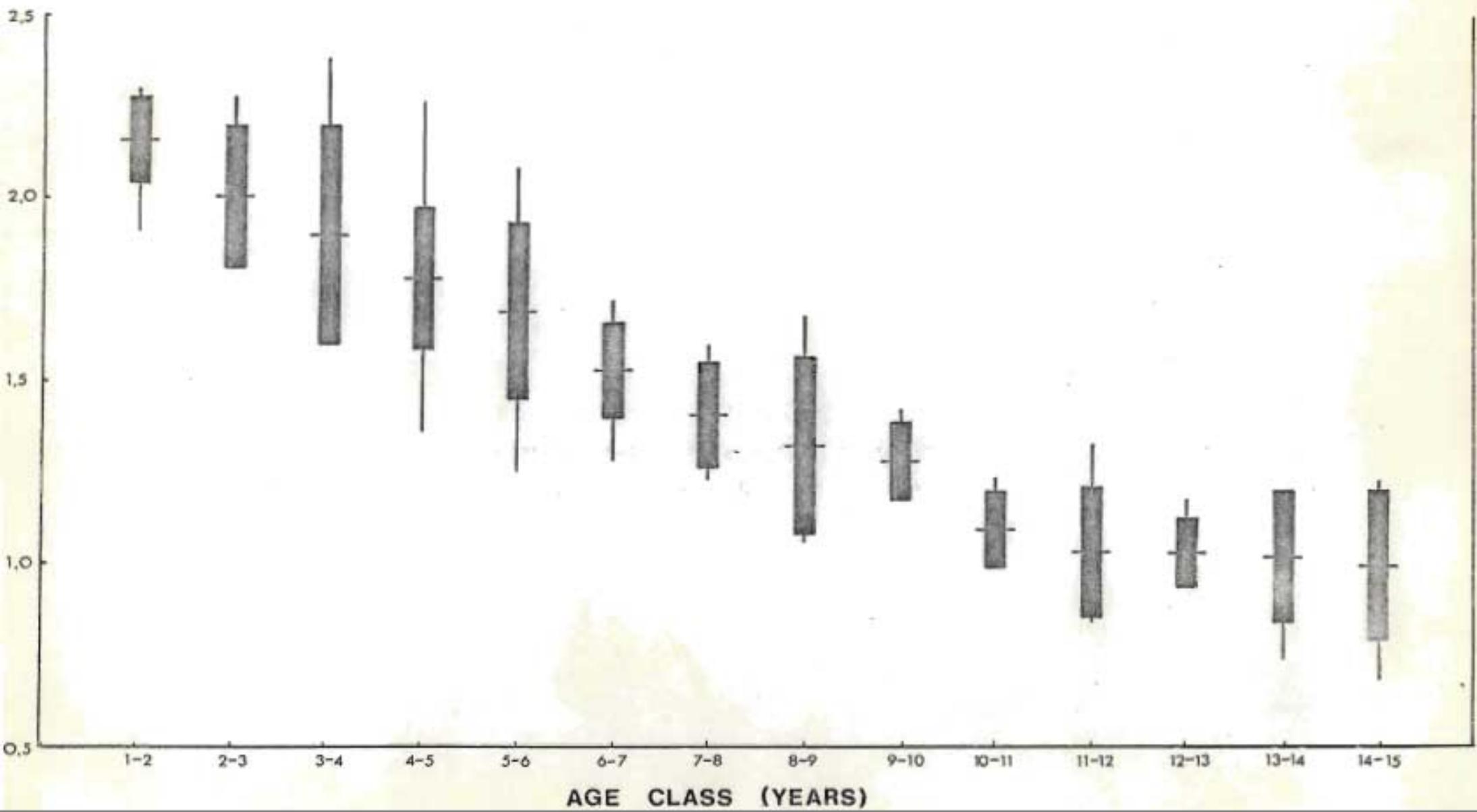
Conversely, with occlusal width (Fig. 3.8.), the rate of change is initially rapid, and then slows down at about the same age. Towards the tooth roots the angle of the "wedge" is less marked and the sides of the tooth tend towards the parallel. At this point little change in occlusal width will occur with wear.

Both graphs illustrate that incisiform wear is not linear. This confirms the findings of Spinage (1967) and Simpson and Elder (1969). A curvilinear relationship is apparent. Similar relationships for molariform teeth have been described by Watson (1967), and Grimsdell (1973).

Spinage (1973) considers that incisiform teeth show greater variability in wear than molariform teeth, and this may account for the overlap between age classes in my results. The overlap is pronounced in older age classes of the occlusal width graph, and in younger age classes of the incisor crown height. The crown height appears to follow a negative exponential wear pattern, which was postulated by Spinage (1967). Again, the results must be used with caution. Spinage (1973) states: "The use of measurements is only pseudo-objective; it may remove observer bias, but it cannot correct for varying rates of wear."

The general conclusion pertaining to the use of dentition in age determination is that eruption sequence is accurate and reliable up to about 3,5 years. The wear chart is less accurate, but is certainly

Fig. 3.8. : Mean values (horizontal lines) of incisor width plotted against age. Bars extend for  $1 X$  Standard Deviation either side of the mean; ranges denoted by vertical lines.



within the requirements for life table data, up till the age of 12 years.

### 3.3.5

#### ANOMALIES IN DENTITION

##### 3.3.5.1.

#### DECIDUOUS DENTITION

The persistence of  $p_2$  into adult life has already been mentioned. In one instance,  $p_2$  of a yearling ♂ was separated from the adjacent  $p_3$  by a gap of 1cm. This occurred on the left side only.

The presence of supernumary maxillary canines was noted in a single calf skull, of about 2 - 3 weeks old, but of undetermined sex (Plate 3.11). The canines were situated at the posterior end of the premaxilla, at the suture between maxilla and premaxilla. An adult female (6 - 7 years, No. 247) showed remnants of maxillary canines. I was not specifically looking for this abnormality, and thus am unable to give a figure for the frequency of this phenomenon, as the small size means that they are easily overlooked. Mitchell (1965) recorded maxillary canines in a 10 month old wildebeest (C.t. taurinus) from Barotseland. The incidence of maxillary canines in white-tailed deer (Odocoileus virginianus) was found by Severinghaus (1949) to be 0,13% ( $n = 18000$ ). For roe deer (Capreolus capreolus), Chaplin and Atkinson (1968) noted an incidence of 3,8% ( $n = 133$ ). Chapman and Chapman (1973) found maxillary canines to be present in as many as 17% ( $n = 68$ ) of fallow deer fawns (Dama dama); the incidence was, however, rare in animals over six months of age.

##### 3.3.5.2.

#### ADULT ERUPTION ABNORMALITIES

Two cases were noted where  $P^2$  did not erupt at all. One occurred on

the left side (5 year old ♂), and the other on the right ( $4\frac{1}{2}$  year old ♂).

Failure of  $P^3$  to erupt was recorded in a single 5 year old ♂, from the right tooth row.

Dental anomalies may be expected in most families of mammals (Colyer, 1936). Child (1965) reported dental abnormalities in 1.19% of impala skulls examined ( $n = 755$ ).

### 3.3.5.3.

#### DEVIATIONS FROM ADULT WEAR PATTERNS

Occasional pronounced discrepancy in wear between incisiform and molariform teeth occurs. In these cases, wear on the incisiforms is far heavier.

Differences in wear also take place between upper and lower jaws. A  $14\frac{1}{2}$  year old male (No. 2566) had maxillary premolars and first molar worn completely flat, whilst the corresponding mandibular surfaces had experienced relatively little wear. (Plate 3.12.).

With heavy wear (in animals older than 13 years),  $M_1$  may split between the buccal and lingual aspects. This is often caused by differential wear: adjacent sides of  $P^4$  and  $M^1$  together form the apex of a wedge which extends beyond the level of other teeth in the tooth row. The "wedge" impinges on  $M_1$ , resulting in highly differential wear of that tooth, particularly on the anterior cusp.

A more frequent phenomenon in adult dentition is seen in the anomalous juxtaposition of the anterior cusp of  $M_1$  with the posterior cusp of  $P_4$ , in both mandible and maxilla. A "shearing" effect results, with enamel worn off at the points of contact, so that the infundibula of the two teeth become confluent.

Plate 3.11. : Supernumary maxillary canines present in a calf, estimated to be about three and a half weeks old. Scale in cm.

Plate 3.12. : Marked differential wear between mandibular and maxillary tooth rows. The anterior end of the mandibular tooth row shows almost no wear, in marked contrast to the maxillary counterparts. Note that  $M^1$  is split. Such disparity in wear does not allow for age estimation from the tooth wear-age chart. Male specimen; cementum age about fourteen and a half years.



PLATE 3.11

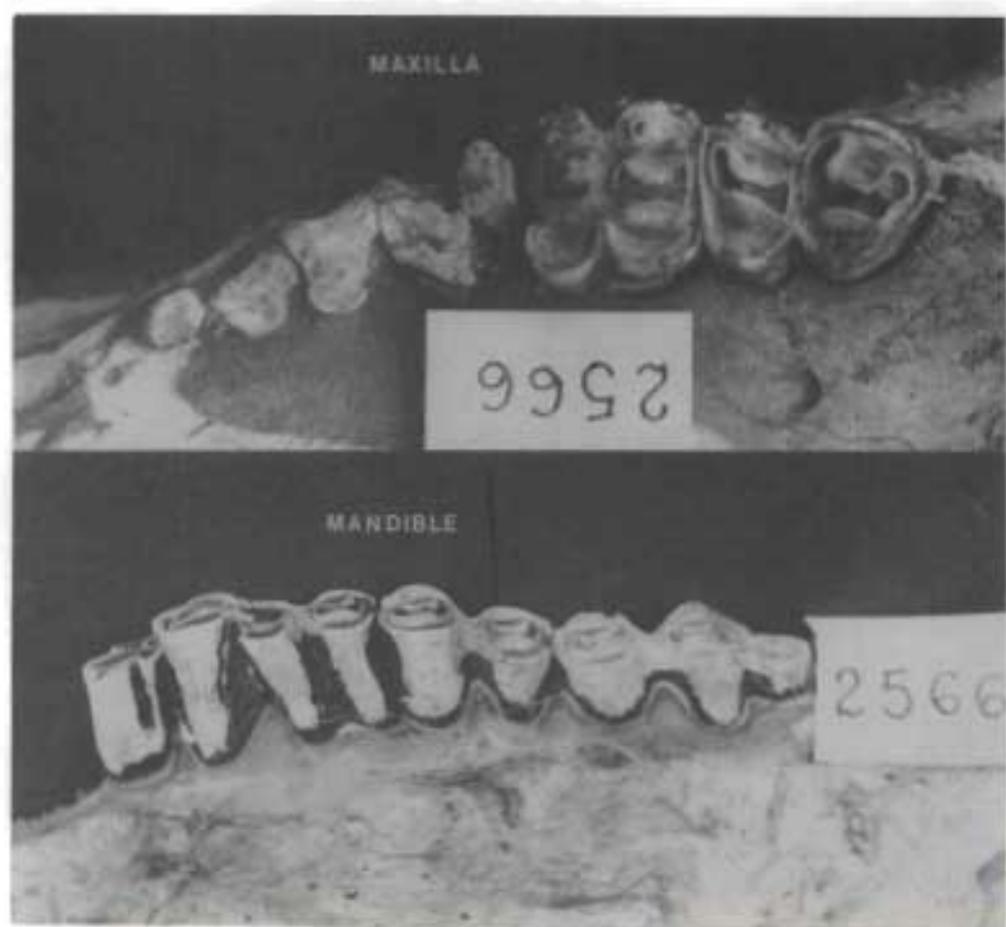


PLATE 3.12

## 3.3.6.

FIELD AGE DETERMINATION

Determination of age in the field requires considerable experience. Talbot and Talbot (1963) differentiated six age classes for females based on horn configuration, and seven for males. Their adult classes were of little use in the field, and the severe wear shown by their oldest male class was never observed in Zululand.

Ansell (1966) produced guidelines for the standardisation of terms used in the field. I did not distinguish between 'infant' and 'juvenile', as the date of observation of young-of-the-year provided an approximate age, owing to the seasonality of parturition. My categories were: calves, yearlings, 2 - 3 year olds, and adults.

The following notes may be of use in distinguishing between age classes:

- a) Calves: Readily distinguishable on size, colour and horn development. The fawn colour contrasts strongly with that of other age classes, but is usually lost by about May (5 - 6 months old), and sometimes as early as the end of February. Fawn colouration is maintained on the face into the yearling class. (A single calf specimen was observed with a wholly black face.) By the end of July, most Zululand calves display full development of brindle stripes on the neck, with faint brindles on the thorax.

The horns first appear at about three months, initially growing straight out but begin to curve outwards and then inwards at about  $7\frac{1}{2}$  months. No field sex differentiation is possible.

- b) Yearlings: The yearling is distinguished by the fawn colouring on the front of the face, between the eyes. Size

may be useful early in the year, but becomes less reliable later. The fawn colouration is not always reliable (it may be lost, or may even be found in adults). A highly reliable characteristic is the degree of exposure of the base of the horns: in yearlings the boss is not visible, and has the appearance of being covered by a tuft of hair. Sexual differentiation is difficult but possible, particularly towards the end of the year when male horn development is more marked. The belly shape (see adults, below) may also be used.

- c) 2 - 3 Year olds: Reliable recognition of this class can only take place in about the first six months of the year. Criteria for sex are as for adults.
- d) Adults: The male is the most easily distinguished. The spread of the horns extends beyond the ears when the latter are extended horizontally. The boss of the horns is well developed, much larger than in females. The scrotum is seldom observed in the field, but the penis shaft extends anteriorly in a downward straight line to the centre of the belly, so that an angular appearance is presented from the flank.\* In contrast the belly of the female is more uniformly rounded, lacking the "angle" of the adult male.

In general, the laterally extended ears of the female project beyond the spread of the horns. No single criterion should however be used, as the above are largely generalisations. The ear/horn-spread feature is fallible, for example, and the angular male belly is lost in animals in very poor condition. Behavioural (\* see frontispiece).

characteristics also serve to separate adult sexes (see Chapter 8.), and it is advisable to use a combination of as many diagnostic features as possible.

Photographs of age classes are reproduced in zur Strassen (1969) and Petersen and Casebeer (1971).

### 3.4.

#### CHAPTER SUMMARY

Age determination methods employed the use of tooth eruption sequence, cementum layers from macroscopic tooth sections, eye lens mass, and tooth attrition. Tooth attrition was considered in terms of the changes in infundibular patterns, and by measurements of incisor height and width.

Eleven eruption classes were arrived at, providing a reliable method of age determination up to 3,5 years. The times of eruption of specific teeth were compared with data from East Africa.

The restricted birth interval of wildebeest enabled some sub-adult animals (ages determined from eruption calendar), to be regarded as "known-age". Ages of these sub-adult animals were used to arrive at a value for the number of cementum layers laid down per annum, and to provide a "correction factor" for the period before eruption and cemental deposition. The nature of tooth cementum lines in wildebeest is discussed. The changes in infundibular patterns were related to cementum or eruption age, thus providing an age-wear chart with fourteen adult classes. A measure of reliability for the chart is provided, and it is considered that the chart is adequate for life-table data.

Incisiform wear in wildebeest appears to follow a curvilinear relationship. When eye lens mass was plotted against cementum or

eruption age, the resultant curve served only to distinguish between animals below one year old and the older age classes.

Anomalies in dentition are discussed.

Some criteria for age determination in the field are presented.

## CHAPTER 4

### GROWTH AND CONDITION

#### 4.1.

##### INTRODUCTION

Growth and condition are closely related factors in the life of an individual animal. As condition may be examined at a demographic level as well, I intend to treat these two factors separately for the sake of clarity.

#### 4.1.1.

##### GROWTH

Sinclair (1969) has defined four main phases in the growth of an animal. The first phase occurs in the early embryo, where everything is subordinated to growth, and there is little differentiation of function. This is followed by a period where a balance exists between growth and differentiated functional activity, which persists until maturity. The third phase is marked by the utilisation of energy chiefly for functional activity. Finally, growth becomes insufficient to maintain the body in balance, and cells are consequently lost without replacement.

Growth in mammals is governed by hormonal interactions. The major hormone controlling growth is APGH (Anterior Pituitary Growth Hormone) or somatotrophin (Needham, 1964). Insulin interacts extensively with APGH, promoting cell proliferation and general metabolism. The third major growth hormonal controller is the corticoid group from the adrenal - these hormones promote protein catabolism.

Early concepts of growth assumed fundamentally some kind of multiplicative process (Stephensen, 1962). As it is clear that the growth tempo of different parts of the body varies considerably, it is essential to distinguish between allometric and isometric growth. If body proportions change with an increase in size, then the relationship is allometric (Hanks, 1972). An isometric relationship exists if the situation appears to be linear. This is illustrated by the work of Smuts (1975), who calculated regression equations for estimating body mass from body dimensions by using logarithmic transformations and fitting linear regressions by the method of least squares. Where experimental curves resulted, the relationships were clearly allometric.

In broad terms, quantitative aspects of growth studies may be separated into those dimensions or parameters which change with age, and those which display a relationship with respect to the animal itself (Hanks, 1972). Results of both these aspects are presented in this section.

Many of the conclusions in this section are based on interpretation of growth curves. Various attempts have been made to provide mathematical expressions to describe postnatal growth curves (Huxley, 1932; Brody, 1945; Thompson, 1962; and Brozek, 1963). Wildlife workers have tended to fit curves by eye (Child, 1964; Rothe, 1965; Hanks, 1969; Pienaar, 1969; Blood, Flook and Wishart, 1970). The use of theoretical growth equations has however been applied to

several species, including elephant (Krumrey and Buss, 1968; Laws and Parker, 1968; and Hanks, 1972), hippopotamus (Laws, 1968), and cottontail rabbits (Bothma, Teer and Gates, 1972).

The collection of morphometric and mass data is basic to most fields of zoological research, but in the case of ungulates these data have important applications. The following are among the uses to which such data may be put:

- a) The collection of representative standard body measurements may be used to compare present growth phenomena with those collected over the same area at future dates, or to compare growth rates of the same species in different habitats or localities. Talbot and McCulloch (1965) emphasize that the size of individuals may vary with race, season, and location. Variations in external measurements may differ significantly from one range to the next without reflecting anything but nutritional variations (Cowan, 1956, quoted by Blood and Lovaas, 1966).
- b) The data may be used to derive mathematical relationships between body dimensions and body mass, thus replacing visual mass estimation methods (Smuts, 1975). Organic growth may be investigated through the use of more sophisticated equations (von Bertalanffy, 1938).
- c) Combined with age structure knowledge, mass data may be used to calculate biomass figures. Biomass data are essential in management considerations of carrying capacity and stocking rates.
- d) For commercial exploitation of game, a knowledge of age of maximum productivity introduces economic considerations into management. Should a game species compete with domestic stock, a comparison of growth rates would aid in management decisions.

- e) The assessment of population age and sex structure in the field is facilitated by recognisable age-specific body dimensions and relationships.
- f) The data may be put to use in taxonomic studies.
- g) Current wildlife management practices employ a range of drugs for immobilisation and sedation. Dosage rates of some drugs require fairly concise data on the mass of an animal of any specific age or sex.

#### 4.1.2.

##### CONDITION

The condition of any individual within a population is related to the chances that animal has of dying, which is determined, among other factors, by deposited fat reserves and the degree to which such reserves may be mobilised in times of stress. At a population level, the measurement of "condition" is not an altogether clearly defined concept. It may be viewed as a function of the demographic fitness (which is given by a measure of age structure, natality and mortality, summarised in the statistic  $\underline{r}$ ) and the physical condition of the individuals making up that population. Condition assessments serve to link growth and reproductive rates with nutritional level of both individuals and populations: these interrelationships may be examined at different seasons and under varying environmental conditions (Hanks, Cumming, Orpen, Parry and Warren, 1976). Ideally, the assessment of condition may be used to compare populations in two different areas, or to compare temporal changes in the same population. Smith (1970) considers that such comparisons may reflect on the effects of current or past management practices, stocking rates, and phenology. Provided measurements of condition are sufficiently sensitive, it should be possible to relate condition to population density, habitat factors, rainfall,

and soil types.

Condition may determine levels of growth, fecundity, and survival. A reduced level of nutrition may be associated with delayed sexual maturity (Pimlott, 1959; Taber and Dasmann, 1954). Poor condition may significantly affect predation (Hirst, 1969), and mortality from infectious diseases. When environmental conditions become critical, mortality is biased towards animals in poor condition (Ferrar and Kerr, 1971; Child, 1972; Keep, 1973). This mortality is marked in calves, possibly as a result of disease: antibodies are produced from serum globulins (proteins), and these may be deficient in cases of hypoproteinaemia resulting from undernutrition (Maynard and Loosli, 1969).

This chapter deals with the assessment of the condition of individuals, and as different techniques for this assessment reflect different physiological processes, techniques and their results are considered separately.

#### 4.1.2.1.

##### CONDITION ASSESSMENT RELATED TO EXTERNAL APPEARANCE AND DEPOSITED FAT RESERVES

Of the techniques available for condition assessment, some are related to the external appearance and morphology of the animal. Hamerstrom and Camburn (1950) used body mass as a condition factor, and Taber and Dasmann (1958) used body mass corrected for skeletal size to compare deer from different habitat types. Christian (1963) has even suggested that the body size of some mammals is reduced in crowded populations owing to density-dependent physiological stress involving adrenocortical hyperplasia. Morphometric data have been utilised to measure condition. Albl (1970), for example, was able to relate the depth of the lumbar region in elephant to condition. More usual is the use of a combination of

measurements, or of the relationship between body mass and a specific body measurement. By using heart girth/body mass relationships, Smart, Giles and Gynn (1973) considered that monitoring of population condition trends for management purposes was justified.

Bandy, Cowan and Wood (1956) derived regressions of body mass against heart girth and hindfoot length from penned animals on a high nutritional status, thus providing an "ideal" relationship. By comparison of estimated body mass with the ideal mass (both derived from regression), an index of condition was arrived at.

Another group of techniques has been concerned with the amount of fat present in the animal. Riney (1955) assessed perinephric, back and abdominal fat percentages. Ledger and Smith (1964) dissected out all body fat and expressed it as a percentage of carcass mass: the tediousness of a total dissection led to a proposal by Whicker (1964) to estimate total fat based on the specific gravity of the body. Smith (1970) differentiated between subcutaneous fat, leg fat and visceral fat.

Of these methods the mass of perinephric fat as a percentage of kidney mass (the Kidney Fat Index, hereafter referred to as KFI) has been the most widely used, on a fairly wide range of species (Riney, 1955; Hughes and Mall, 1958; Taber, White and Smith, 1959; Ransom, 1965; Blood and Lovaas, 1966; Allen, 1968; O'Gara, 1968; Caughley, 1970; Flook, 1970; Bear, 1971; and Flux, 1971). Smith (1970) found significant correlations between kidney fat and body fat in eight species, except hippopotamus and lesser kudu (Tragelaphus imberbis).

The fat content of bone marrow was initially used as a qualitative index based on texture and colour (Cheatum, 1949). Subsequently, a quantitative approach was standardised by Sinclair and Duncan (1972) who found that the dry weight of bone marrow expressed as a percentage of the fresh weight was an accurate measure of the fat content.

## 4.1.2.2.

CONDITION ASSESSMENT RELATED TO BLOOD AND URINE CONSTITUENTS

Another approach to condition estimation is through the use of standard medical techniques in the analysis of blood components, such as Glucose levels, and Packed Cell Volume (PCV). Serum cholesterol levels have also been used (Dillman and Carr, 1970). Urine analysis has been used to derive a Hydroxyproline Index (McCullagh, 1969) - this amino acid is derived from the breakdown of collagen: low levels of hydroxyproline are associated with malnutrition.

## 4.1.2.3.

THE RELATIONSHIP OF THE ADRENAL GLAND TO CONDITION

Endocrine glands respond in a predictable manner to changes in population density or in environmental factors, and they may be used as indicators of population status for the purposes of management. The adrenal gland has been found to be particularly sensitive to these changes, and may be regarded simply as an indicator of the trend of a complex of adaptive events within the body in response to its overall environmental situation (Welch, 1962). A clear example of adrenal response of this nature has been provided by Christian, Flyger and Davis (1960), who found the adrenals of Sika deer (Cervus nippon) to be larger during the year of a major die-off than in those years preceding or following it.

A simplified chain of events leading to an increase in adrenal mass may be summarised as follows: stress (which may take numerous forms, as described below), results in an increase of ACTH (Adrenocorticotrophic hormone) production from the anterior pituitary. This hormone causes hypertrophy of the adrenal cortex, with concomitant increase in adrenal mass.

The adrenal medulla is chiefly responsible for the production of

the catecholamines: adrenaline and noradrenaline. Release of the catecholamines is controlled by nervous impulses from the hypothalamus. Liberation of these hormones is accompanied by generalized sympathetic effects in all tissues of the body provided with catecholamine receptor sites. Both catecholamines increase the depth and rate of respiration. Noradrenaline increases the total peripheral vascular resistance, whilst adrenaline constricts the skin vessels and dilates skeletal muscle. The most important effect of adrenaline is on carbohydrate metabolism, resulting in the production of free energy.

Almost fifty corticosteroids have been isolated from the cortex itself, but only a few from the adrenal venous blood. It would consequently appear that the remainder are precursors or degradation products of the venous components. Originally, corticosteroids were divided into glucocorticoids and mineralocorticoids (the former affecting carbohydrate metabolism and the latter electrolyte metabolism). Overlap of function no longer justifies the use of this arbitrary classification. The major corticosteroids are cortisol (hydrocortisone) and aldosterone. The action of cortisol is extremely complex, influencing carbohydrate metabolism, glucose synthesis, the availability of fatty acids for energy, water metabolism, and the regulation of blood pressure. Aldosterone increases electrolyte metabolism by modifying the rate of active transport of sodium and potassium across membranes.

Stress situations, ranging from muscular exertion to hypoglycaemia, result in secretion of the catecholamines and cortisol. Any specific stressor, or combination of stressors, will result in the General Adaptation Syndrome, which was proposed by Selye (1950, 1956). This syndrome comprises a standard set of physiological responses which occur irrespective of the nature of the stressor acting on the animal. Among these responses is adrenocortical hypertrophy. Such animals may be more susceptible to disease. Turner (1955) suggests that

the increased glucocorticoid activity leads to the suppression of the reticulo-endothelial system with consequent diminution of antibody formation.

Attempts to use total corticosteroids in the blood as a measure of adrenal mass have been largely unsuccessful (Krebs and Myers, 1974). The reason for this has only recently been elucidated by Lee, Bradley and Braithwaite (in press). These workers have shown that total corticosteroids are not equivalent to active corticosteroids; thus total corticosteroid levels may be unrelated to stress. In man, for example, only some 20% of corticosteroids are biologically active, as the remainder are bound to a globulin, transcortin.

Changes in adrenal mass may be caused by normal physiological processes such as changes in reproductive status, but the main extrasomatic factors are population density, disease, and the availability of food. The effects of inanition and malnutrition on adrenal mass have been documented by Selye (1951), Kennedy and McCaone (1958), and Slater (1962).

Most work relating population density to adrenal status has centred on rodents. Chitty (1952) found enlargement of adrenal glands during population peaks of the vole Microtus agrestis. This phenomenon was confirmed by Christian and Davis (1956), who found a density-dependent adrenocortical response in Rattus norvegicus, which was independent of food supplies. The same authors (1966) found an excellent correlation between adrenal mass and population size for Microtus pennsylvanicus, provided reproductive status was taken into consideration. A similar relationship was found in Ruffed Grouse Bonasa umbellus by Neave and Wright (1968), indicating that the phenomenon was not solely mammalian. Little work of this nature has been performed on ungulates, although Welch (1962) was able to demonstrate larger adrenals in white-tailed deer Odocoileus virginianus on densely populated ranges when compared to sparsely populated regions.

## 4.2.

MATERIALS AND METHODS

## 4.2.1.

GROWTH

Two hundred and five animals were made available during the culling programme from which mass and morphometric data could be taken. Horn measurements were based on two hundred and ninety skulls, the additional material being derived from skulls collected in the field and from culling operations prior to the start of the study. The method of measurement followed that recommended by Ansell (1965). A flexible steel tape was used, and measurements recorded to the nearest 10<sup>-1</sup>cm. Measurements were taken "over the curves". Smuts (1975a) points out that this technique is preferable to the alternative "between pegs" (Ansell, *ibid*) method, as the latter consistently fails to register changes in condition or muscular development. Shoulder height was recorded as the distance from the base of the hoof to the median line of the body between the scapula. Chest or heart girth was taken as the minimum circumference of the chest measured just posterior to the front legs. Hindfoot length was recorded cum ungue (c.u.). Ear length was not measured routinely, but when recorded, this measurement was from ear tip to notch.

Crown-rump and head length were recorded in foetuses where development was sufficiently advanced. Again, methods followed were those of Ansell (1965).

Horn measurements recorded were: Distance between tips, spread, outer curvature, and basal circumference of the boss. The first two measurements are standard "trophy" dimensions as used in Rowland Ward (Best, 1962), except that "spread" is termed "greatest width outside" in big game records. Outer curvature was measured from

the ventral side of the boss, proceeding outwards along the maximum curve of the horn to the tip. Basal circumference of the boss is self-descriptive. These last two differ from the standard Rowland Ward in method, and are not comparable. Big game horns of wildebeest or buffalo form employ "Breadth of Palm" across the top of the boss, and length on the front curve of the horn.

Body mass was recorded on a 400 lb. Salter spring scale to the nearest pound, and subsequently converted to kg. For various reasons, it was not possible to weigh every animal, and mass data are consequently limited. Dressed carcass mass conformed in most respects to the definition given by Ledger (1963), except that kidneys and kidney fat were not included.

Ages of animals were determined as described in Chapter 3. Foetal ages were estimated by the method of Huggett and Widdas (1951). A full description of this method is provided in Chapter 5.

Mass and length data were analysed by computer (University of Natal IBM 1130), using the von Bertalanffy growth equation. The von Bertalanffy relationship is of outstanding value in its ability to fit actual results to confirm and predict other facts about growth and metabolism (Needham, 1964). Based on the theory of von Bertalanffy (1938), Beverton and Holt (1957) derived a suitable equation. Further concepts and derivations are discussed by Gulland (1969). Hanks (1972) provides a lucid account of uses and concepts of the von Bertalanffy equation, and methods of computerisation. Basically, the equation is of value in that it eliminates the subjectivity which frequently limits the comparative value of growth data (Smuts, 1975a). This means that the theoretical growth rates of animals in different populations can be objectively compared, providing results of taxonomic value.

The program used in this study was identical to that used by Hanks

(1972). The program uses iteration to produce values of the coefficients that minimize the sums of squares of the deviations about the fit, taking into account the standard errors of the mean values of the specific parameters. A curve-fitting subroutine provides an objective method of fitting curves to growth data.

#### 4.2.2.

##### CONDITION

The lack of suitable field laboratory facilities precluded the use of techniques more sophisticated than KFI estimation and the collection of bone marrows. Material collected from Vernon Crookes reserve on the Natal South Coast subsequent to the Zululand field work allowed for the determination of minimal data on blood components.

#### 4.2.2.1.

##### DEPOSITED FAT RESERVES

##### a) KIDNEY FAT

The estimation of kidney fat was based on one hundred and twenty four animals. Female material was derived largely from deaths resulting during game capture operations: these operations take place during the dry season, with the result that the female data are limited to the dry season only. (Although culling took place throughout the year, the sample obtained from this source was highly biased in favour of adult males). The method of Riney (1955) was adopted unchanged. Perinephric fat extends anteriorly and posteriorly within the kidney mesentary. Both kidneys were removed, and excess fat extending beyond the anterior and posterior borders of the kidneys was trimmed away at right angles to the long axis of the kidney. Kidneys were weighed on a triple beam balance to 10-1g, before and after removal of the fat.

The KFI was then given by:

$$\text{Kidney Fat Index} = \frac{\text{perinephric fat mass}}{\text{kidney mass}} \times 100$$

b) BONE MARROW FAT

Bone marrow samples were collected from forty-six females and ninety-one males. The marrow was obtained from either the metatarsus or the metacarpus: the bone was shattered with a hammer, and up to 10g of marrow removed. After removal of bone chips, samples were deep frozen until they could be processed. Before drying, samples were weighed to  $10^{-2}$ g. They were then placed in an oven and dehydrated at  $100^{\circ}\text{C}$  until constant mass was achieved, when dry mass was recorded. For the determination of fat content, some of the dried samples were transferred to a Soxhlet apparatus, where the fat was extracted with Petroleum spirit (b.p.  $40^{\circ}$ -  $60^{\circ}\text{C}$ ) for eight hours. The residue was weighed, and fat content derived from the difference in mass before and after extraction. Fat content was correlated with percentage dry mass of fresh mass, and the regression so obtained was used to estimate fat contents for the remaining samples.

Marrow texture and colour were recorded into one of three categories, following the criteria of Riney (1955); these categories were "good", "fair" or "poor".

4.2.2.2.

BLOOD ANALYSES

A small sample (seven males and six females, all older than two years) of culled animals from Vernon Crookes reserve on the Natal South Coast provided material for the determination of PCV and blood glucose levels. PCV values were obtained in the standard medical manner, by centrifugation. Blood glucose levels were

determined semi-quantitatively by the use of 'Dextrostix' reagent strips. Blood was spread over the reagent area, and visual estimation of blood glucose was achieved by reference to a colour chart with assigned values.

#### 4.2.2.3.

##### ADRENAL GLANDS

For various reasons, it was not practical to conduct a complete collection from every animal, but where possible, adrenal glands were collected, trimmed of surrounding connective tissue, and weighed to the nearest  $10^{-1}g$  on a triple beam balance. Histological sections were prepared from a small sample only (four animals) for descriptive purposes. Histological processing followed the procedure in Appendix 1. The main zones of the gland were described and their relative transverse extents measured using a micrometer eyepiece (further details of the use and calibration of the micrometer scale are given in Chapter 6, Section 6.2.2.). By using mean adrenal mass as an index, various tests were made to investigate changes in mass induced by age, sex, body mass, reproductive status, and season.

#### 4.3.

##### RESULTS AND DISCUSSION

#### 4.3.1.

##### GROWTH

#### 4.3.1.1.

##### VON BERTALANFFY EQUATIONS AND GROWTH CURVES

Growth in mass with age in the von Bertalanffy equation takes the cubic form:

$$m_t = M_{\infty} (1 - e^{-K(t - t_0)})^3, \quad \text{where}$$

$m_t$  = mass at age  $t$ .

$M_{\infty}$  = asymptotic mass; the maximum mass that an animal can attain under given conditions.

$K$  = coefficient of catabolism, a constant representing the catabolism of body materials per unit mass and time. Further explanation of  $K$  is given by Hanks (1972).

$t$  = age of animal.

$t_0$  = theoretical age at which the animal would have zero mass with the same growth pattern as that observed in later life.

Growth in length of any specific body measurement takes the non-cubic form:

$$L_t = L_{\infty} (1 - e^{-K(t - t_0)}) \quad (\text{Howells and Hanks, 1972}).$$

The computer printout provides values for the three coefficients, namely asymptotic mass or length ( $L_{\infty}$  or  $M_{\infty}$ ),  $K$ , and  $t_0$ . For each age class, a fitted value of the variable under consideration was also given, enabling a curve to be drawn. An example of the printout is reproduced in Table 4.1..

From the growth curves, it was apparent that standard errors of a specific mean parameter often extended above the computer-derived asymptote before the projected asymptote from the  $y$ -axis met the fitted curve. For this reason, and because I was not consistent in the choice of scale for all parameters, the asymptotic age was considered to be attained when that parameter was within 2,5% of the von Bertalanffy equation asymptotic value. This arbitrary figure of 2,5% was arrived at in that it was considered that a

TABLE 4.1. : Example of computer printout for von Bertalanffy growth curve. Curves were drawn using the fitted values.

AGE	MEAN VALUE OF HINDFOOT LENGTH (♀)	FITTED VALUE	S.E.M.
0,75	46,85	46,84	0,74
1,25	49,80	49,86	0,45
1,75	50,76	50,28	0,71
2,50	50,50	50,34	0,30
3,50	49,00	50,34	0,66
4,50	50,25	50,34	0,52
5,50	51,01	50,34	1,33
7,00	50,33	50,34	0,42
9,00	50,35	50,34	0,59
12,00	50,43	50,34	0,37

higher figure (say, 5%) would be approaching discernible differences in the field, especially with regard to parameters such as shoulder height. Hence, in the following results, all von Bertalanffy asymptotic projections onto the fitted curve are in fact 2,5% less than the computer-given asymptotic value.

a) Growth in mass with age

The theoretical von Bertalanffy equations for growth in mass for wildebeest are:

$$\sigma M_t = 252,96 (1 - e^{-0,7471 (t + 0,8597)})^3 \quad \text{kg}$$

$$\text{♀ } M_t = 192,97 (1 - e^{-1,56 (t + 0,15)})^3 \quad \text{kg}$$

(pregnant animals included)

$$\text{♀ } M_t = 187,4 (1 - e^{-1,41 (t + 0,28)})^3 \quad \text{kg}$$

(pregnant animals excluded)

The growth curves for mass are illustrated in Figs. 4.1. and 4.2.. By projecting the von Bertalanffy asymptotic value onto the curves, it can be seen that males achieve the asymptote of 253 kg by about six years, and females their asymptote of 193 kg (pregnant) or 187 kg (non-pregnant) by about three years.

b) Growth in shoulder height with age.

The theoretical growth equations for this parameter are:

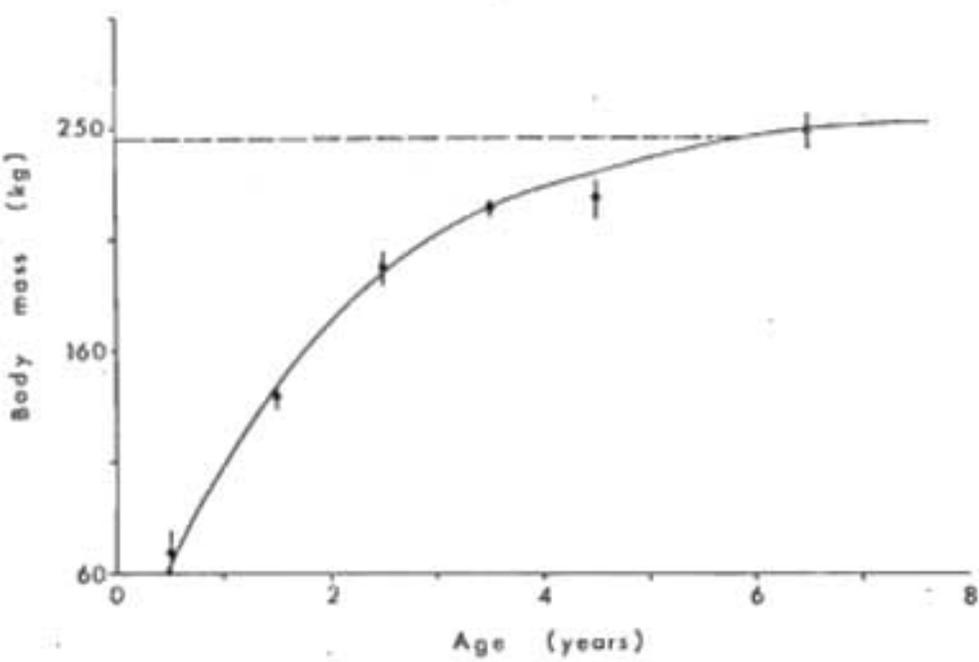
$$\sigma h_t = 145,57 (1 - e^{-0,69 (t + 1,52)}) \quad \text{cm}$$

$$\text{♀ } h_t = 136,06 (1 - e^{-0,47 (t + 3,16)}) \quad \text{cm}$$

Males attain their asymptote of 145,6 cm at about four years of age, in comparison to the female asymptote of 136 cm which is attained at four and a half years (Figs. 4.3. and 4.4.).

Fig. 4.1. : Theoretical Von Bertalanffy growth in mass curve for males. Standard error denoted by vertical line. Circles denote mean mass at age. Dashed line within 2,5% of asymptote.

Fig. 4.2. : Theoretical Von Bertalanffy growth in mass curves for female wildebeest. The lower curve excludes pregnant animals. Standard errors omitted to avoid confusion. Dashed lines within 2,5% of asymptote.



— Pregnant included  
 - - Pregnant excluded

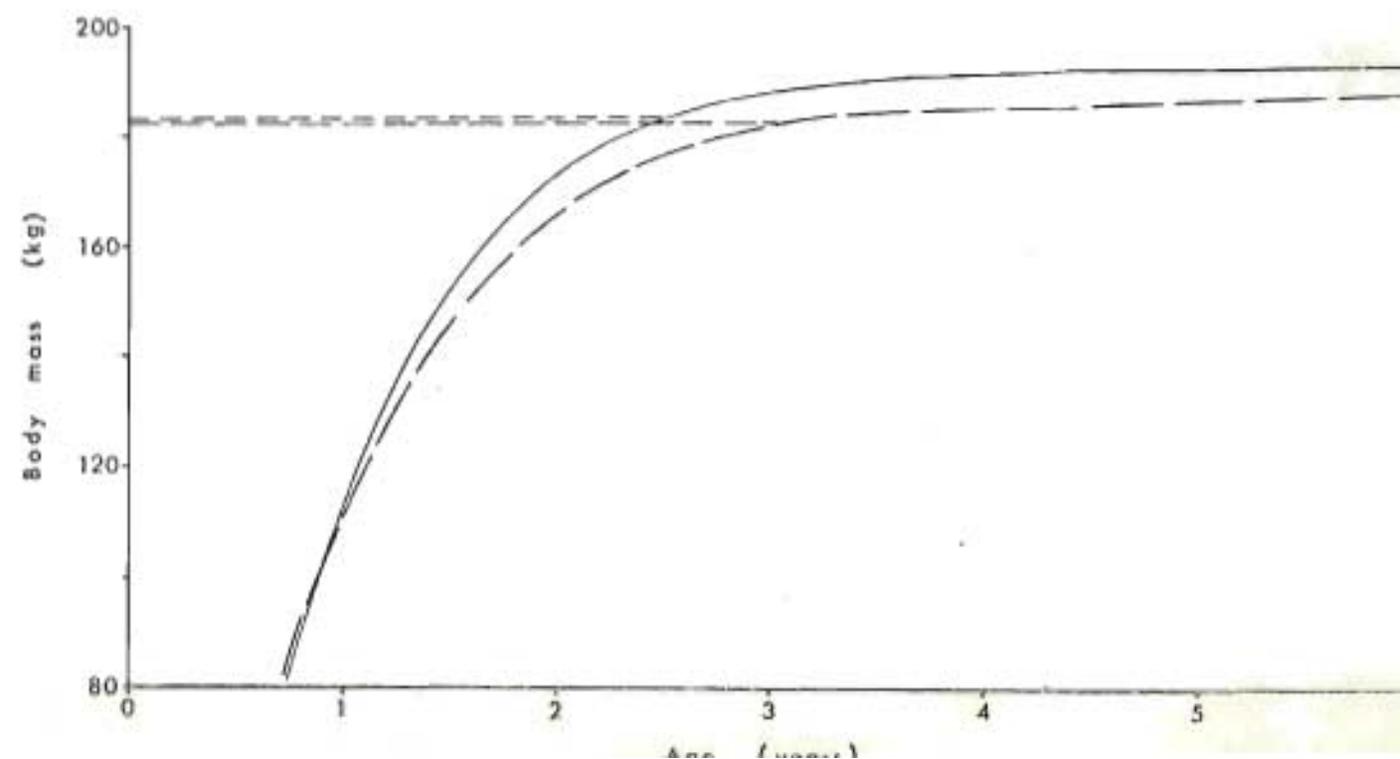
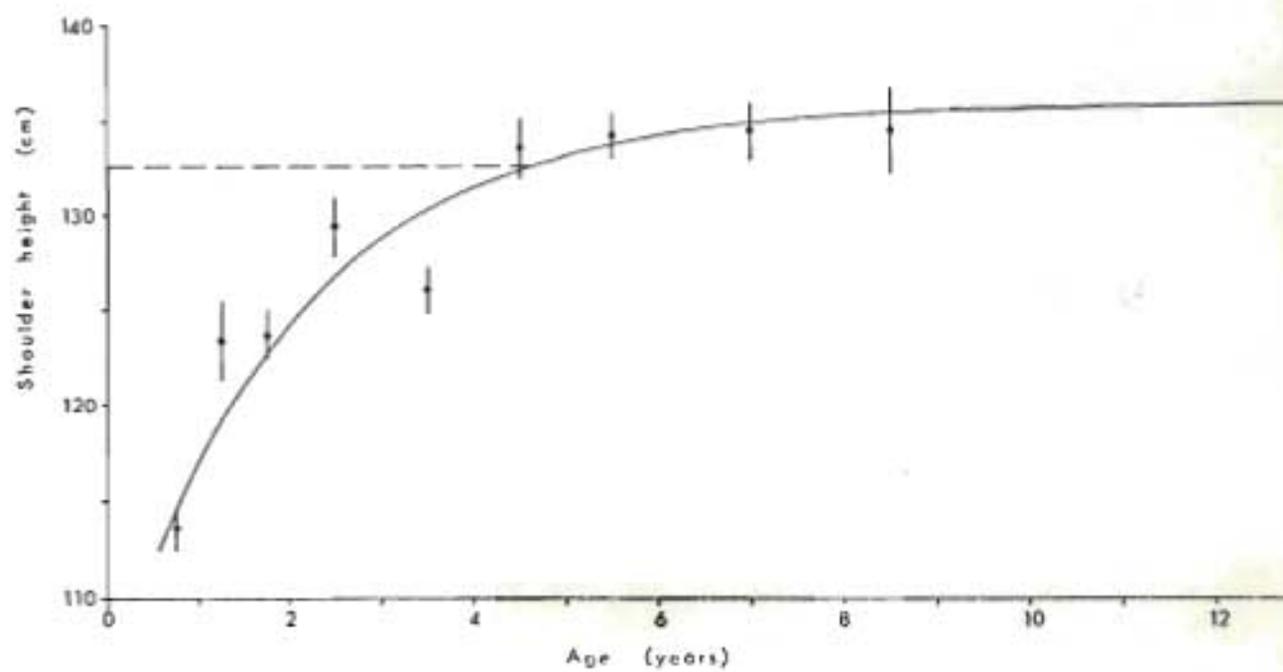
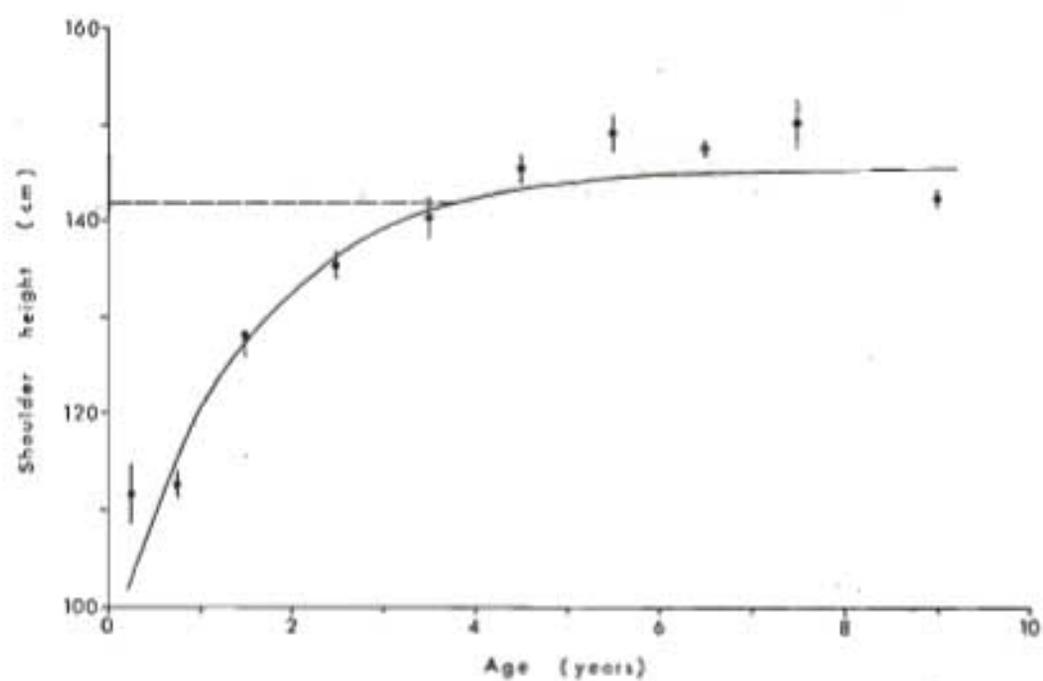


Fig. 4.3. : Theoretical Von Bertalanffy growth in male shoulder height curve, together with mean height at age (circles). Standard error denoted by vertical line; dashed line within 2,5% of asymptote.

Fig. 4.4. : Theoretical Von Bertalanffy curve for growth in female shoulder height, with mean height at age (circles). Vertical line is one standard error; dashed line within 2,5% of asymptote.



c) Growth in hindfoot length (c.v.) with age.

The theoretical von Bertalanffy equations for growth in hindfoot for male and female wildebeest are:

$$\sigma L_t = 52,73 (1 - e^{-0,83 (t + 2,34)}) \quad \text{cm}$$

$$\text{♀ } L_t = 50,34 (1 - e^{-3,98 (t - 0,081)}) \quad \text{cm}$$

Asymptotic lengths are achieved by two years in males (Fig. 4.5) and by one year in females (Fig. 4.6).

The female asymptote is attained particularly early, and differs markedly from the age of attainment given by Talbot and Talbot (1963), which was between thirty and thirty-six months. The same authors estimated that the growth in male hindfoot length normally continued into the fourth year of life.

Although Taber and Dasmann (1958) consider hindfoot length to be the most convenient external index of skeletal size, it clearly is valueless in female wildebeest after one year. Howells and Hanks (1975) have questioned the value of recording parameters which attain asymptotic values early in life. Despite this, hindfoot length has been put to some use (Bandy, Cowan and Wood, 1956) in evaluating range conditions, and in comparative growth studies (McEwan and Wood, 1966).

d) Growth in chest girth with age.

The theoretical growth curves for this measurement are illustrated in Fig. 4.7. (males) and Fig. 4.8. (females). The von Bertalanffy equations are:

$$\sigma g_t = 159,75 (1 - e^{-0,81 (t + 0,90)}) \quad \text{cm}$$

$$\text{♀ } g_t = 147,23 (1 - e^{-0,96 (t + 0,75)}) \quad \text{cm}$$

The male asymptotic value of 159,7 cm is achieved by 3,5 years, and the female value of 147,2 cm by three years.

Fig. 4.5. : Theoretical Von Bertalanffy growth in male hind-foot length curve, together with mean length at age (circles). Standard error denoted by vertical lines; dashed line within 2,5% of asymptote.

Fig. 4.6. : Theoretical Von Bertalanffy growth in hindfoot length curve for females, together with mean length at age. Vertical line represents standard error; dashed line within 2,5% of asymptote.

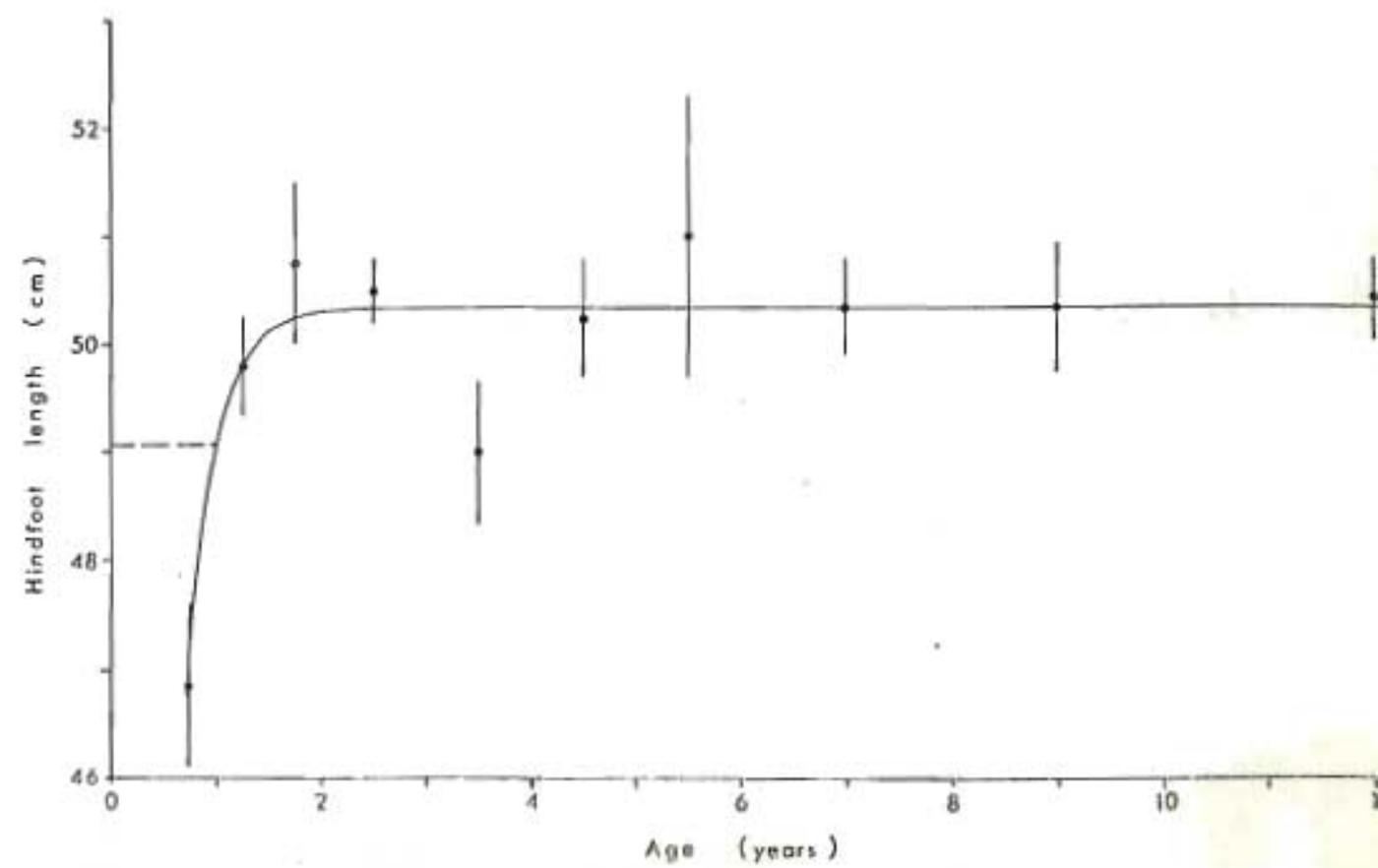
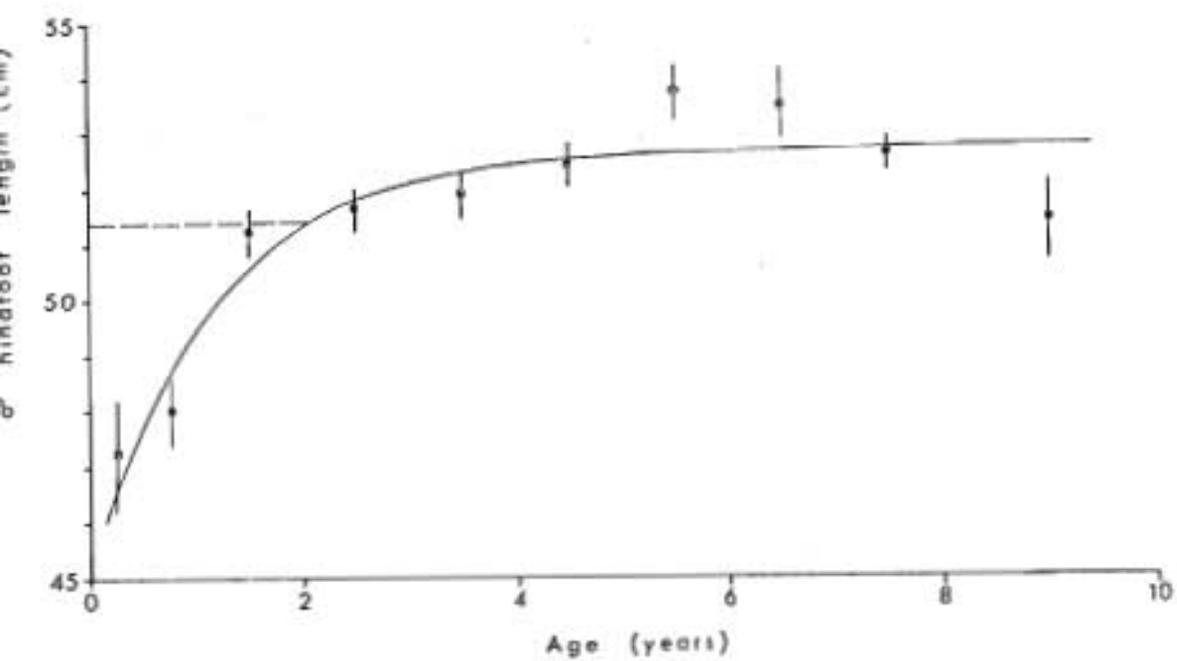
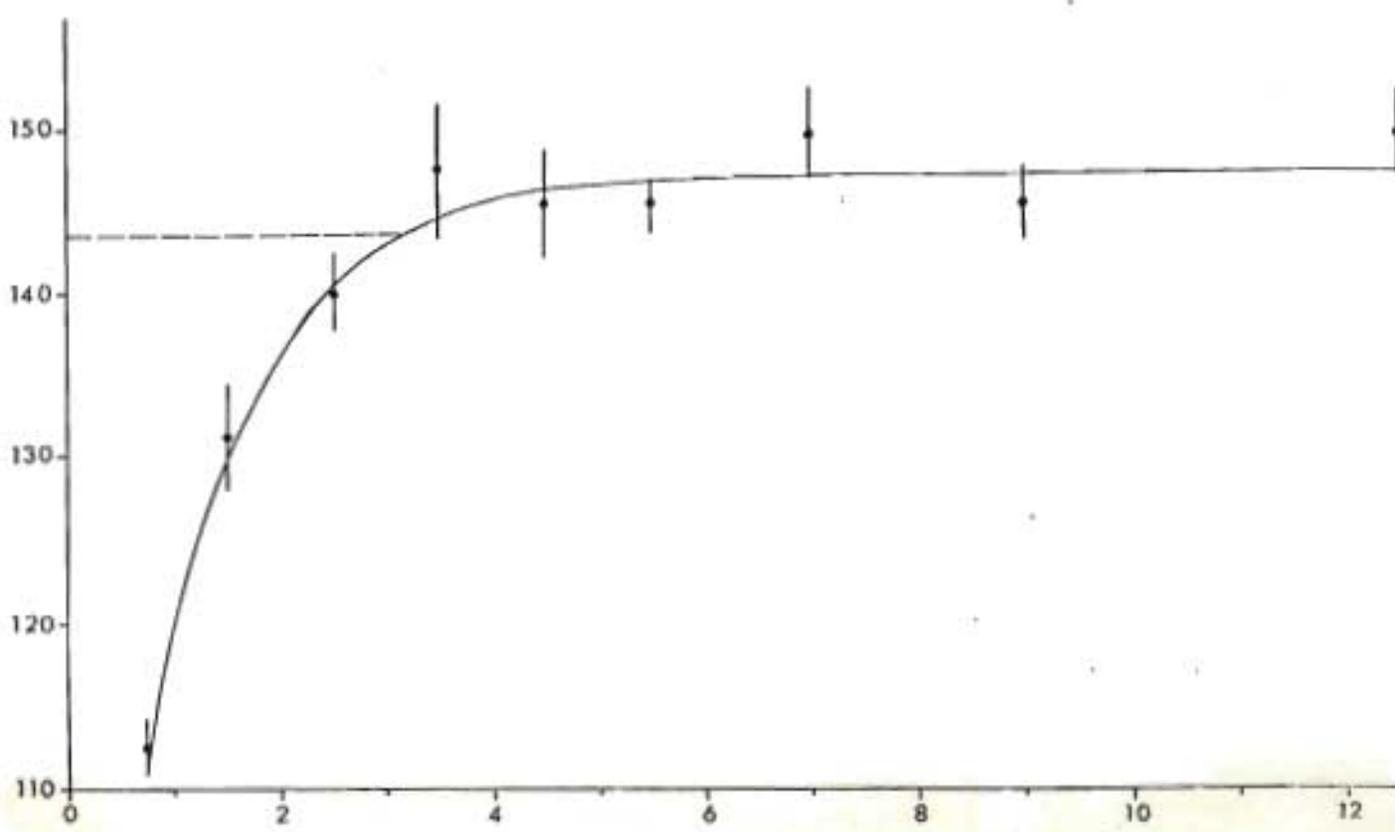
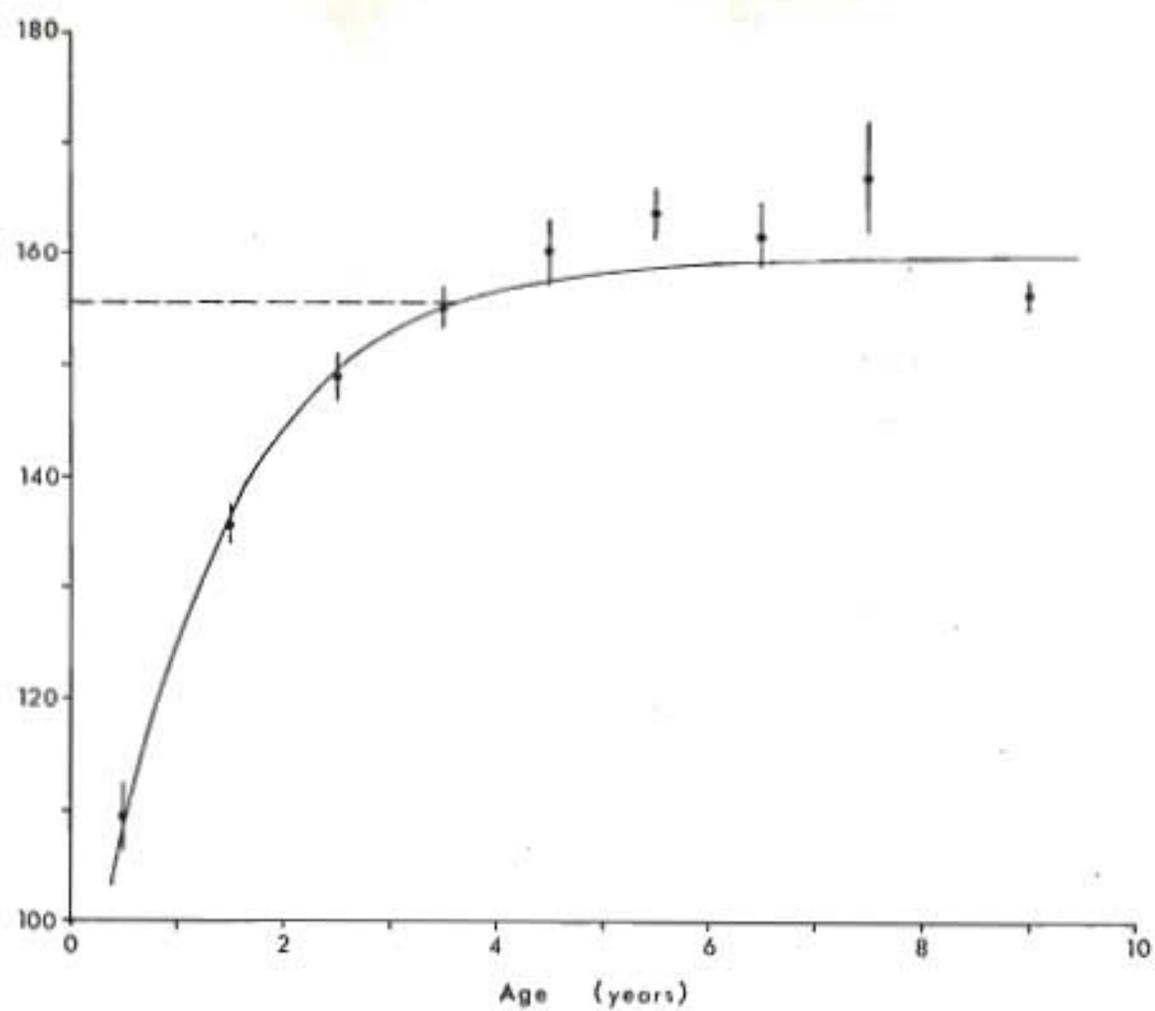


Fig. 4.7. : Theoretical Von Bertalanffy growth curve for male heart girth, with mean values at age. Standard error denoted by vertical line; dashed line lies within 2,5% of asymptote.

Fig. 4.8. : Theoretical Von Bertalanffy growth in female heart girth curve with mean girth at age. Standard error denoted by vertical line; dashed line lies within 2,5% of asymptote



e) Growth in ear length with age.

Von Bertalanffy equations for growth in ear length are given by:

$$\sigma L_t = 20,82 (1 - e^{-0,50 (t + 2,83)}) \quad \text{cm}$$

$$\text{♀ } L_t = 19,04 (1 - e^{-1,36 (t + 1,06)}) \quad \text{cm}$$

The respective growth curves with asymptotes in dotted lines are shown in Figs. 4.9. and 4.10.. By 4,5 years, the male asymptote is reached, compared to about two years in the female.

f) Growth in horn spread with age.

Theoretical equations for horn spread growth are:

$$\sigma S_t = 68,0 (1 - e^{-1,09 (t - 0,23)}) \quad \text{cm}$$

$$\text{♀ } S_t = 51,2 (1 - e^{-2,01 (t - 0,45)}) \quad \text{cm}$$

By referring to Figs. 4.11. and 4.12., it can be seen that the male asymptote (68cm) is reached by 3,5 years, and the female asymptote (51cm) by 2,5 years.

g) Growth in horn basal circumference with age.

Theoretical equations for the basal circumference growth pattern are:

$$\sigma C_t = 35,40 (1 - e^{-0,77 (t + 0,14)}) \quad \text{cm}$$

$$\text{♀ } C_t = 24,45 (1 - e^{-1,57 (t - 0,003)}) \quad \text{cm}$$

Figs. 4.13. and 4.14. display the respective growth curves, providing asymptotic value attainment at 4,5 years in males, and 2,5 years in females.

h) Change in distance between tips with age.

These data were considered unsuitable for the von Bertalanffy equation, as animals below two years of age show a decrease in the tip to tip measurement, resulting from the inward growth

Fig. 4.9. : Theoretical Von Bertalanffy growth in ear length curve for males, together with mean length at age. Standard error denoted by vertical line; dashed line within 2,5% of asymptote.

Fig. 4.10. : Theoretical Von Bertalanffy growth in ear length curve for females, together with mean length at age. Vertical line represents one standard error; dashed line lies within 2,5% of asymptote.

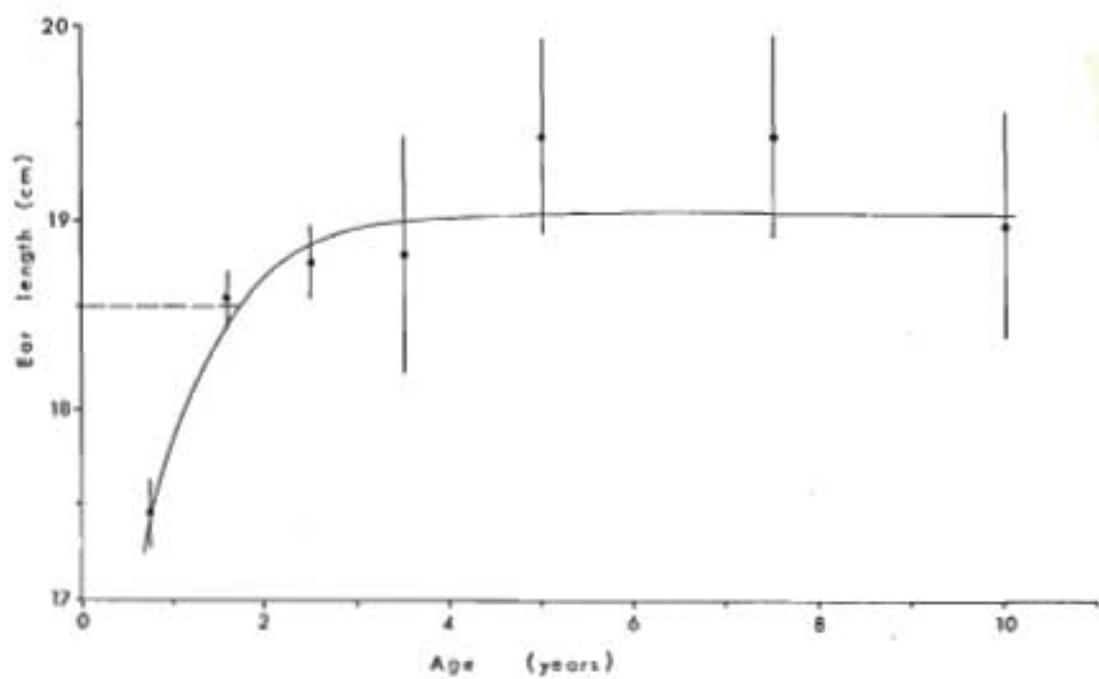
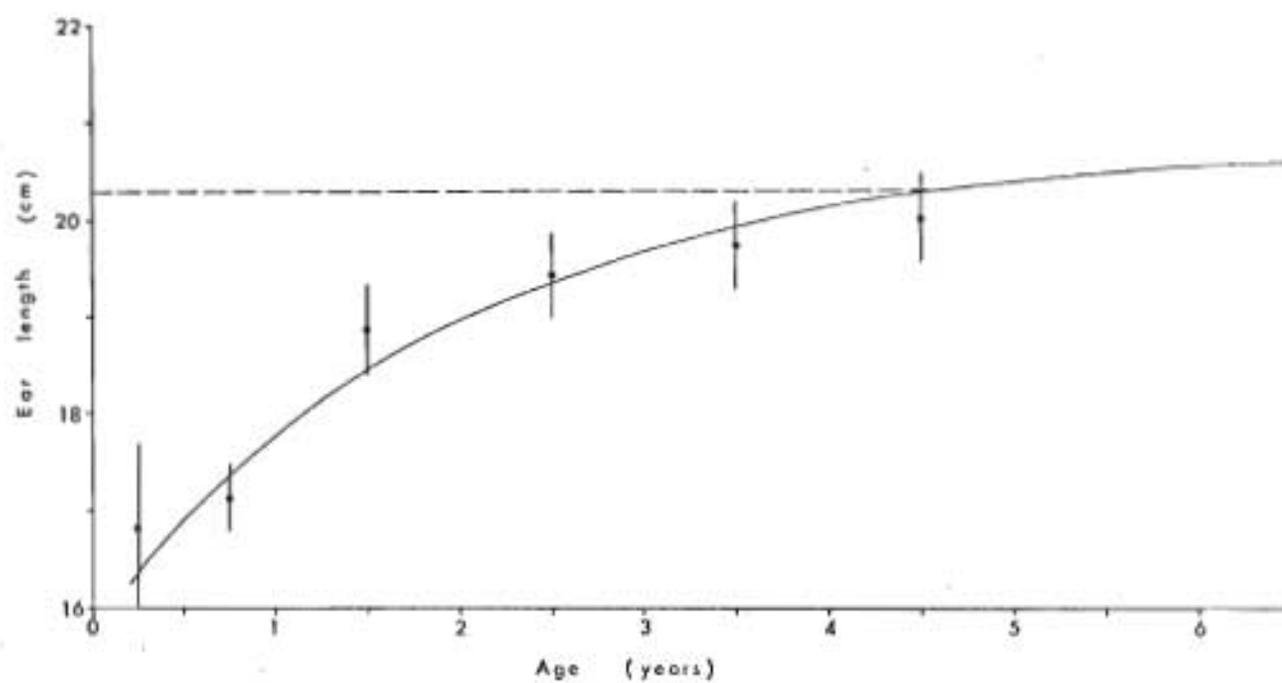


Fig. 4.11. : Theoretical Von Bertalanffy growth curve for male horn spread, together with mean spread at age. Standard error denoted by vertical line; dashed line lies within 2,5% of asymptote.

Fig. 4.12. : Theoretical Von Bertalanffy growth in female horn spread, together with mean spread at age. Standard error denoted by vertical line; dashed line lies within 2,5% of asymptote.

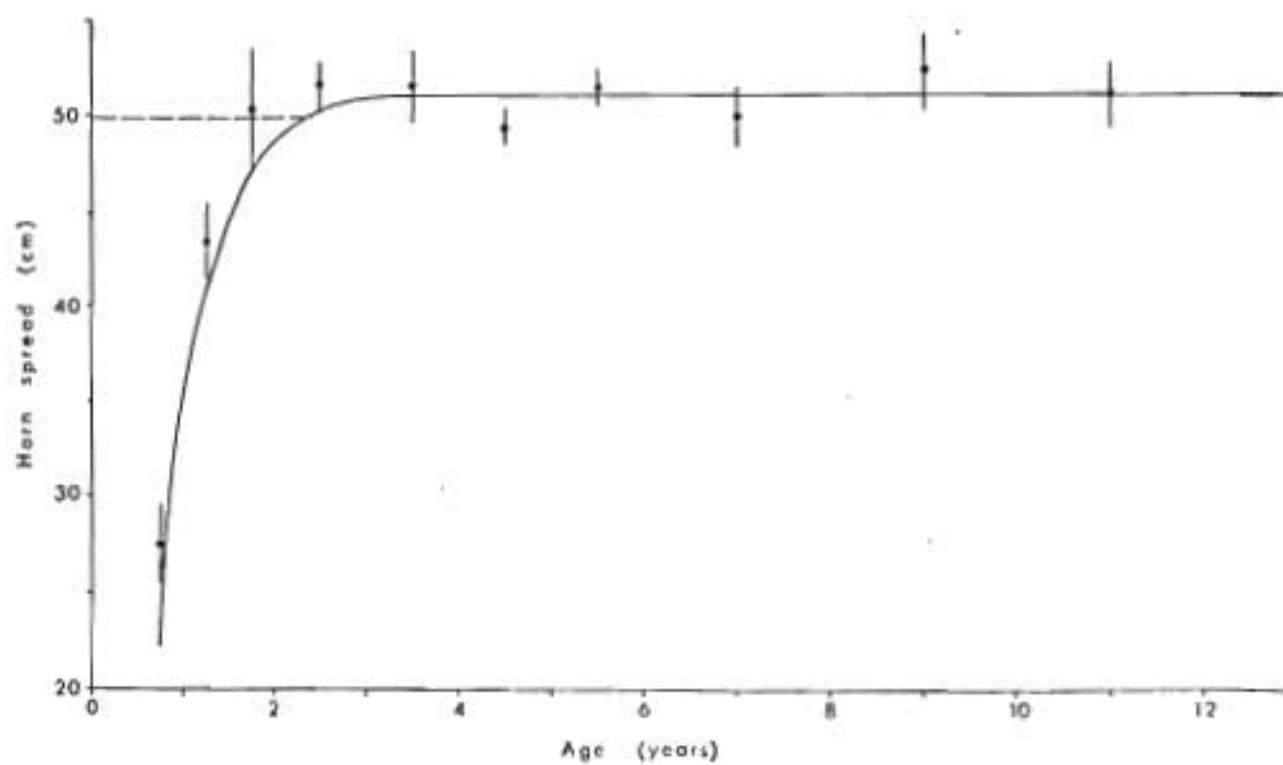
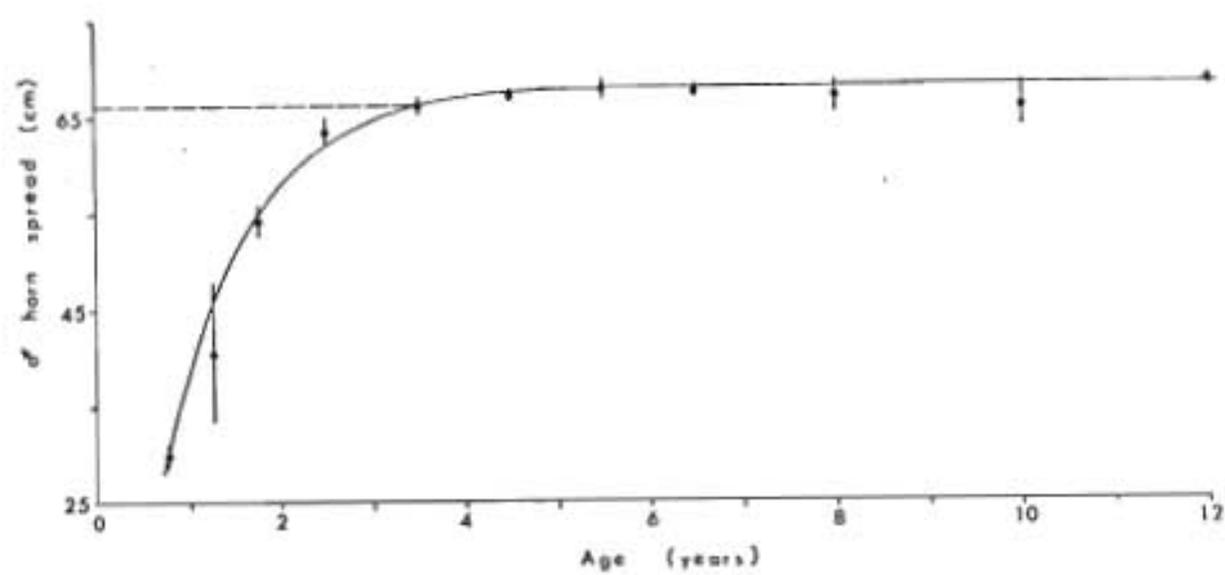
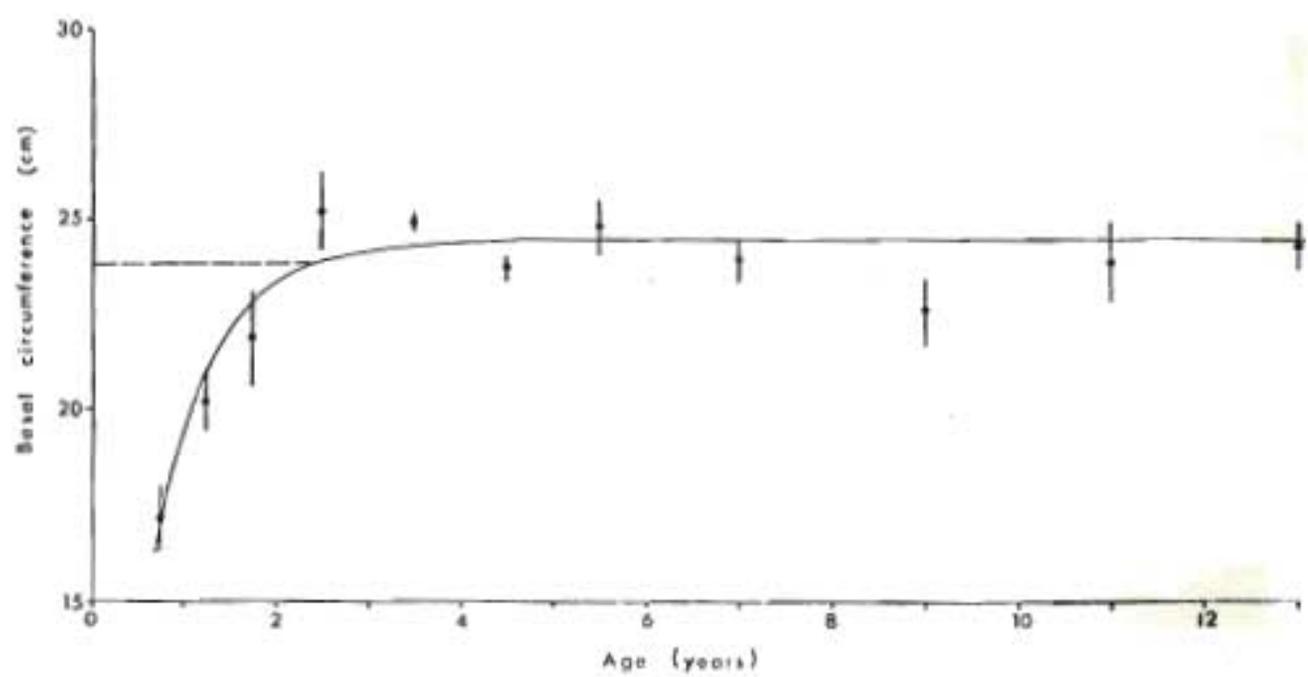
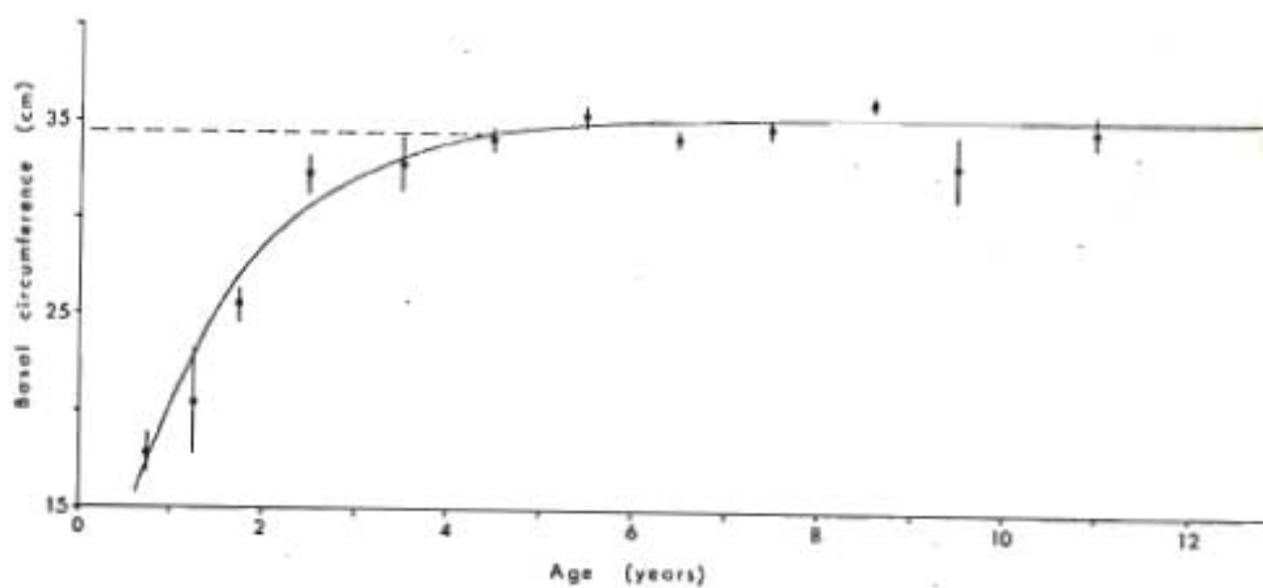


Fig. 4.13. : Theoretical Von Bertalanffy growth in male horn basal circumference curve, together with mean circumference at age. Vertical lines represent one standard error; dashed line lies within 2,5% of asymptote.

Fig. 4.14. : Theoretical Von Bertalanffy growth in female horn basal circumference curve, together with mean circumference at age. Standard error denoted by vertical line; dashed line lies within 2,5% of asymptote.



of calf "spike" horn tips as they tend towards the elliptical adult shape. This parameter thus tends to reflect change in horn conformation rather than true organic growth. For this reason, only raw data are presented (Table 4.2.).

i) Change in horn outer curvature with age.

As older males tend to blunt the tips of the horns through rubbing, thus lessening the outer curvature measurement with increasing age, this parameter was also unsuitable for inclusion in the von Bertalanffy equation. The raw data are shown in Table 4.3.. Male wear in tips exceeds growth at about six years, which corresponds almost exactly to the situation in impala (Spinage, 1971).

In any discussion on the use of growth curves, one is confronted by the limitations of the particular method adopted. Hanks (1972) states that an ideal function gives a good fit to the data, and is of use in analytical studies of growth phenomena. These requirements are met by the von Bertalanffy function, but it is of value to quote Needham's (1964) conclusion on the fitting of algebraic functions:

"..... measurements are rarely sufficiently precise to distinguish between the possible alternative relations which could be fitted to them and that in any event the gross curve probably represents the summation of many contributory processes and only by chance approximates to some simple relation also with a single biological meaning".

A summary of the differences in ages between sexes in their attainment of the various asymptotic values is provided in Table 4.4.. Data from other localities shown in the Table are not strictly comparable; only in the case of Braack's (1973) value for male body mass asymptotic age was the value computed from a von Bertalanffy equation

TABLE 4.2. : Mean values of distance between horn tips corresponding to mean ages, with standard errors.

F E M A L E S			M A L E S		
MEAN AGE (YRS)	MEAN VALUE (CM)	STANDARD ERROR	MEAN AGE (YRS)	MEAN VALUE (CM)	STANDARD ERROR
1,75	21,75	2,94	0,75	29,67	1,04
2,5	26,91	2,05	2,5	33,63	1,57
3,5	26,00	2,51	3,5	35,28	0,93
4,5	24,95	1,17	4,5	37,78	0,89
5,5	25,81	1,71	5,5	39,42	0,94
7,0	27,55	1,59	6,5	41,15	1,58
9,0	27,42	2,02	7,5	42,25	2,77
11,0	26,33	1,30	8,5	44,57	3,59
13,0	26,70	1,45	10,0	45,10	1,71
			12,0	46,29	1,42

TABLE 4.3. : Mean values of horn outer curvature for male and female wildebeest, with corresponding mean ages and standard errors.

F E M A L E S			M A L E S		
MEAN AGE (YEARS)	MEAN OUTER CURVATURE (CM)	S.E.M.	MEAN AGE (YEARS)	MEAN OUTER CURVATURE (CM)	S.E.M.
0,75	22,50	1,52	0,75	21,78	1,41
1,25	36,75	1,13	1,25	27,25	11,25
1,75	42,63	4,13	1,75	43,56	5,02
2,5	41,93	1,00	2,5	53,81	0,92
3,5	40,39	1,44	3,5	52,38	1,01
4,5	39,06	0,94	4,5	52,52	0,63
5,5	40,71	0,87	5,5	53,16	0,91
7,0	38,88	1,10	6,5	50,94	0,02
9,0	40,90	2,09	8,0	48,14	1,25
11,0	39,75	1,91	10,5	46,13	1,00
12,5	41,50	1,04			
13,5	41,00	0,70			

**TABLE 4.4.** : Comparison of ages at which males and females attain asymptotic values of specific parameters. (See text for comments on ages of animals from Kruger National Park and East Africa.) The age at which a particular asymptote is attained is taken when the parameter is within 2,5% of the asymptote.

Parameter	Age at which asymptote is attained in Zululand (Yrs)		Kruger National Park (Braack, 1973)	East Africa (Talbot & Talbot, 1963)	
	♂	♀	♀ + ♂	♂	♀
Body Mass	6	3	6	3,3	-
Shoulder Height	3,5	4,5	6	-	-
Hindfoot Length	2	1	-	4	3
Chest Girth	3,5	3	6	-	-
Ear Length	4,5	2	2	-	-
Horn Spread	3,5	2,5	-	3	3
Basal circumference(horns)	4,5	2,5	-	3	3

and curve. Other values for ages were estimated by simple comparison of the mean values of specific parameters between different age classes. The results from this study indicate that, except in the case of shoulder height, males take far longer than females to attain asymptotic values for the parameters recorded.

#### 4.3.1.2.

##### SEX DIFFERENCES IN BODY MASS AND MEASUREMENTS

By taking data on measurement and mass from those animals older than the ages at which a particular asymptote was attained, Table 4.5. was constructed. t-tests between the means showed that there were highly significant differences for every parameter between the sexes ( $p < 0,001$  for all tests, except ear length and horn outer curvature, where  $p < 0,01$ ). Comparative figures for mean body mass from the same study area are 237,2 kg (males) and 190 kg (females). These results (Hitchins, 1968) are more accurate than mine owing to a larger sample size ( $\sigma^{\text{m}} = 98$ ;  $\text{f} = 95$ ).

The Table also includes maximum and minimum values for the various parameters. Braack (1973) also recorded similar values from the Kruger National Park, and comparison of his maximum values with those from the complex are made in Table 4.6.. Braack's sample size was larger than mine, particularly with respect to body mass data of females. Thus it is more meaningful to compare Braack's maximum mass data with those of Hitchins (1968) for Zululand. Hitchin's maximum male figure is virtually identical with mine (294,5 kg), but his female maximum value is 252,1 kg, which is far more realistic. Maximum mass values for Zululand and Kruger Park (Transvaal) are then very similar. The other measurements show little difference, except in the case of shoulder height. The discrepancy arises because Braack's measurements were not taken

TABLE 4.5. : Summary of morphometric data for comparison between sexes. Data are derived from animals older than ages at which theoretical von Bertalanffy values are attained. Body mass in kg; all other measurements in cm.

	Body Mass		Shoulder Ht.		Hindfoot		Chest girth		Ear Length		Horn Spread		Outer Curvature		Basal Circumference	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Maximum	295,4	215,9	156,5	141,0	57,0	52,5	177,0	160,5	22,5	21,0	75,5	59,0	65,0	46,0	37,0	27,5
Minimum	231,8	164,1	141,0	129,0	48,5	45,5	153,0	139,5	19,0	17,4	60,0	42,5	42,0	33,0	30,0	20,5
Mean	249,8	182,7	147,2	135,3	52,8	50,2	161,4	148,5	20,5	19,3	67,5	51,4	51,2	39,4	34,6	24,04
Asymptote	252,9	187,4	145,6	136,1	52,7	50,3	159,7	147,2	20,8	19,03	68,0	51,2	-	-	35,4	24,4
Difference between means	67,1		11,95		2,56		12,6		1,24		16,05		11,78		10,6	
Sample size	14	11	17	17	50	49	17	17	10	13	60	58	100	50	37	52
t value	6,57**		8,84**		8,06**		5,61**		2,83*		22,43**		14,21*		28,08**	

\*  $p < 0,01$

\*\*  $p < 0,001$

TABLE 4.6. : Comparison of maximum morphometric values between Zululand and Kruger National Park wildebeest populations, geographically separated but belonging to the same sub-species.

	BODY MASS		SHOULDER HT.		CHEST GIRTH		EAR LENGTH		HORNS : TIP TO TIP		HORN SPREAD		HORNS : OUTER CURVATURE		HORNS : BASAL CIRCUM.	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
ZULULAND	295,4	215,9	156,5	141,0	177,0	160,5	22,5	21,0	52,5	36,5	75,5	59,0	65,0	46,0	37,0	27,5
KRUGER PARK	307,5	254,9	142,2	132,1	170,2	160,7	22,2	21,6	51,4	41,9	75,6	61,0	62,2	50,2	38,1	28,6

"over the curves". The high maximum value of 177 cm for male Zululand shoulder height should be viewed with caution, as the animal in question was extremely bloated when the measurement was taken, although bloating should not affect the anterior thoracic region unduly. Thus, if we take maximal values as a basis for comparison, there is little difference between the two populations of the same subspecies in different areas. A more valid comparison is presented by Table 4.7..

#### 4.3.1.3.

##### SUBSPECIES COMPARISONS OF MORPHOMETRIC DATA

A summary of mean values for body mass and measurements from different subspecies is presented in Table 4.7.. The mean values provided by Braack (1973) were for mass, shoulder height, chest girth, horns tip-to-tip, and horn spread. The remaining Kruger Park mean values were determined from his data, by averaging the mean values for adult age classes, which he tabulated. Hence these values only approximate to the true means, which could only have been obtained from his raw data. Apart from body mass, all my values are based on animals older than the age at which a particular asymptote is attained. For this reason they are greater than those values which would have been obtained by considering all adults (based on dentition), because in many cases asymptotes are attained long after adult dentition. The values from all other authors in Table 4.7. are based on "adults".

The absence of raw data on which the means are based prohibits statistical treatment of differences between the different populations. Despite this, differences in mean body mass are considerable and probably significant when comparing C.t. taurinus with the East African subspecies. Using the data of Sachs (1967) for C.t. albojubatus, the Zululand mean male body mass exceeds that of

TABLE 4.7. : Comparison between subspecies of mean values for adult body mass and measurements. Zululand body mass data from Hitchins (1968). Body mass in kg; all other units are in cm. Note that Broeck's shoulder height is not comparable, owing to the method of measurement. Body mass for females given by Ledger (1964) are exclusive of conceptus. I have adopted Ansell's (1971) nomenclature for the Serengeti subspecies, as opposed to that used by Talbot and Talbot (1963), which was *C.t. hecki*.

	NATAL ZULULAND <i>C.t. taurinus</i> (This study)				TRANSVAAL KRUGER NATIONAL PARK <i>C.t. taurinus</i> (Broeck, 1973)				TANZANIA GRUMETI <i>C.t. albojubatus</i> (Sachs, 1967)				TANZANIA/KENYA SERENGETI-MARA <i>C.t. nearnsi</i> (Talbot & Talbot, 1963)				ZAMBIA LUANGWA VALLEY <i>C.t. cooksoni</i> (Wilson, 1968)				KENYA S. KENYA <i>C.t. albojubatus</i> (Ledger, 1964)			
	n	♂	n	♀	n	♂	n	♀	n	♂	n	♀	n	♂	n	♀	n	♂	n	♀	n	♂	n	♀
BODY MASS	98	237,2	95	190,4	97	251,7	106	214,8	40	201,1	11	163,0	40	210	43	164,9	2	238,4	2	221,1	10	243,3	10	192,4
HINDFOOT	50	52,8	49	50,2	-	-	-	-	40	50,1	11	48,9	?	52	?	48	-	-	-	-	-	-	-	-
SHOULDER HT.	17	147,2	17	135,3	97	129,9	99	121,6	40	135,9	11	128,0	?	144	?	131	-	-	-	-	-	-	-	-
CHEST GIRTH	17	161,4	17	148,5	95	156,4	98	146,9	40	144,7	11	136,1	?	155	?	135	-	-	-	-	-	-	-	-
EAR LENGTH	10	20,5	13	19,3	96	19,9	94	19,5	40	20,2	11	19,5	-	-	-	-	-	-	-	-	-	-	-	-
TIP TO TIP	92	38,6	63	26,4	101	39,8	97	29,1	40	37,6	11	25,9	-	-	-	-	-	-	-	-	-	-	-	-
SPREAD	60	67,5	58	51,4	100	67,3	97	53,8	40	56,0	11	45,3	-	-	-	-	-	-	-	-	-	-	-	-
OUTER CURVE.	100	51,2	50	39,4	96	46,6	99	37,0	-	-	-	-	?	57	-	-	-	-	-	-	-	-	-	-
BASAL CIRCUM.	37	34,6	52	24,0	106	37,1	106	27,4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

HORNS

C.t. albojubatus by 15%, and the mean female figure is in excess by 14,4%. Similar values result when comparing mean body mass of C.t. taurinus with C.t. mearnsi. If one uses Braack's data for C.t. taurinus, the percentages by which mean body mass exceeds that of the East African subspecies are even greater. The differences are caused by a combination of factors, of which genetic and nutritional aspects probably dominate. Migrational phenomena may also influence loss in body mass of the East African subspecies. Bergmann's Rule must also be taken into consideration. Similar results have been reported by Smuts (1974), who found mean male body mass from Kruger Park zebra (Equus burchelli antiquorum) to exceed the mean Tanzanian figure for E.b. böhmi by 22%. The corresponding percentages for excess in female mean body mass was 32%.

Subjectively, body measurements between the C.t. taurinus populations in Zululand and Kruger National Park appear much the same (shoulder height incomparable owing to different methods of measurements). In contrast, body mass differences may be more real (i.e. significant). Kruger Park male mean body mass exceeds that from Zululand by 5,7%, and female mean body mass is also in excess, by 11,3%. Clearly, these differences, assuming they are significant, are related to environmental and nutritional factors. A further consideration may relate to differences in social interactions between the two populations. Klein and Strandgaard (1972) investigated differences in body size of roe deer (Capreolus capreolus) in different study areas of equal forage quality but differing in soil quality. Soil quality did not appear to regulate body size, but appeared instead to determine population density. These authors considered that differences in body size were related to population density. Social pressures were increased with a rise in density, resulting in greater energy expenditure and decreased food intake. It is suggested that the same phenomena might apply to the apparent

differences in body size between the Complex and Kruger Park populations. In 1974, I calculated that the density or stocking rate for wildebeest in Umfolozi, measured by the number of hectare available per animal, was 35,7. This is approximately half the value given by Braack (1973) for the Central District of the Kruger National Park, which was 69 hectare/wildebeest. Relative to the Kruger Park, the Complex is an extremely small area, which might aggravate competition (and hence increase social interaction) for preferred habitat.

#### 4.3.1.4.

#### BIOMASS CALCULATIONS BASED ON SEX AND AGE STRUCTURE RELATED TO BODY MASS

For the calculation of biomass values, the mean mass of an "average" wildebeest is required; consequently sex and age structure must be taken into account. The population structure shown in Table 4.8. was that determined for the Complex in August 1974, by helicopter counts. Details of the methods of arriving at the relative percentages of the sex and age groups are given in Chapter 8. I have assumed equal sex ratios for yearlings and two to three year-olds, which is a source of error. The mean wildebeest mass of 174,05 kg will clearly vary with changes in population structure. This value may be taken as approaching the maximum, because the percentage calves in Table 4.8. is approaching a minimum value, following dry season mortality. A higher calf percentage earlier in the year would mean a lower mean mass figure.

The Complex mean value is lower than those computed in a similar manner for Kruger Park (181,4 kg : Pienaar, Van Wyk and Fairall, 1966; 189,4 kg : Young, Wagener and Bronkhorst, 1969; 200,4 kg : Braack, 1973). The differences between the Zululand and Kruger Park figures are a reflection of possible mass differences, but certainly of variation in population structure. The value of

TABLE 4.8. : Calculation of mean wildebeest mass using relative age and sex composition with corresponding mean values of body mass.

Age Class	Number of animals ( $n_t$ )	Mean Body Mass (kg) per animal ( $m_t$ )	Total Averaged Mass of each age class (kg) ( $n_t m_t$ )
Adult ♂♂	158	237,2	37477,6
2 - 3 yr ♂♂	54	198,1	10697,4
Adult ♀♀	254	190,4	48361,6
2 - 3 yr ♀♀	54	184,9	9984,6
Yearling ♂♂	78	148,9	11614,2
Yearling ♀♀	78	146,0	11388,0
Calves (♂ + ♀)	122	76,8	9369,6
	$\Sigma n_t = 798$		$\Sigma n_t m_t = 138893,0$

$$\text{Mean wildebeest mass} = \frac{\Sigma n_t m_t}{\Sigma n_t} = 174,05\text{kg}$$

174,05 kg is used subsequently (Chapter 9) for the calculation of biomass.

#### 4.3.1.5.

#### COMMERCIAL EXPLOITATION RELATED TO AGE OF MAXIMUM INCREASE IN MASS

Table 4.9. compares liveweight gain for different age classes in Zululand. Data from Braack (1973) are included for comparison. Braack's mean mass at parturition (21,74 kg) was used as the "zero age" value. Gain in body mass was then derived from the von Bertalanffy growth curves (Figs. 4.1. and 4.2.). Productivity is highest during the first year of life, after which it tapers off rapidly, particularly in females. Female body mass gain during the first year is greater than males in both populations, but in subsequent years the male increase in mass exceeds that of females for the Zululand population. Talbot and Talbot (1963) found that for C.t. mearnsi, males and females gained mass at the same rate for the first eighteen months; thereafter male mass gain exceeded females. In terms of meat production the optimal age at which to harvest wildebeest would be approximately one year. Commercial exploitation requires management aimed at maximum rate of increase, and concern must consequently be given to maintaining a specific sex and age structure. These aspects receive further consideration in Chapter 9.

#### 4.3.1.6.

#### FOETAL GROWTH

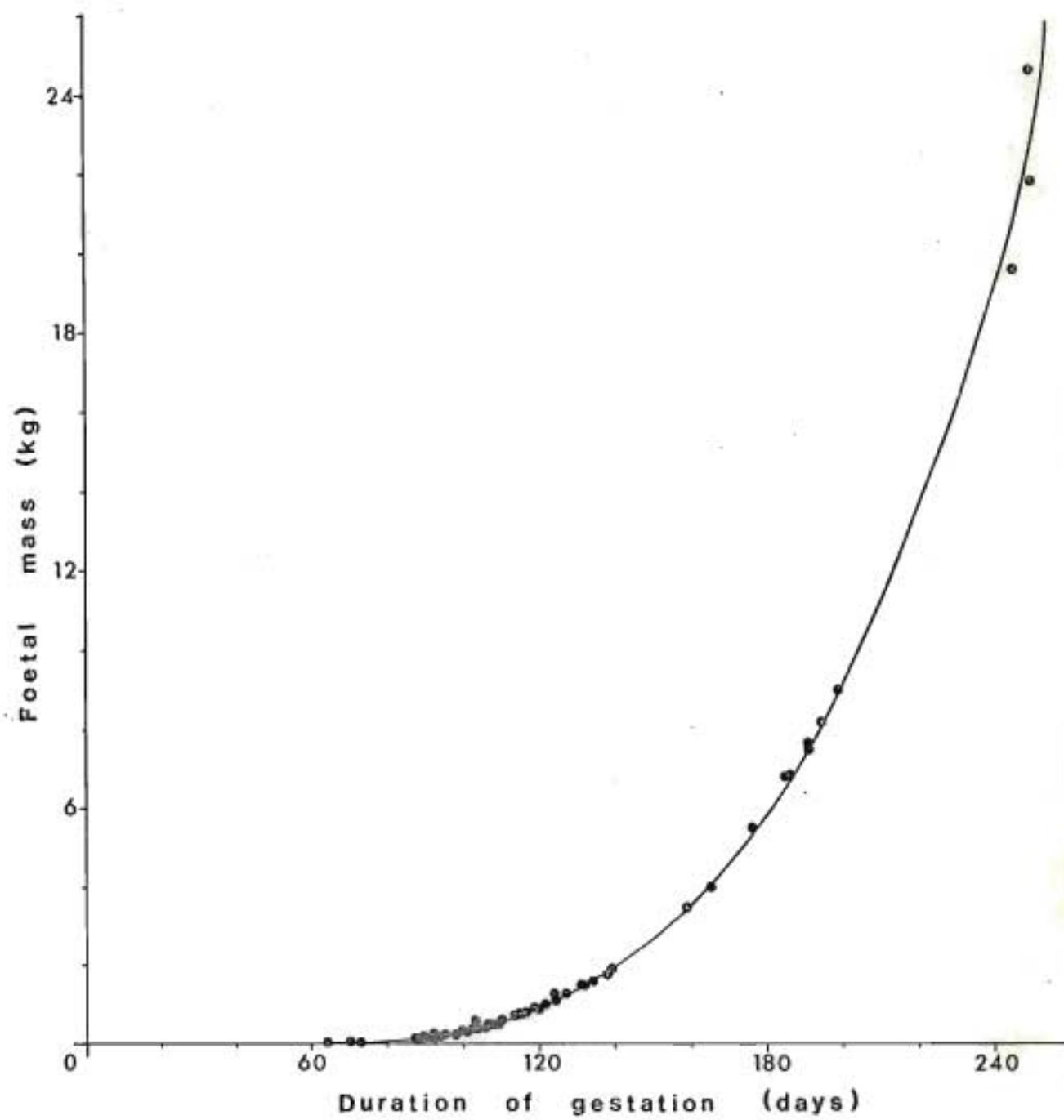
##### (a) Growth in mass

Fig. 4.15. shows the growth in foetal mass during pregnancy. The standard increasing exponential curvilinear relationship is apparent. The curve agrees with the findings by Stephensen (1962) in sheep, where after eighty to ninety days from conception the growth of the foetus changes to a constant pattern

TABLE 4.9. : Changes in increase in body mass gain with age for C.t. Taurus populations from Zululand and Kruger National Park.

Age Interval (Years)	Increase in body mass (kg)							
	ZULULAND (This study)				KRUGER NATIONAL PARK (Braack, 1973)			
	♂	gain/day	♀	gain/day	♂	gain/day	♀	gain/day
0 - 1	88,26	0,242	94,3	0,258	90,1	0,247	96,6	0,265
1 - 2	62,5	0,171	49,0	0,134	55,1	0,151	57,2	0,157
2 - 3	39,5	0,108	17,5	0,048	32,1	0,088	44,5	0,122

Fig. 4.15. : Foetal growth in mass. Both sexes are considered. Curve fitted by eye. My data are supplemented by additional mass data collected by Anderson in 1963 and by Vincent in 1967 (both personal communications) from the Complex.



which is maintained until birth, conforming to a cubic model. Smuts (1974) has listed some factors affecting foetal growth. Among these is the plane of nutrition during the second half of pregnancy.

(b) Growth in Crown-Rump and Head Length

Growth in these foetal measurements appear to be strictly linear (Figs. 4.16. and Fig. 4.17). The regression equations for the lines drawn are:

$$\text{Crown-Rump} : y = 0,4015x - 20,323 \quad (r = 0,9913)$$

$$\text{Head Length} : y = 0,1303x - 5,7580 \quad (r = 0,9880).$$

4.3.1.7.

PREDICTIVE RELATIONSHIPS BETWEEN CHEST GIRTH AND BODY MASS, AND DRESSED CARCASS MASS

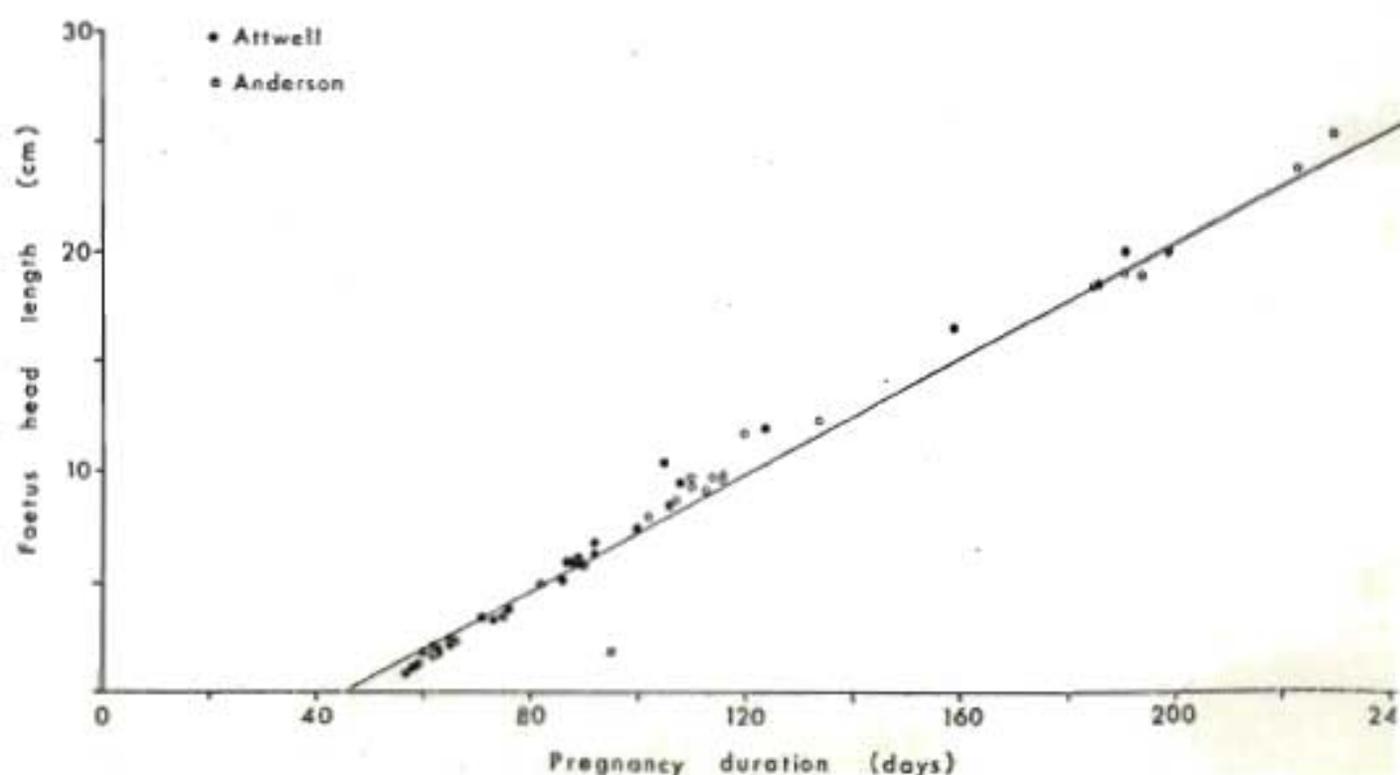
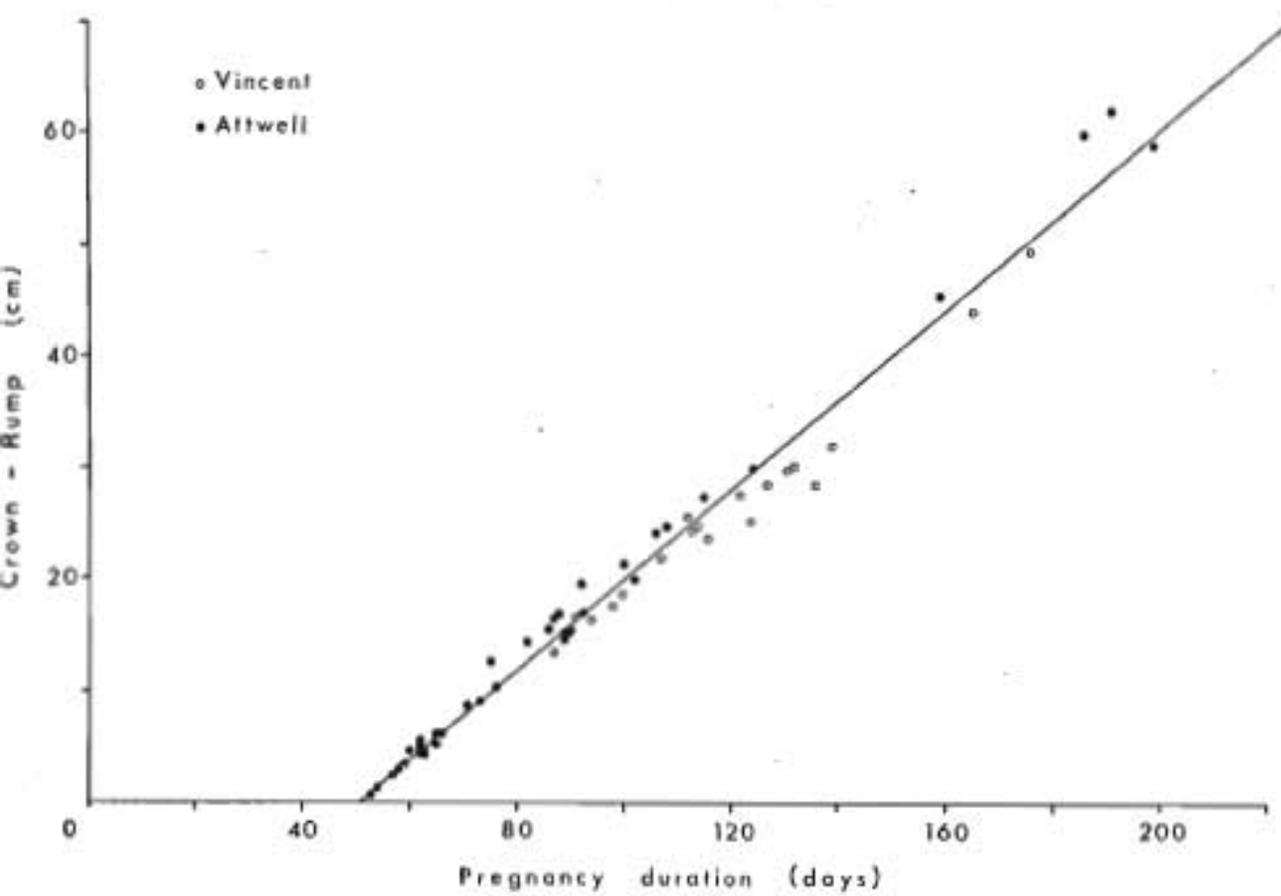
a) Chest girth and body mass

Predictive equations relating chest girth to body mass have been used by various workers (Bandy, Cowan, and Wood, 1956; McCulloch and Talbot, 1965; McEwan and Wood, 1966; Smart, Giles and Guynn, 1973; and Hanks et al, 1976).

McCulloch and Talbot (1965) have pointed out the necessity for deriving statistical relationships for specific populations, as opposed to using a relationship for the same species but from a different population. Thus, although such relationships have been calculated for wildebeest, it is necessary to include a further relationship which is specific to C.t. taurinus from Zululand. A simple plot of chest girth against body mass is given in Fig. 4.18.. The scatter appears to be curvilinear, but I consider predictive relationships to be adequately represented by two straight line regressions, and there appears to be no advantage in devising

Fig. 4.16. : Growth in foetal crown-rump length. Additional data collected from the Complex in 1967 by Vincent (pers. comm.). Regression equation in text.

Fig. 4.17. : Growth in foetal head length. Additional points from data collected from the Complex by Anderson in 1963 (pers. comm ). Regression equation in text.



more complicated mathematical equations which would be more difficult for field workers to apply (McCulloch and Talbot, 1965).

For calves the relationship is as follows:

$$M = 1,90 \text{ CG} - 118,76 \quad (r = 0,9998 ; p < 0,001) , \text{ where}$$

M = Mass

CG = Chest Girth.

For all animals older than calves, the relationship is:

$$M = 2,97 \text{ CG} - 242,24 \quad (r = 0,9133 ; p < 0,001)$$

Comparative equations for the same subspecies from Kruger National Park (Braack, 1973) are given for males:

$$\text{For all males: } M = 2,745 \text{ CG} - 182,49 \quad (r = 0,959)$$

For males with chest girth exceeding 120 cm:

$$M = 1,682 \text{ CG} - 84,05 \quad (r = 0,972)$$

Hanks et al. (1976) have illustrated the limitations of using girth measurement in condition assessments, as high values of girth measurements may be present in animals which have already mobilized substantial quantities of fat reserves.

#### b) Dressed Carcass Mass in relationship to Liveweight

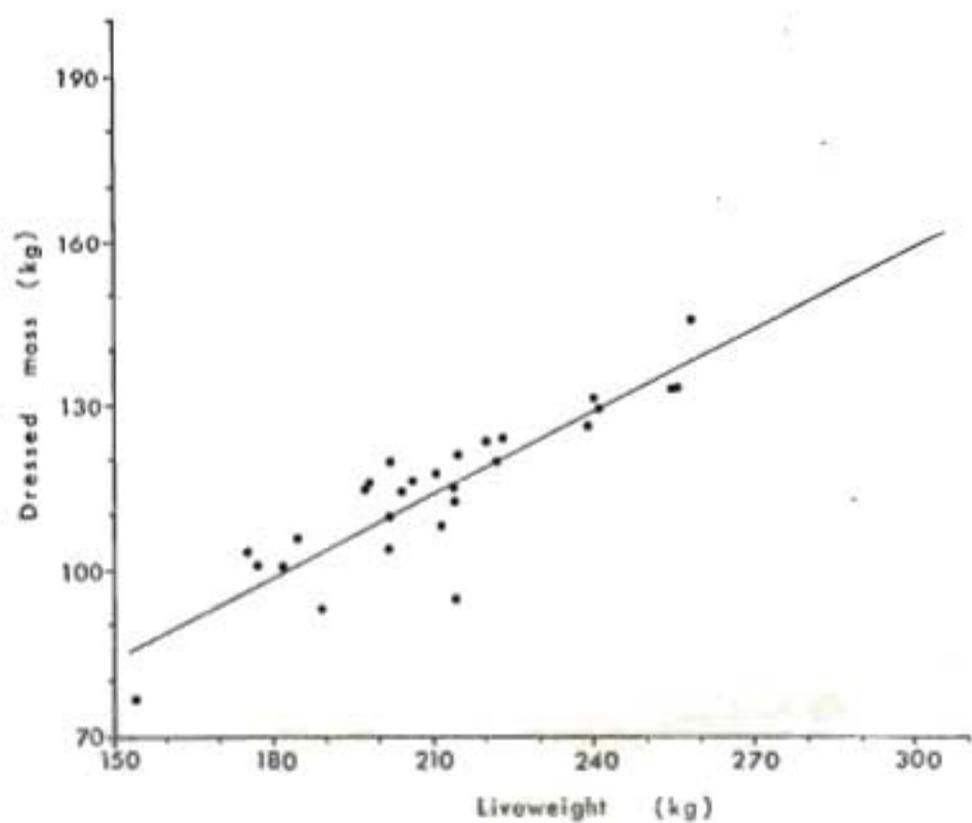
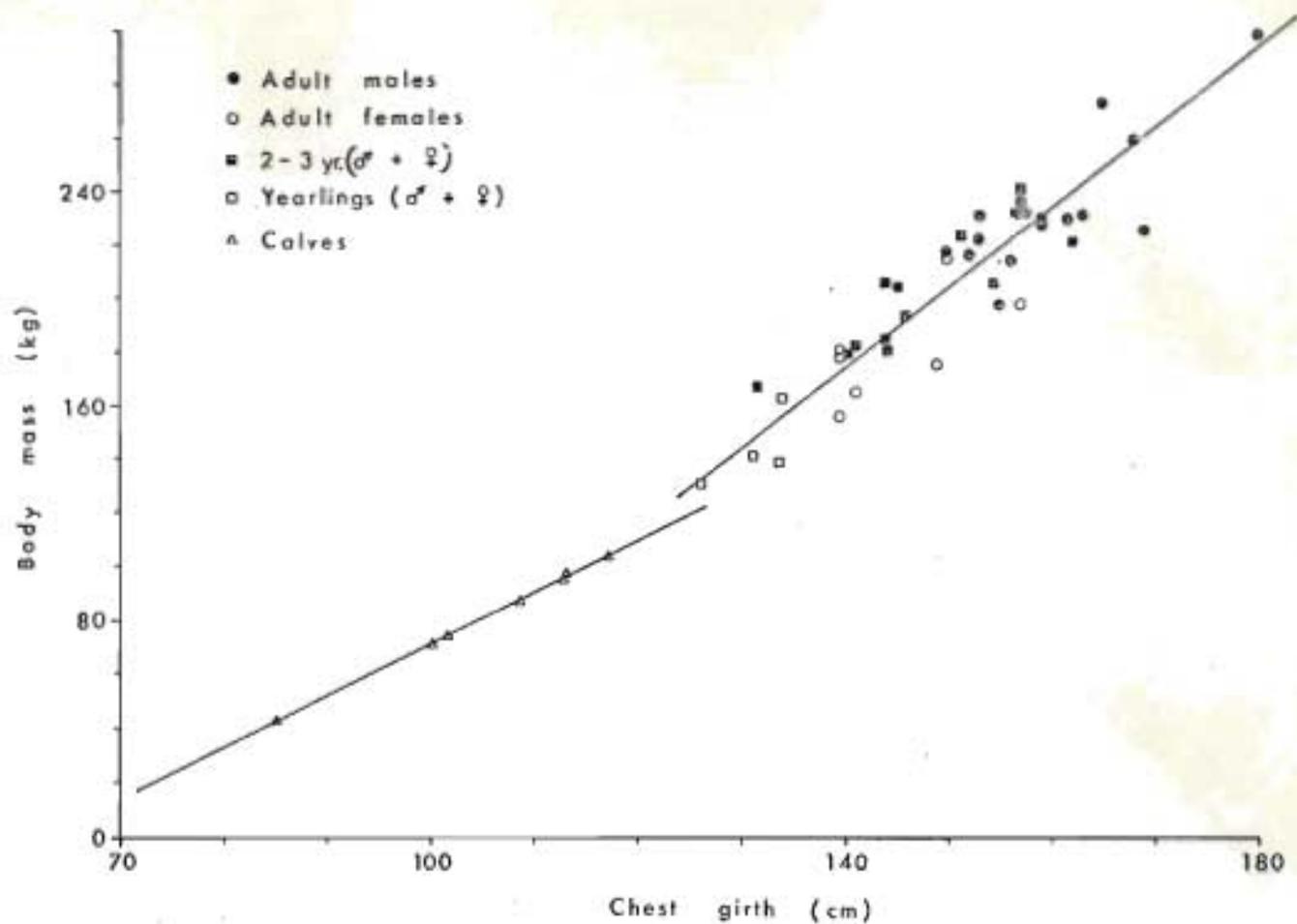
From 28 animals, the dressed mass as a percentage of liveweight was 54,79%. This result appears to be remarkably constant within the species. Hitchins (1966) recorded values of 56% for adult males (n = 33) and 55,7% (n = 22) for adult females from the Complex. The Kruger Park figure given by Young et al. (1969) was 57,7% for both sexes.

Fig. 4.19. provides a regression line for dressed mass against live mass, with an equation:

$$DM = 0,50 LM + 8,75 \quad (r = 0,88; p < 0,001).$$

Fig. 4.18. : Relationship between chest (heart) girth and body mass. Regression equations in text.

Fig. 4.19. : Relationship between dressed carcass mass and liveweight. Regression equation in text.



## 4.3.2.

CONDITION

## 4.3.2.1.

DEPOSITED FAT RESERVESa) THE KIDNEY FAT INDEX

For both sexes, a highly significant difference was found between KFI values of animals below three years of age and animals of three years and older ( $p < 0,001$ ). This is in accordance with the findings in impala (Hanks, Cumming, Orpen, Parry and Warren, 1976). Consequently, for the investigation of seasonal changes in KFI, animals below three years were discarded. Flook (1970) also states that differences in body size and therefore nutritional requirements may influence the levels of condition attained. The basal metabolism in calories/day of larger adults is greater than that of the smaller, younger age classes, although proportionately lower in terms of calories/kg body mass.

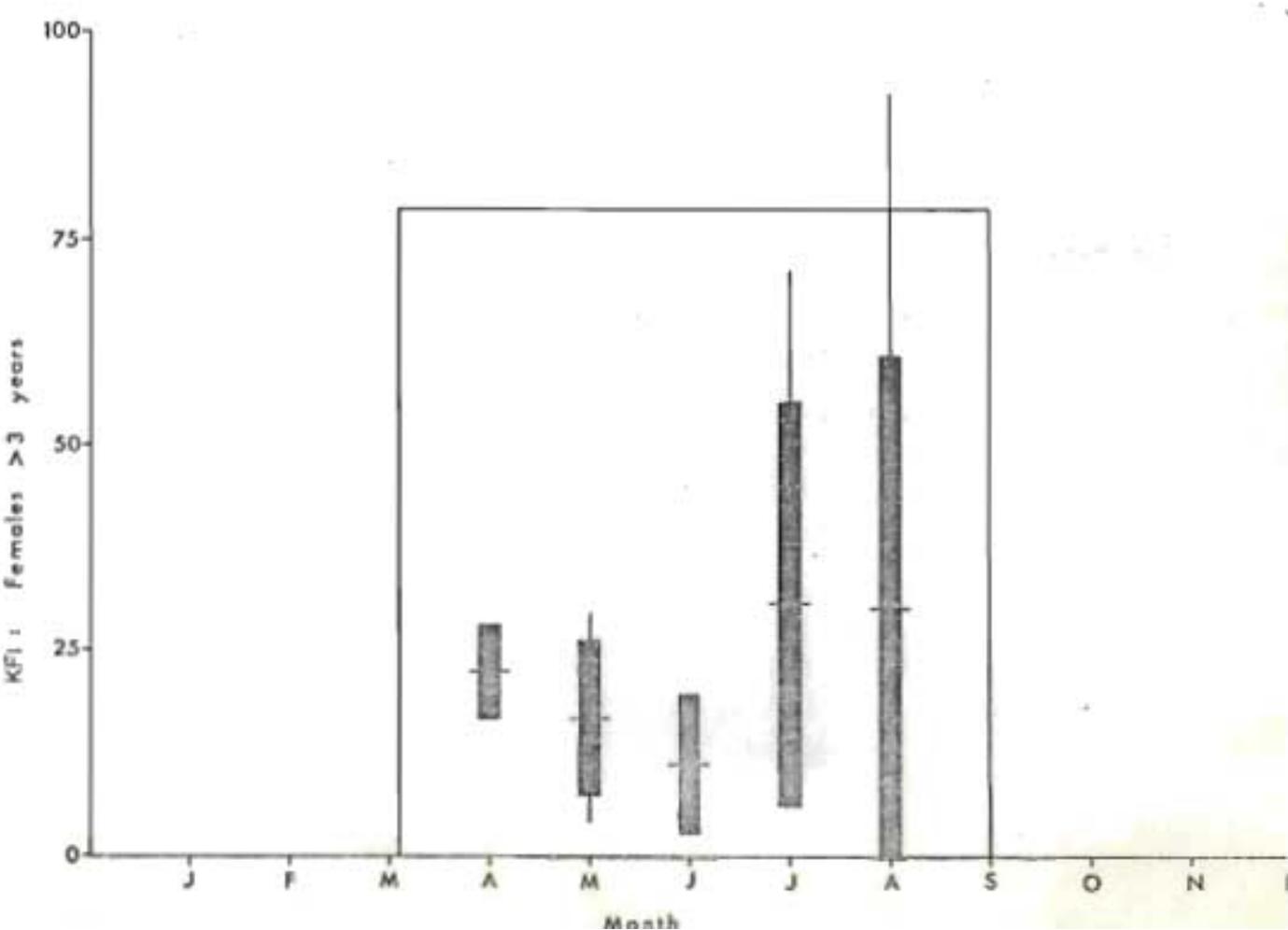
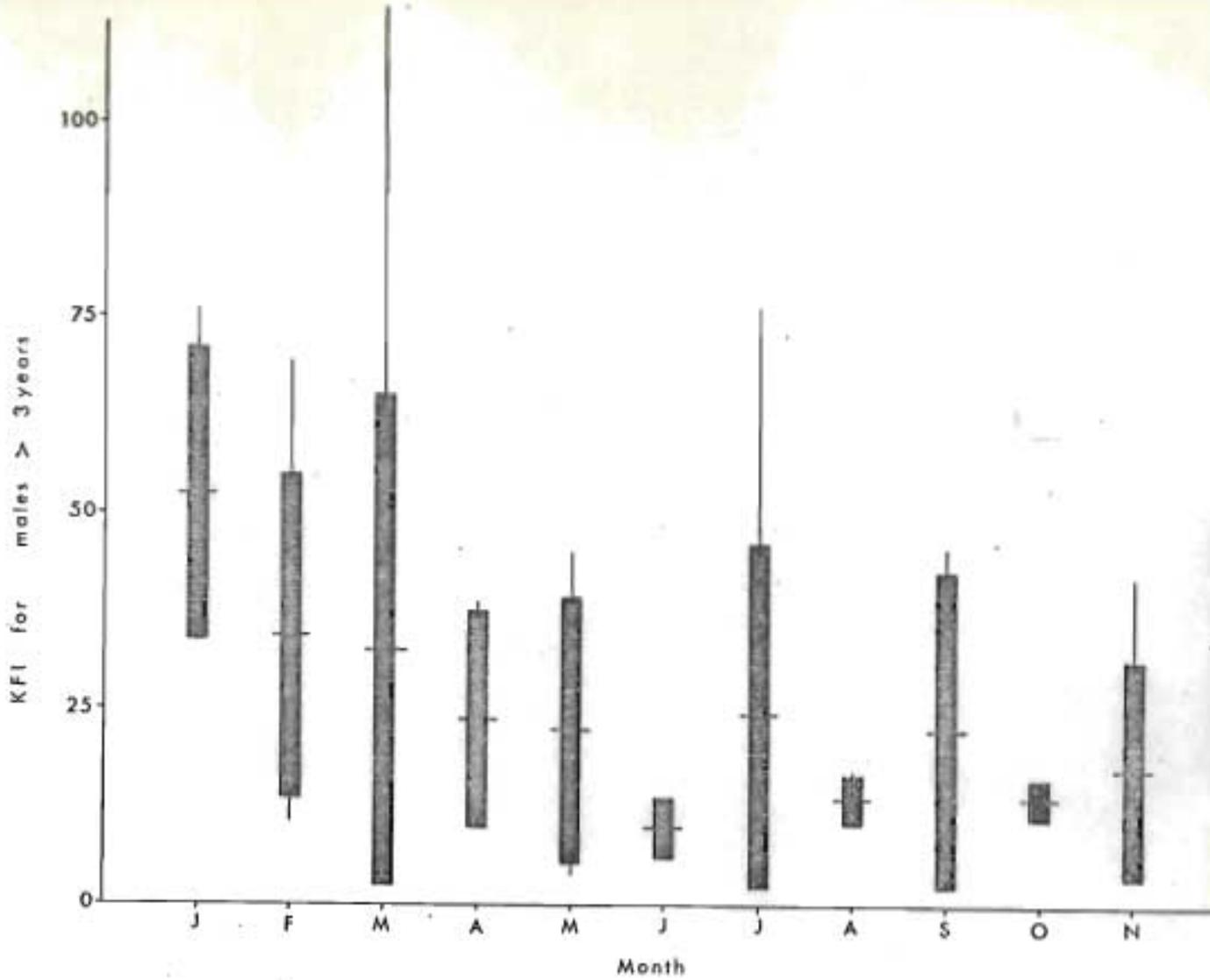
The KFI in wildebeest was found to range from 3,3 (2,5 year old ♂, shot in July) to 115,3 (4,5 year old ♂, shot in March). Smith (1970) reported a range of 6,7 to 127,3 for the same species in East Africa. As he found a correlation between KFI and total body fat at the 0,01 level of significance, he assumed that the wide range of KFI values indicated a wide range of total fat. Anderson, Medin and Bowden (1972) found the KFI variable for mule deer, as did Hesselton and Sauer (1973) for white-tailed deer.

Fig. 4.20. depicts the change in KFI values with season for males older than three years. There is no significant difference in comparison of wet season and dry season values, but the lowest mean KFI value (June) differs significantly from the

December and January values ( $p < 0,001$ ). Loss in condition is generally related to a change in quantity and quality of food, and to phases in the reproductive cycle. Forage grasses lose both palatability and nutrient content during the drier months. Palatability changes are related mainly to the fall in protein and carbohydrate content at the expense of an increase in cellulose. The results serve only to indicate broad seasonal differences, and parallel the findings of McCulloch and Talbot (1965) for East African ungulates, where animals appeared not to respond to changes in food or environmental factors by depositing or utilising significant quantities of body fat. The results certainly show no relationship to the pattern of seasonal KFI change in elephants described by Albl (1970), where KFI values decreased through the latter months of the dry season in a linear relationship, such that KFI values could be predicted should the rainy season be delayed. In general, males with fixed breeding seasons lose condition during the rut (Anderson, 1965; Flock, 1970; Skinner, 1970; Skinner and Huntley, 1971b; Bear, 1971; and Hanks et al., 1976). This is not apparent from Fig. 4.20, which appears more in line with the findings of Huntley (1971) on blesbok (Damaliscus dorcas) and kudu, where there was no evidence for condition being related to a sexual cycle. These two species do exhibit peaks in calving (and hence peaks in male reproductive activity), but in no way are these peaks as distinct and well-defined as in the wildebeest. Fig. 4.21. shows the dry season variation in KFI values for females older than three years. There was no significant change in condition as the dry season progressed. Assuming that kidney fat changes are normally related to reproductive events, the KFI was used to investigate changes in condition during pregnancy. A general improvement in the physical condition during pregnancy

Fig. 4.20. : Seasonal change in KFI values for ♂♂ older than three years. (Range denoted by vertical line, mean by crossbar, standard deviation by broad portion of line.)

Fig 4.21. : Dry season changes in KFI values for ♀♀ older than three years. (Range denoted by vertical line, mean by crossbar, standard deviation by broad portion of line.)



and loss of fat during lactation are common in most mammals (Albl, 1970). The seasonally biased female sample meant that significant amounts of data were confined to about the first half of pregnancy only. Pregnant animals were grouped according to their duration of pregnancy by using thirty-day intervals, up to 120 days. (Determination of duration of pregnancy is explained in Chapter 5.). No significant differences were found between the mean KFI values for any of the groups. Abrams (1968) maintains that the nutritive drain on female ungulates is greatest during the last one third of pregnancy. Anderson (pers. comm.) was however unable to find any obvious trend in KFI during any stage of pregnancy in nyala. Both his results and mine are subject to the errors inherent in the KFI method, which are discussed below.

Although Smith (1970) concludes that the KFI best fulfills the need for a workable method for condition estimation, the results must be interpreted with extreme caution. Firstly, variation may arise when perinephric fat is trimmed, as in this study. Monson, Stone, Weber and Spadaro (1974) compared KFI values derived from Riney's (1955) trimming method with those derived by using total perinephric fat. They found no significant correlation in adult deer, and further stated the inadvisability of using either index in a strictly quantitative manner, on account of the great individual variation in animals from the same range.

The second and more important source of variation results from the seasonal change in kidney mass. In the use of the KFI, most workers have assumed that changes in the index were related to fat changes and not fluctuations in kidney mass. Batcheler and Clarke (1970) however found that in red deer (Cervus elaphus) kidney mass was constant during summer, but

higher in early winter, declining to a minimum in late winter/early spring. As a result the KFI was distorted, tending to displace the measure of peak condition until later in the season. Dauphine' (1975) described a similar phenomenon in caribou (Rangifer tarandus): mature kidneys of adult males showed a seasonal fluctuation of 45% of the maximum (42% in females). These findings showed conclusively that kidney mass is an unsuitable correction for body size in an index intended to reflect seasonal changes in perinephric fat.

In Fig. 4.22, seasonal fluctuation in adult male kidney mass is presented. The dry season (April - September) values differ significantly from the wet season (October - March) values ( $p < 0,001$ ). The maximum mean value (November) is decreased by 47% (June), a fluctuation almost identical with that shown by caribou (Dauphine', ibid.). Loss in kidney mass may be related to inanition (Wood, Cowan and Daniel, 1965), or to adaptive and voluntary food intake restriction, signalling a decline in basal metabolism in a nutritionally poor winter environment (Batcheler and Clarke, 1970). Dauphine' (ibid.) suggests that heat stress or changes in body water kinetics may also play a role.

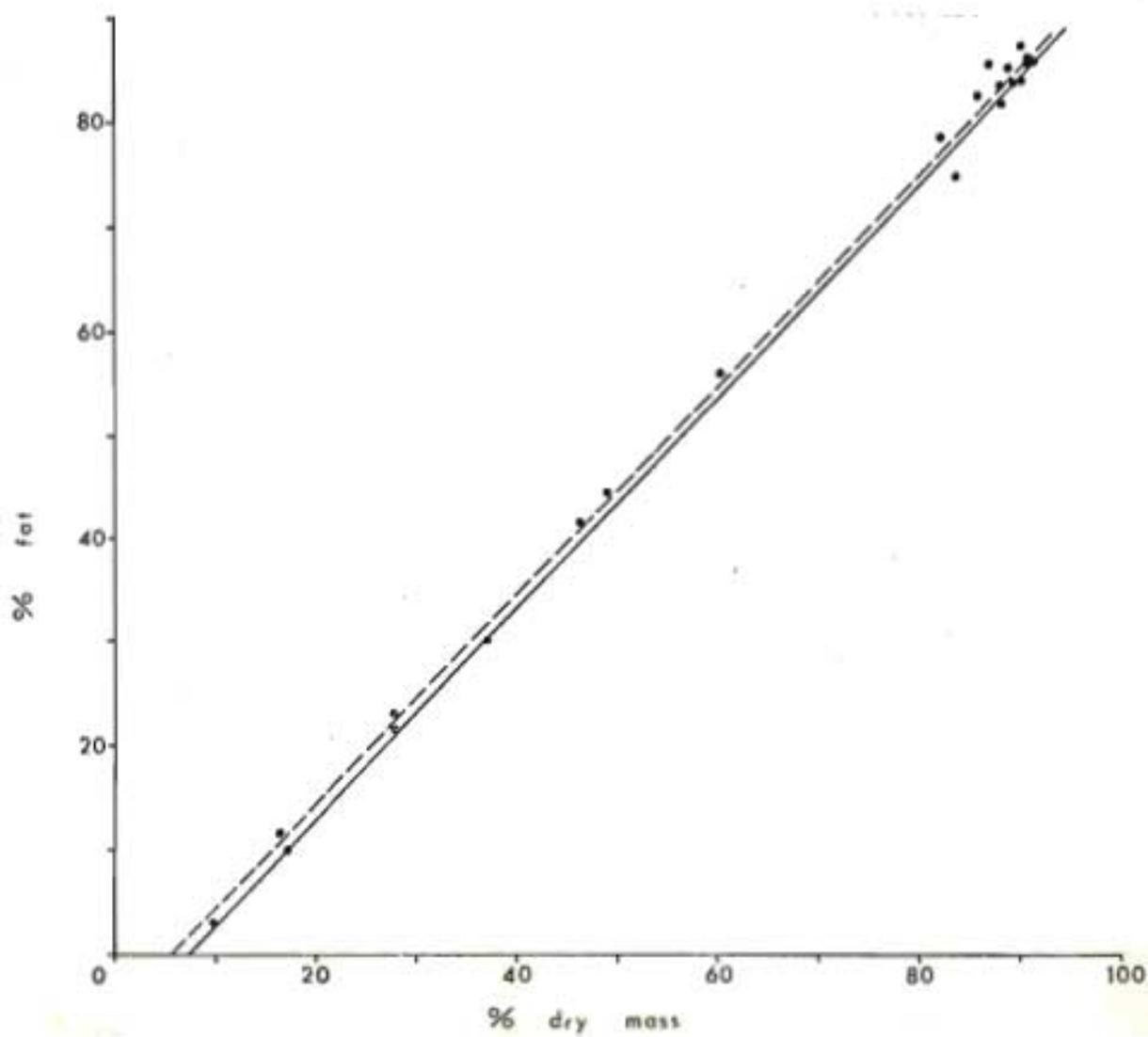
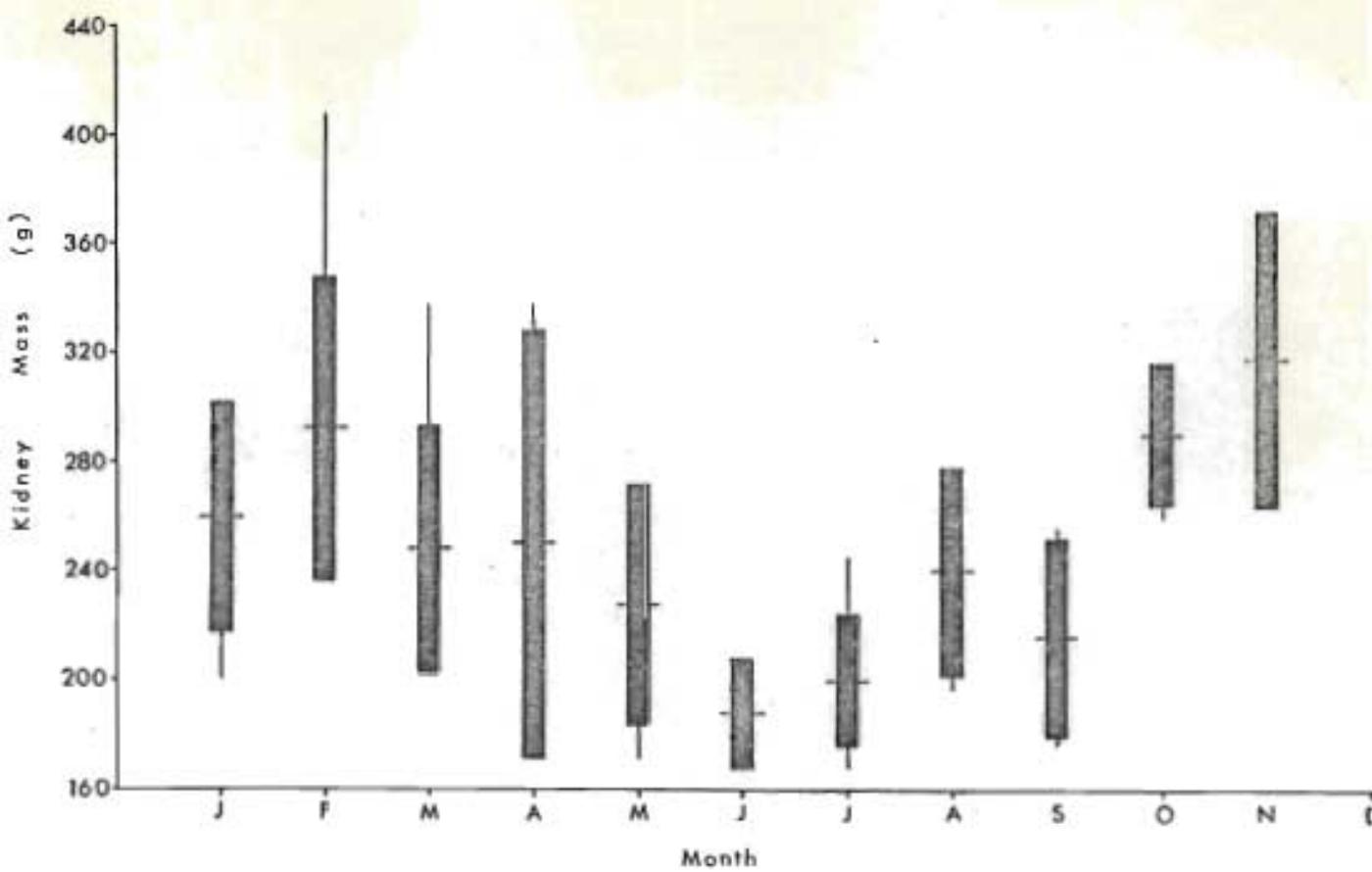
The conclusion from these results is that the KFI may only be of use in comparing populations at the same time.

#### b) PERCENTAGE FAT IN BONE MARROW

In Fig. 4.23, the percentage dry mass of fresh mass for bone marrows has been plotted against percentage fat content. The dotted line is a regression for the points shown (this study); the unbroken line is the regression for wildebeest from East Africa obtained by Sinclair and Duncan (1972).

Fig. 4.22. : Seasonal changes in kidney mass for adult male wildebeest. (Range denoted by vertical line, mean by crossbar, standard deviation by broad portion of line.)

Fig. 4.23. : Regressions of % dry mass of fresh mass (bone marrow) against fat content. Points relate to dashed line (this study); unbroken line is regression derived by Sinclair and Duncan (1972). Both regression equations in text.



The regression equations are:

$$\text{Sinclair and Duncan} : y = 1,0042x - 7,2829$$

$$\text{This study} : y = 1,0047x - 5,76 \quad (r = 0,998).$$

The results from this study are closely similar, and agree to the generalised relationship in most ungulates:

$$\% \text{ marrow fat} = \% \text{ dry weight} - 6$$

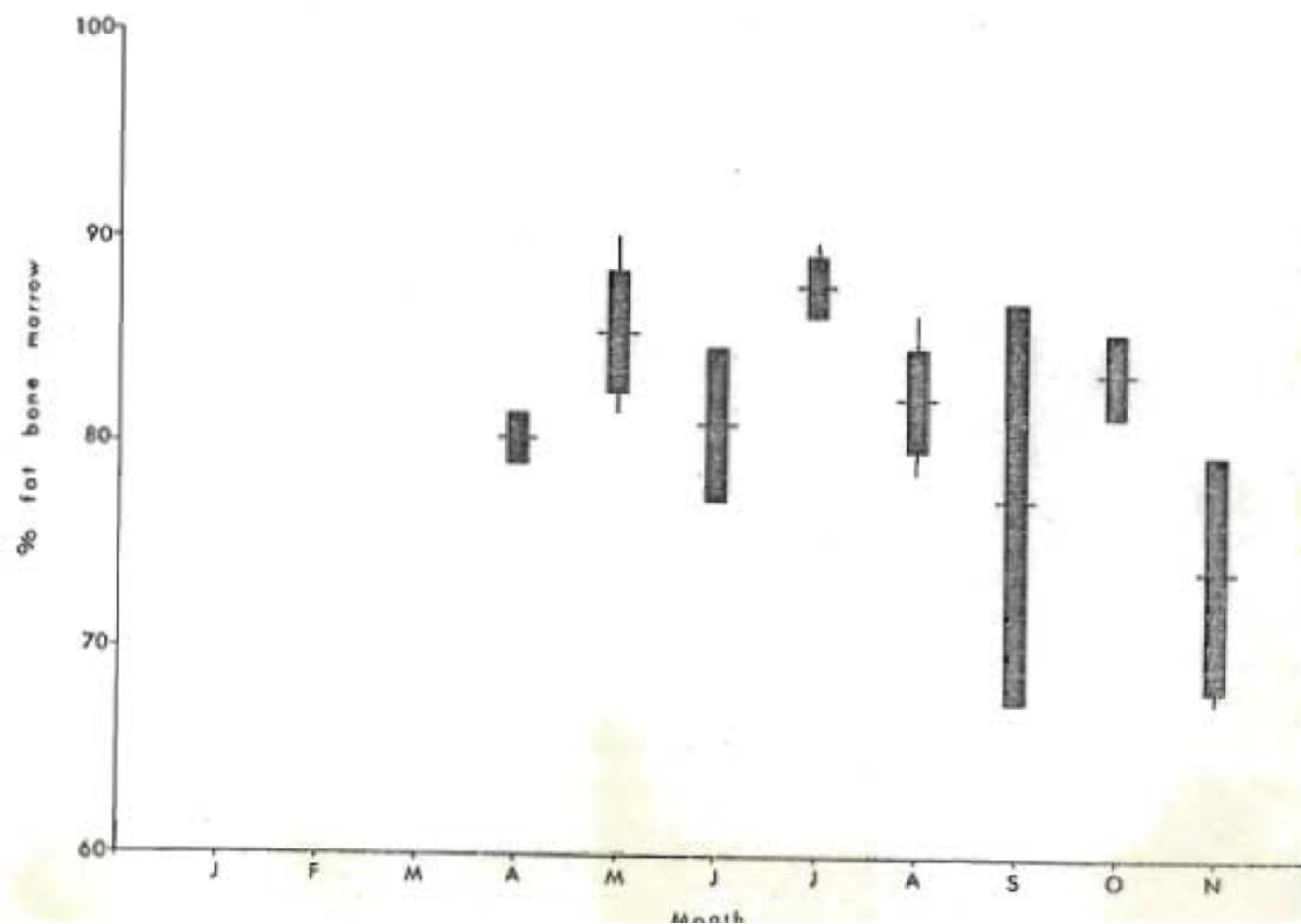
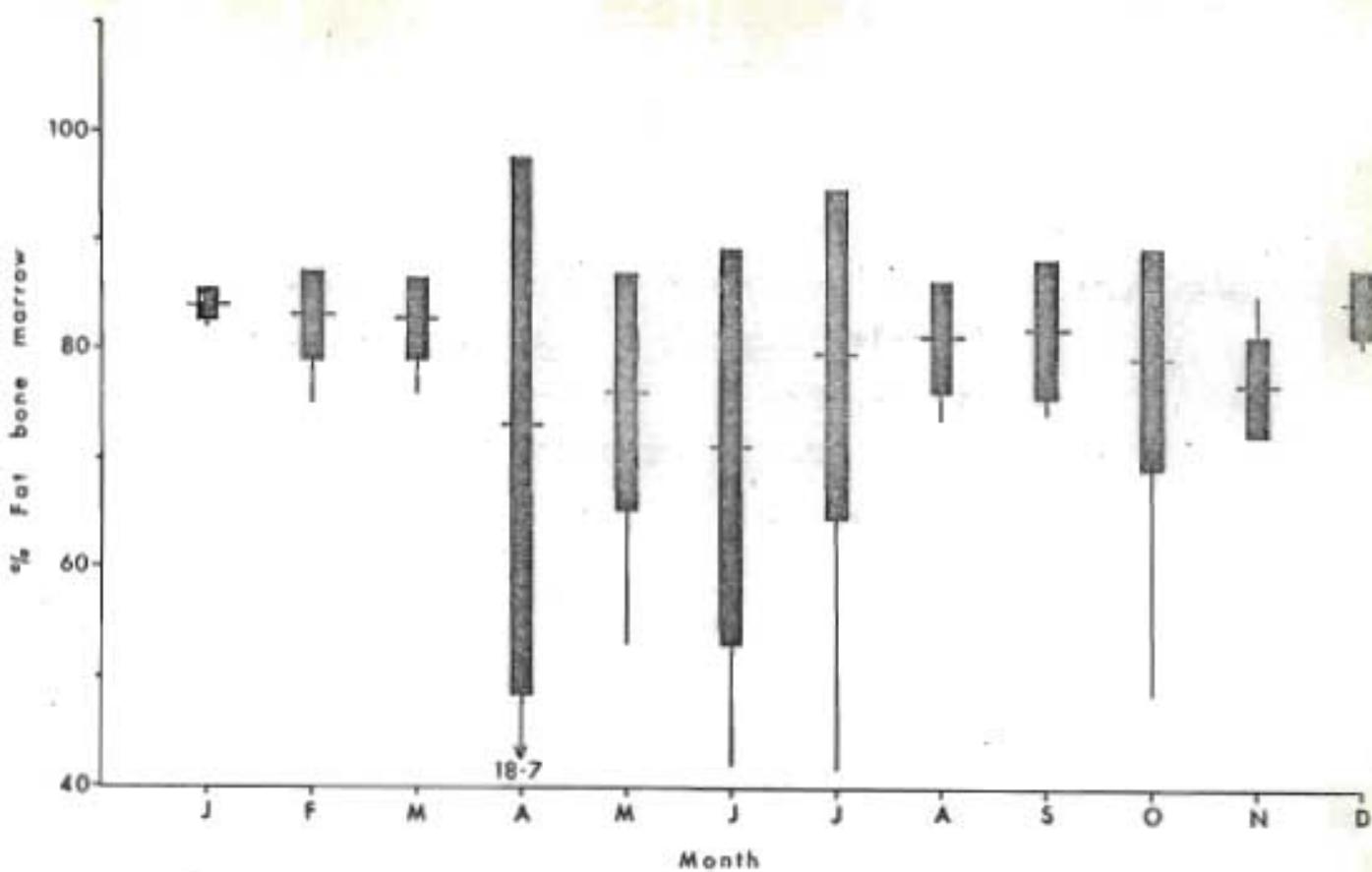
(Sinclair and Duncan, 1972; Brooks, Hanks and Ludbrook, in press).

Analysis of variance performed on percentage fat content of bone marrow between all age classes (both sexes considered together) showed no significant differences. Thus, in the seasonal changes in percentage fat (Figs. 4.24. and 4.25), all ages are considered. In the graph for the male (Fig. 4.24.), no clear pattern emerges. The graph for the female (Fig. 4.25), which is limited to the dry season for the same reasons as for KFI values, exhibits a degree of complexity which may be accounted for by the fact that both pregnant and non-pregnant animals are included (insufficient data prevent separation of these reproductive states). As with the KFI seasonal graph for females (Fig. 4.21) there is a rise in July, which in this case is significant, ( $p < 0,05$ ). If this results from placental progesterone output, then the effects of this hormone are most marked three to four months after conception, and may relate to foetal skeletal development.

The reasons for the absence of any clear pattern in seasonal change of male percentage bone marrow fat may become explicable when one compares percentage bone marrow fat with KFI. In Fig. 4.26, KFI has been plotted against percentage fat in the bone marrow. It is clear that below a KFI value of about 12, the percentage bone marrow fat cannot be accurately determined

Fig. 4.24. : Seasonal changes in fat content of bone marrow for males of all ages. (Range denoted by vertical line, mean by crossbar, standard deviation by broad portion of line.) The minimum April value of 18,7% extends below the x-axis.

Fig. 4.25. : Dry season changes in fat content of bone marrow for females of all ages. (Range denoted by vertical line, mean by crossbar, standard deviation by broad portion of line.)



from the curve. Above about 30, the KFI increases without any appreciable corresponding change in percentage marrow fat. This irregularity between KFI and percentage marrow fat in bone marrow has been noted by other workers (Harris, 1945; Ransom, 1965; Allen, 1968; Sinclair and Duncan, 1972). Only below a certain KFI value does the percentage fat start to decline - this is indicative of the fact that the bone marrow fat is utilised after kidney fat; bone marrow fat may indeed be the last body fat reserve to be utilised (Harris, 1945). Further, there is evidence (Brooks et al., in press) that mobilisation of bone marrow fat reserves does not occur simultaneously in all long bones: it appears that reserves are mobilised first from the femur or humerus in preference to the radius/ulna or tibia/fibula.

It is assumed that changes in kidney fat are governed more by physiological events related to reproduction (Sinclair and Duncan, 1972). Bone marrow fat is a desirable method of measuring condition when an animal is suffering from more extreme environmental pressures. The insignificant fluctuation in male percentage bone marrow fat with season tends then to indicate that the Complex population is not subjected to environmental pressures extreme enough to result in significant marrow fat mobilisation. The more significant seasonal fluctuations in female marrow fat would tend to support the conjecture of Hanks et al. (1976) that in special cases (relating to reproduction, for example) demands on fat reserves may be such that bone marrow may be utilised when substantial kidney fat remains. The findings in this study reinforce the statement by Hanks et al. (ibid.), that our understanding of the use of a simple index (like KFI or % fat) is not altogether clear.

## 4.3.2.2.

PCV VALUES AND BLOOD GLUCOSE LEVELS

These results were obtained from an isolated sample outside the Zululand Complex, from a small reserve (Vernon Crookes), which I consider to be essentially unsuitable wildebeest habitat. I include them only to serve as a baseline for subsequent similar work on the same population, and to provide an indication of the range of such values in the wildebeest for comparison with other ungulates. All blood glucose levels (six animals including both sexes; all adult) were in the order of 45 mg/100 ml. Table 4.10. shows the PCV values. I was unable to relate PCV values to either KFI or percentage fat in any way.

## 4.3.2.3.

ADRENAL RELATIONSHIPSa) MORPHOLOGY AND HISTOLOGY

The external appearance of the wildebeest adrenal glands corresponds to the standard ungulate pattern. Both glands are bi-lobed and flattened dorso-ventrally, but the left gland is more elongate (Plate 4.1), with the posterior lobe longer. They are associated with the antero-mesial borders of the corresponding kidneys. Typical mass and measurement data for adult animals are given in Table 4.11.. There was no significant difference between the mass of left and right adrenals ( $p > 0,1$ ). The maximum mass of an adrenal gland collected during this study was 12,5 g, from a ten-year old female which died in the Capture pens at Hluhluwe Game Reserve, several days after capture in Umfolosi. No such hypertrophy was found in other animals that had experienced the same trauma, and it is thus not considered to result from the stress of capture operations, particularly as it has been

TABLE 4.10. : PCV values from an isolated sample of wildebeest from Vernon Crookes reserve. All animals shot in June, 1976.

Sex	Age (years)	PCV (%)	K F I	% marrow fat
♀	12 - 13	35	16	77
♀	4 - 5	30	11	82
♂	2,5	40	10,5	81,53
♂	6 - 7	36	13	82,3
♂	2 - 3	34	9,5	42,2
♀	12 - 13	32	27	75,7
♂	7 - 8	43	15,5	84,3

TABLE 4.11. : Adrenal gland measurements and mass for adult wildebeest. Material from animals shot in June, 1976.

	ADULT ♂♂						ADULT ♀♀					
	LEFT ADRENAL			RIGHT ADRENAL			LEFT ADRENAL			RIGHT ADRENAL		
	MEAN	S.D.	n	MEAN	S.D.	n	MEAN	S.D.	n	MEAN	S.D.	n
Length (ant.-post.) (cm)	5,04	0,10	6	3,44	0,33	6	4,51	0,31	7	3,25	0,06	7
Width (cm)	2,09	0,09	6	2,32	0,09	6	2,17	0,26	7	2,51	0,61	7
Height (cm)	0,74	0,04	6	0,83	0,15	6	0,83	0,05	7	1,01	0,21	7
Weight (g)	4,92	0,93	38	4,19	1,24	38	4,88	0,76	29	4,62	1,63	29

established that there is considerable delay between stress and hypertrophy (Hanks, pers comm.; Taber, White and Smith, 1959). Histologically, the adrenal coincides with the generalised description of that of eutherian mammals as given by Bourne (1949). The cortex is peripheral to the medulla, except at the hilum, where the adrenal vein leaves the gland. The histology of the gland may vary with sex and season (Bourne, 1949), and for this reason it is necessary to state that the following histological description is from a ten-year old female. The section was taken through the centre of the gland. This animal was parous, but was neither pregnant nor lactating. Ovarian analysis showed that the animal was not about to ovulate. If one assumes that hypertrophy is related to reproductive physiological processes (among other "stressors"), then this animal may be taken to represent a "normal" stress situation. There was no evidence of any pathological condition in the animal.

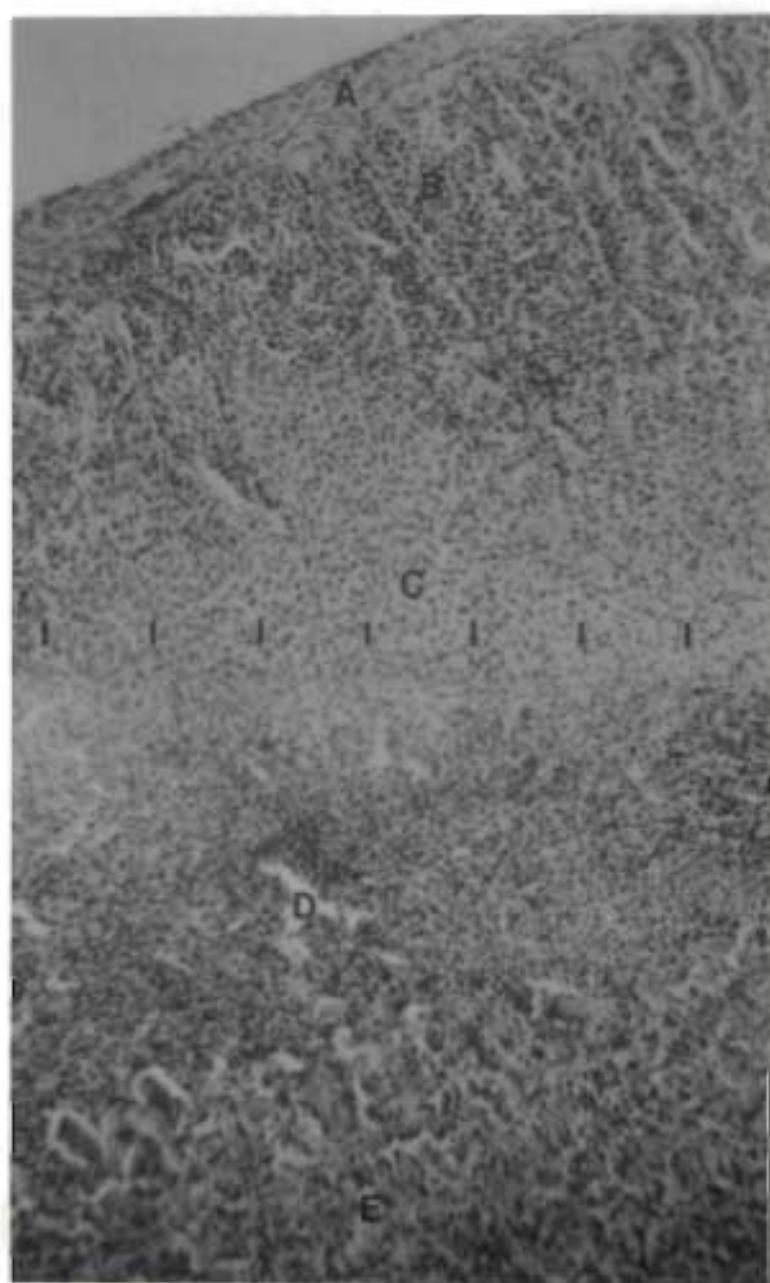
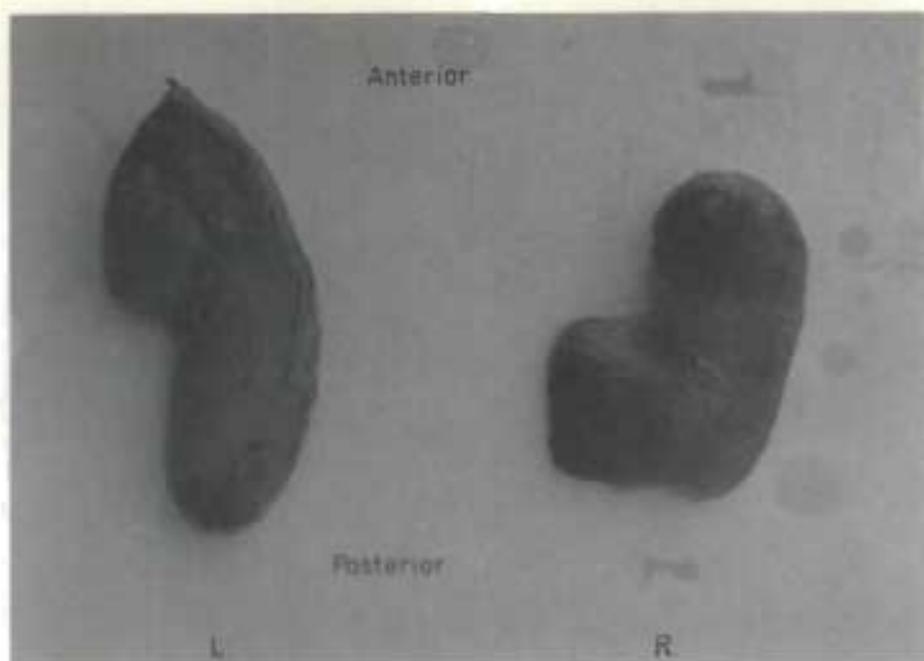
A fibrous capsule, about  $66\mu\text{m}$  thick, surrounds the gland (Plate 4.2.). Proceeding centripetally, the next zone is the zona glomerulosa ( $269\mu\text{m}$ ) which contains columns of columnar cells which bend through  $180^\circ$  near the capsule to proceed back in the original direction. The broad zona fasciculata follows, composed of parallel columns of squarish cells. This layer characteristically contains lipid droplets in mammals, but these did not show up in the section, possibly because a fat stain was not used, although cells would have shown a vacuolated appearance had lipid content been pronounced. Nicander (1952) maintains that a "lipid-poor" cortex is characteristic of ruminants. The zona fasciculata is the broadest zone in the cortex, extending for about  $1136\mu\text{m}$ . It merges into the zona reticularis, which has a denser appearance, possibly as a result of cellular degeneration. The zona reticularis may be separated from the medulla by a band

Plate 4.1. : External appearance of adrenal glands from adult male wildebeest. See Table 4.11. for measurements.

Plate 4.2. : Section through adrenal gland. The plate is composed of two juxtaposed prints: the depth of the zona fasciculata is greater than appears in the plate.

A = fibrous capsule; B = zona glomerulosa;  
C = zona fasciculata; D = zona reticularis;  
E = medulla.

Further details in text. Scale divisions on the photomicrograph are  $10^{-1}$ mm.



of connective tissue. This zone (termed the X-zone by Delost, 1953) may be transitory. In some mammals it is present in juveniles only; Krumrey and Buss (1969) referred to this zone as the 'fetal cortex' when describing the elephant adrenal. The X-zone is not apparent in Plate 4.2., but was observed in other sections (a five-year old ♀ and a 4,5 year old male both had readily discernible X-zones). Insufficient adrenals were sectioned to be able to relate disappearance of the zone to physiological or other processes. There has been little success in relating microscopic appearance of cortical cells to hormonal production (Frandsen, 1965).

The medulla is about 3708  $\mu\text{m}$  in section, and has a mosaic of three types of cells, distinguishable by differential staining with Haematoxylin and Eosin. Groups of closely-packed cells (staining pink) tend to occur around the central blood sinus. The other two types of cells are larger: light-staining cells with polyhedral to rounded shapes are enclosed by connective tissue, and dark-staining cells, irregularly shaped, with somewhat less connective tissue. By summation of the thicknesses of the cortical zones, the medulla was found to be 2,23 times as thick as the cortex.

#### b) ADRENAL GROWTH WITH AGE

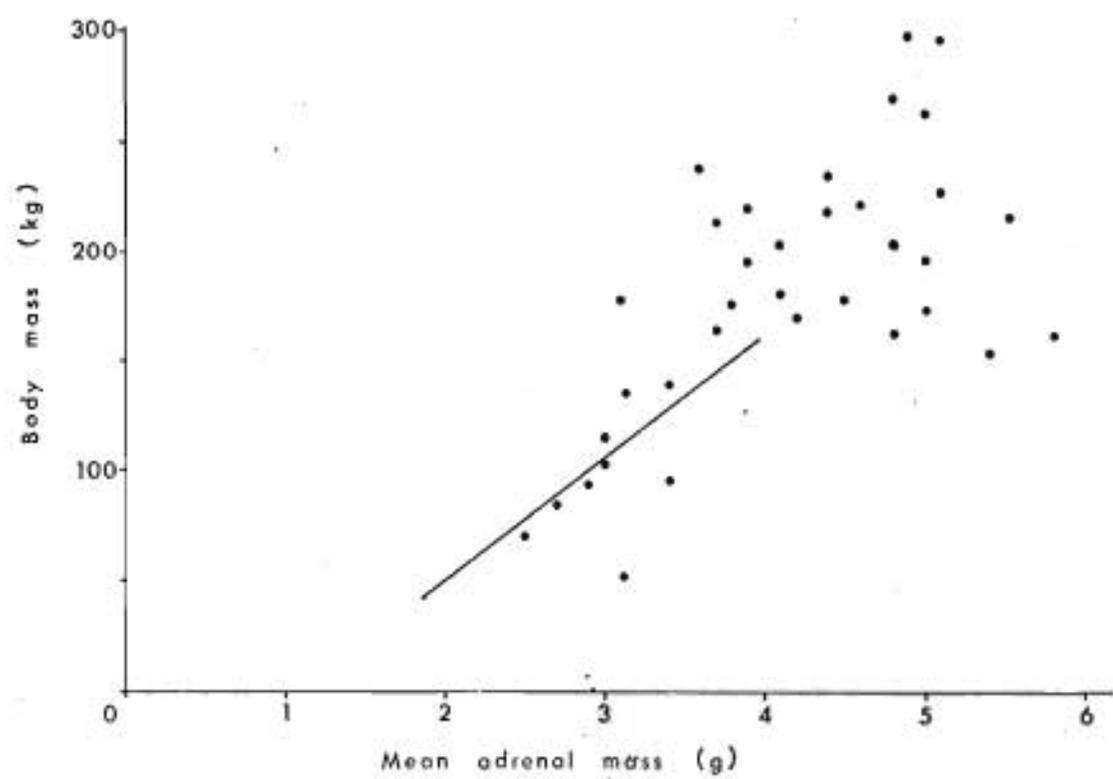
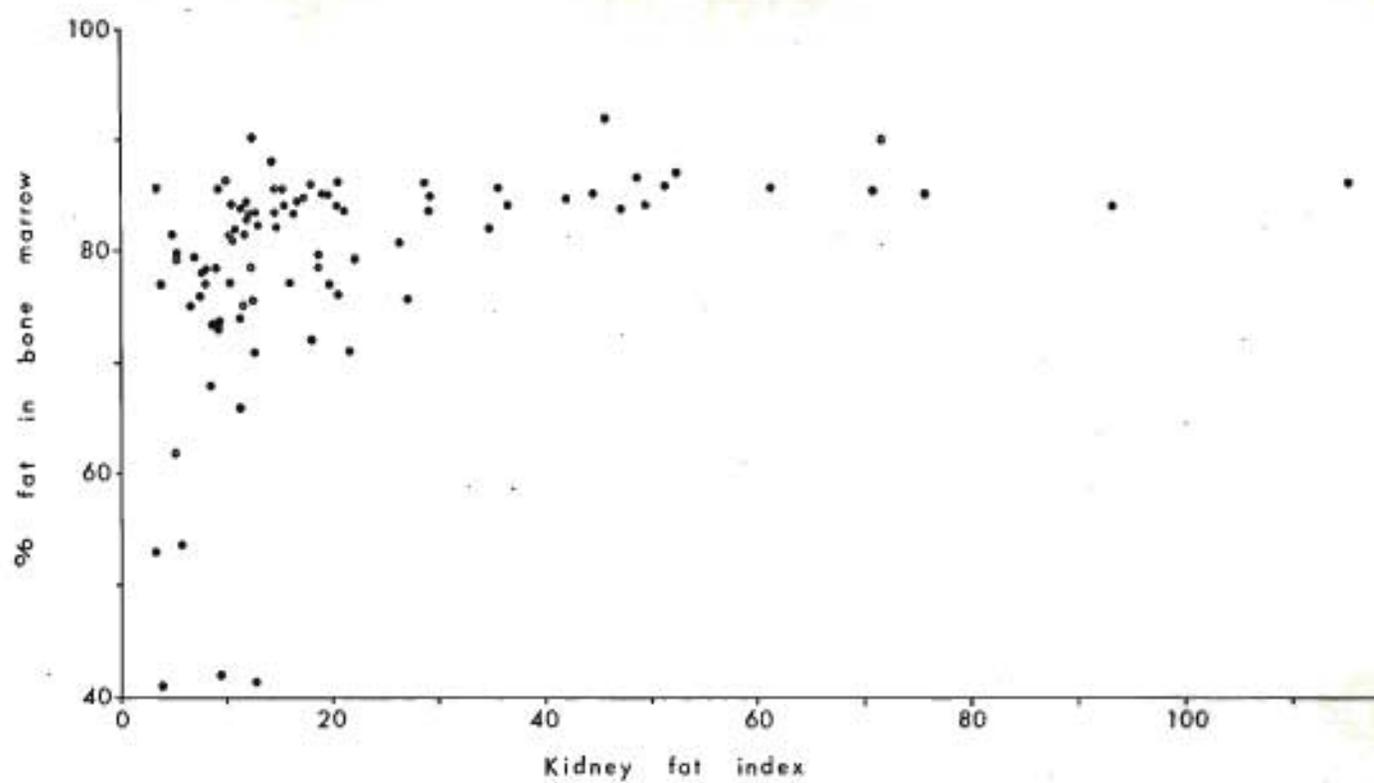
Most workers have assumed adrenal mass to be proportional to body mass, and for this reason have used an Adrenal Index rather than adrenal mass on its own. An Adrenal Index may take the following form:

$$\text{Adrenal Index} = \frac{\text{mean adrenal mass in g} \times 100}{\text{body mass in kg}}$$

The results of plotting mean adrenal mass against body mass (Fig. 4.2Z) indicate a linear relationship below 150 kg ( $r = 0,73$ ;  $p > 0,05$ ), but this relationship was absent above

Fig. 4.26. : The relationship between KFI and % fat in bone marrow.

Fig. 4.27. : Relationship between mean adrenal mass and body mass. Both sexes are considered. Regression equation for animals < 150 kg:  
 $y = 55,73x - 62,44.$



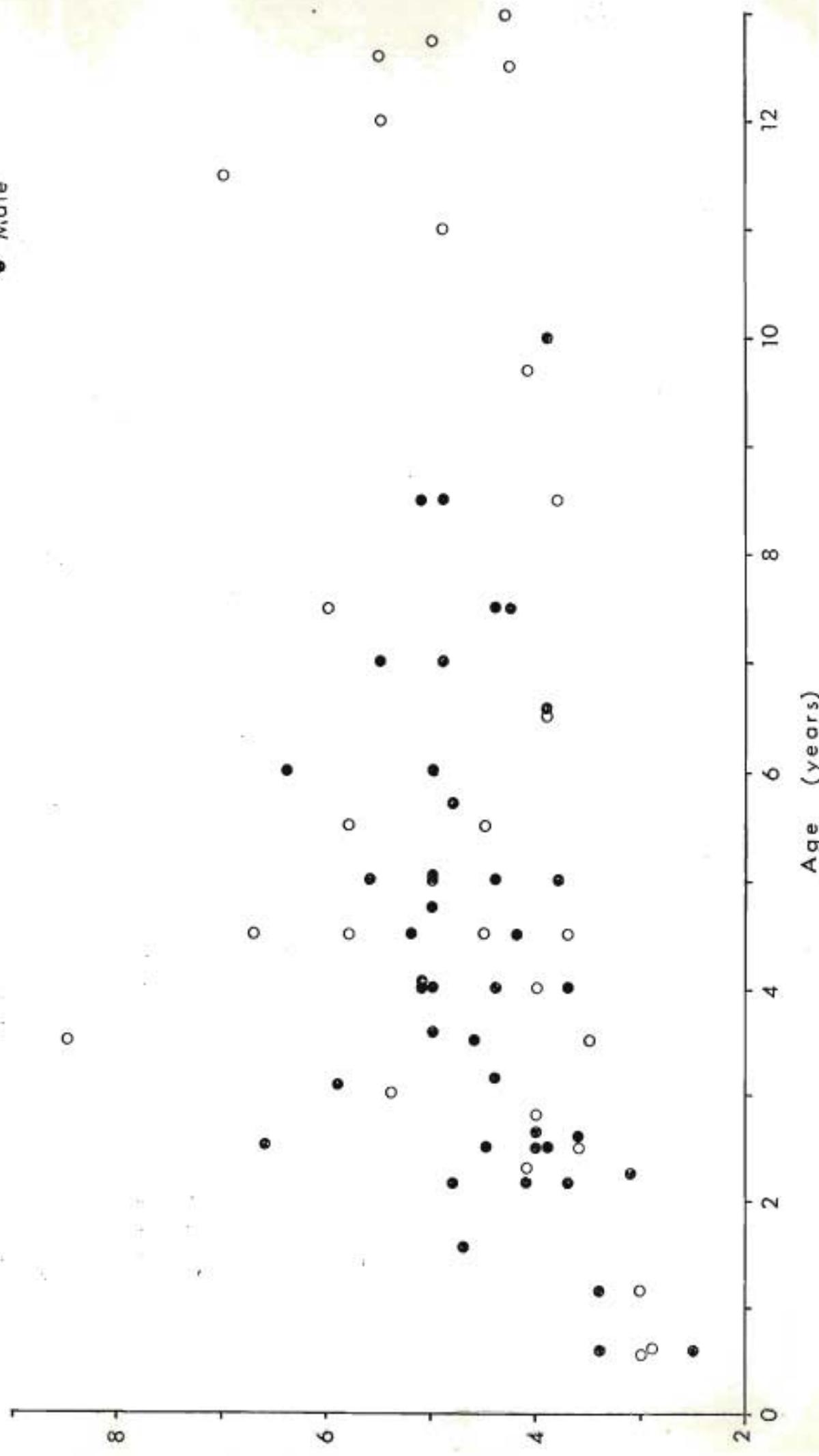
150 kg,  $r = 0,17$  (not significant,  $p > 0,1$ ). In both sexes, a body mass of 150 kg is attained by about eighteen months (Section 4.3.1.1.). It would thus appear that it may be meaningless to use an Adrenal Index in animals older than yearlings, particularly as errors in body mass computation may be in the order of  $\pm 10$  kg, which result from blood loss, scale inaccuracies, and ingestion of food or water before death. Payne and Hutchison (1963) have shown that liveweight of zebu steers may increase as much as 17% after a single drinking. Consequently, all relationships have been investigated based on animals older than eighteen months, by using mean adrenal mass unrelated to body mass.

Fig. 4.28. shows the relationship between age and mean adrenal mass. Adrenal mass increases at sexual maturity (male puberty is achieved at the end of the second year, and females first ovulate during their third year - Chapters 5 and 6), but thereafter there is no obvious relationship between mean adrenal mass and age. Of note is the fact that adrenal mass of juvenile white-tailed deer was significantly higher than that of adults (Hoffman and Robinson, 1966).

There was no significant difference in mean adrenal mass between males and pregnant, lactating females ( $p > 0,1$ ), nor between males and pregnant, non-lactating females ( $p > 0,1$ ). When all females were grouped together, difference between the mean adrenal mass of the total group and that of the male group was again not significant ( $p > 0,05$ ). These results deviate from the standard mammalian pattern, in which female adrenal glands tend to be heavier than those of males. This results from an enlarged zona reticularis (Bourne, 1949), and has been documented for cotton rats *Sigmodon hispidus* (Goertz, 1965); for elephant (Krumrey and Buss, 1969); and for bushbuck

Fig. 4.28. : Relationship between age and mean adrenal mass.

○ Female  
● Male



(Morris, 1973). An exception to this rule occurs in the cottontail rabbit (Christian, 1953).

c) RELATIONSHIP OF MEAN ADRENAL MASS TO THE FEMALE REPRODUCTIVE CYCLE.

In most mammals the size of the adrenal gland varies seasonally with sexual activity, stage of oestrus, or during pregnancy and lactation (Zalesky, 1934; Beer and Meyers, 1951; McKeever, 1959; Christian, 1962; Chitty and Clark, 1963; and Krumrey and Buss, 1969). Females were divided into three groups:

- (i) prepubertal or nulliparous,
- (ii) pregnant but not lactating,
- (iii) pregnant and lactating.

The mean adrenal mass of any particular group did not differ significantly from that of the other two ( $p > 0,1$ ), indicating that the wildebeest might be an exception to the general mammalian pattern. Similar findings have been reported for voles (M. pennsylvanicus) by Christian and Davis (1966). In this species, adrenal mass relative to body mass did not vary with changes in reproductive status once maturity was obtained.

By grouping females into duration of pregnancy intervals, and by testing the mean adrenal mass between groups, it was found that there was no significant difference ( $p > 0,05$ ). The biased female sample did not allow for comparison with females in the later stages of pregnancy. It appears that up to mid-term, mean adrenal mass in the wildebeest is unaffected by the stage of pregnancy. This is unusual for a ruminant, for Bell and Weber (1959) have reported on the variation in adrenal mass with stage of pregnancy in ruminants.

d) SEASONAL EFFECTS ON MEAN ADRENAL MASS

Insufficient adrenal data from females during the rainy season prevented seasonal comparison for that sex. Males older than eighteen months had a mean adrenal rainy season mass of 4,81 g compared to a dry season mean of 4,70 g, but this difference was not significant ( $p > 0,1$ ). Using an Adrenal Index, Cowley (1975) was unable to clearly relate impala Adrenal Index to season. In non-tropical mammals, there is a tendency for adrenals to weigh less during winter when temperatures are lowest and food supplies least available (Christian, 1962; Goertz, 1965; Hoffman and Robinson, 1966).

e) RELATIONSHIP BETWEEN ADRENAL MASS AND CONDITION

Hughes and Mall (1958) found adrenal mass to be a function of condition in deer, which was not related to size of the animal. They found a good correlation between adrenal mass and kidney fat mass and between  $\frac{\text{adrenal mass}}{\text{body length}}$

and kidney fat. The results from this study indicate that adrenal mass bears little relationship to fat reserves in wildebeest. The correlation coefficient for mean adrenal mass and KFI was 0,14 (not significant,  $p > 0,1$ ). For mean adrenal mass and % bone marrow fat,  $r = 0,36$  ( $p < 0,01$ ). Adrenal mass may vary from about 3 to 7 g without any appreciable change in either KFI or % marrow fat. Smith (1970) found an extremely low correlation coefficient (0,044) between his adrenal index and total fat from East African wildebeest. His result is not conclusive, for he based his adrenal index on kidney mass, and did not take kidney mass fluctuations into account. The failure to relate adrenal mass to condition is perhaps explicable in that one is using

simple indices to relate extremely complex relationships involving, among other systems, feed-back mechanisms of a diversity of hormones.

#### f) CONCLUSION

There are numerous factors which alter endocrine function which are not density-dependant. These may include thermo-period, photoperiod, nutrient limitations and even genetic factors. A further complication is that it is difficult to separate climatic influences from those of breeding. The variability induced by non-density-dependent factors means that it is somewhat specious to attempt to use adrenal mass to compare different populations. Rather, it is more meaningful to use trends in adrenal mass for comparing the same population from year to year at the same season. Consequently, I see this aspect of the study as establishing a base-line for future comparisons. Work on rodents has demonstrated a relationship between population density and reproductive success. In ungulates, I consider the adrenal mass/population density/reproductive success relationships to be extremely complex. No attempt is made to relate these parameters: the data are presented simply to describe the situation relating to a specific population over a specific period.

#### 4.4.

##### CHAPTER SUMMARY

Mass and measurement data were incorporated into von Bertalanffy growth equations. Computer-derived growth curves for specific parameters allowed for the determination of the age at which the asymptote for that parameter was attained. Generally, males took far longer to attain asymptotes than females. Some comparisons were made between different populations: for example, the mean mass

of the Zululand subspecies exceeds that of East African subspecies. Foetal growth curves are presented. Regression equations relate chest girth to body mass.

Condition of wildebeest was investigated using the Kidney Fat Index (KFI), the percentage of fat in the bone marrow, and the blood Packed Cell Volume (PCV). In adult males, seasonal changes in KFI values were not pronounced; similar results were found for adult females during the dry season. Interpretation of KFI values was complicated by the fact that kidney mass itself showed significant seasonal variation. Bone marrow fat was utilised after body fat, and it appears that adult males were not subjected to environmental pressures extreme enough to result in significant marrow fat mobilisation. Significant mobilisation may however occur in females, in which case it may be related to reproductive events. PCV values from a small sample could not be related to KFI or % fat in bone marrow.

The adrenal histology is described. The adrenal mass increased at sexual maturity, but thereafter no obvious relationship between adrenal mass and age was found. There was no significant difference in mean adrenal mass between males and females, nor did adrenal mass in females appear to be affected by stage of pregnancy. In wildebeest, adrenal mass was shown to bear little relationship to fat reserves.

## CHAPTER 5

### REPRODUCTION IN THE FEMALE

#### 5.1.

##### INTRODUCTION

Mammals may generally be grouped on the basis of fundamental breeding patterns. The wildebeest belongs to a group which is clearly defined: those mammals which produce a single young annually. Characteristics of this group have been outlined by Lloyd (1969). Long gestation periods are the rule and nutritional changes at the conception period bear little relationship to food availability at birth. Young are born at the most favourable stage in terms of food resources, and possibly cover and concealment. In general, lactation is prolonged. Longevity is great, and survival of the young is generally high, such that favourable conditions may in the long term reflect a dramatic increase in numbers despite their low reproductive performance.

In the social structure of the wildebeest (see Chapter 8), a single territorial male is associated with a breeding herd of females which display a high degree of synchrony with respect to oestrus. Consequently, there is an excess of males over and above those required for breeding, and the sex ratio is not of primary importance in reproduction. The implication is that the female plays a prime role

in determining the levels of recruitment to a population.

One of the fundamental steps in management is knowledge of the reproductive cycle, and the limiting factors imposed upon reproduction. Whether the aim of management is to maximise productivity or to maintain a population in harmony with the ecosystem, an understanding of those factors controlling reproduction and population growth is essential.

In broad terms, those aspects of reproduction in the female which are subject to variation are:

- a) the onset of the breeding season;
- b) the duration of the breeding season or rut;
- c) the age of attainment of puberty;
- d) the pregnancy or conception rate;
- e) the extent of out-of-season breeding;
- f) the extent of intra-uterine mortality, and the proportion of successful to unsuccessful pregnancies;
- g) the duration of lactation. Nalbandov (1964) considers lactation to be the culmination of the reproductive process, and indeed as much a part of this process as the oestrous cycle or gestation.
- h) the age at reproductive senescence.

When considering the factors regulating the aspects outlined above, it is necessary to differentiate between proximate and ultimate factors. The former are environmental events that serve as a trigger to the animal's physiology, and synchronise events for a given population. Ultimate factors are concerned with the ecological reasons for such triggering. Owen (1966) has pointed out that a proximate factor may also act as an ultimate factor, citing the example whereby decreasing food supply could act as both proximate and ultimate stimuli for a population to move. Proximate factors

tend towards complexity in some cases: for example, it is difficult to separate the direct consequences of climate on animal reproduction from those resulting from the indirect influence of climate on the quality and quantity of food.

Of the proximate factors, the most important could be grouped as follows (Lloyd, 1969):

- a) population density;
- b) food availability and quality;
- c) age and sex structure of the population;
- d) climate and other physical factors.

This chapter is an attempt to outline the major reproductive phenomena in the life cycle of the female wildebeest, with a possible bias towards reproductive physiology. It does not include behavioural data, as these have been adequately covered by Estes (1966) and Watson (1969). These authors included descriptions of parturition and adult-calf relationships.

## 5.2.

### MATERIALS AND METHODS

Material was obtained from seventy-four females of all age classes, but chiefly adult. As explained in Chapter 4, the sample was not representative of all seasons, but was biased in favour of the dry season. Additional data were made available from some sixty animals culled during 1963 in HGR (Anderson, pers. comm.), and from a further eighty-nine culled in 1967 (Vincent, pers. comm.).

### 5.2.1.

#### FIELD COLLECTION METHODS

The reproductive tract was exposed by slitting the animal from the sternum to the pubis. For the single detailed dissection of the

tract, the pubic symphysis was cut through and the vagina dissected away. If the animal was visibly pregnant, the foetus was weighed and sex was determined when development was sufficiently advanced. The site of implantation (i.e. left or right uterine horn) was recorded. Foetal data were recorded from forty-five foetuses in this study; these were supplemented by limited data from Anderson (sixty foetuses) and Vincent (thirty-five foetuses).

Both ovaries ( $n = 126$ ) were collected where possible, the left with a filament of attached mesentery or fallopian tube to allow for subsequent distinction from the right. The ovaries were stored in Bouin's solution, or 10% formalin. Those destined for histological processing were stored in 10% formol saline. Vincent (pers. comm.) recorded ovarian parameters (mass, diameter of larger follicles and corpora lutea) from 173 ovaries: these additional data were utilised where possible.

The mammary gland was dissected away and weighed and its activity noted.

Blood samples were limited to the small sample from Vernon Crookes reserve (see Chapter 4.), and were collected from the carotid artery or jugular vein in evacuated heparinised tubes. Collection was made as soon after death as possible, and delay seldom exceeded several minutes. Tissue samples for histology were limited to the vagina and endometrium.

Data were recorded directly onto data sheets, specimens of which are shown by Figs. 5.1. and 5.2..

### 5.2.2.

#### SUBSEQUENT PROCESSING OF MATERIAL AND DATA

##### a) OVARIES

After fixation, the ovaries were rolled on filter paper to promote

Fig. 5.1. Examples of data sheets used in the field. Both  
and : examples were subject to deletion, alteration or  
Fig. 5.2. addition in some cases.

## WILDERBEE DATA SHEET

DATE: \_\_\_\_\_ HERD: \_\_\_\_\_ LOCALITY: \_\_\_\_\_

SPECIMEN NUMBER: \_\_\_\_\_ SEX: \_\_\_\_\_ AGE CLASS: \_\_\_\_\_

TOOTH WEAR: \_\_\_\_\_ CEMENTUM AGE: \_\_\_\_\_

SHOULDER HEIGHT: \_\_\_\_\_ HORN WIDTH: \_\_\_\_\_

KNEEFOOT: \_\_\_\_\_ EAR WIDTH: \_\_\_\_\_

CHEST GIRTH: \_\_\_\_\_ RATIO: \_\_\_\_\_

BODY WEIGHT: \_\_\_\_\_ ROMEN + CONTENTS WEIGHT: \_\_\_\_\_

ROMEN WEIGHT: \_\_\_\_\_ CONTENTS WEIGHT: \_\_\_\_\_

RUMEN SAMPLE COLLECTED: YES/NO

KIDNEY WEIGHT: \_\_\_\_\_ KIDNEY FAT WEIGHT: \_\_\_\_\_ INDEX: \_\_\_\_\_

BARRAGE SAMPLE COLLECTED: YES/NO CONDITION: \_\_\_\_\_

BSE COLLECTED: YES/NO

PREGNANT: YES/NO LACTATION: YES/NO UDDER WEIGHT: \_\_\_\_\_

PONTUS: L/R HORN WEIGHT: \_\_\_\_\_ SEX: \_\_\_\_\_

HEAD LENGTH: \_\_\_\_\_ CROWN-HEMP: \_\_\_\_\_ AGE: \_\_\_\_\_

UTERINE HORN LENGTHS: LEFT: \_\_\_\_\_ RIGHT: \_\_\_\_\_

OVARIES: FOLLICLES: NUMBER: \_\_\_\_\_ SIZE: \_\_\_\_\_ (State L or R)

CORPORA LUTEA: NUMBER: \_\_\_\_\_ SIZE: \_\_\_\_\_

CORPORA ALBICANTIA: NUMBER: \_\_\_\_\_ SIZE: \_\_\_\_\_

TESTIS + EPIDIDYMIS WEIGHT: \_\_\_\_\_ TESTIS WEIGHT: \_\_\_\_\_

EPIDIDYMAL SMAR: \_\_\_\_\_ TESTIS TISSUE SAMPLE: YES/NO

TUBULE DIAMETER: \_\_\_\_\_

REMARKS: \_\_\_\_\_

## WILDERBEE CULL - VERNON CROOKS

No.: \_\_\_\_\_ DATE: \_\_\_\_\_ SEX: \_\_\_\_\_ AGE: \_\_\_\_\_

KIDNEY + FAT WT. L: \_\_\_\_\_ R: \_\_\_\_\_

KIDNEY WT. L: \_\_\_\_\_ R: \_\_\_\_\_

K.F.I. L: \_\_\_\_\_ R: \_\_\_\_\_

ADRENAL WT. L: \_\_\_\_\_ R: \_\_\_\_\_ (Collect whole)

BARRAGE WT. FRESH: \_\_\_\_\_ ( ) \_\_\_\_\_ ( ) \_\_\_\_\_ ( )

DRY: \_\_\_\_\_

SKELETAL EXTRACTION: \_\_\_\_\_

(BRACKETS DENOTE SOURCE OF BARRAGE)

HISTOLOGY SAMPLES: FOLLICLES PEDAL; PREORBITAL GLANDS

MIN. 90 ml. BLOOD (3 SAMPLES)

{ PCV : \_\_\_\_\_

{ SERUM CHOLESTEROL : \_\_\_\_\_

FSH : \_\_\_\_\_

LH : \_\_\_\_\_

OESTROGEN : \_\_\_\_\_

PROGESTERONE : \_\_\_\_\_

PREGNANT : YES / NO

LACTATION : YES / NO

UDDER WT. : \_\_\_\_\_

FOETUS : SEX : \_\_\_\_\_ L/R

C/R : \_\_\_\_\_ HEAD : \_\_\_\_\_

OVARIES WT. L : \_\_\_\_\_ R : \_\_\_\_\_

HISTOLOGY SAMPLES :

ENDOMETRIUM, VAGINAL EPITHELIUM

(MILK SAMPLE IF COPIOUS)

MIN. 90 ml. BLOOD (3 SAMPLES)

{ PCV : \_\_\_\_\_

{ SERUM CHOLESTEROL : \_\_\_\_\_

TESTOSTERONE : \_\_\_\_\_

TESTIS WT. L : \_\_\_\_\_ R : \_\_\_\_\_

EPID. WT. L : \_\_\_\_\_ R : \_\_\_\_\_

BULBOURETHRAL WT. L : \_\_\_\_\_ R : \_\_\_\_\_

PROST. ATE WT. L : \_\_\_\_\_ R : \_\_\_\_\_

SEM. VESICLE WT. L : \_\_\_\_\_ R : \_\_\_\_\_

(EITHER COLLECT WHOLE, OR PORTIONS OF

ABOVE AFTER FIELD WEIGHING, FOR HISTOLOGY)

OTHER : . . . . .

. . . . .

. . . . .

peripheral drying, and then weighed to  $10^{-3}$ g on a Mettler electrical balance. A Vernier caliper was used to take three measurements of each ovary, to  $10^{-2}$ mm. Length was recorded from end to end, parallel to the mesovarium. Width was taken from the side of attachment of the mesovarium to the opposite side. Depth was recorded at right angles to the previous measurements. The volume of the ovary was determined by displacement of water in a measuring cylinder, to  $10^{-1}$ ml.

Macroscopic examination of ovarian structure followed the technique of Cheatum (1949a) which was subsequently expanded by Golley (1957). A razor blade was used to section ovaries at 1mm intervals along the axis: each section was left joined to its neighbour at the point of attachment of the mesovarium. The resultant "book" appearance reduced the chance of double counts of ovarian structures. In addition, the coagulated liquor folliculi of each follicle was scraped out on counting. Follicles were grouped into eleven size classes, and counted. Corpora lutea were measured from those sections showing maximum diameter. Counts were made of corpora nigra (= albicantia), and measurements taken using a Vernier caliper. Selected sections were processed (Appendix I) for microscopic examination, in order to confirm microscopically the nature of the structures counted.

Twenty corpora lutea were removed completely from their ovaries and weighed to  $10^{-4}$ g on an electrical balance. The results were plotted against mean diameter, after the method of Laws (1969).

#### b) STEROID ANALYSES FROM BLOOD SAMPLES

Samples were centrifuged for 10 minutes, and the plasma was drawn off with a syringe, and then stored in a deep freeze until

the assays could be undertaken. FSH (Follicle Stimulating Hormone), LH (Luteinizing Hormone), Oestradiol -  $17\beta$ , and Oestriol were determined using radioimmunoassay procedures. The gonadotrophins (FSH and LH) were determined with the use of a CEA - IRE - SORIN kit, as was Oestradiol -  $17\beta$ . In the gonadotrophin kit the principal stages of the assays were:

- (i) incubation of the hormone with the anti-hormone antibody for 18 - 20 hours at room temperature;
- (ii) agitation with the anti -  $\gamma$  antibody and the immunoabsorbant for 5 hours at room temperature;
- (iii) centrifugation at room temperature and counting of the precipitate.

Oestradiol -  $17\beta$  assay involved the following main steps:

- (i) extraction of oestradiol from plasma;
- (ii) incubation of the reaction mixture for 30 minutes at  $37^{\circ}\text{C}$  and for two hours at  $4^{\circ}\text{C}$ ;
- (iii) adsorption of free oestradiol on charcoal - dextran;
- (iv) centrifugation at room temperature and counting of the supernatant.

Oestriol levels were determined by using an Oestriol RIA kit (Radiochemical Centre, England). Oestriol conjugates in the samples were hydrolysed using an enzyme preparation. An iodine -  $125$  labelled oestriol derivative was allowed to compete with the sample oestriol for binding sites on a specific anti-oestriol antibody. The amount of  $\text{I}^{125}$  - labelled oestriol which is bound by the antibody is then inversely proportional to the concentration of unlabelled oestriol in the samples.

#### c) FOETAL MASS DATA

The mass of the foetus may be used as an estimate of gestational age, following the relationship derived by Huggett and Widdas

(1951). There exists a linear relationship between foetal mass and gestational age, such that:

$$M^{1/3} = a (t - t_0)$$

where  $M$  = mass of foetus,  
 $a$  = slope of line (specific foetal growth velocity),  
 $t$  = gestational age,  
 $t_0$  = x - axis (age) intercept.

$t_0$  varies with gestation length, and for gestation periods of 100 - 400 days (which includes the wildebeest),  $t_0 \approx 0,2$  X gestation period.

The ages of foetuses were then extrapolated forwards to provide a sample of birth dates, and backwards to provide a sample of conception dates.

### 5.3.

#### RESULTS AND DISCUSSION

##### 5.3.1.

#### DESCRIPTION OF THE REPRODUCTIVE TRACT

The reproductive tract conforms to the standard bovid pattern. In the non-pregnant animal, there is no difference between lengths of left and right uterine horns ( $p > 0,5$ ). Mean lengths of uterine horns are 8,3cm for calves; 8,8cm for yearlings; 12,6cm for 2 - 3 year olds; and 14,0cm for parous non-pregnant adults. Caudally, the uterine horns are united by peritoneal connective tissue; they open independently into the uterine body.

A detailed dissection was made of the reproductive tract of a pregnant animal of about twelve years of age. The duration of pregnancy (as determined following Huggett and Widdas, *ibid.*) was 98 days. An overall view of the entire tract is given in Plate 5.1.. The

urethra measured 80mm, and entered the vagina 205mm from the cervix. From the point of entry of the urethra, the urogenital canal continued for a further 45mm, terminating in the vaginal opening. Vaginal length was thus 250mm. The vaginal opening (undistended) measured 55mm from dorsal to ventral ends of the vulvar cleft. Ventrally in the vaginal opening was situated a cream-coloured clitoris (5 X 5 X 2,5mm), which is shown in Plate 5.2..

Placentation is of the placenta cotyledonaria type, as shown in Plate 5.3.. Cotyledons in the animal described above measured 32 X 17mm.

### 5.3.2.

#### THE OVARY AND THE OESTROUS CYCLE

##### 5.3.2.1.

#### OVARIAN MASS/VOLUME RELATIONSHIPS

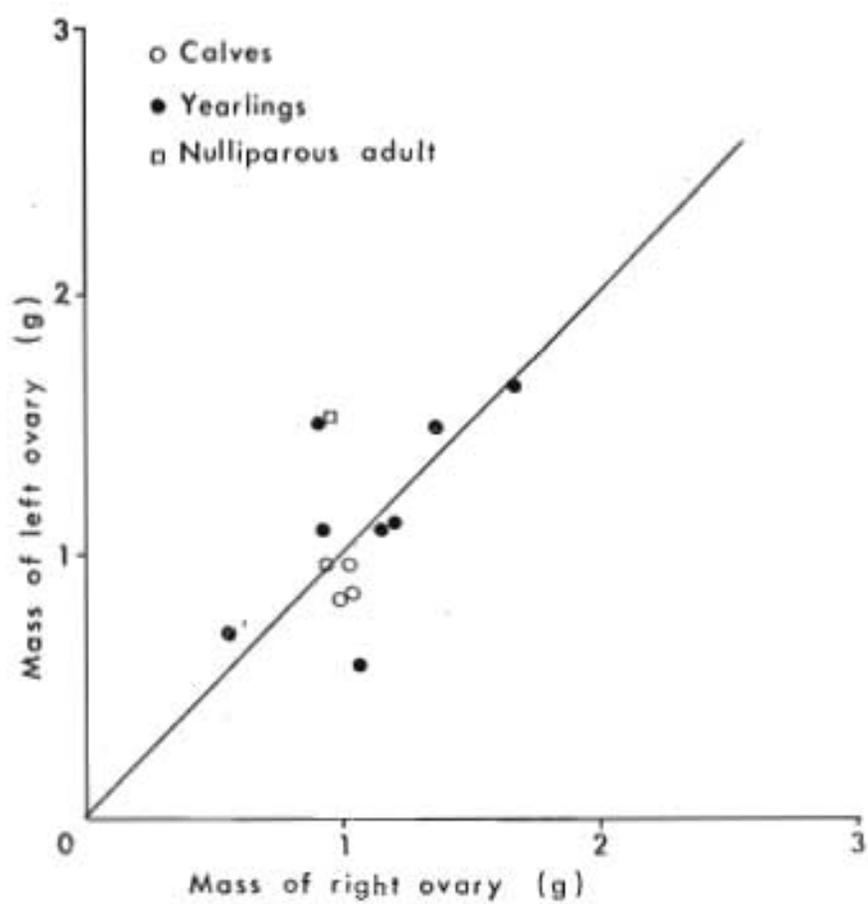
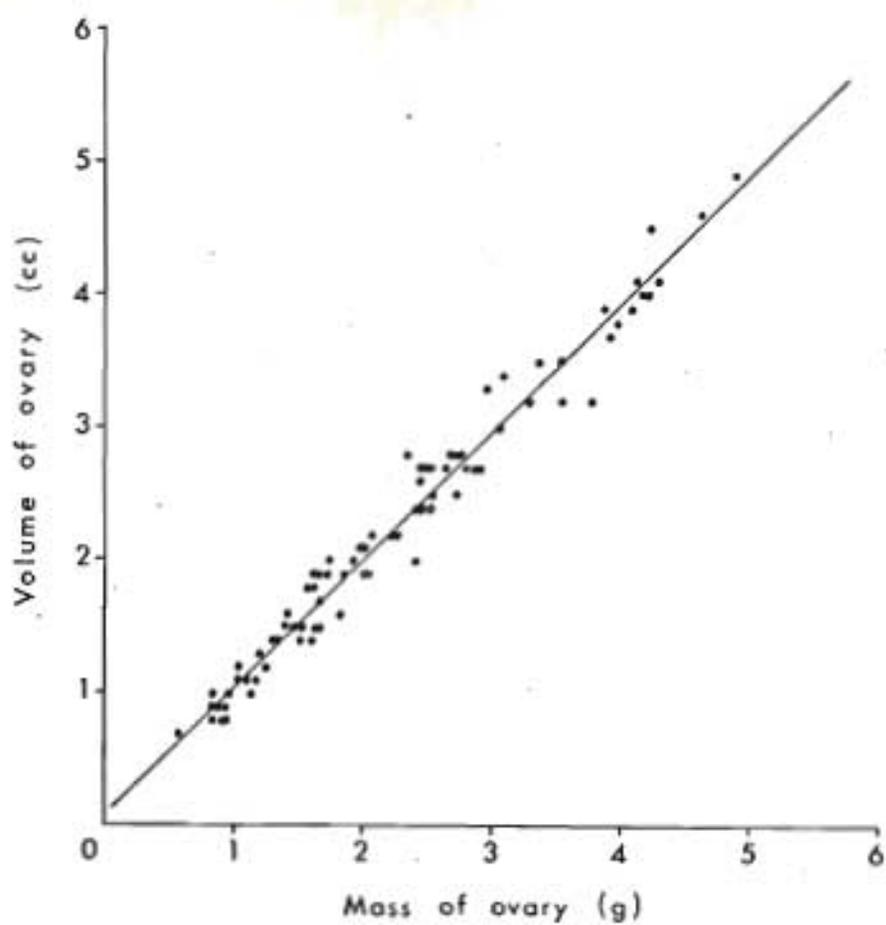
The three ovarian measurements were used to calculate volume, using the formula for an ovoid sphere:  $\frac{4}{3} \pi r_1 \cdot r_2 \cdot r_3$ . The calculated volumes were compared with the observed volumes, and gave a correlation coefficient of 0,9388 ( $p < 0,001$ ). The observed volumes were very well related to mass ( $r = 0,98$ ;  $p < 0,001$ ), as seen in Fig. 5.3., so that volume could with confidence be substituted for mass in relationships involving the latter.

On the assumption that difference in mass between left and right ovaries may imply a propensity for the heavier to ovulate first, the masses of left and right prepubertal ovaries were plotted in Fig. 5.4.. From the data available, it does not appear that differences exist between the mass of the left and right prepubertal ovaries.

In Fig. 5.5., volume of the ovary has been related to age. The

Fig. 5.3. : The relationship between observed ovarian volume and ovarian mass. The equation for the regression line is  $y = 0,96x + 0,08$ .

Fig. 5.4. : Comparison between mass of left and right prepubertal ovaries. (A single nulliparous adult is included). The straight line represents parity in mass of the two ovaries.



presence of a corpus luteum has a marked effect on the volume (and hence mass) of the ovary. As the volume of ovaries lacking corpora lutea from adult animals falls within the range of prepubertal animals, it does not appear that a critical volume (or mass) need be attained before ovulation occurs. This conclusion must however be viewed with caution, as mass or volume alone can be deceptive. Hanks (1973) found that in elephants pronounced hypertrophy of foetal ovarian interstitial tissue took place, to the extent that, in the second half of gestation, foetal ovarian mass could exceed that of neonatal or prepubertal animals.

#### 5.3.2.2.

##### OVARIAN HISTOLOGY

Microscopic examination of ovaries allowed confirmation of structures seen macroscopically. The wildebeest ovary is in every way consistent within the generalised mammalian form. The main structures studied in microscopic sections were those in the zona parenchymatosa (cortex). Plate 5.4. shows the germinal epithelium, from which are derived the primordial follicles, surrounded by a single layer of flattened epithelial cells. Proceeding inwards, a typical Graafian follicle can be seen, containing a primary oocyte of about 100 $\mu$ m in diameter.

After rupture of the follicle, the granulosa cells are transformed into luteal cells to form the corpus luteum. In Plate 5.5. a section of a corpus luteum of pregnancy is shown. The corpus luteum is in a non-regressive phase, with luteinization progressing.

Only a small sample of ovaries was processed for histological purposes: consequently, no microscopic assessment of ovarian abnormalities could be made. A single macroscopic abnormality was noted; this took the form of a large (approximately 2mm) cyst in the centre

Plate 5.1. : Reproductive tract of the adult wildebeest female:  
overall view. Dimensions in text.

A = Uterus with foetus; B = ovary; C = vagina;  
D = ureter; E = urinary bladder; F = urethra;  
G = vulvar cleft; H = anus; I = rectum.

Ruler is 12cm long.

(Photograph: J. Hanks).

Plate 5.2. : Vaginal opening, showing situation of clitoris (C).

A = Anus.

Ruler is 12cm long.

(Photograph: J. Hanks).

Plate 5.3. : Exposure of uterine wall to show cotyledonary  
placentation. The foetus is approximately  
three months old.

C = Cotyledon.

Ruler is 12cm long.

(Photograph: J. Hanks).

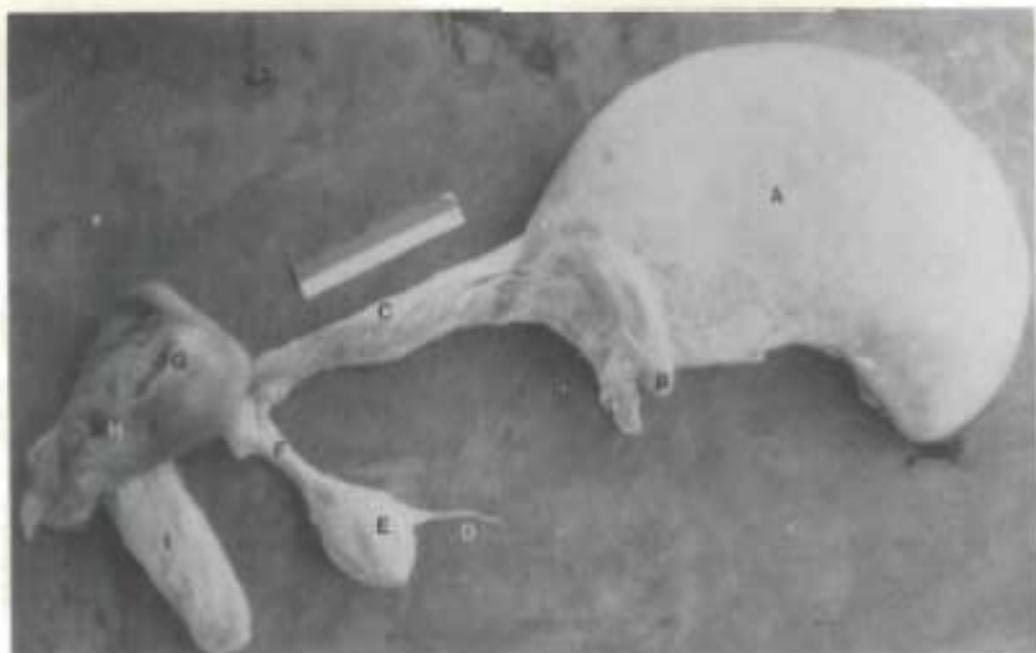


PLATE 5.1



PLATE 5.2



PLATE 5.3

of a corpus luteum of a recently pregnant seven-year old animal. Luteal tissue from this ovary is shown in Plate 5.6.. The presence of this cyst was not related to any foetal abnormality, and its effect on the reproductive physiology of the animal is unknown.

### 5.3.2.3.

#### RESULTS OF MACROSCOPIC OVARIAN SECTIONING

##### a) FOLLICLES

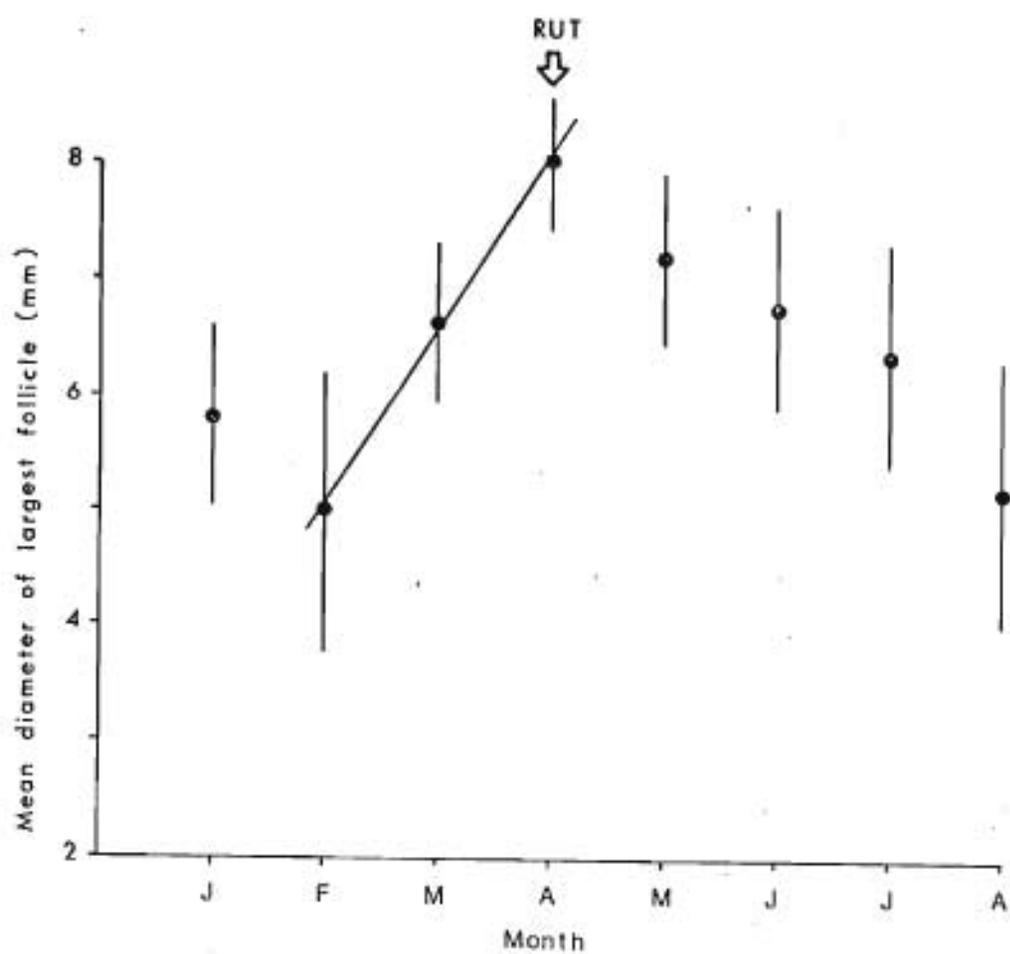
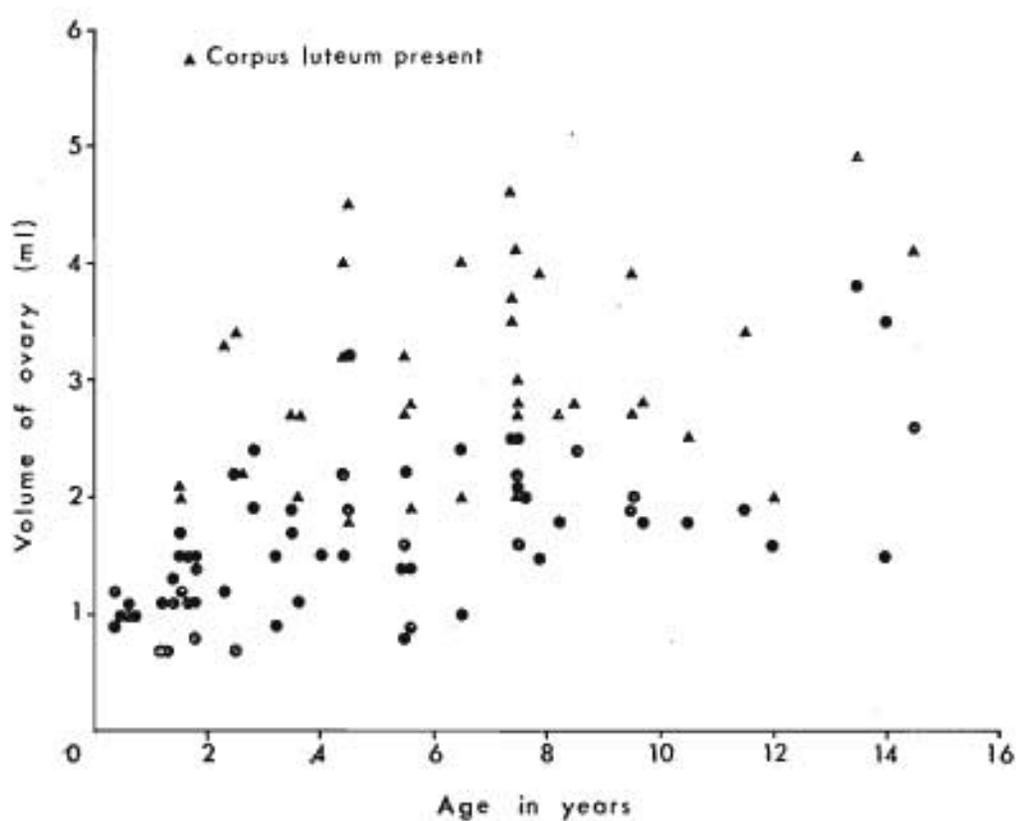
There is considerable variation in the number of macroscopic follicles in the wildebeest ovary. The minimum figure of eleven (both ovaries) was found in a 7,5 year old pregnant animal. The maximum value of 171 follicles was counted in a 12,5 year old pregnant animal.

A plot of the number of macroscopic follicles and age of the animal showed no obvious trend, possibly because small sample size necessitated the inclusion of both pregnant and non-pregnant animals.

The maximum mean diameter of a follicle was 11mm (from an 8,5 year old animal, shot on 8.5.1974), and it was assumed that this follicle was about to rupture, as it was very close to the periphery. The seasonal change in mean diameter of the largest follicle is shown in Fig. 5.6.. The April mean is significantly greater than the means of the preceding months ( $p < 0,01$ ), and corresponds exactly to the period of oestrus during the rut. The wildebeest thus deviates from the standard mammalian pattern where lactation inhibits follicular development, ovulation and oestrus (Perry and Rowlands, 1962). All wildebeest females with calves at heel are still lactating at the time of the rut. A similar situation is found in other species, for example the

Fig. 5.5. : The relationship between observed ovarian volume and age.

Fig. 5.6. : Seasonal change in mean diameter of the largest follicle for post-pubertal animals. . Insufficient data for September to December. Circles represent means; vertical lines 2 X S.E..



Uganda kob Adenota kob thomasi (Morrison and Buechner, 1971).

Fig. 5.6. indicates a decrease in mean follicle diameter after conception in April. This trend was investigated further by plotting maximum follicle diameter against gestational stage in Fig. 5.7.. The regression line for mean values for 20 day intervals was given by  $y = 0,03x + 9,49$ ; the line indicates that for every twenty days advance in the stage of pregnancy the mean maximum follicle diameter decreases by 0,5mm.

Although the data in the latter stages of pregnancy are limited, it would appear that a similar phenomenon exists in Uganda kob, where mature follicles greater than 5mm were found to be absent in the last 60 days of gestation (Morrison and Buechner, 1971). The results of plotting total number of follicles against gestational stage showed no meaningful relationship. Similarly, when total number of follicles were plotted against the mean diameter of the corpus luteum of pregnancy, no obvious relationship emerged.

#### b) CORPORA LUTEA

The majority of the corpora lutea were oval in section, although some were spherical. When fixed in formalin these structures had a characteristic yellowish-brown colour. Watson (1969) was able to differentiate between corpora lutea of cycle and those of pregnancy on the basis of colour. This was not the case in this study, possibly as a result of small sample size during oestrus, when corpora lutea of cycle would be encountered. Höfliger (1948), quoted by Harrison (1962), stated that in the cow the corpus luteum of pregnancy could not be distinguished from that of cycle.

The relationship between luteal tissue mass and mean diameter was established by dissecting out twenty corpora

Plate 5.4. : Low-power photomicrograph of section through a wildebeest ovary.

A = germinal epithelium; B = primary follicle;

C = theca interna; D = cumulus oophorus;

E = oocyte; F = liquor folliculi.

Scale divisions are  $10^{-1}$ mm.

Plate 5.5. : Photomicrograph of section through corpus luteum of pregnancy.

Scale divisions are  $10^{-1}$ mm.

Plate 5.6. : Photomicrograph of section through cystic corpus luteum of pregnancy.

Scale divisions are  $10^{-1}$ mm.

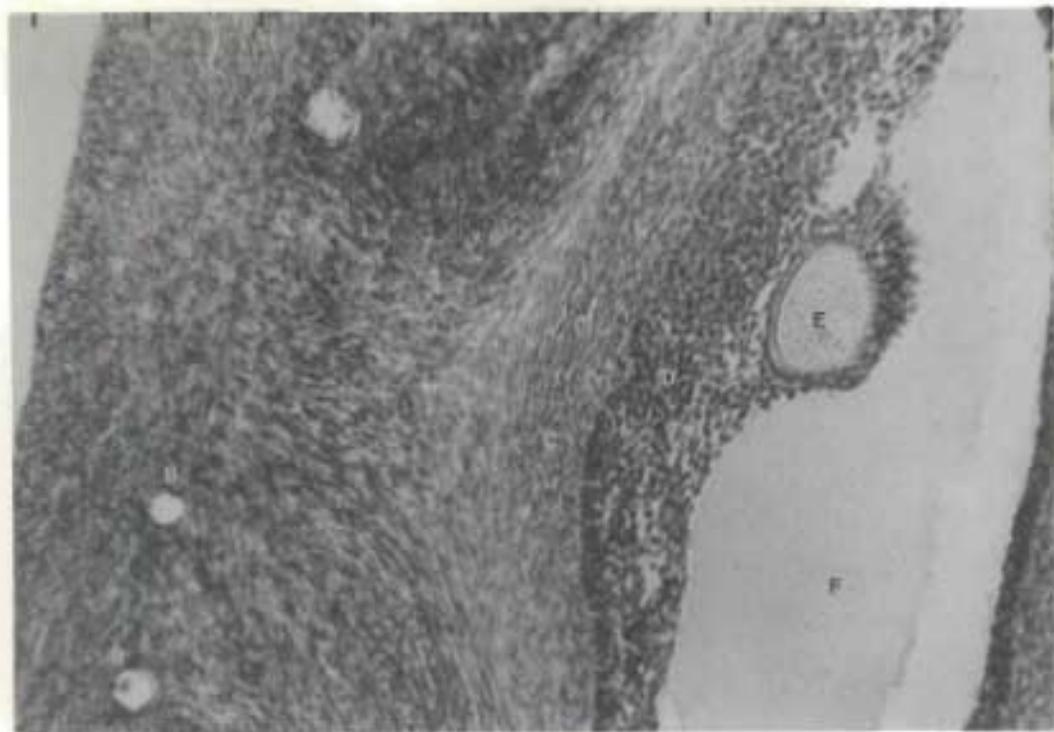


PLATE 5.4

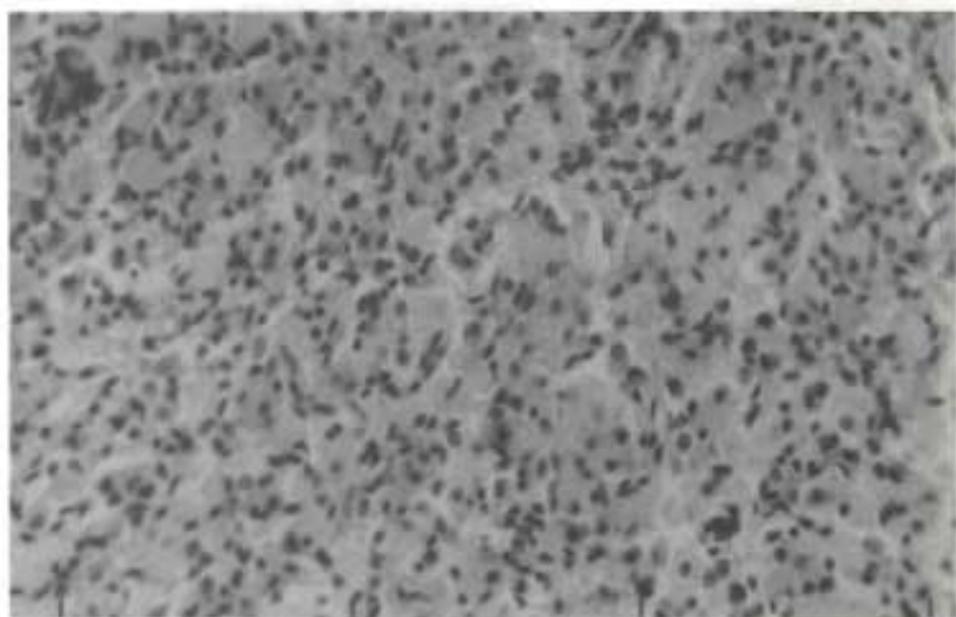


PLATE 5.5

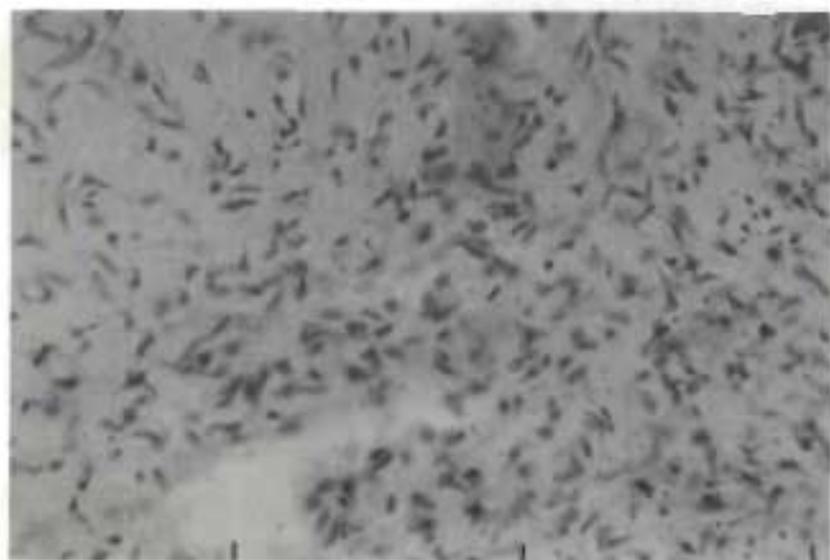


PLATE 5.6

lutea and weighing them to  $10^{-3}$ g. This relationship (Fig. 5.8.) gave a correlation coefficient of 0,91 ( $p < 0,001$ ), and a regression equation of  $y = 0,16x - 0,92$ . Thus it was considered justifiable to use mean diameter as an index of luteal tissue mass. By dividing pregnancy into forty-day intervals, and considering the mean corpus luteum diameter for each interval, Fig. 5.9. was prepared. Only in the final stages of pregnancy was there a significant ( $p < 0,05$ ) increase in mean diameter. The findings parallel those of Watson (1969), who described a regression in size of the corpus luteum by about 16% in the middle of pregnancy, followed by a gain towards the end of pregnancy. This change towards the end of pregnancy contrasts with the situation in impala (Kayanja, 1969) where regression takes place after a certain stage of pregnancy, and is not followed by a period of hypertrophy. In the Uganda kob, the size of the corpus luteum appears to be unaffected by the gestational stage (Morrison, 1971). Artiodactyls showing no appreciable regression before parturition include the hippopotamus, the cow, the giraffe and the domestic pig (Amoroso and Finn, 1962). The domestic sheep, the black rhinoceros, and the peccary Pecari tajacu all experience considerable regression before parturition, suggesting that extra-ovarian tissues supply enough progesterone for the maintenance of pregnancy. The African elephant appears to be almost solely dependent on extra-ovarian sources, as the corpus luteum has been found to contain minimal or no levels of progesterone (Short and Buss, 1965; Short, 1966; Hanks and Short, 1972; Ogle, Braack and Buss, 1973). The inference from this study is that the corpus luteum of the wildebeest is a major source of progesterone during the terminal stages of pregnancy.

Fig. 5.7. : Maximum diameter of follicles related to gestational stage. Animals with no macroscopic embryo were assumed to be 10 days pregnant. Squares denote mean values for 20-day intervals, except in the case of absence of macroscopic embryos. The regression equation for the mean values is :  $y = -0,03x + 9,49$ .

Fig. 5.8. : Relationship between mean corpus luteum diameter and corpus luteum mass. Regression equation in text.



## 5.3.2.4.

OVULATION, OESTRUS, AND IMPLANTATION

The wildebeest exhibits a remarkable synchrony of oestrus. The social environment and the presence of rutting males have been postulated as the final psychological triggers inducing synchronous oestrus in several species, the females of which are already "primed" by photoperiodicity (Fairall, 1972; Grubb and Jewell, 1973).

The relationship between oestrus and ovulation in the wildebeest is not altogether clear: there is evidence that the wildebeest experiences a "silent" ovulation (Watson, 1969), which is ovulation without overt oestrus. It has been suggested that, in species displaying silent ovulation, a regressing corpus luteum of cycle is necessary to permit the full expression of oestrus in association with the next ovulation (Perry, 1971). The phenomenon has been reported in several species of wild ungulates, including buffalo (Grimsdell, 1973a) and Uganda kob (Morrison, 1971; Morrison and Buechner, 1971).

Watson (*ibid.*) based his conclusions regarding the "silent" ovulation of wildebeest on the simultaneous presence of a regressing corpus luteum of cycle and a corpus luteum of pregnancy, or on a regressing corpus luteum together with a large follicle. No animal in this study was found to have more than one corpus luteum. Evidence for the possibility of "silent" ovulation was based on only two animals, although the female sample over the rut was limited. The first specimen had two follicles in the 8 - < 9mm size class (the only occasion on which more than one follicle was recorded in this size class), at the beginning of April 1974, and could consequently be assumed to be approaching oestrus. The second specimen, collected during the rut, had a large follicle of 10mm together with a corpus luteum. This may also be interpreted as a possible instance of impending postconception ovulation, which has been recorded for elk (Halazon and Buechner, 1956), and need not

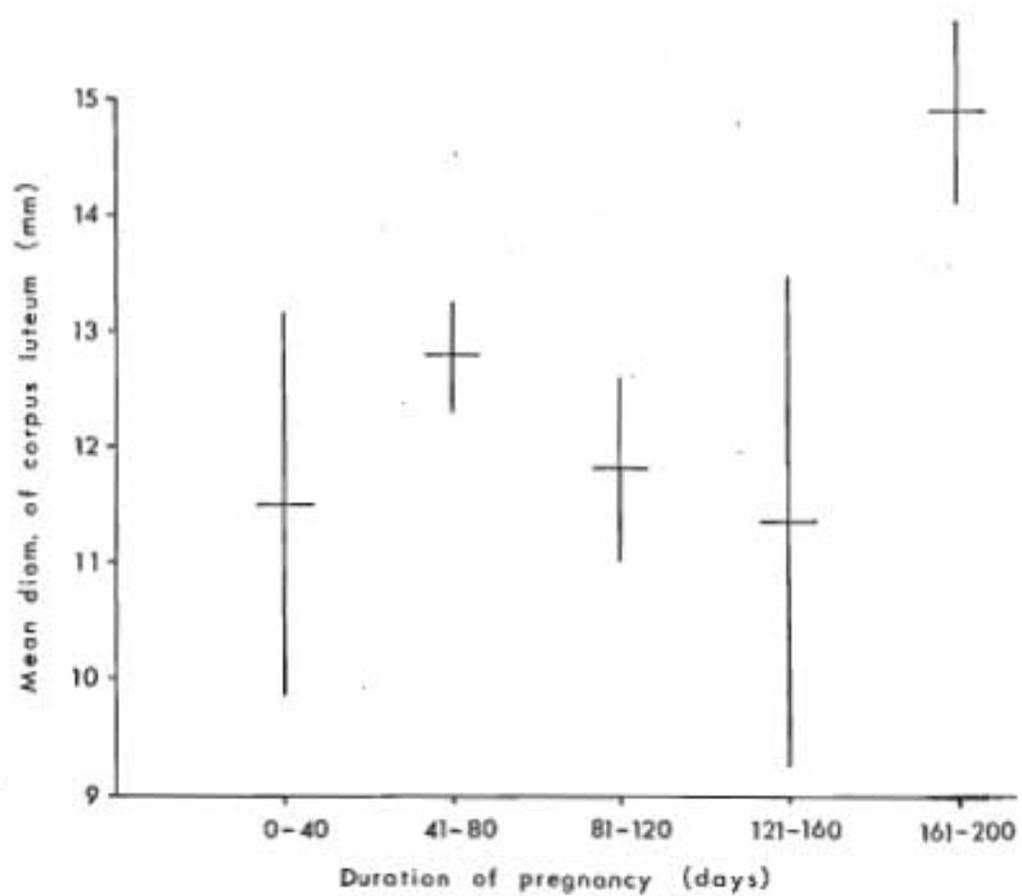
necessarily relate to a "silent" ovulation. Further, the presence of two corpora lutea need not imply two ovulations, as accessory corpora lutea may be derived from unruptured follicles.

A small percentage of calves is born out-of-season, indicating that some females are asynchronous in their cycles. Eight cases were recorded of aseasonal newly-born calves (two of these were recorded by other observers: Brooks and Keep, both pers. comm.). By back-dating from the gestation period (see Section 5.2.2.(c)), the month of conception and hence oestrus could be ascertained. In both June and July there were single "records" of oestrus determined in this manner; in August there were three, in September two, and in October one. Braack (1973) reports that in the Kruger Park a few calves are born in March and April. This would mean cases of oestrus in July and August the previous year, assuming an 8,5 month gestation period. Anderson (1975) states that in impala from the Complex most "out-of-season" calves are dropped during April, corresponding to conception during September and October.

Thus there is some evidence that out-of-season young of wildebeest tend to be conceived over a specific period. On the limited data, one can only state the possibility of the peak of out-of-season oestrus occurring in August and September. It is possible that cows that lose calves soon after birth are more likely to come into oestrus earlier (Watson, 1969), but I wish to introduce an alternative or additional hypothesis for aseasonal births. Fig. 5.10. provides an indication of the frequency of occurrence of follicles of different diameters. As there is a marked discrepancy between the frequency of occurrence of follicles below and above about 4mm in diameter, one may assume that follicles in the larger size classes (>4mm diameter) will eventually ovulate. This is further supported by the fact that follicles in these larger classes almost always occur singly in each ovary.

Fig. 5.9. : Mean diameters (horizontal lines) of corpora lutea for five gestational stages. Vertical lines indicate 2 X standard error.

Fig. 5.10. : Relative percentage frequency of numbers of follicles in specific size classes. Number of follicles counted = 4042, being a total from all ovaries sectioned. All ages taken into consideration.



The maximum follicle sizes of non-pregnant yearlings collected after the rut were all larger than 4mm, except for one ( $n = 6$ ). If one assumes a linear increase in follicular diameter prior to ovulation, then from Fig. 5.6. the diameter of a follicle would increase by approximately 1,5mm over a one-month period. In Fig. 5.11., the maximum follicle size of non-pregnant yearlings has been plotted against calendar month. Assuming that ovulation corresponds to attainment of the 10 - <11mm follicle size class, then, by applying the growth rate derived from Fig. 5.6., it is possible to predict tentatively when ovulation would occur. In three cases, predicted oestrus falls approximately in August, and the suggestion is that, if a second rut exists, then it is likely that the females displaying oestrus at this time are mainly yearlings which failed to conceive at the first rut in March and April.

When ovulation occurs, there is no evidence that preference is given to either ovary. Combined totals of corpora lutea, corpora nigra and the frequency of occurrence of the largest follicle produced the results in Table 5.1.. Chi-square values did not depart significantly from a 1 : 1 ratio ( $p > 0,1$ ). In every case implantation occurred in the same side as ovulation i.e. homolateral. Both these findings agree with those of Braack (1973) from the Kruger Park. Watson (1969) however recorded a single case where right ovary ovulation resulted in left horn implantation. His data indicated that the first fertilised ovulation tended to be from the right side, but after this both ovaries contributed equally to fertilisation.

There appears to be a discrepancy between persistence of corpora nigra in the Complex population and in the Serengeti population described by Watson (ibid.). In the latter population, corpora nigra persisted in the ovaries to the extent that Watson was able to derive a linear relationship between the number of corpora nigra and reproductive age. Table 5.2. shows the relative frequency of occurrence of corpora nigra

**TABLE 5.1.** : Frequency of occurrence of corpora lutea and largest follicles in left and right ovaries, with numbers of corpora nigra counted. Data from Vincent were extracted from his raw data, collected in 1967. Assuming that the ovary with the largest follicle is that one which will ovulate, the totals represent the number of possible ovulations.

	<u>LEFT OVARY</u>	<u>RIGHT OVARY</u>	
Corpora lutea	20	33	} Vincent
Corpora nigra	85	81	
Largest follicle	29	25	
Corpora lutea	16	23	} This study
Corpora nigra	47	60	
Largest follicle	36	29	
	<u>233</u>	<u>251</u>	

**TABLE 5.2.** : Frequency of occurrence of corpora nigra counts in single ovaries. Vincent's data unpublished, collected in the Complex in 1967. Source of Vincent's data as for Table 5.1..

NO. OF CORPORA NIGRA	NO. OF OVARIES AND PERCENTAGE			
	VINCENT		THIS STUDY	
	NO.	%	NO.	%
1	78	66,1	39	55,7
2	31	26,3	20	28,6
3	9	7,6	7	10,0
4	0	0	4	5,7

in single ovaries. When both ovaries are combined, the maximum count was 6, which occurred in 2,4% of paired ovaries. In comparison, Watson recorded a maximum of 10 from paired ovaries.

### 5.3.3.

#### STEROID ASSAY RESULTS

The results of gonadotrophin and gonadal steroid assays are given in Table 5.3., together with the age, reproductive condition and some ovarian features of the animals from which the samples were taken.

#### a) FSH AND LH

On the few data presented, there appears to be little obvious relationship between FSH levels and maximum follicle diameter; a clear-cut relationship would in any case probably not be expected during pregnancy. The LH values serve to provide a range of ratios of FSH to LH during pregnancy.

The lowest value of LH (2,2 mIU/ml) is recorded from the single non-pregnant animal, and it is possible that the higher values in pregnant animals result because LH may be necessary for corpus luteum formation (in addition to its effect on the synthesis of ovarian steroids), although the high levels of progesterone in the luteal phase of pregnancy may prevent any sudden surges of LH release (Short, 1974).

#### b) OESTROGENS

In the non-pregnant female the ovary is the principal site of oestrogen production, but during pregnancy the placenta becomes a more potent source. Oestradiol -  $17\beta$  is the form in which oestrogen is probably secreted in the ovary. Oestrone, the second major natural oestrogen, is also found in the ovary and

**TABLE 5.3.** : Hormonal levels for seven females, six of which were pregnant.  
Reproductive condition and major ovarian features are included.

DURATION OF PREGNANCY (DAYS)	AGE CLASS (YEARS)	LACTATION	TOTAL NO. OF FOLLICLES (BOTH OVARIES)	SIZE CLASS OF LARGEST FOLLICLE DIAMETER (mm)	FSH (mIU/ml)	LH (mIU/ml)	OESTRADIOL - 17 $\beta$ (pg/ml)	OESTRIOL (ng/ml)
NON-PREGNANT	10 - 11	No	132	3 - 4	0,9	2,2	132	0
64	4 - 5	No	ovaries not collected		0,3	5,9	132	0
75	2 - 3	No	31 (Right ovary only)	6 - 7 (Right ovary only)	2,6	3,9	292	0
77	12 - 13	No	171	4 - 5	<0,28	3,9	160	0
80	5 - 6	Yes	46	5 - 6	0,5	2,6	120	0
85	4 - 5	Yes	34	8 - 9	0,6	4,2	72	0
98	12 - 13	No	49	7 - 8	1,0	6,6	120	0

as an excretion product in the urine. Oestriol is the least active of the natural oestrogens, and appears to be a metabolic breakdown product of the other two. Oestrogens specifically stimulate tissues derived from the Mullerian duct and the urogenital sinus, and promote growth of mammary glands. Further effects include proliferation of vaginal mucosa, endometrial hypertrophy and metabolic manifestations (Eckstein, 1962).

The oestrogen results are included in Table 5.3.. The single non-pregnant animal had an oestradiol level of 132 pg/ml, which is below the level found in cattle. Mason, Krishnamurti and Kitts(1972) reported values in a standardised cattle 21-day cycle to range from 17,6 to 117,5 ng/100ml (equivalent to 176 pg/ml to 1175 pg/ml).

The rise in oestrogen output during pregnancy is due to the presence of placental cells. Oestradiol in wildebeest is present in animals at least two months pregnant (Table 5.3.). This contrasts with the findings in cattle, where oestrogenic activity was not detected until the last month of pregnancy (Saba, 1964). Pope, Jones, and Waynforth (1965) found no detectable oestrogen in cattle 2 - 3 months pregnant. Both sets of results used the mouse uterine mass method, and are thus not strictly comparable with my results.

The complete absence of any detectable oestriol is in accord with the contention of Austin & Short (1972c) that this oestrogen is not produced at all by most mammals. Short writes (in litt. to J. Hanks, 1976): "... we still don't know to what extent it is an important hormone in its own right (this seems highly doubtful) and to what extent it is just a biological, rather inert, metabolite. It is certainly only produced in large amounts by man and the other Great Apes, and although there

have been claims to have isolated it from blood or urine from sub-human primates, these claims have seldom been substantiated by rigorous chemical identification, and I would still stand by the statement that it is not produced by most mammals."

#### 5.3.4.

#### LACTATION AND WEANING

The anatomy of the wildebeest mammary gland is essentially the same as that of the domestic cow, described, for example by Hammond (1927). The initiation of milk secretion is dependent upon the combined effect of ovarian steroids, pituitary growth hormones, ACTH, and lactogenic hormone (Amoroso, 1969). The duration of lactation, and the seasons over which it extends, are of the utmost importance. Sadleir (1969a) considers lactation to produce even more strain on the female than pregnancy, and concludes that it must consequently result in an increased food intake. Nutrition during lactation may govern subsequent reproductive events in the female.

Fig. 5.12. depicts mammary gland mass changes during pregnancy, showing the major changes which occur in mass between lactating and non-lactating glands. The mean mass of non-lactating glands from parous females was 379,4g, compared to a value of 961,9g for lactating, parous animals. On average, lactation induces a 2,5 times increase in mass of the mammary gland.

The percentages of lactating females per month are shown in Fig. 5.13.. Nulliparous or primiparous animals were excluded. Negligible calf loss in January and February is the probable cause of the entire sample for those months being in lactation. From March to July, the lowered percentages of lactating animals reflect those females which had ceased lactating following calf loss. The sudden drop in August reflects either maximum calf mortality at the

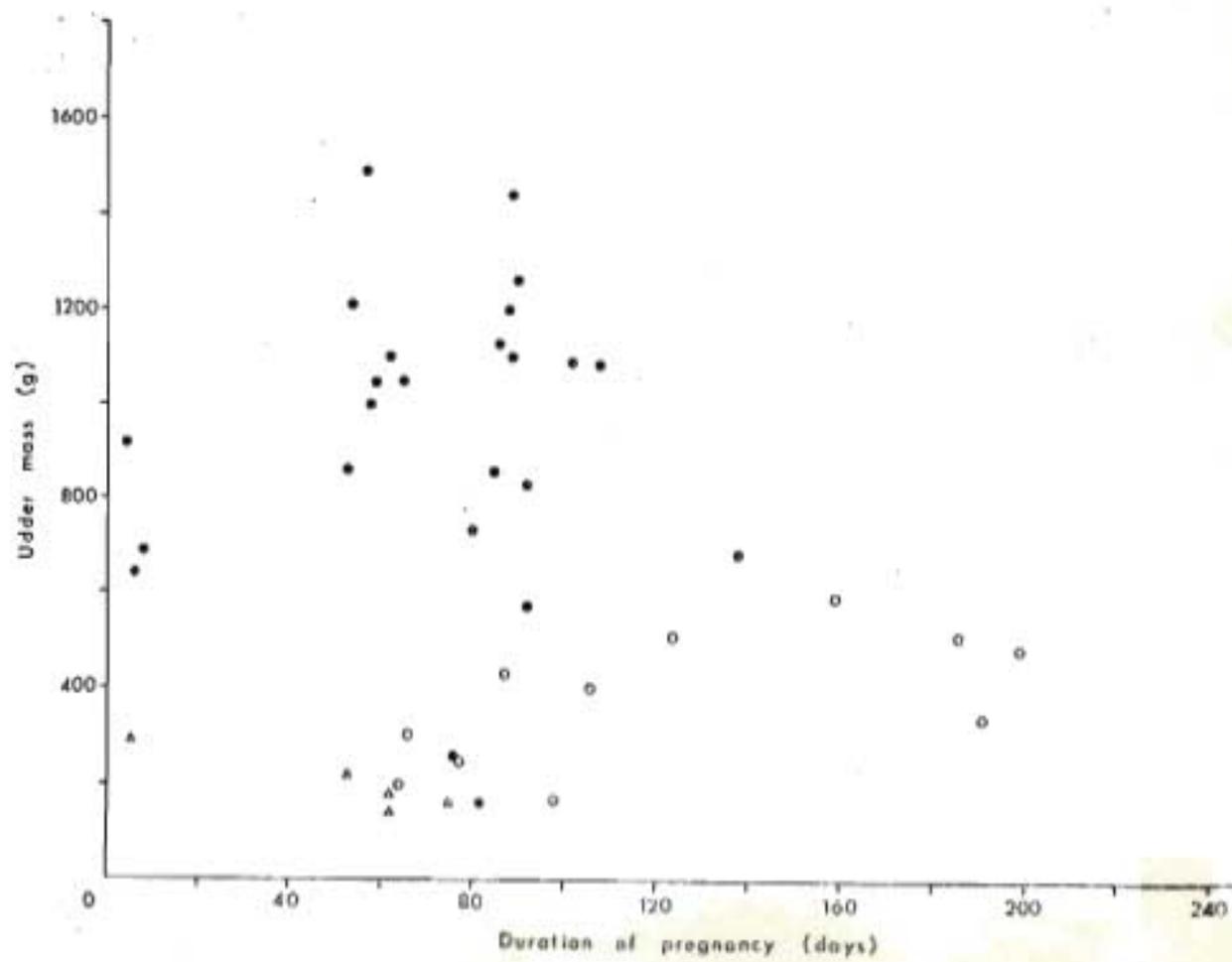
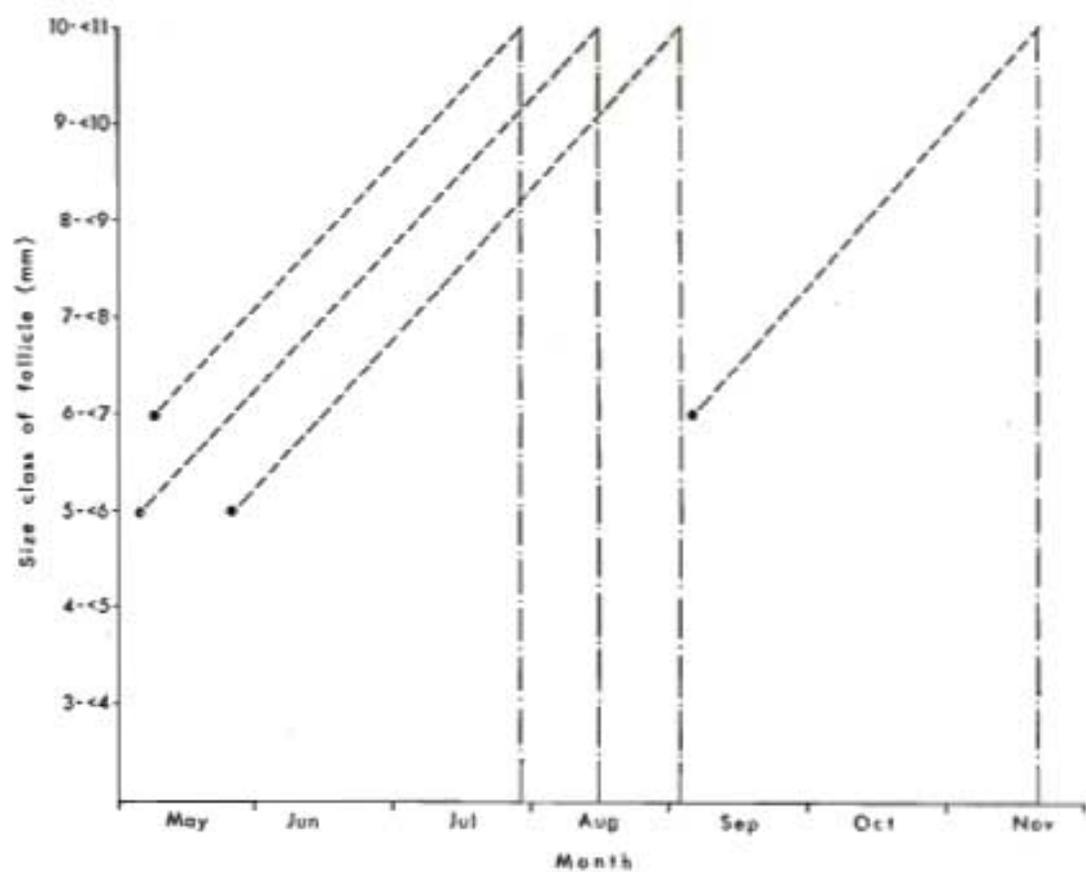
Fig. 5.11. : Maximum follicular diameter (circles) of non-pregnant yearlings which had failed to conceive at the rut in March and April. Dashed diagonal lines are projected growth rates (see text). Vertical dashed lines relate attainment of the 10 - < 11mm size class (at which ovulation occurs) to month.

Fig. 5.12. : Variation in mammary gland mass with duration of pregnancy.

Open circles = non-lactating, parous.

Closed circles = Lactating and parous.

Triangles = non-lactating, primiparous.



end of the dry season, or the onset of weaning, or a combination of both. Whatever the factor, weaning appears to be completed by September. The small percentage of lactating animals in November corresponds to early calves of the next season.

Assuming a December calving peak (see section 5.3.6.2.), and bearing in mind the inaccuracies resulting from combining data from different years, calves are weaned at about eight months. The cessation of lactation apparently does not reflect the calf's willingness to continue suckling, for Talbot and Talbot (1963) found milk in the stomachs of animals up to sixteen months old, suggesting they will suckle again when lactation follows the next parturition.

Further, lactation extends through most of the dry season, so that critical years in which nutrition is a limiting factor would consequently have immediate impact on lactating females, and possibly secondary effects as well. Mitchell, McCowan and Nicholson (1976) have shown that red deer which breed successfully one year may fail the following year on account of poor condition from the effects of pregnancy and lactation in a nutritionally poor environment.

### 5.3.5.

#### ATTAINMENT OF PUBERTY AND AGE-SPECIFIC CONCEPTION RATES

##### 5.3.5.1.

##### PUBERTY

Eckstein (1962) considers that puberty cannot be equated with the attainment of full reproductive capacity, but that it is a stage of variable length during which reproductive processes are perfected and synchronised. On this basis, all female yearlings in the Complex could be taken as pubertal, despite the fact that some are conceiving. The culmination of puberty is sexual maturity, and if

this is defined by ovulation (i.e. by the presence of a corpus luteum or corpus nigricans), then 22% of the yearlings are sexually mature i.e. they conceive in their second year of life.

From Table 5.4. it is clear that the yearling conception rate (equivalent to attainment of sexual maturity) is highly variable geographically. It is also likely that it varies in time within the same area. Sadleir (1969b) has reviewed the effects of light and temperature on the attainment of puberty. Nutritional factors are most often cited as causes for delayed puberty. Daniel (1963) related early oestrus in red deer to areas with good food. Pimlott (1959) found conception in 29% of yearling elk Alces alces in one area in Newfoundland compared to 67% for the rest of the province. Reduced availability of food resulting in delayed puberty may be associated with the attainment of a minimal critical body size (Joubert, 1963; Sadleir, 1969a; Mueller and Sadleir, 1975).

Population structure has even been shown to affect puberty: Snyder (1962) demonstrated that alteration of the sex ratio in woodchucks Marmota monax led to a delayed female puberty. Edaphic factors may also influence the timing of puberty (Moustgaard, 1959). It has also been shown that under certain conditions various grasses possess sufficient oestrogenically active material to cause infertility in livestock. Although to my knowledge no signs of hyperoestrogenicity have been reported in Africa, Symington (1965) has shown that the oestrogenic activity of veld grazing can reach levels higher than those reported to produce this hyperoestrogenic syndrome.

Clearly it is presumptuous to isolate factors which may cause the somewhat delayed puberty in the Complex populations in comparison to other populations, as it is likely that a combination of the factors discussed above is responsible.

## 5.3.5.2.

CONCEPTION RATES RELATED TO AGE CLASS

In the conception rates presented in Table 5.4., four age classes only are considered. Adult conception rates appear to be fairly consistent when comparing different populations, except for data from Wankie. There is evidence of temporal variation in the Complex adult conception rate, but it is uncertain whether the differences would exert much impact on the dynamics of the population. If the differences between years are real (i.e. do not result from sampling or other errors), then these would probably be caused by differences in range conditions. Conception rates have been related to different nutritional conditions for North American cervids (Cheatum and Severinghaus, 1950; Taber and Dasmann, 1958; Pimlott, 1959). Field and Blankenship (1973) related conception rates of some East African ungulates to rainfall, biomass of vegetation, and crude protein. Tassell (1967) found a high conception rate in cattle if good feeding conditions occurred between parturition and oestrus.

Talbot and Talbot (1963) reported that cows in their very old age classes were not pregnant. There was no sign of reproductive senescence in animals older than 16 years in the Complex. Neither Watson (1969) nor Braack (1973) found any indication of decreasing conception rates in older animals.

Of those animals for which pregnancy was recorded in the Complex, 107 had fetuses sufficiently advanced for the determination of sex (these results include data collected by Anderson in 1963, and by Vincent in 1967). Fifty-seven of these were male, and fifty female. This does not represent a significant departure from a 1 : 1 ratio. This is in accordance with the findings of other workers on wildebeest (Talbot and Talbot, 1963; Watson, 1969; Braack, 1973).

TABLE 5.4. : Percentages of each age class conceiving, from different localities, and in different years.  
 In many cases, figures have been arrived at from raw data, either published or unpublished.

LOCALITY	YEAR	YEARLINGS (A)	2 - 3 YRS. OLD (B)	3 YRS. OLD (C)	(B) + (C)	SOURCE
HGR + CORRIDOR COMPLEX COMPLEX	1963	0% (n = 5)	No data	No data	91,8% (n = 64)	Hitchins (pers. comm.)
	1967	No data	No data	No data	94% (n = 50)	Vincent (pers. comm.)
	1973 - 74	22% (n = 9)	100% (n = 14)	86% (n = 36)	90% (n = 50)	This study
KRUGER NAT. PARK " " "	1967	11,8%	100%	91,5%	92%	Braack (1973)
	1972	57,1%				
MASAI MARA, KENYA	1959 - 61	83%	No data	No data	95%	Talbot & Talbot (1963)
SERENGETI, TANZANIA	1962 - 65	37%	83%	96%	No data	Watson (1969)
WANKIE, RHODESIA	1968	0%	No data	No data	74% (n = 61)	Higgins (1969)

## 5.3.6.

SEASONALITY OF CONCEPTIONS AND BIRTHS

## 5.3.6.1.

HUGGETT AND WIDDAS RELATIONSHIP

The Huggett and Widdas regression is shown in Fig. 5.14.. The gestation period (t) was taken as 250 days, as this is the mean figure of five estimates extracted from the literature by Mentis (1972). It also corresponds to Braack's (1973) estimation of gestation period in the Kruger Park, arrived at by measuring the intervals between calving peaks and rutting peaks. The mass at birth was taken directly from Braack (*ibid.*) as 21,74kg, a figure based on three animals. By substitution in the equation:

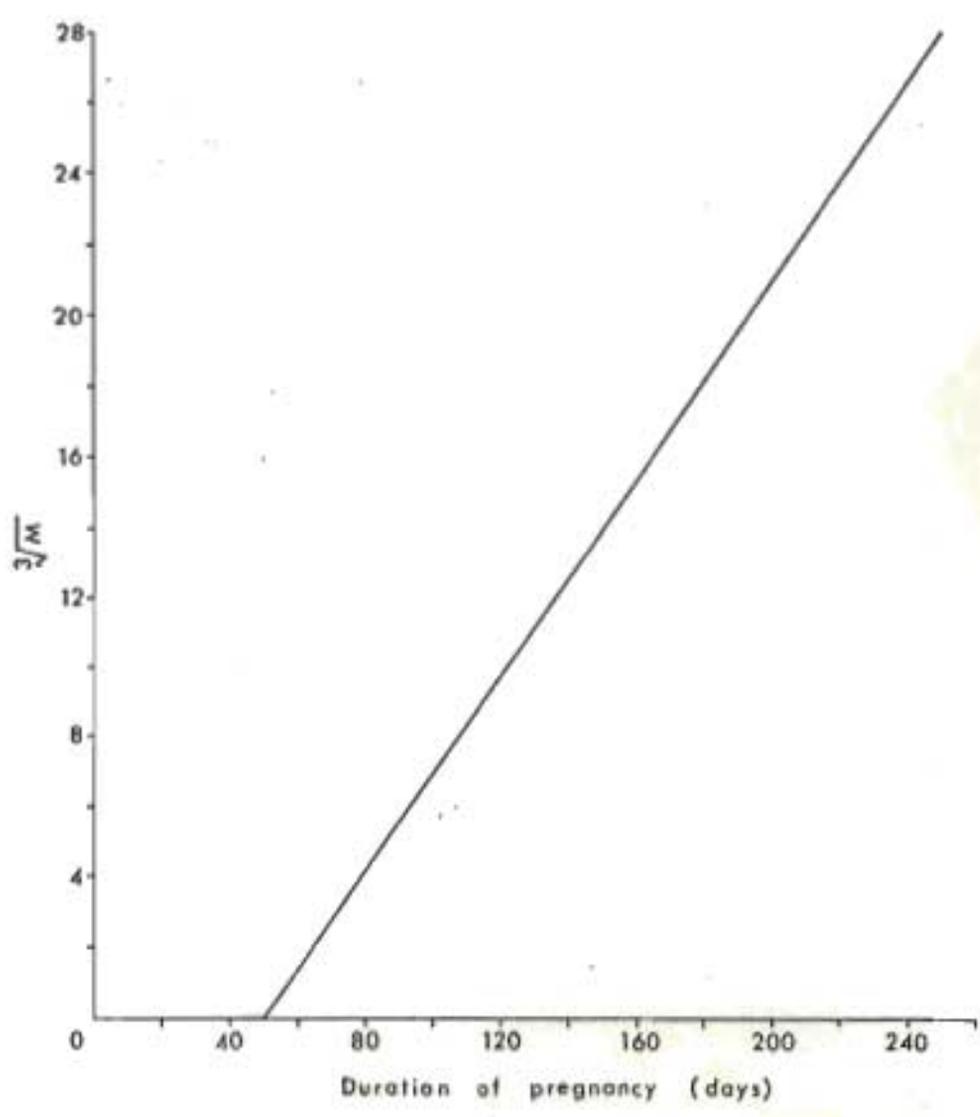
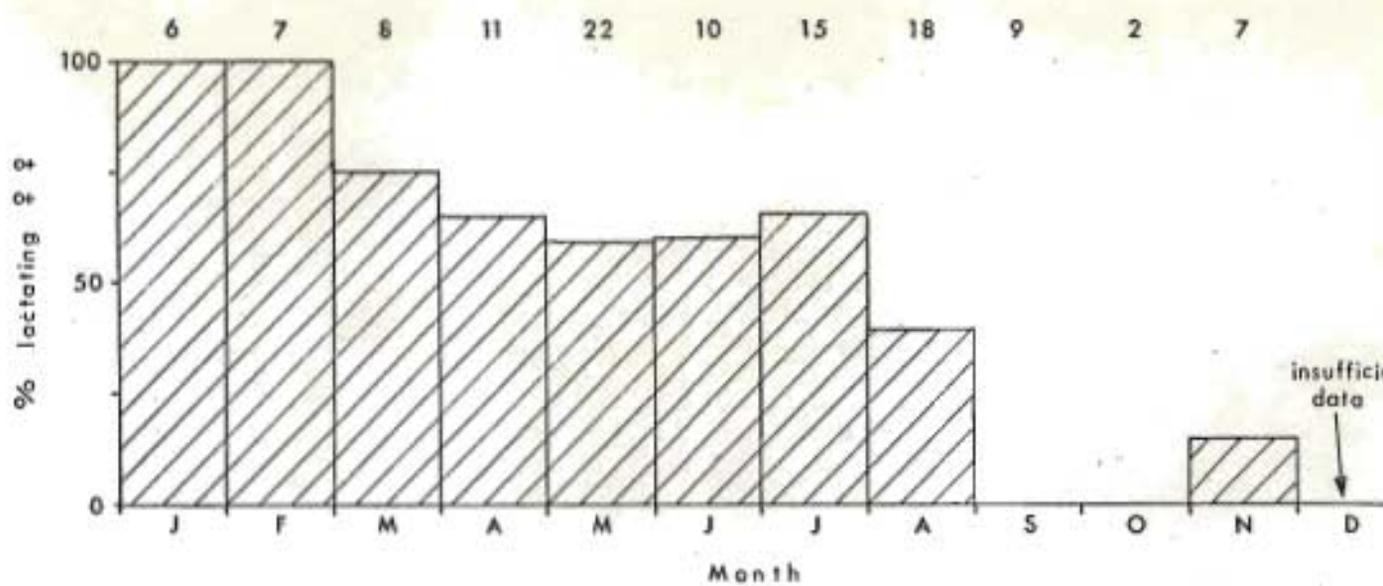
$$M^{1/3} = a (t - t_0)$$

(explanation of terms given under Methods), the value of a (the specific foetal growth velocity) was 0,1395. This is similar to the values derived by Watson (1969) for two separate years, on a population basis: 0,124 and 0,128.

The accuracy of the Huggett and Widdas regression has been adequately discussed by Perry (1953), Buss and Smith (1966), Laws and Parker (1968), and Frazer and Huggett (1974). Specific growth rates are averages for a species, and individual variation may be caused by factors such as nutrients available to the foetus (Frazer and Huggett, *ibid.*). The value of the regression is questionable in the estimation of age of small foetuses and embryos. Fig. 5.14. suggests that the foetal mass can be determined only after about fifty days post conception; Smuts (1974) estimates that in the zebra the conceptus is visible ten to fifteen days after fertilisation. Mass would readily be detectable on a triple beam balance by thirty days.

Fig. 5.13. : Percentages of lactating females in each month. Nulliparous, primiparous and parous animals which have not given birth the previous season are excluded from the totals. Figures for each month are total sample size for parous females. Data from Vincent (pers. comm.) collected during 1967 and 1968 also included.

Fig. 5.14. : The Huggett and Widdas regression of cube root of foetal mass against duration of pregnancy.



When comparing seasonal peaks in conception or parturition from different years, the error in the method will be constant for each year i.e. although absolute dates of projected conception or birth for any specific foetus may be in error, the differences between such dates for different foetuses would probably be real.

#### 5.3.6.2.

##### SEASONALITY

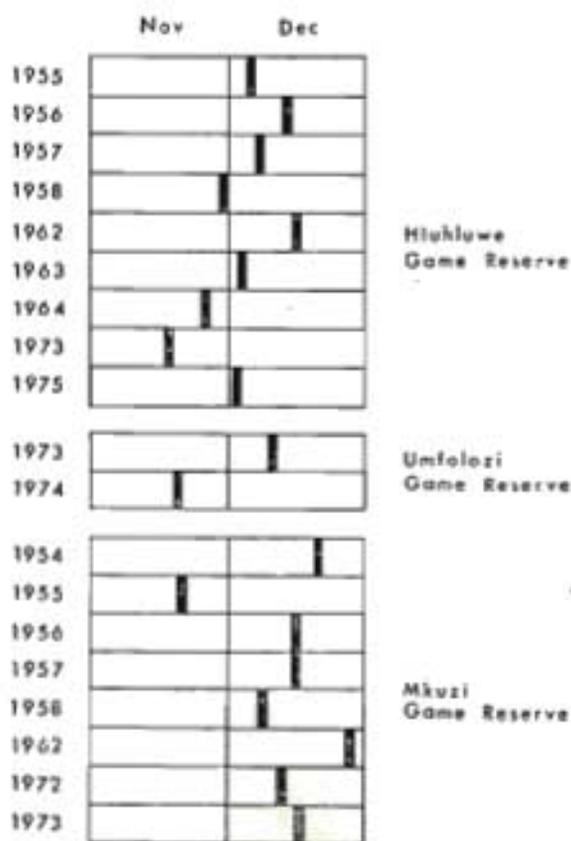
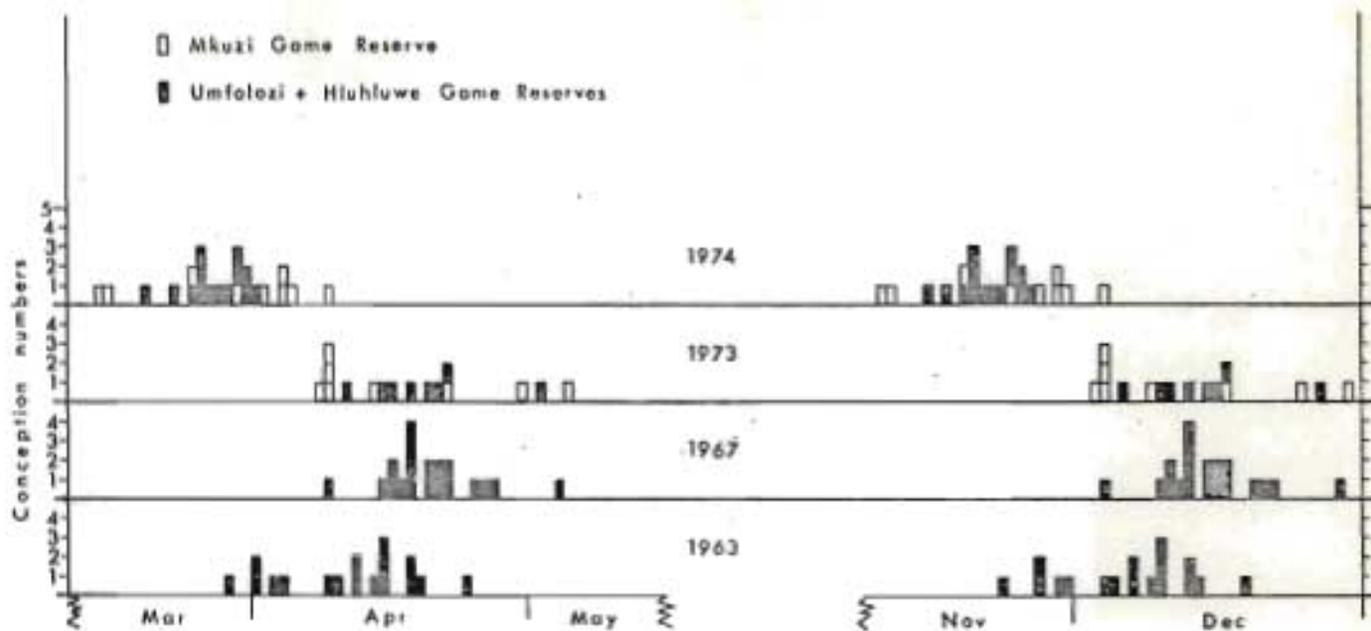
Sadleir (1969b) classified breeding seasons into six types. The wildebeest appears to fulfill most of the Type 1 conditions, where "length of time from conception to weaning is longer than a single optimal season ..... (and) where birth and weaning occur during the fixed optimal season, but the time of conception is pushed back so that it occurs either in a poor season or in the previous season."

Calving peaks for wildebeest in Africa have been summarised by Mentis (1972), and by Spinage (1973a). Local variation occurs in most populations, but calving peaks invariably fall within the rainy season. Birth peaks in the wet season are well documented for other animals as well (Laws and Clough, 1966; Spinage, 1969; Grimsdell, 1973a, and others).

The results of extrapolation from foetal mass to conception and birth dates are shown in Fig. 5.15.. In every case, conceptions and births are spread over about a one-month period, with the rut generally in April, and with parturition generally in December. Comparison with the dates on which first calves were observed (Fig. 5.16.), suggests that the Huggett and Widdas projections are in fact fairly reliable. The duration of the rut and of parturition appears shorter than in Kruger Park. Braack (1973) describes the rut in that area as extending from the first week in April to the first week in June, almost double the duration in the Complex. Similarly, calving extended from the first week in December to

Fig. 5.15. : Peaks of conception and parturition as determined from the Huggett and Widdas regression. Raw data for 1963 from Anderson (pers. comm.) and for 1967 from Vincent (pers. comm.).

Fig. 5.16. : Records of first calves. Data from personal observations, Natal Parks Board files, and personal communications from NPB officers.



mid-February, with a peak during the latter half of December and the first week of January (in all, ten weeks).

Sadleir (1969b) has reviewed the proximate factors controlling the onset of breeding. Classically, the onset of breeding is markedly affected by the level of nutrition, and in the majority of tropical to subtropical situations it is controlled by rainfall. Photoperiod is the proximate factor with green vegetation and rainfall the ultimate factor. "The very presence of a breeding season ..... shows that selection of individuals has worked to alleviate the detrimental effects of poor nutrition on the reproductive processes of the population concerned." (Sadleir, (1969b).

Estes (1976) has discussed the significance of breeding synchrony in the wildebeest, and maintains that it is necessary for specialised feeding on short green grass. He suggests that predation pressures help to maintain a short, sharp birth peak (the majority of births in the Ngorongoro population units occurred in a three-week period). The fact that seasonality produces offspring when grazing conditions are ideal is entirely consistent with the findings in this study: Chapter 7 discusses the high leaf to stem ratios found in grazing at the time of parturition, which are equivalent to a high level of available protein. It is pertinent to include the comments of Eckstein and Zuckerman (1955) on seasonality: "The teleological statement that an animal's breeding season is so timed, and the mechanism of its oestrous cycle so arranged, that its young are born at a season of the year favourable to the survival of the species, is not an explanation, but merely an expression of the fact that the physiological processes of animals are adapted to their particular ways of life. And in itself this is no more than a tautology."

Spinage (1973a) points out that it need not necessarily follow that it is natural to produce when conditions are optimal, as overproduction could threaten the survival of the species. He maintains that

random survival of the young might equally be selected for.

In Fig. 5.17., I have related conception and birth peaks (from Fig. 5.15.) to rainfall. Spinage (ibid.) has presented data to support the view that a proximate photoperiodic stimulus induces the rut in wildebeest: the species shows a short-day response i.e. breeding is initiated by decreasing daylength. Braack (1973) has shown that the rut corresponds with a period of most rapid decline in daylight hours and temperature. If photoperiodicity is the proximate factor for the rut, and as this factor is constant from year to year, what accounts for the variations in timing of the rut, as shown in Fig. 5.17. ?

Smuts (1974) argues that in any natural area the seasonal condition of the veld is largely due to three climatic variables - rainfall, daylight hours, and temperature. As the last two are relatively constant at any particular time of the year, only rainfall and concomitant increase in green vegetation can account for the irregularities in timing of the rut. Fig. 5.17. appears to support this contention: in both cases where the rut was early in the season (1963 and 1974), it was preceded by abnormally high rainfall. The relationship may appear clear, but one should be wary of drawing conclusions from short-term studies: when an ecological event (for example, heavy rainfall) coincides with a physiological event (early oestrus), the two need not be causally related.

By inspection of Figs. 5.15. and 5.17., it can be seen that the post-partum interval is about four months. This is confirmed from a gestation period of 250 days.

#### 5.4.

#### CHAPTER SUMMARY

The reproductive tract of the female wildebeest was described, and

Fig. 5.17. : Relationship of conception and birth periods to rainfall.

C = conceptions

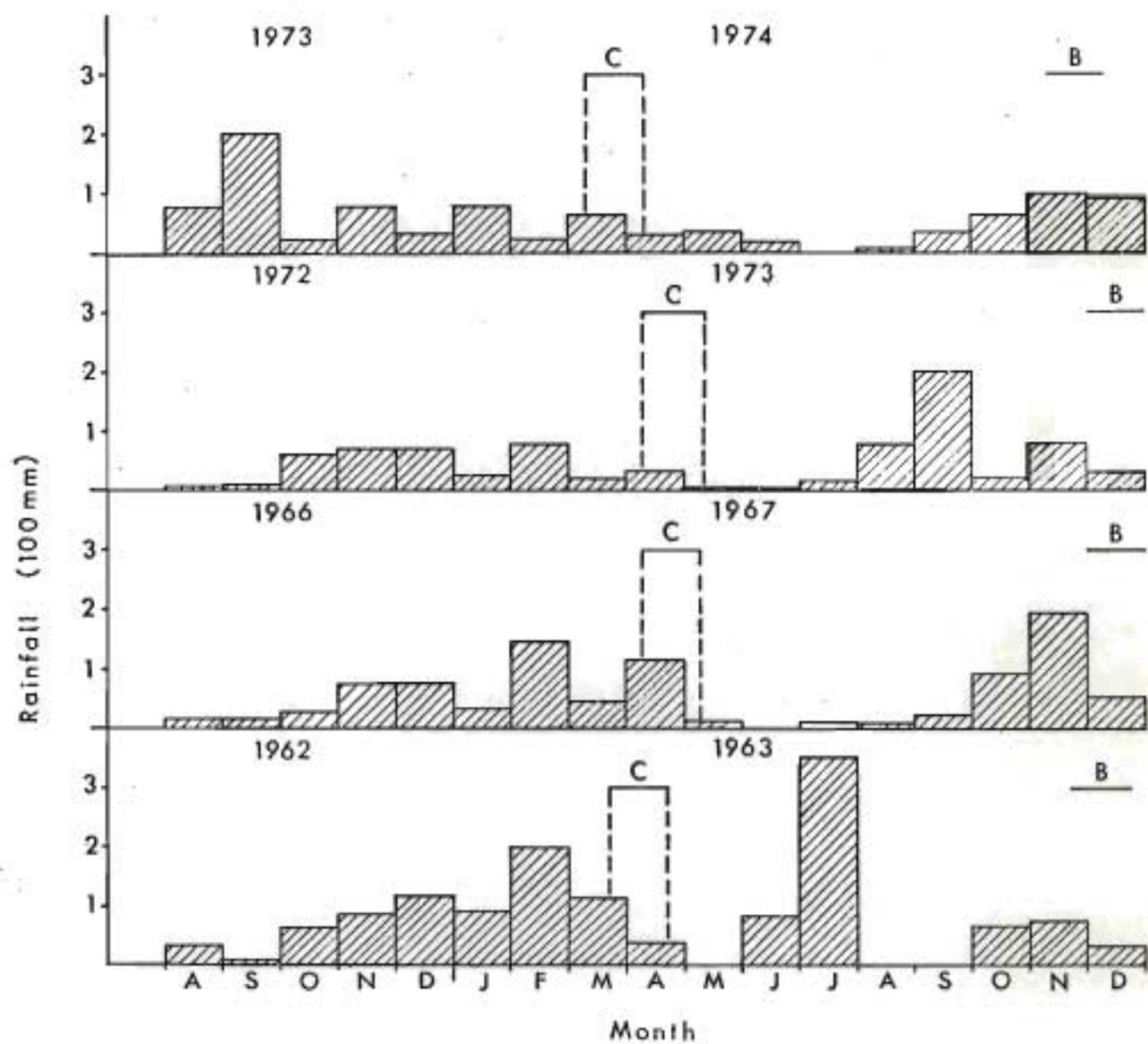
B = births

Rainfall figures : Aug. 1973 - March 1974 : 782mm

Aug. 1972 - March 1973 : 341mm

Aug. 1966 - March 1967 : 446,7mm

Aug. 1962 - March 1963 : 714,3mm



found to conform to the standard bovid pattern.

It did not appear that significant differences in mass existed between prepubertal left and right ovaries. Mean diameter of the largest follicles increased to a peak coinciding with oestrus in April. Lactation was found to inhibit neither follicular development nor oestrus.

Increase in mean diameter (and hence mass) of the corpus luteum during the terminal stages of pregnancy suggested that the corpus luteum of the wildebeest might be a major source of progesterone.

Evidence was presented to suggest that out-of-season calves were conceived over a specific period, and that such conceptions might occur in yearlings which had failed to conceive during the "true" rut.

Ovulation favoured neither left nor right ovary, and implantation was homolateral. Foetal sex ratios did not depart significantly from parity.

FSH, LH and oestrogen levels were determined from a small female sample. The absence of detectable oestriol is in accordance with findings in most mammals.

Calves are weaned at about eight months of age. Variation in yearling and adult conception rates is discussed.

Foetal mass data were used to provide peaks of conception (April) and parturition (December). There is evidence that an early rut is preceded by abnormally high rainfall, but this may be circumstantial.

## CHAPTER 6

### REPRODUCTION IN THE MALE

#### 6.1

##### INTRODUCTION

As in most polygamous mammals, the male is relatively dispensable in comparison to the female, and in terms of reproduction is consequently less important. However, Smuts (1974) has pointed out that the enhanced vulnerability of the male (see Chapter 9) to predation favours calf survival, with resultant effects on the perpetuation of the species.

The significance of puberty and sexual maturity in the dynamics of a population has been discussed in the previous chapter. Puberty is more important in the female, since the timing of puberty relative to the longevity of the species governs the total number of young produced (Sadleir, 1969b). The concepts of puberty and maturity are however more complex in the male, as in many ungulates sexual maturity does not necessarily imply successful mating, as this is often mediated by behavioural and social factors.

The reproductive cycles of few male mammals have been adequately investigated (Chapman, 1972). The necessity for such investigation is exemplified by the case of the Muntjac (Muntiacus sp.), where

fawns are born throughout the year. Chapman (1970) highlights the need for knowledge of the male cycle of the Muntjac by suggesting reasons for the year-round parturition: either the males are fertile throughout the year, or a male is fertile only for a restricted period, but these periods are not the same for all males.

The wildebeest male segment of the population experiences a well-defined rut, such that the males themselves act as environmental factors in the reproduction of the females: the rut forms part of the environment in which mating is taking place. Sadleir (1969b) categorises the timing of male breeding relative to the female into two main possibilities: either the males are capable of breeding throughout the year, or the males have a fixed breeding season coinciding with the female. In the former category the females either breed continuously, or they experience a discrete breeding season. Categorisation of this type requires understanding of seasonal changes in spermatogenesis, and in the morphology and histology of the reproductive and associated organs. In spermatogenesis, for example, the quality of the sperm (as measured by motility, longevity and proportion of live spermatozoa) shows characteristic seasonal variation even in those mammals that are fecund throughout the year (Chapman, 1972).

## 6.2.

### MATERIALS AND METHODS

The phenomenon of seasonality in the male may be investigated by a number of techniques:

- a) The change in testis mass. This is now so standard a procedure that reference is made only to earlier workers: Kellas (1955); Robinette and Child (1964); Anderson (1965); Wright (1969).

- b) The change in mass of accessory glands. Chapman (1972) lists those organs which should be investigated, including prostate glands, seminal vesicles, ampullary glands, bulbo-urethral glands, urethral glands and preputial glands.
- c) The change in seminiferous tubule diameter. This technique has been applied by numerous workers including Watson (1969), Dryden (1969), and Skinner and Huntley (1971 a and b).
- d) Changes in epididymal sperm number (Skinner and Huntley, 1971 a and b).
- e) Measurement of sperm motility (Skinner 1971 a; Skinner, Van Heerden and Van Zyl, 1971).
- f) The measurement of spermatogenic activity (Johnson and Buss, 1967 a and b).
- g) The use of gonadotrophin and androgenic hormone assays (Fairall, 1972).
- h) The assessment of vesicular and ampullar fructose and citric acid concentration (Skinner and Huntley, 1971 a and b). There exists a close correlation between testicular testosterone and fructose and citric acid concentration in many ruminants (Lindner and Mann, 1960; Short and Mann, 1966; Skinner, Booth, Rowson and Karg, 1968).

The simplicity of a) and c) led to their choice in this study. Furthermore, there is now substantial evidence that the two techniques are valid indicators of seasonality: Skinner and Huntley (1971 a) have demonstrated the validity of the techniques by the simultaneous undertaking of more refined methods such as those listed under d) and h). The diameter of the seminiferous tubule is considered to be a reliable index of ruminant sexual function (Hay, Lindner and Mann, 1961; Short and Mann, 1966), and has subsequently been used in various studies including those of Dryden (1969), Watson (1969),

Smuts (1976), and Hanks, Cumming, Orpen, Parry and Warren (1976).

### 6.2.1.

#### METHODS IN THE FIELD

As soon after death as possible, the testes were removed from the scrotum by cutting through the latter and the tunica vaginalis. If time permitted, the testes were weighed in the field on a triple beam balance to  $10^{-1}$ g, after dissecting away the pampiniform plexus, and including the epididymis. A second weighing was taken after removal of the epididymis. A small portion of the testis was excised from the centre, and fixed in Bouin's solution for subsequent histological processing. When several animals required processing it was considered that the delay in field weighing might result in autolysis of testicular cells in those animals still awaiting processing: in these cases the testes and epididymides were fixed in 10% formalin for subsequent weighing. Material was collected in this manner from one hundred and twenty-four animals.

In one adult male a complete dissection of the reproductive tract was performed after chopping through the pubic symphysis. For various reasons, it was not possible to make a routine collection of accessory glands.

### 6.2.2.

#### MICROSCOPY

Histological processing of the testes followed the sequence in Appendix II. After embedding, sections were cut at  $7\ \mu\text{m}$ , and stained with Haematoxylin and Eosin. From a small sample, (seven animals from Vernon Crookes reserve - see Chapter 4), further sections were prepared from epididymides, vasa deferentia, ampullae, bulbo-urethral glands, seminal vesicles and penis. These tissues were fixed in 10% formol saline, and histological processing followed that in Appendix I.

Using a micrometer eyepiece (8 x), and an objective of 45x, the testis sections were examined for the presence of spermatogenesis. Testes were considered prepubertal when a single layer of cells was apparent along the basement membrane of the seminiferous tubule, together with an absence of spermatids in the lumen of the tubule, which was usually filled with cytoplasmic extensions from the basement membrane. Sections were taken as postpubertal when there were several cell layers present, together with spermatids in the lumen.

The eyepiece micrometer was calibrated against an objective micrometer for the purpose of measuring tubule diameter. Measurements were taken in  $\mu\text{m}$  of thirty round tubules, and the mean value derived. Where autolysis or tubule shrinkage were apparent, then measurements were taken from the basement membrane.

### 6.3.

#### RESULTS AND DISCUSSION

##### 6.3.1.

#### THE REPRODUCTIVE TRACT

The reproductive tract (excluding testes) from an eight-year old male is displayed in Plate 6.1.. The terminal parts of the vasa deferentia thicken to form the ampullae, which are about 1cm across at the widest point, and about 9cm long. The seminal vesicles enter the ampullae just before the latter joins the urethra. The vesicular glands or seminal vesicles have faintly lobulated surfaces, and are about 5cm long, 3cm wide, and 0,75cm thick. They are situated at the anterior end of Wilson's muscle (urethralis muscle), which surrounds the urethra. Macroscopically, the seminal vesicles appear to be composed of individual lobules separated by trabeculae of connective tissue and muscle. Microscopically (Plate 6.2.),

Plate 6.1. : Reproductive tract (excluding testes) of eight-year old male wildebeest. Dimensions in text.

VD = Vas Deferens; Ur = Ureter; BL = Bladder;  
Am = Ampulla of Vas Deferens; S = seminal vesicle; W = pelvic urethra surrounded by Wilson's muscle (urethralis muscle); BU = Bulbo-urethral gland surrounded by bulboglandularis muscle;  
M = Bulbocavernosus muscle; N = Bulbospongiosus muscle; R = Retractor penis muscle; F = sigmoid flexure of penis; E = external urethral orifice.

Plate 6.2. : Photomicrograph of section through seminal vesicle of adult male collected in June. Numerous alveoli are present, separated by strands of inter-alveolar connective tissue, lined by columnar epithelium. Scale divisions on plate are  $10^{-1}$ mm.



PLATE 6.1

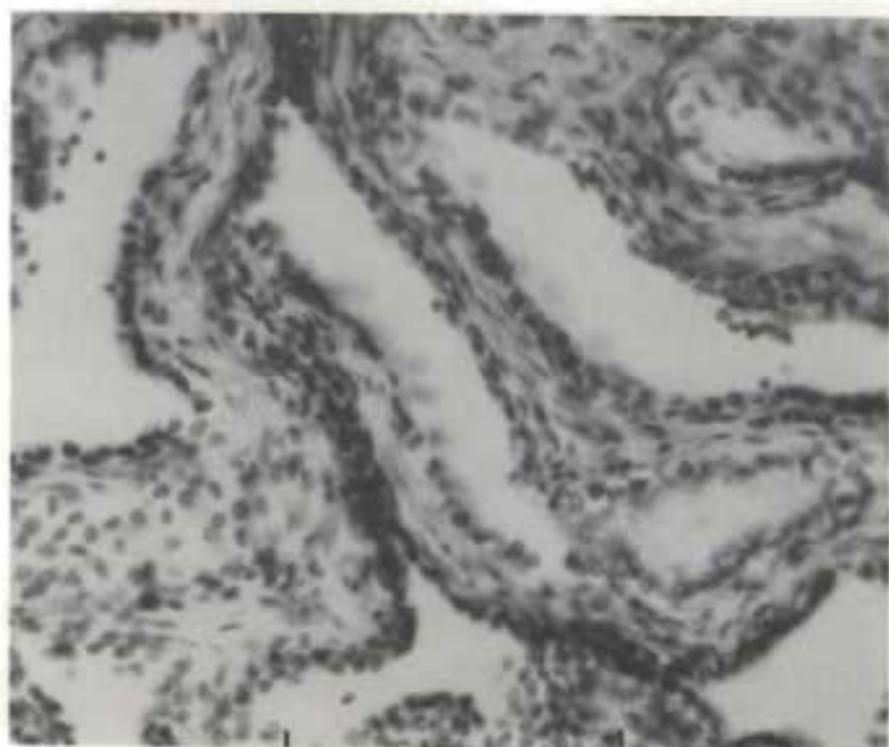


PLATE 6.2

each lobule contains numerous alveoli, which are separated by thick strands of inter-alveolar connective tissue. The alveoli are lined by columnar epithelium, which is presumably secretory in nature.

There was no distinct sign of a prostate gland, but bulbo-urethral glands were prominent, measuring 3cm long, 2,5cm wide and about 1,5cm thick. The bulbo-urethrales were also lobulated, and contained alveoli which were richly supplied by secretory cells (Plate 6.3.). The unerect penis measured 65cm; a microscopic section showed the typical mammalian form.

### 6.3.2.

#### PUBERTY AND TESTIS CHARACTERISTICS RELATED TO AGE

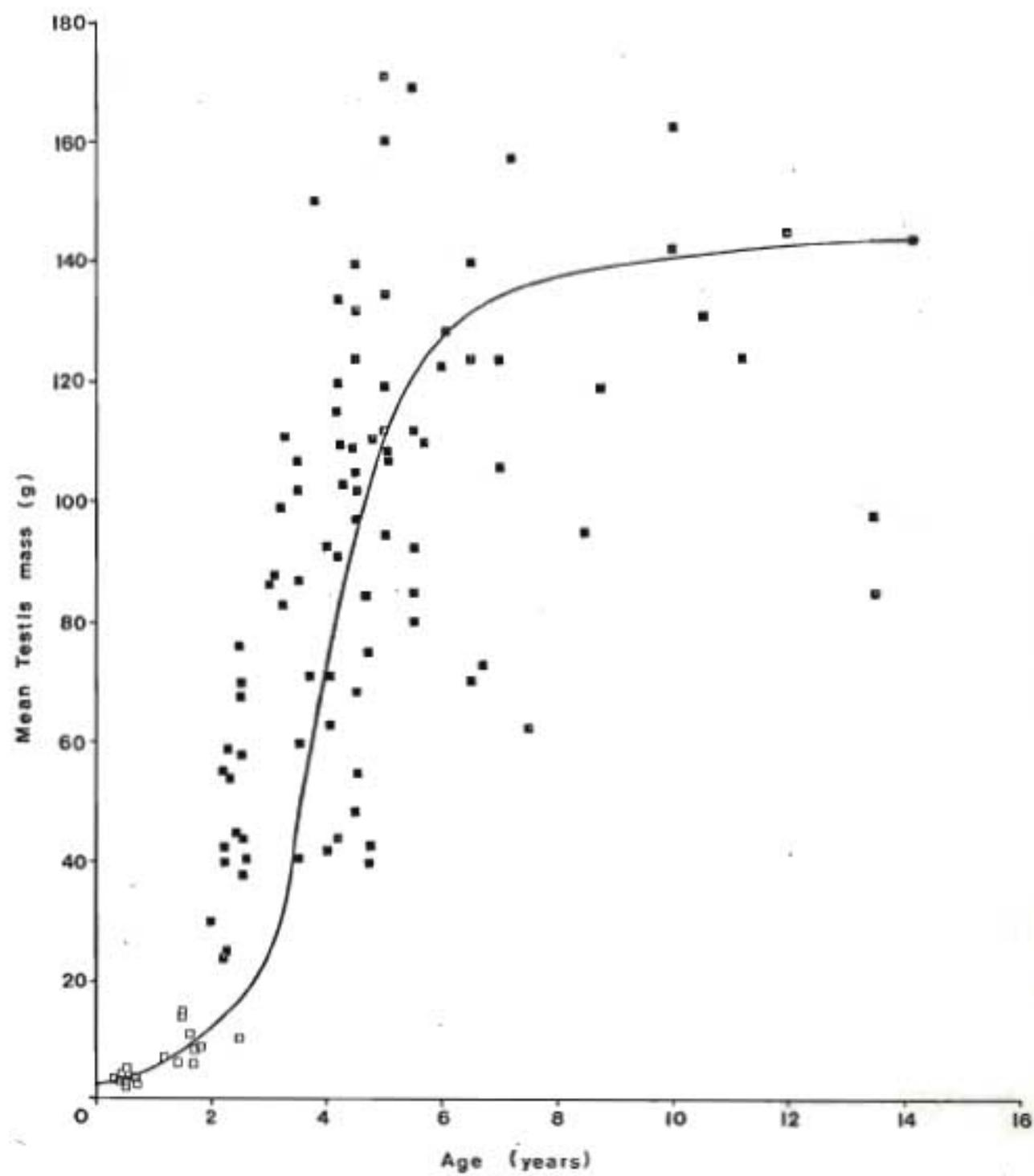
The concepts of puberty and sexual maturity have been dealt with in Chapter 5. In the male, some workers have used the attainment of minimum adult mass of testes and epididymides as criteria of sexual maturity (Laws and Clough, 1966). Skinner (1969) favours the concept that the onset of male puberty coincides with the time when the testes become androgenically active, the accessory glands begin to secrete fructose and citric acid, and the animal assumes the characteristic male appearance. He further states that spermatozoa appear some time after the onset of puberty. It is spermatogenesis that is chiefly used as the criterion for puberty in the following results.

#### 6.3.2.1.

##### TESTIS MASS RELATED TO AGE

This relationship is illustrated in Fig. 6.1., and appears to follow a sigmoid pattern. The attainment of a critical adult value of testis mass can only be very approximate, because animals from all months were included, and there exists seasonal change in testis mass (see 6.3.3.1.). The age of attainment of adult testis mass

Fig. 6.1. : Change in mean testis mass with age. Closed squares indicate at least some through to full spermatogenesis. Open squares indicate no spermatogenesis. The curve was fitted by eye.



is estimated to lie between about five and six years. A more accurate figure can be given with respect to the mean testis mass at which spermatogenesis begins: this figure is about 20g, and is attained at about two years of age. Based on the subjectively fitted sigmoid curve, the mean adult testis mass would be in the order of 130g. Watson (1969) found the mean mass of the right testis in animals over five years old to be 153,5g; adult testis mass was achieved in the fourth year. The mean testis mass in animals over five years old in this study (118,0g) was far lower than Watson's figure.

I consider the concept of "minimum adult testis mass" in animals displaying seasonal cycles to be somewhat spurious, unless one's sample is adequate enough to cover a specific stage of the sexual cycle.

#### 6.3.2.2.

#### SEMINIFEROUS TUBULE DIAMETER RELATED TO AGE

##### a) The Seminiferous Tubule

The seminiferous epithelium is composed of concentric layers of germ cells that are at stages of development progressively more advanced (Austin and Short, 1972a). A typical section through a pre-pubertal testis is shown in Plate 6.4.. During early growth of the testis only two types of cells are clearly distinguishable: these are the supporting cells located along the basement membrane, and the gonocytes which are fewer in number and centripetal to the supporting cells. It is now currently accepted (Ortavant, Courot and Hochereau, 1969) that the supporting cells are transformed into Sertoli cells and the gonocytes into spermatogonia.

The post-pubertal testis (Plate 6.5) displays the characteristic

Plate 6.3. : Photomicrograph of section through bulbo-urethral gland of an adult male. Alveoli of the gland are lined by secretory cells.  
Scale divisions marked on plate are  $10^{-1}$ mm.

Plate 6.4. : Photomicrograph of section through pre-pubertal testis, to illustrate supporting cells and gonocytes lining the basement membrane of the seminiferous tubules. Note the absence of spermatids; cytoplasmic extensions project into lumina of tubules.  
T = Interstitial tissue.  
Scale divisions are  $10^{-1}$ mm.

Plate 6.5. : Photomicrograph of section through post-pubertal testis, showing spermatids and germ cells in various stages of spermatogenesis. The circular shape of the tubule indicates that it has been cut transversely: such tubules were selected for the measurement of tubule diameter using an eyepiece micrometer.  
Scale divisions are  $10^{-1}$ mm.

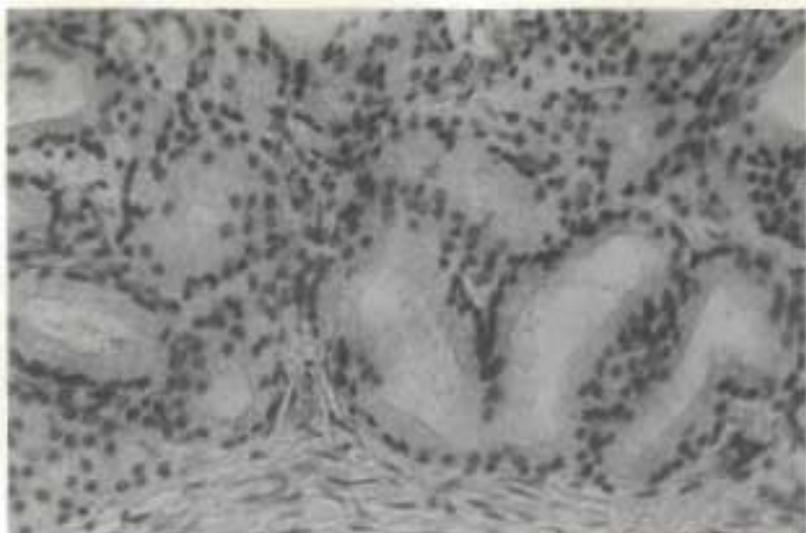


PLATE 6.3

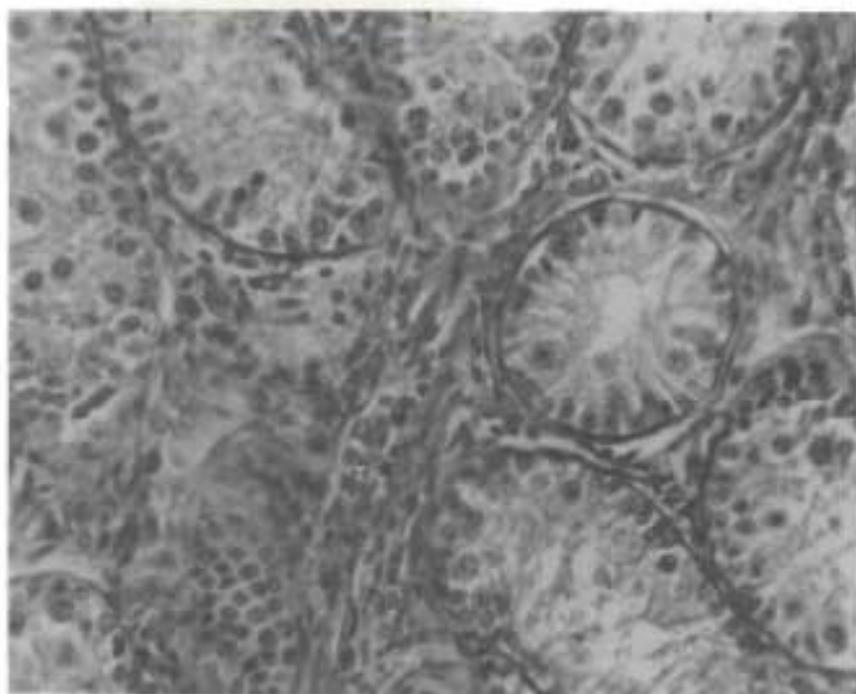


PLATE 6.4

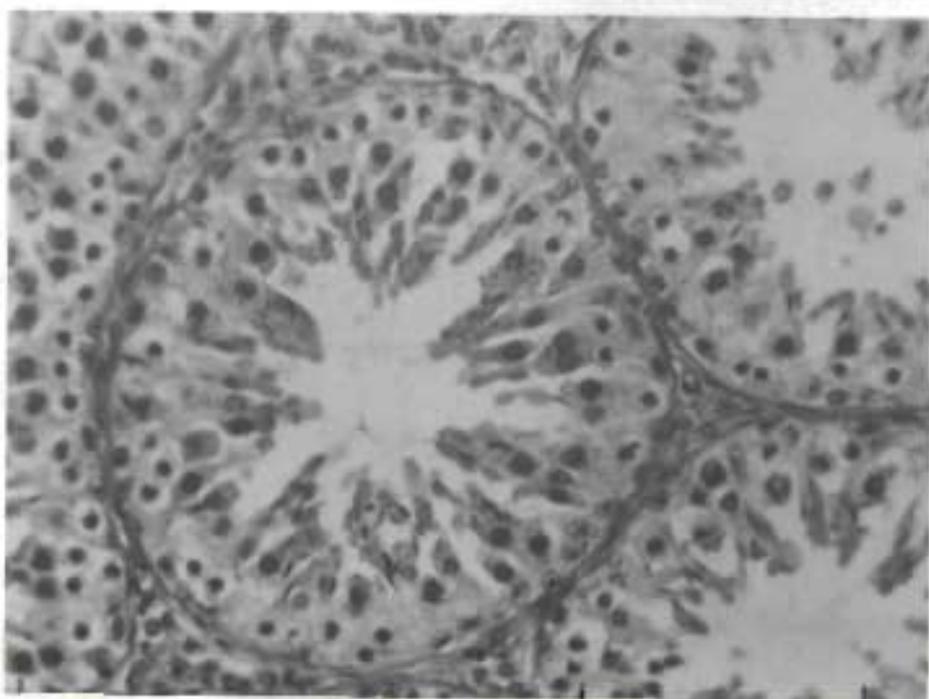


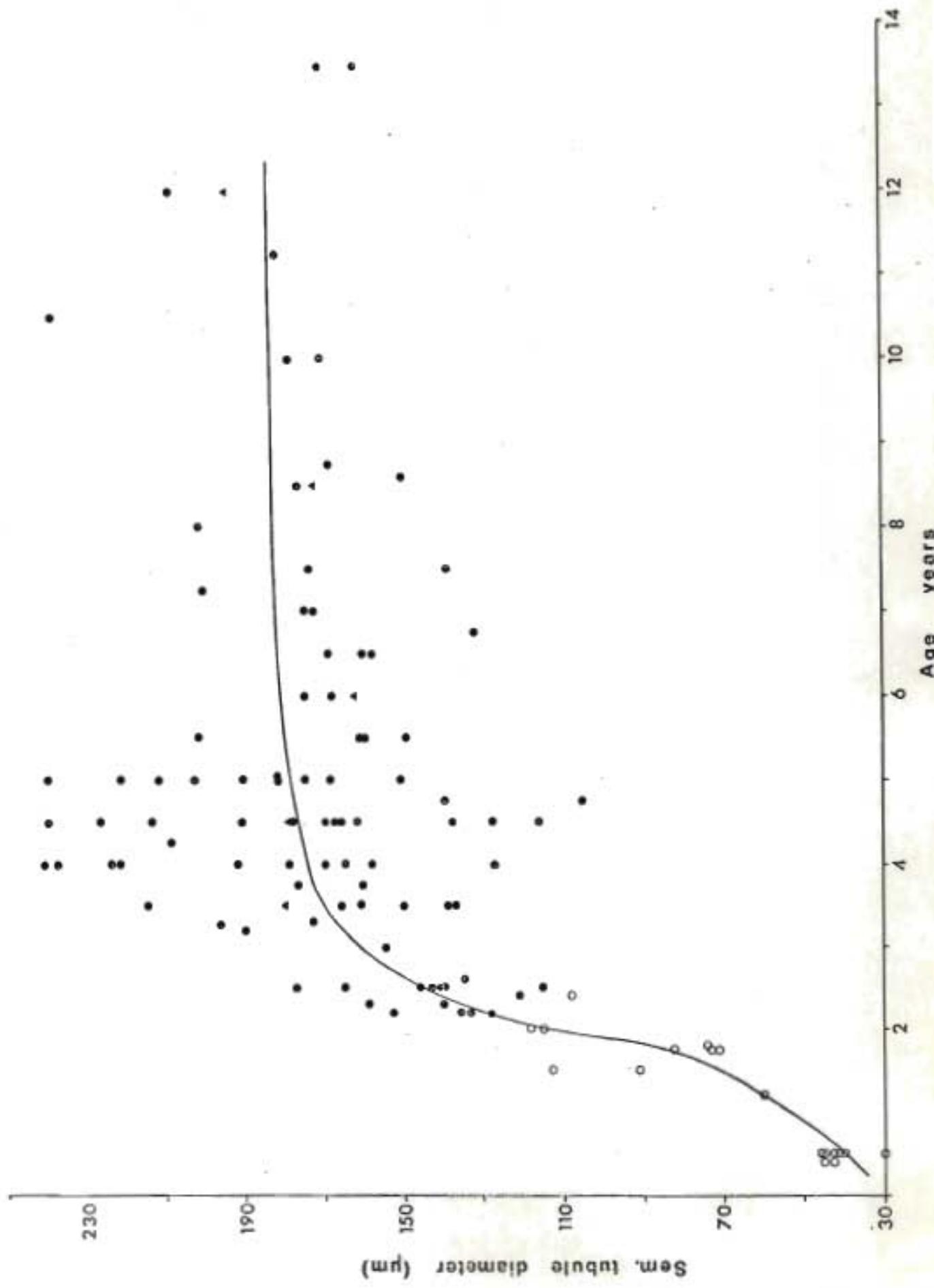
PLATE 6.5

progression of germ cells at various stages of spermatogenesis, culminating in late spermatids. The presence of spermatids was taken as an indication of spermatogenesis: this was confirmed by comparing epididymal sections from animals judged to be prepubertal or postpubertal from the appearance of seminiferous tubules. Plate 6.6. shows a section through the caput epididymidis of a prepubertal animal. The lumina of the ducts are devoid of spermatozoa. The post-pubertal appearance is strikingly different (Plate 6.7.) : the lumina are full of mature spermatozoa and occasional spermatids. In both cases the lumina are lined with tall stratified columnar epithelium with stereocilia on their free surfaces. The basement lamina is surrounded by a circular layer of smooth muscle fibres, which is probably contractile in nature to aid the passage of sperm.

b) Change in Tubule Diameter with Age.

This relationship is depicted in Fig. 6.2.. It is evident that spermatogenesis begins in the second year of life, when tubule diameter is about  $116\mu\text{m}$ . The single prepubertal animal older than two years was from outside the Complex (Vernon Crookes reserve), and is suggestive of nutritional differences affecting puberty. The figure of  $116\mu\text{m}$  is extremely close to that given by Watson (1969) for Serengeti wildebeest:  $120\mu\text{m}$ . Again, it is somewhat dubious to give a value for adult tubule diameter (for reasons given in 6.3.2.1.), but Watson (*ibid.*) felt justified in calculating this value, for he found no evidence of male seasonality. His mean value of  $169,9\mu\text{m}$  seems to agree fairly well with the point where the eye-fitted curve in Fig. 6.2. flattens out. Again, the curve agrees well with Watson's statement that the mean adult value is attained at the end of the third year or early in the fourth year. The mean value of tubule diameter from animals over four years of

Fig. 6.2. : Change in tubule diameter ( $\mu\text{m}$ ) with age. Open circles indicate no spermatogenesis; closed circles indicate at least some through to full spermatogenesis. Curve fitted by eye. Triangles represent means of age classes (2 -<3; 3 -<4; 4 -<5; 5 -<7; 7 -<10; 10 -<14).



age was 177,8  $\mu\text{m}$ . The curve has a faintly sigmoid appearance, which is typical for mammals (Dryden, 1969). Thus, spermatogenesis continues for about two years until the "adult" value for mean tubule diameter is attained. The maximum value in buffalo is only attained by about eight to nine years (Grimsdell, 1969).

The age when spermatogenesis first occurs in springbok is 36 weeks, and spermatozoa are present by 48 weeks (Skinner and Van Zyl, 1970). Epididymal smears showed the presence of spermatozoa in impala at 13 months (Kerr, 1965). In both these species, spermatogenesis begins about a year earlier than in the wildebeest.

In order to determine whether there was any indication of a peak or decline in tubule diameter (i.e. reproductive activity) within any age group, an analysis of variance was performed on the following age classes: 2 -<3 years; 3 -<4 years; 4 -<5 years; 5 -<7 years; 7 -<10 years; and 10 - 14 years. The results showed significant differences ( $p < 0,001$ ), and t-tests were consequently performed between individual means. The 2 -<3 year old class was significantly lower ( $p < 0,001$ ) than both the 3 -<4 and 4 -<5 year old classes. The 10 - 14 year old age class was significantly greater than the 5 - 7 year old class ( $p < 0,05$ ). This can be taken as an indication that there is no sign of reproductive senescence. Anderson (pers. comm.) found no evidence of decrease in tubule diameter in older nyala age classes. A similar situation was reported for impala by Hanks, Cumming, Orpen, Parry and Warren (1976). Grimsdell (1969), however, found a slight reduction in tubule diameter in buffalo over twelve years old.

## 6.3.2.3.

RELATIONSHIP BETWEEN TUBULE DIAMETER AND TESTIS MASS

This relationship is shown in Fig. 6.3.. Two separate regression equations have been calculated, one for prepubertal testes and the other for postpubertal.

Prepubertal :

$$y = 38,25 + 3,27x \quad (r = 0,8737 ; \text{significant at } p < 0,001)$$

Postpubertal :

$$y = 115,91 + 0,59x \quad (r = 0,6479 ; \text{significant at } p < 0,001).$$

Although both correlation coefficients are highly significant, in post-pubertal animals there can be considerable reduction in testis mass with little corresponding change in tubule diameter. Thus a reduction in testis mass with season need not necessarily be due to change in seminiferous tubule diameter.

## 6.3.2.4.

MEAN TESTIS MASS RELATED TO BODY MASS

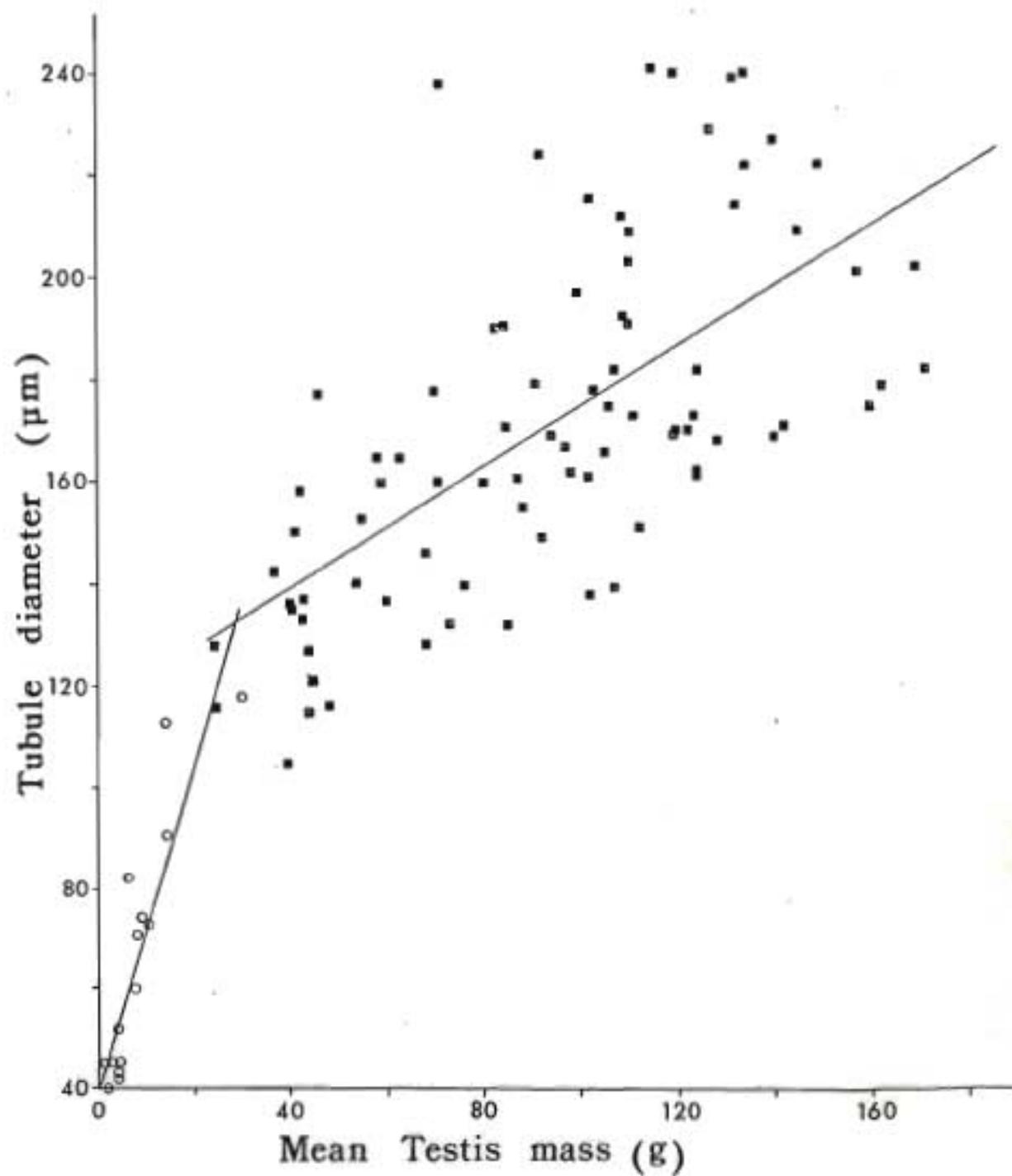
The results of plotting mean testis mass against body mass are shown in Fig. 6.4.. Frisch (1974) has demonstrated a close relationship between a critical body mass and the onset of puberty. The critical body mass in wildebeest would appear to be about 160kg. This differs from the situation in impala, where Hanks *et al* (1976) were unable to clearly define a critical body mass coinciding with spermatogenesis.

The regression equations for Fig. 6.4. are :

$$\text{Prepubertal : } y = 14,48x + 30,70 \quad (r = 0,87 ; p < 0,01)$$

$$\text{Postpubertal: } y = 0,39x + 189,91 \quad (r = 0,62 ; p < 0,001)$$

Fig. 6.3. : Relationship between tubule diameter and mean testis mass. Open circles indicate no spermatogenesis; squares indicate some through to full spermatogenesis. Regression equations and correlation coefficients in text.



## 6.3.2.5.

SIGNIFICANCE OF PUBERTY AND SEXUAL MATURITY IN THE MALE

In summary, spermatogenesis commences at two years of age, when the mean testis mass is about 20g, the seminiferous tubule diameter about 116 $\mu$ m, and the body mass about 160kg.

Analysis of ages of animals derived from different social groups during culling showed that the youngest territorial males or males with breeding herds were 4,5 years. On the assumption that only territorial males and single adult males in breeding herds take part in mating, then at least 2,5 years elapse between spermatogenesis and active breeding. This is a minimum figure, for the mean age of territorial males (including those with breeding herds) is 5,7 years. These results are similar to those of Watson (1969). He considered that the Serengeti male wildebeest, although physiologically capable of reproducing between the ages of two and three, and physically mature between three and four, do not breed until over five years old. The Uganda kob is subject to a similar delay: spermatogenesis occurs at about one year, but breeding is unlikely until about three and a half years (Buechner, Morrison and Leuthold, 1966). A very pronounced delay between puberty and mating occurs in buffalo. Grimsdell (1969) places puberty at two and a half to three years, sexual maturity at four and a half years, but considers it doubtful whether the males take an active part in mating until eight years old.

Emlen (1973) has put forward an hypothesis as to why, in most mammals, the females reach reproductive age sooner than males. An experienced male is more successful in the defence of a territory; consequently, young males have less chance of successfully mating, and selection for early reproduction is opposed. With lessened selection for efficiency in reproductive behaviour early in life, the male segment of the population will respond to any existing selection pressure

opposing mature sexual characteristics, and delayed maturity should result.

An alternative speculation has been proposed by Smuts (1974). He suggests that in zebra, selection has operated to reduce competition for mares by extending the pubertal interval to stallions. If the pubertal interval were shortened, and the age of psychological maturity reduced, then the potential number of males competing for oestrous females would be increased. The involvement of young animals could directly affect their survival, while increased contact between stallions would indirectly disrupt family units, with possible effects on the dynamics of the entire population.

### 6.3.3.

#### THE MALE SEXUAL CYCLE

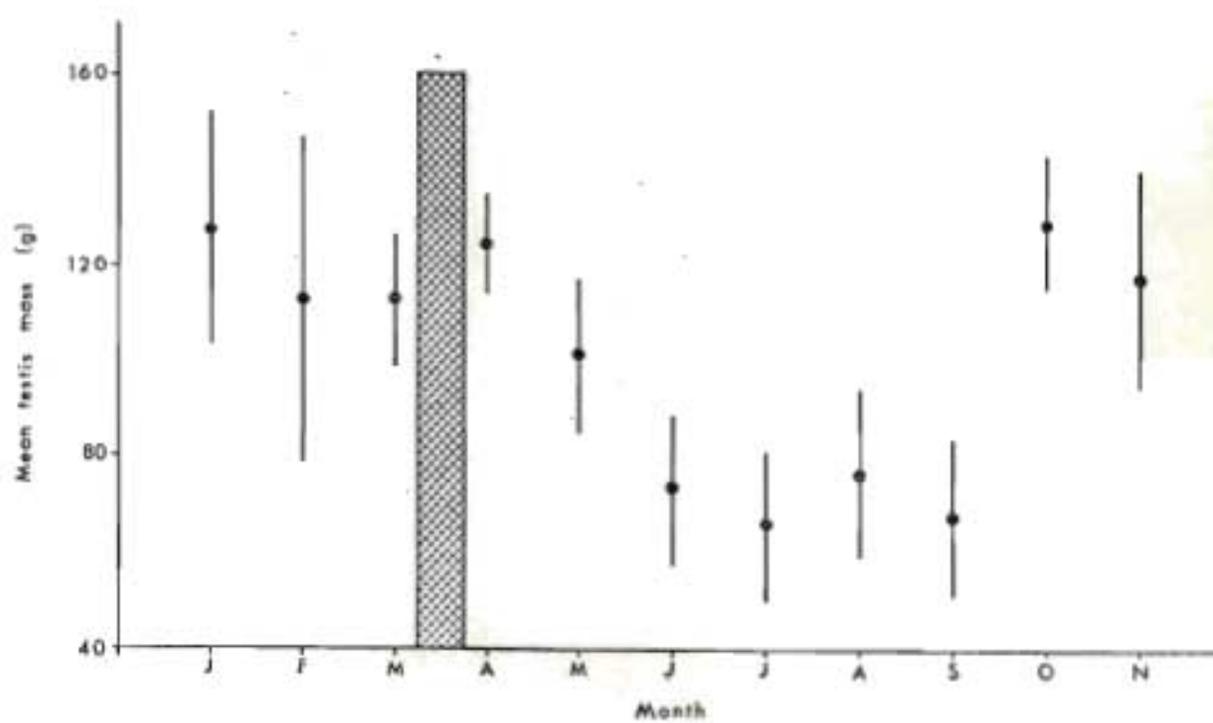
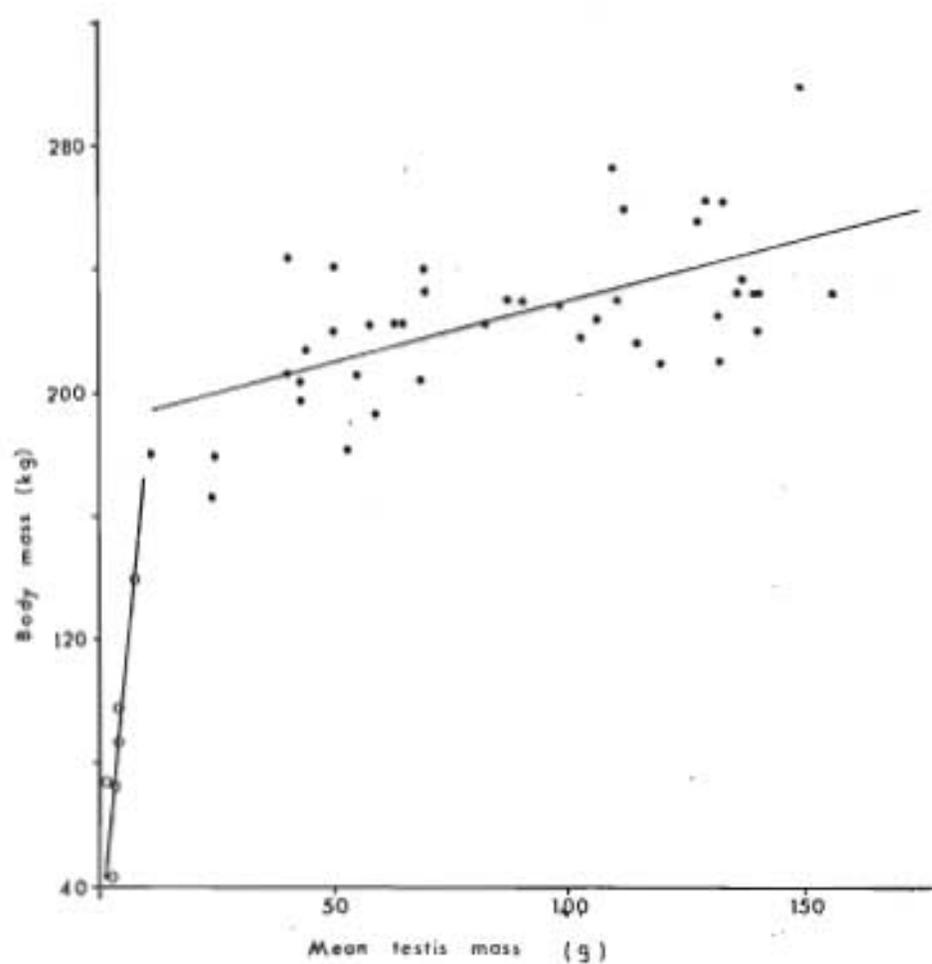
##### 6.3.3.1.

#### SEASONAL CHANGES IN TESTIS AND EPIDIDYMAL MASS

In considering seasonal changes in the male, only those animals older than three years were utilised. This was based on Fig. 6.2., where tubule diameter in the 3 - 4 year old age class was significantly larger than the 2 - 3 year old class, and it was assumed that spermatogenesis was complete after three years of age. Fig. 6.5. illustrates the change in mean testis mass with month. The pre-rut means of testis mass were significantly higher ( $p < 0,05$ ) than those towards the end of the dry season (July, August and September). The means at the beginning of the rains (October, November and December) were significantly higher ( $p < 0,01$ ) than those for the preceding three months. The maximum pre-rut mean value decreased by 48,6% to the minimum dry season mean value in July. Watson (1969) was unable to find any seasonal variation in testis mass of Serengeti wildebeest, but warned that further information was required before absence of

Fig. 6.4. : Mean testis mass related to body mass. Open circles indicate no spermatogenesis; closed circles indicate at least some through to full spermatogenesis. Regression equations in text.

Fig. 6.5. : Change in mean testis mass with month for males older than three years. Circles indicate means; vertical lines are 2 X standard error. Shaded band indicates the rut.



seasonal variation could be confirmed. The pattern illustrated in Fig. 6.5. is rather similar to that of the black wildebeest (Skinner, Van Zyl, and Van Heerden, 1973) where peak testis values were reached in March before the rut, declining to a minimum in September. Spingage (1969) recorded lowest testis mass in July for waterbuck, which corresponded to the driest month. Impala show maximum testis mass two months prior to the rut (Anderson, 1965; Skinner, 1971b). Hanks et al (1976) found a significant difference in impala testis mass during the rut and at the end of the dry season. In general, the results from this study indicate that testis mass fluctuates seasonally along the lines shown by most other seasonal breeders including blesbok, impala and springbok (Skinner, 1971a). The pattern of pre-rut testis mass peaks, or peaks coinciding with the rut, is also found in Cervids (Chapman, 1972).

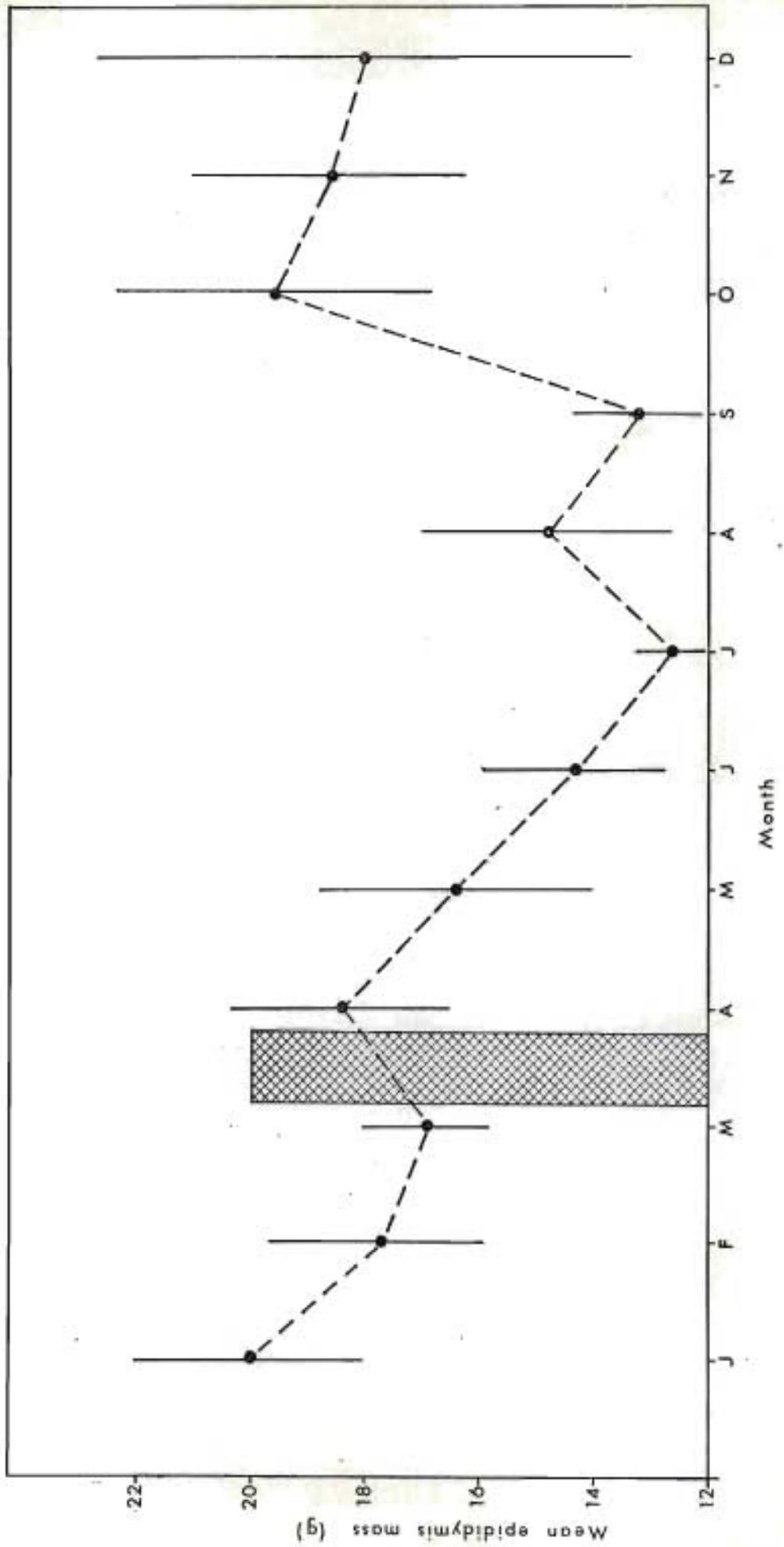
The change in mean epididymal mass (Fig. 6.6.) is almost identical with that of testis mass. An increase or decrease in testis mass would thus appear to be directly related to a similar change in epididymal mass. This pattern, where an equally pronounced change in epididymal mass occurs, is also found in blesbok and springbok (Skinner, 1971a). In general, the situation is the same in Cervids: Chaplin and White (1972), for example, found that in Fallow deer Dama dama the development of the epididymides paralleled that of the testes. The impala appears to be an exception: Skinner (1971b) found that testis mass was maximal prior to the rut, whereas epididymal mass peaked at the rut, when testis mass had already started to decline.

### 6.3.3.2.

#### RELATIONSHIP BETWEEN TUBULE DIAMETER AND MONTH

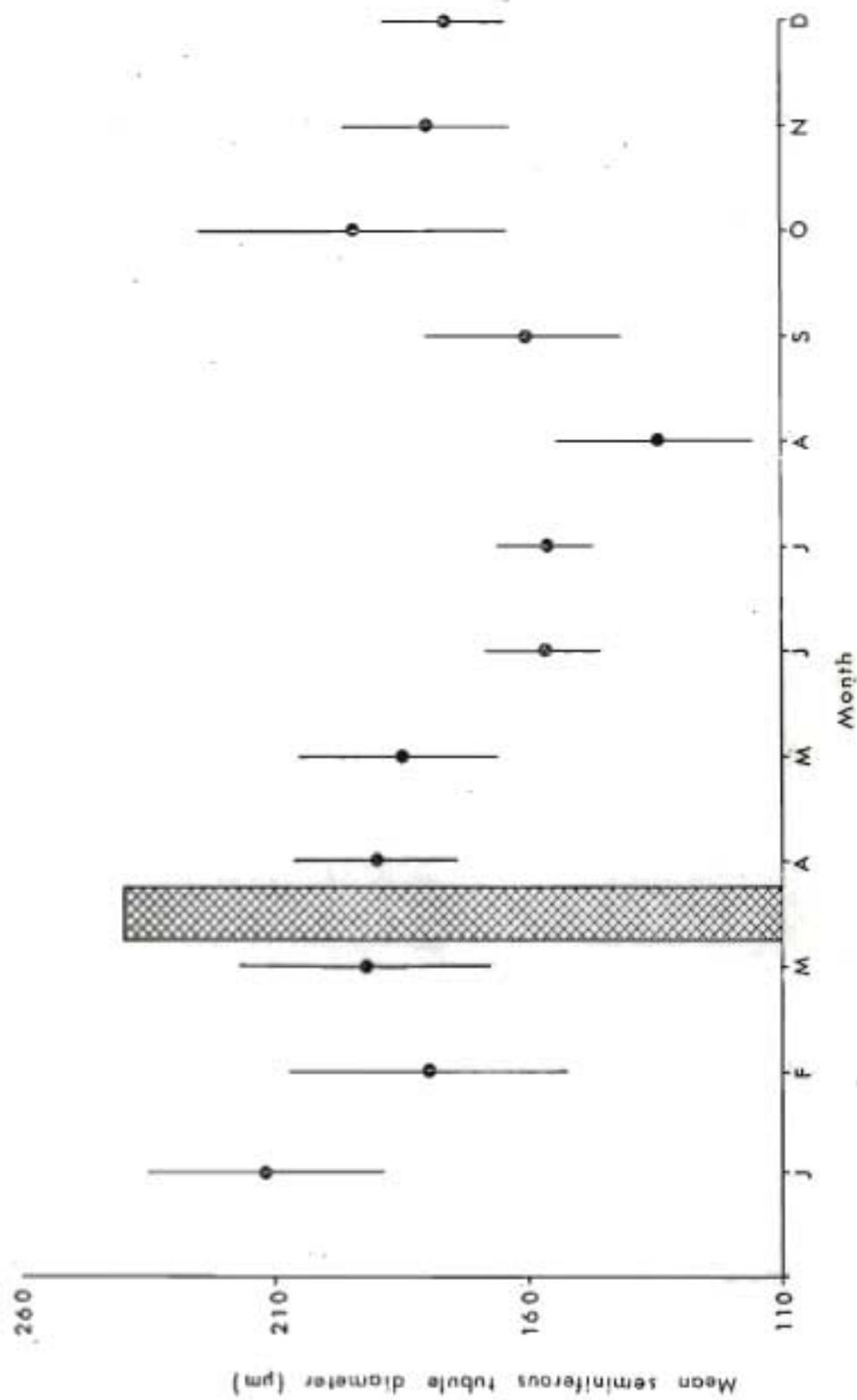
The mean values of seminiferous tubule diameter for males older than three years are plotted against month in Fig. 6.7.. The seasonal changes follow a similar trend to that of testis and epididymis

Fig. 6.6. : Mean values of epididymal mass plotted against month. Shaded bar indicates the rut. Vertical lines extend for 2 X S.E. either side of the mean.



mass. The August mean value at the end of the dry season is significantly smaller ( $p < 0,05$ ) than the pre-rut values. The maximum mean value in January decreases by 36,5% to the minimum in August. This was very close to the percentage increase shown by impala during the rut (Skinner, 1971a) which was about 30%. In the black wildebeest, Skinner, Van Zyl and Van Heerden (1973) also found maximal tubule diameter values in January. The decreasing trend in diameter after the rut corresponds to the general pattern shown by other seasonal breeders (Skinner, 1971a). In this study, tubule diameter change was temporally reflected in testis mass change; this does not hold for the springbok, where Skinner and Van Zyl (1970) described how the peak in tubule diameter preceded the testis peak by about two months. Watson (1969) reported no seasonal change for wildebeest tubule diameter in East Africa, but mentioned the need for further investigation. At no stage during the year did spermatogenesis cease. Plate 6.8. illustrates the state of the seminiferous tubules from an adult male collected during the rut. This may be compared with Plate 6.5., also from an adult animal, but collected early in September, at the end of the dry season. Skinner, Van Zyl and Van Heerden (1973) made a similar finding as regards year-round spermatogenesis in the black wildebeest, but histochemical changes in testicular interstitial tissue and the concentration of vesicular fructose indicated a decline in spermatogenesis in spring. Spermatogenesis throughout the year has been demonstrated in kudu, springbok, impala and blesbok (Skinner, 1971a) and in the pronghorn Antilocapra americana (O'Gara, Moy and Bear, 1971). A cessation of spermatogenesis and a period of infertility occurs in most Cervids (Cheatum and Morton, 1946; Short and Mann, 1966; Chapman, 1970; Lincoln, Youngson and Short, 1970; Lincoln, 1971; Chapman, 1972; and Chaplin and White, 1972.)

Fig. 6.7. : Mean values (circles) of seminiferous tubule diameter plotted against month. Only animals older than three years are considered. Vertical lines indicate 2 X standard error; shaded bar corresponds to the rut.



The presence of breeding males at seasons of the year when female breeding does not occur has been discussed by Sadleir (1969b), who suggests that the phenomenon may be necessary to maintain the male in a certain behavioural state for reasons of ethology or population dynamics. The presence of year-round spermatogenesis in the wildebeest implies that testosterone levels are maintained at a specific level. This could account for the fact that many wildebeest bulls are territorial throughout the year. This has important consequences on population structure (see Chapter 8) and even on habitat utilisation (Chapter 7).

### 6.3.3.3.

#### THE QUESTION OF THE "SECOND RUT."

Evidence was presented in Chapter 5 that suggested that some females were conceiving outside the main rut, towards the end of the dry season. The percentage of single (i.e. territorial) males in the population changed seasonally, and two peaks occurred (see Fig. 8.2.). The first peak coincided with the rut, and the second took place in August and September. Anderson (1972) and Vincent (1972) have shown similar secondary peaks for impala in Zululand.

If indeed mating does take place at this time, then it coincides with the lowest point in the male sexual cycle. However, it need not necessarily follow that a low point in the sexual cycle is inconsistent with mating, for Bigalke (1970) has reported on a second calving peak in springbok, which coincides with a September or October conception period. This period has been shown by Skinner and Van Zyl (1970) to correspond to the lowest point in the male cycle. Furthermore, Chapman (1972) stresses that morphological changes, whether macroscopic or histological, do not necessarily reflect the secretory activity of the gland. In red deer and roe deer, spermatogenesis did not coincide with the rut (Short and Mann,

Plate 6.6. : Photomicrograph of section through caput epididymidis of pre-pubertal wildebeest. The ductus epididymis is devoid of spermatozoa. Note stereocilia extending from tall epithelium toward the lumen. Scale divisions in  $10^{-1}$ mm.

Plate 6.7. : Photomicrograph of section through cauda epididymidis from post-pubertal wildebeest. Alveoli are densely packed with spermatozoa. Scale divisions on micrograph are  $10^{-1}$ mm.

Plate 6.8. : Photomicrograph of section through testis of adult male collected during the rut. The appearance is essentially the same as that in Plate 6.5., which was taken from an animal collected at the end of the dry season.

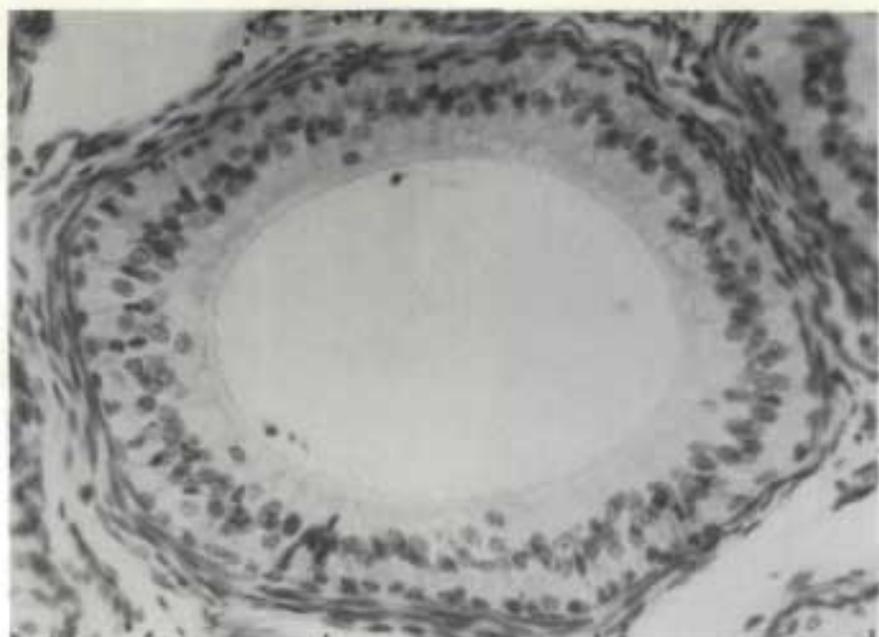


PLATE 6.6

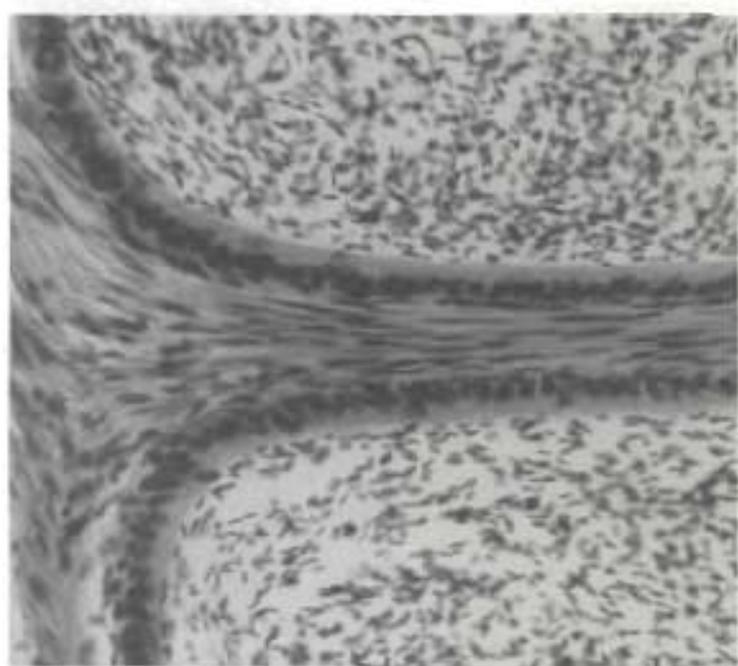


PLATE 6.7

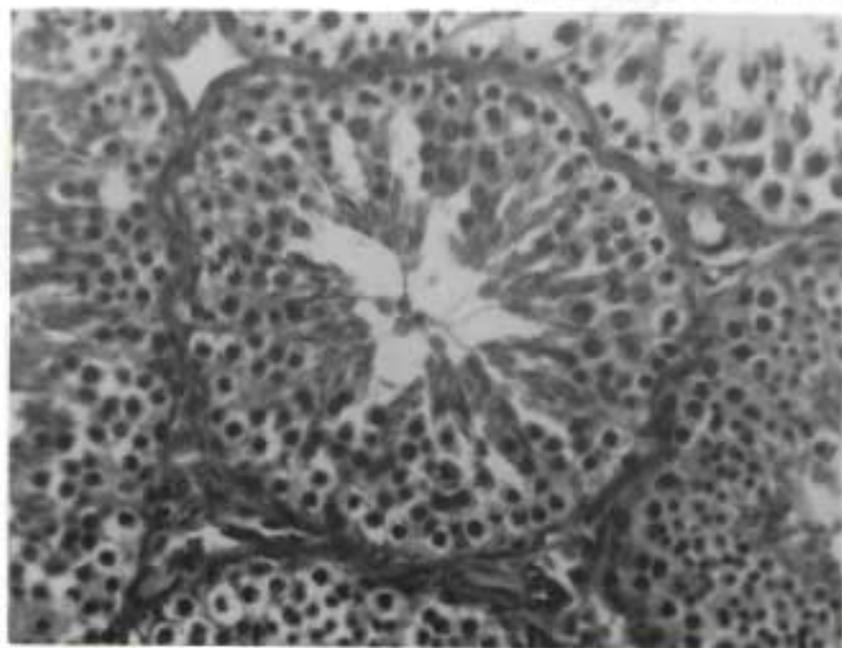


PLATE 6.8

1966; Lincoln, Youngson and Short, 1970), and one can infer that at least in Cervids the rut does not provide a good indication of the seasonal changes which take place in male organs.

An alternative explanation for the second peak in single males may be unrelated to sexual activity. Estes (1969) also recorded two peaks in territorial activity of wildebeest in Ngorongoro crater; the second peak was related to the start of the rains, when the restoration of abandoned pastures afforded opportunities for prospecting males to establish themselves on a territory without meeting the same degree of resistance encountered in an intact territorial network. This argument would possibly explain the rise in testis mass, epididymal mass, and tubule diameter in my results at the beginning of the rains: these phenomena may be due solely to increased nutritional status. The question of a second rut in wildebeest is discussed further in Chapter 8.

#### 6.3.3.4.

##### DISCUSSION ON THE RUT AND MALE SEASONALITY.

The wildebeest rut has been described in detail by Estes (1966, 1969) and by Watson (1966, 1969). No attempt was made in this study to duplicate their ethological work, but field observations support the view that behaviour was essentially the same as described by the above authors, except that the Complex population, being non-migratory, did not exhibit the phenomenon of "pseudo-territories" described by Watson (1969).

The synchronisation of the male is subject to the same factors discussed in Chapter 5 for the female. In the Soay sheep, rams and ewes respond independently to environmental factors, but it is well established that the social environment itself may affect the onset of oestrus (Grubb and Jewell, 1973). Lincoln and Guinness (1973)

suggest that in red deer, both the stag and the hind play important roles in initiating the rut. In the same species, Lincoln (1971) proposes that the cessation of rutting activity is probably due to the onset of a period of behavioural "refractoriness", brought on by sexual exhaustion after a period of intense rutting behaviour.

The cyclical changes in the male reproductive organs could be due to changes in photoperiodicity. Specifically, in the Zululand wildebeest, this would be decreasing daylength. Chapman (1972) has reviewed other environmental factors which may affect the male cycle.

An alternative explanation is that the cyclical changes shown by Zululand male wildebeest are unrelated to a sexual cycle. These changes may be due solely to nutritional changes following rainfall. This would support available evidence as to why no male "sexual cycle" was found in the same species in East Africa (Watson, 1969), and in East African buffalo (Grimsdell, 1969). These populations are subject to a bimodal rainfall pattern with the result that condition is maintained at a relatively high level throughout the year, and male reproductive organs consequently show little or no cyclical change. If one defines a male sexual cycle in terms of a period when spermatogenesis ceases or when the male is incapable of sexual activity, then the wildebeest does not display a true sexual cycle at all, as conceptions are taking place at the lowest "ebb" of the "cycle." There are indeed cyclical changes, but it is quite possible that these chiefly morphological changes are wholly unrelated to a sexual cycle. Bramley and Neaves (1972) compared the reproductive activity of territorial and bachelor impala males, and found that differences in testis mass, seminiferous tubule diameter, and spermatogenic activity were negligible. They suggested that the similarity of the testis in these two social groups, where only the one group (territorial animals) was partaking

in breeding, implied that testicular development did not reflect sexual activity.

Correlation was tested between tubule diameter and KFI, and between testis mass and KFI. The results do not tend to substantiate my argument that the cycles are related to condition: for tubule diameter and KFI,  $r = 0,46$  ( $p < 0,01$ ); and for testis mass and KFI,  $r = 0,47$  ( $p < 0,01$ ). This need not necessarily negate the argument, as a time-lag effect between kidney fat deposition and testicular morphology changes may be apparent. The hypothesis that the seasonal changes in the male reproductive organs are not reflecting a sexual cycle requires further investigation. Other species for which a male sexual cycle have been described and which also require investigation along these lines include: impala, springbok, blesbok, and kudu (Skinner, 1971a).

#### 6.4.

##### CHAPTER SUMMARY

The male reproductive organs are described.

Onset of spermatogenesis was found to occur at about two years of age, when the mean testis mass was about 20g, the seminiferous tubule diameter about 116  $\mu\text{m}$ , and body mass about 160kg. There was no evidence of reproductive senescence, based on decrease in seminiferous tubule diameter. Considerable reduction in testis mass could take place without concomitant change in tubule diameter. At least 2,5 years elapsed between spermatogenesis and active breeding.

Despite the fact that seasonal changes took place in testis mass, epididymal mass and tubule diameter, both spermatogenesis and conceptions took place at seasonal "lows." Some doubt is cast on whether the male wildebeest (in addition to some other ungulates) experiences a true sexual cycle, as the seasonal changes in reproductive organs may be related merely to nutrition.

## CHAPTER 7

### FEEDING AND HABITAT RELATIONSHIPS

#### 7.1.

##### INTRODUCTION

Five different aspects were considered in this study to investigate the relationships of wildebeest with their habitat: habitat selection, rumen content analysis, ecological separation, grazing succession, and distribution coupled with movement. These aspects are essentially a continuum, but I have chosen to present results separately for the sake of clarity. Cross-references are made where applicable to reinforce the concept that the aspects considered are intimately related.

A knowledge of habitat selection and other ecological requirements is basic to any management program. Ungulates have been shown to exhibit a heterogeneous distribution over African vegetation types, and this heterogeneity may be directly related to varying degrees of habitat selectivity (Petrides, 1956; Darling, 1960; Grzimek and Grzimek, 1960; Lamprey, 1963; Vesey-Fitzgerald, 1965; Anderson and Talbot, 1965; Simpson and Cowie, 1967; De Vos, 1969; Field and Lows, 1970; Ferrar and Walker, 1974; Pienaar, 1974; and Hirst, 1975). Attachment to habitat is not only linked with the availability of

desirable food plants but with other features which include shelter and water availability. Pienaar (1974) has listed some factors whereby distribution of herbivores within habitats is influenced. Nutritional deficiencies can be avoided to some extent through habitat selectivity; conversely, such deficiencies may be magnified by the selection of habitats or food plants notably deficient in essential nutrients.

One of the most important conditions for the maintenance of a population is that the available food should be sufficient both in quantity and nourishment value (Jensen, 1968). Consequently, investigation of rumen contents can provide insight into seasonal changes in quality, which may be related to the condition of the population. Klein (1970) has demonstrated that North American deer show direct responses in physiology and population dynamics to qualitative aspects of their food supply. Analysis of rumen contents may also be related to the question of a grazing succession. Gwynne and Bell (1968) postulate that if a grazing succession is apparent, then one would expect that different species in the succession would display different proportions of grass structural components in the rumen.

With respect to the ecological separation of sympatric species, previous work has been largely concerned with the principle of competitive exclusion. This principle (Lack, 1971) implies that those species which differ primarily in habitat differ in their adaptations to their respective habitats, and that those which differ primarily in their foods differ in their feeding adaptations. For example Darling (1960) has shown that sympatric herbivores occupy separate niches, while Lamprey (1963) suggested behavioural, temporal and other means whereby animals may co-exist.

Most animal groups show increased speciation in the tropics, and considerable ecological theory has been directed towards this

phenomenon (Klopfer and MacArthur, 1961; Connell and Orias, 1964). One ecological interpretation of this is niche width and niche overlap (Klopfer and MacArthur, *ibid.*), and in general the hypothesis is that tropical organisms have narrower niches. Whereas the concept of ecological niche is old (Grinnell, 1917), the quantitative evaluation of niche width is relatively new (Levins, 1968). Hutchinson (1957) formalised the niche concept by considering the niche as a hypervolume in an n-dimensional hyperspace, with each axis corresponding to some relevant environmental variable. This concept of the niche was used by Ferrer and Walker (1974) to determine the nature and relative importance of those factors separating the major herbivores in Kyle National Park, Rhodesia. Their approach was adopted relatively unchanged in this study.

The phenomenon of a "grazing succession" was originally described by Vesey-Fitzgerald (1960) in East Africa, where a sequence of herbivores (heavier followed by light) used different pastures in rotation, resulting in alternate periods of optimum use and rest. Major contributions to the understanding of a grazing succession were made by Bell (1969, 1970, 1971). The species relationships to a grazing system have been interpreted in terms of maintenance requirements, rate of assimilation of food from the gut, rate of intake of food, and availability of food (Bell, 1969). The level of the herb layer selected corresponded to the position in the grazing succession (Bell, 1970). This work was the foundation for the Bell - Jarman principle (Geist, 1974), which relates forage choice, body size and digestive techniques to each other and to social organisation. Basically, the body size of an ungulate species is a function of the fibre content (digestibility) and density of the forage they exploit. More recent work (McNaughton, 1976) has underlined the importance of grazing successions. McNaughton was able to demonstrate how heavy grazing by migratory

wildebeest prepared the plant community for subsequent dry season exploitation by gazelle, Gazella thomsonii.

From an understanding of the requirements of wildebeest based on the above studies, one may assume that the animal is adapted to a very specific herb layer structure, and that changes in this structure will initiate movement, which may be related to a succession. The objects of this aspect of the study were to determine those times of the year when wildebeest were independent of other species, when they competed with other species, and under what herb layer conditions competition (or lack of competition) was apparent.

The final aspect considered was movement and distribution. Western (1975) classified large mammal communities into three broad categories on the basis of seasonal movement: migratory, dispersal (wet season dispersal and dry season concentration), and resident. Whatever categorisation is employed, the reason is closely related to habitat. Pienaar (1974), in classifying the environmental factors governing distribution (physical, historical, and biotic), maintained that vegetation was all-important. This has been confirmed by numerous studies (references include those in the introductory paragraph on habitat selection), especially that of Blankenship and Field (1972). The response of a population to a vegetation structure that differs from the optimum is to move away from it. Bell (1968) showed that, in the case of wildebeest, when the grass was too long it differed from the optimum in that the proportion of structural to cytoplasmic constituents was too high to allow the species to harvest and assimilate a maintenance diet.

Wildebeest movement patterns have been studied in detail in East Africa (Talbot and Talbot, 1963; Watson, 1966; Pennycuik, 1975; and Inglis, 1976). In most cases, rainfall was the proximate factor initiating movement. The East African situation is dominated

by the migration spectacle, and is hardly comparable to movement patterns in Southern Africa. Migration does occur in the Kruger National Park (Braack, 1973; Joubert, 1974), but no true migration occurs in Zululand. The absence of a true migration necessitates a closer understanding of movement which does occur, as this movement complicates the present system of game removal undertaken in the Complex. Game removal is centred on areas considered to be degraded, and the size of these areas often means that they have been vacated by the time capture is to take place. The objective of a movement study in the Complex is ideally to delimit subpopulation boundaries or ecological units, based on the area in which a given sub-population normally moves. Additional objectives are a knowledge of the extent and speed of recolonisation of removal areas (which relates to the validity of establishing "vacuum" areas), and the utilisation of burns and upland areas (which relates to the possibility of sighting additional waterpoints).

## 7.2.

### MATERIALS AND METHODS

#### 7.2.1.

##### HABITAT SELECTION

Although data on habitat selection were collected throughout the Complex, only those from UGR and the southern Corridor were analysed. Not only did the majority of observations come from the last two areas, but the HGR populations were found consistently in approximately the same areas, with the result that habitat selection for that reserve may be deduced from the HGR vegetation map, compiled by Whateley in 1975 (HGR Herbarium).

When an observation was made, the habitat type recorded was based on the dominant tree or shrub species, coupled with a standardized

description of the plant community form. Any observation could be related to one of nine possible plant community forms (Porter, Scotcher and Downing, 1973 ): floodplain grassland, dry grassland, bush clump grassland, wooded grassland, open woodland, closed woodland, riverine forest, or thicket. Dominant grass species were recorded where possible. Because on many occasions more than one dominant species was recorded, and owing to the variation in community form, the resulting number of "possible" habitat types was of a magnitude (in the order of seventy) incompatible with statistical analysis. Reduction was essential, and this was performed by assigning each sighting to one of Downing's (1972) broad woody community divisions. This was considered justifiable, in that Downing (pers. comm.) maintained that his major divisions reflected environmental trends with characteristic soil and vegetation features. A further advantage lay in the fact that the major divisions were plotted on a vegetation map (Downing, 1972 ), and their relative areas could be deduced. A slightly revised version of Downing's original woody community divisions was used: Open woodland, comprising five communities (Acacia caffra, A. tortilis, A. nigrescens, A. burkei, and Combretum apiculatum); Closed woodland, with three woody communities (A. nilotica, A. grandicornuta, Spirostachys africana); and the Riverine Association represented by a single woody community, A. robusta/Phoenix reclinata. For the purposes of assigning areas in BGR to these communities, the A. grandicornuta and S. africana communities had to be combined, as they were not wholly distinct on Downing's (ibid.) vegetation map. The areas of the communities were determined by cutting out separate communities marked on the map, and by weighing the combined "snippets" for each community to  $10^{-4}$ g. Relative areas of the communities enabled selection to be considered when habitat sightings were weighted on an equal area basis.

## 7.2.2.

RUMEN CONTENT ANALYSIS

Rumen contents of both buffalo (fifty-nine samples) and wildebeest (forty-seven samples) were analysed according to grass structural components only. No attempt was made to analyse on a species composition basis. Buffalo were included because culled material was available during the study, and because their ability to graze in long grass areas would provide a favourable comparison with the short grass selectivity of wildebeest.

The method followed closely that of Gwynne and Bell (1968).

Samples were collected from the rumen and stored in an alcohol-acetic acid-formalin solution (AFA : 18 parts 70% ethanol, 1 part glacial acetic acid, and 1 part 40% formaldehyde) until analysis could be made. Subsamples were washed in a sieve, and placed in a large petri dish, overlain by a sheet of perspex which was scored with an 11 X 11cm grid of 1cm<sup>2</sup> blocks to give 100 line intersections. The grass part beneath each intersection was examined through a binocular microscope, and assigned to one of three categories: leaf, sheath, or stem (culm). If it was impossible to identify a specific component beneath an intersection, then the nearest identifiable component was recorded. In this manner, a direct percentage occurrence could be ascribed to each grass component. Gwynne and Bell (ibid.) showed that there were no significant differences between the results of analyses of different sub-samples from the same sample, nor between synthetic mixtures of known plant parts and their analyses performed by this method.

No measure of availability of grass components was made in this study; consequently, the results could not be directly related to selectivity. Although limited data were collected on direct observations of plant species eaten in the field, the results are not considered, as the data available from this technique are subject to the danger pointed

out by Stewart and Stewart (1971), namely that the choice of food plants will depend, among other factors, on the choice of plant species available. Records of grass species eaten by wildebeest have however been compiled from field observations by Anon. (1960), Hitchins (1968a), Braack (1973), and Hirst (1975).

### 7.2.3.

#### ECOLOGICAL SEPARATION

Four herbivores were selected for an investigation of the structural features of the habitat which might serve to separate them. Three (wildebeest, zebra, and white rhinoceros) were chosen for their apparently similar grazing requirements, and the fourth (buffalo) was included on account of its impact on the habitat, and because there existed the possibility of relating that species separation to rumen content analysis. Data were initially collected on impala as well (on account of their wide distribution and high numbers), but this species was later discarded owing to the complexity which resulted from inclusion of habitat variables for a species which was both a browser and a grazer. Data collection was limited to UGR as it was considered that herbivore-habitat stresses were more marked in that reserve (in comparison to other areas in the Complex), and it was felt that, for management purposes, a knowledge of herbivore-habitat interactions would be more valuable from an area in which culling was becoming increasingly essential. Further, it was considered that any attempt at ecological separation would only be meaningful in a relatively homogeneous environment, and the inclusion of data from HGR (which differs essentially in habitat from UGR) might render interpretation of the results more difficult. Habitat variables were recorded at feeding sites for the four species. Green (1971) states that the choice of environmental parameters (i.e. habitat variables in this case) for a multivariate analysis

should have a reasonable theoretical possibility of affecting feeding site, and should be readily determinable in the field. The latter factor meant that many variables had to be visually estimated (see Table 7.1.), but Ferrar and Walker (1974) maintain such estimation is justified, as the choice of site by a herbivore is likely "to encompass variability of the same order of magnitude as would result from such estimates."

The original variables considered are shown in the data collection form (Fig. 7.1.). HOM/HET refers to homogeneity or heterogeneity of the feeding site. This variable was included to allow for the presence of "grazing mosaics" (a patchwork appearance of short and long grass areas, which is prevalent in many parts of UGR); it was subsequently discarded in the analysis as Walker (pers. comm.) considered absolute categorisation at this level ecologically unwarranted, on account of the continuum nature of habitats. The variable "% browse-not-forbs below 3m" was omitted early in the study to coincide with the exclusion of impala from the species under consideration. In practice, it was seldom possible to assign a value to "Distance to nearest water," owing to the constantly fluctuating status of pans as water sources. "Distance to nearest burn" was found to be another variable which lost significance in the field, as burns could be up to 30km away, and could not possibly reflect on choice of feeding site. Both these variables were omitted for the analysis.

The majority of variables are self-explanatory, but some require definition: "forb" refers to a non-woody dicotyledonous plant (Hofmann and Stewart, 1972); "shrub" was defined as woody vegetation less than 2m in height; "litter" was defined as unattached plant material; "moribund material" referred to all dead herbaceous material not lying on the soil surface; and "bare patch" included any natural or induced patch > 2m in radius. "Degree of range degradation" was

Fig. 7.1. : Original data collection form for the multivariate analysis. See text for amendments to the variables shown here.

	SPECIES
	DATE
	LOCALITY
	TIME
	CALVES
	YEARLINGS
	♂
	♀
	A D U L T S
	T O T A L
	ACTIVITY
	VEGETATION TYPE
	HOM/HET
	BURN
	MEAN HEIGHT TREE CANOPY
	% CANOPY COVER TREES
	% AERIAL COVER SHRUBS
	MEAN HEIGHT SHRUB LAYER
	AVERAGE MAXIMUM HEIGHT HERB LAYER
	MEAN HEIGHT HERB LAYER
	% AERIAL COVER HERB LAYER
	% FORBS IN HERB LAYER
	% MORIBUND MATERIAL IN HERB LAYER
	% BROWSE-NOT-FORBS BELOW 3m
	% SITE WITH BARE PATCHES
	DEGREE OF ROCKINESS (0 - 5)
	DISTANCE TO NEAREST H <sub>2</sub> O
	DISTANCE TO NEAREST BURN
	DEGREE OF RANGE DEGRADATION (0 - 5)

finally defined in terms of scores: 1 = no erosion; 2 = soil movement apparent; and 3 = eroded. Similarly, "Degree of rockiness" was scored as follows: 1 = no rocks present; 2 = rocks present, but unlikely to affect herb layer variables; and 3 = rocks present to the extent that herb layer variables are affected. The final variables considered in computerisation are shown in Table 7.1., where each variable has been assigned a code number for the analysis.

The main danger behind selection of feeding sites at which to record the above variables lay in oversampling (Walker, pers. comm.). To obviate this, transects were initially based on the UGR vegetation map in order to include all (or as many as possible) of the major habitat types. Wildebeest distribution was found early in the study to be discontinuous, with the result that many kilometres were often walked along a predetermined transect without obtaining a single set of data for that species. This problem was subsequently overcome by mapping wildebeest distribution from a fixed-wing aircraft approximately every month; transects were then made through areas with highest concentrations, but in conjunction with the UGR vegetation map so as to minimise sample bias. Data were collected only at feeding sites; for a herd, this was estimated as the herd "centre", and for single animals a standard site size of 5m radius was used (Ferrar and Walker, 1974). In this manner, the data collected consisted of four herbivore species (groups), each made up of varying numbers of sites (sets of observations at feeding localities), with each site characterised (in the final analysis) by twelve variables or site attributes. For all species, 124 sites were recorded.

Discriminant function analysis may be used to provide an ordering of the variables according to their importance (Shugart and Patten, 1972). This multivariate technique reduces the number of criteria used for discrimination, providing "discriminant functions" or

TABLE 7.1. : Final variables considered in the multivariate analysis, together with computer code numbers. Variables 1, 2, 3, 7, 8, 9 and 10 were visually estimated in the field; 4, 5 and 6 were determined by measurement.

<u>CODE</u>	<u>VARIABLE</u>
1	Mean height tree canopy
2	% canopy cover trees
3	% aerial cover shrubs
4	Mean height shrub layer
5	Average maximum height herb layer
6	Mean height herb layer
7	% aerial cover herb layer
8	% forbs in herb layer
9	% moribund material in herb layer
10	% site with bare patches
11	Degree of rockiness (1 - 3)
12	Degree of range degradation (1 - 3)

"canonical variates." The value of correlation between a given variable and the discriminant function indicates how well that variable separates the species. Green (1971) has outlined the statistical assumptions for the valid use of multiple discriminant analysis.

The discriminant function program used in this study was identical to that used by Ferrar and Walker (1974), which was adapted by C.T. McCabe (Dept. of Zoology, Univ. of Rhodesia) from the procedure given in Hope (1968). Computation was carried out on an IBM 370 computer at the University of the Witwatersrand. In the analysis, univariate F-ratios were computed for all attributes (variables) separately, identifying those for which the ratio of between-species to within-species variance was sufficiently large to enable discrimination between the four herbivore species. The discriminant functions were extracted from the total set of species matrices, thus expressing the difference between species in terms of a few common gradients of variation. The mean of the discriminant scores for all sites is termed the species centroid, and may be equated with the niche centre.

The centroids were plotted by computer (IBM 1130, University of Natal), using a program written by D. Chalton (Dept. of Biometry, Univ. of Natal). This plot provided for the inclusion of 90% confidence limits, based on the technique of Delany and Healy (1964), who used a similar approach to investigate the within-species morphological variation in a rodent.

#### 7.2.4.

##### GRAZING SUCCESSION

Three study areas were chosen in UGR in which wildebeest populations were consistently recorded, either throughout the year or for a major portion of the year. These areas were approximately 4ha in

area, and the following considerations were taken into account in their choice:

- a) homogeneity of the herb layer.
- b) accessibility of the area. In order to maximise the number of observations of different herbivores on the study areas, they were chosen within visibility range of a main tourist road.
- c) proximity to permanent water. Areas were chosen which were sufficiently close to permanent water so as to ensure that absence of water was not a factor inducing movement away from the study areas. The areas were nevertheless sufficiently far from water points to negate the effects on the herb layer of animal congregation around a watering point.

Within each study area, four  $1\text{m}^2$  plots were pegged out. This is the usual sampling area size for pasture production determinations (Brown, 1954).

For various reasons, it was not possible to construct an enclosure plot. A convenient site was however found on the slopes of Dengezi hill - a pen had been constructed for the re-introduction of cheetah; these had been released some years previously, but the fencing was still sufficiently intact to exclude large herbivores. This pen was conveniently sited in Acacia nigrescens habitat, and the area had year-round wildebeest populations.

Study Area 1 was situated approximately 0,25km SW of the Black Umfolosi river, where the latter forms a bend around the Nonqishi "peninsula" (Fig. 7.16). The area lay adjacent to the tourist roads, on the lower slopes of the Mbulunga hills, in the region of the Mbuzana stream. A description of Study Areas 2 and 3 is not included, as the results from those areas are not presented: in Area 2, wildebeest moved out of the area, and were not recorded again during the study period; Area 3, although its choice as a favoured area was justified, did not receive sufficient attention from other herbivores to enable

meaningful interpretation of the results.

Study Area 1 was in Acacia nigrescens open woodland. Plot (a) was sited away from any tree canopy, and corresponded to Downing's (1972) Panicum coloratum grass community. It was dominated by P. coloratum, P. maximum and Digitaria argyrograpta. Plot (b) was chosen beneath the tree canopy, and was maintained in a moderately short condition, in comparison to Plot (c) which contained a tall stand, but also beneath the tree canopy. Both (b) and (c) belonged to Downing's (*ibid.*) Themeda-Panicum grass community, and the main dominants were Themeda triandra, P. maximum, and P. deustum. Plot (d) was similar to (a), but the former comprised a medium stand of grasses, as opposed to the well-grazed appearance of Plot (a).

Measurements of the herb layer were taken in each plot approximately at monthly intervals, and these measurements were identical to those used for herb layer variables in the multivariate analysis. A subjective record of utilisation was made according to the following scale: 1 = no grazing noticeable; 2 = sporadic grazing; 3 = moderate grazing; 4 = heavy grazing; 5 = overgrazed. Data of this nature were also collected from the "enclosed" plot, and compared with those from a heavily utilised plot in the immediate vicinity.

Except in the case of the enclosure and its adjacent comparison plot, records were taken as often as possible of the numbers and species of herbivores utilising the Study Areas. The enclosure plot was situated too far from a road to allow comparison with the relatively high number of observations made on the other Study Areas.

#### 7.2.5.

#### MOVEMENT AND DISTRIBUTION

Twelve flights were made in the Natal Parks Board's fixed-wing aircraft, from which distribution of herds and single animals was plotted

onto a 1 : 50,000 map of the Complex. It was found impossible to cover accurately the entire area in one day; consequently, the wet season distribution map was constructed from consecutive flights during that season. In addition maps were available from previous censuses performed by the Natal Parks Board: censuses are normally performed during the dry season, with the result that such data could be used to provide an accurate picture of dry season distribution both during the study period and in previous years.

One requirement of the Natal Parks Board for this study was that movement patterns be investigated. The Board rejected the use of collars to mark animals during the study period, and trials were made on the cryobranding of wildebeest. Some twelve animals were branded, but the methods will not be discussed here, as results were so unsatisfactory that the technique was abandoned.

### 7.3.

#### RESULTS AND DISCUSSION

##### 7.3.1.

#### HABITAT SELECTION

The distribution of wildebeest populations in HGR and the N. Corridor coincides with the following habitats (reference should be made to Fig. 7.16): the north-eastern populations utilise valley floors, where a Panicum maximum - Cyperus textilis grassland community is found. Upland areas, particularly hillslopes, are selected for the Themeda triandra grassland found in such areas. Other habitats in NE HGR in which wildebeest occur include A. korroo and A. caffra thicket communities, and A. nilotica woodland.

Distribution along the SE boundary (on the slopes of Mthole and in the Nomageje valley) coincides with thicket communities comprising Euclea divinorum and A. korroo as dominants. Proceeding SW, the

populations centred around HlokoHloko are found particularly in A. nilotica woodland, but may also occur in Spirostachys africana woodland, and in Dichrostachys cinerea - A. karroo thicket communities.

The NW boundary of HGR is utilised only towards the south: virtually no wildebeest are found in the northern forested hills of HGR. Populations of wildebeest may consistently be found on the slopes of hills forming the southern NW boundary: Mpanzakazi, Tshempofu, and Zangomfe. The Mpanzakazi area is dominated by a Themeda triandra grassland community; Tshempofu is essentially Dichrostachys cinerea-A. karroo thicket habit; and Zangomfe shows an A. burkei-dominated woodland community.

Distribution of wildebeest in the western corner of HGR occurs predominantly in A. nilotica woodland, or in A. karroo woodland. In the northern Corridor, where the Ziqhumeni area was consistently found to harbour wildebeest populations, A. nilotica woodland was again the dominant community. This community may be interspersed with patches of thicket composed of Euclea divinorum, Dichrostachys cinerea, and A. karroo as dominant plant forms. Range may be extended onto the slopes of Seme hill, particularly during the wet season, in order to utilise the Themeda triandra grassland.

In UGR and the southern Corridor, the results are more detailed. Fig. 7.2. shows histograms representing the percentage frequency of sightings for the nine habitat types considered. The histograms have been unadjusted for the difference in areas between habitat types, and include all social groups (single males, bachelor herds, and breeding herds). Table 7.2. contains the relative areas of the different habitats (note that the Spirostachys africana and A. grandicornuta communities have been combined, as explained under 7.2.1.). The ratio of these areas provided a means of weighting or adjusting the number of sightings on an equal area basis, shown in

TABLE 7.2. : Relative areas of eight communities in UGR.

COMMUNITY	AREA IN UGR (ha)	CORRECTION FACTORS
<u>A. nigrescens</u>	11098,5	1
<u>A. tortilis</u>	6474,0	1,7143
<u>A. nilotica</u>	6909,5	1,606
<u>A. grandicornuta</u> + <u>Spirostachys africana</u>	9767,0	1,136
<u>A. caffra/Themeda grassland</u>	1816,0	6,111
<u>A. burkei</u>	2549,0	4,354
<u>Combretum apiculatum</u>	8116,5	1,367
<u>A. robusta/Phoenix reclinata</u>	3268,5	3,396

Fig. 7.3.. Comparison between Figs. 7.2. and 7.3. indicates that habitat selection is not greatly influenced by area of the habitats, except in the case of A. caffra/Themeda triandra grassland. Acacia nigrescens is clearly the community of choice.

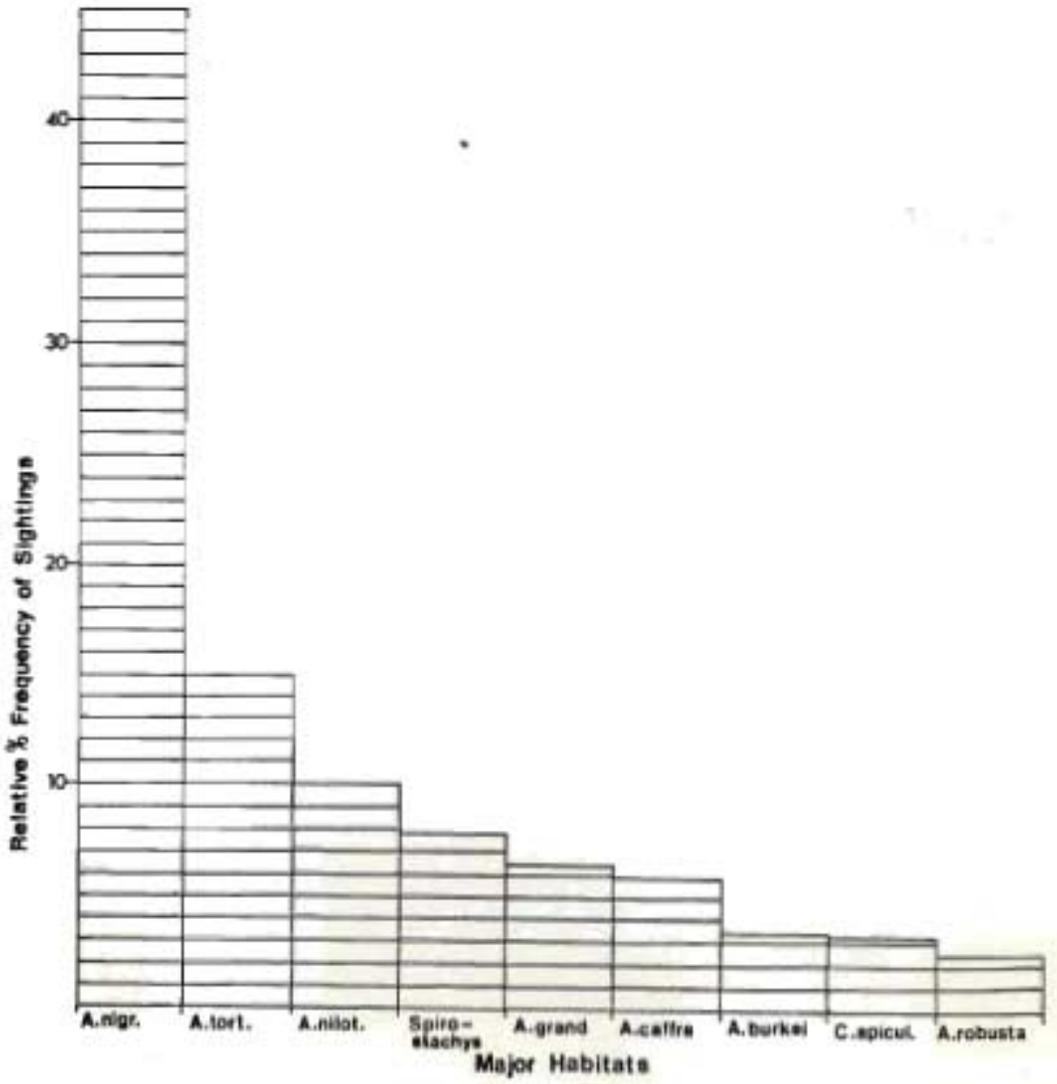
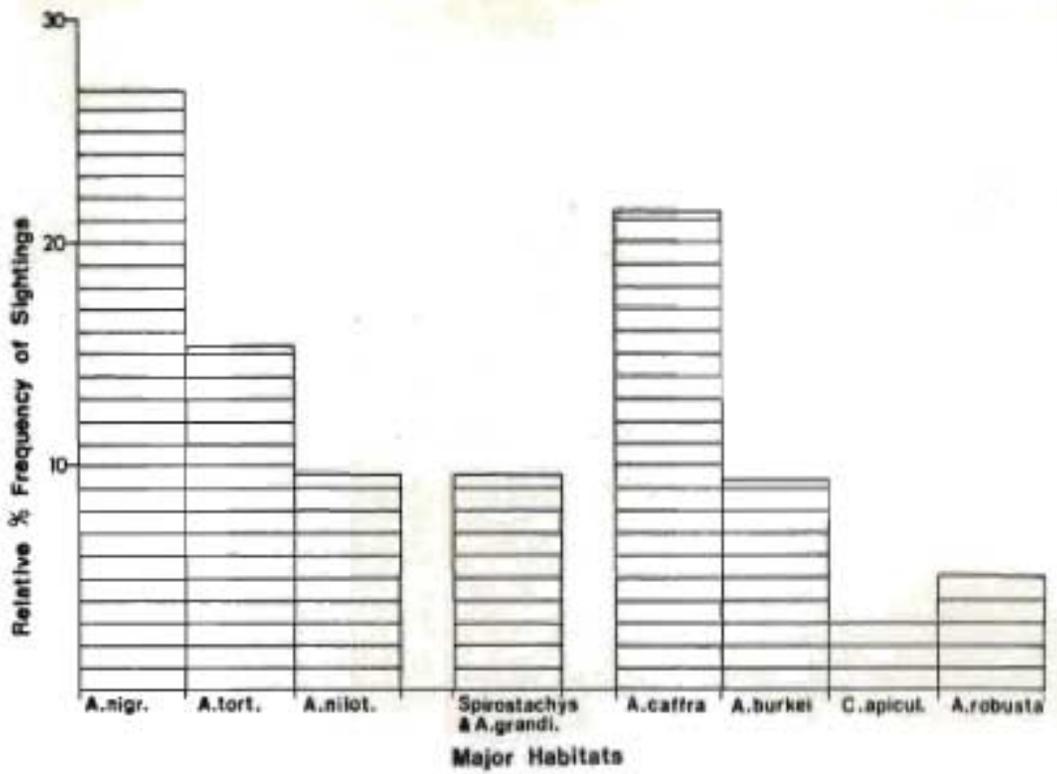
The selection of the grassland community is not surprising, for the animals probably evolved in a plains environment. But the available grassland in UGR comprises the smallest community in terms of area (Table 7.2.), and it appears that, in UGR, wildebeest have adapted themselves to a woodland environment. Leopold (1969) maintains that the adaptability of many species depends not only on their genetic plasticity, but also on their capacity to learn and consequently adjust their behaviour to an altered environment. Hirst (1975) found that in the Timbavoti reserve in the Transvaal, wildebeest were most often associated with "open short-grass savanna." Other habitats frequently utilised included the related "wooded short- and tall-grass savanna" and "sparsely wooded/grass forbland." A further habitat selected for in his study was "mixed thorn and evergreen woodland", which include Acacia nigrescens as a dominant. These findings are similar to the situation in UGR.

Hirst (ibid.) also considers that the selection of preferred habitats may essentially be a behavioural process of "keying in" to structural habitat features, but suggests that the ultimate reason for this is the minimisation of interspecific competition. The choice of A. nigrescens woodland may well be related to structural features, but pedological factors may be equally important. The Kiaora soil form which develops in situ over dolerite is the commonest soil in the A. nigrescens habitat (Downing, 1972). Grasses sampled from the carbonate rich, illuviated soils of the Bottomland Association were found by Downing (ibid.) to reflect a higher nutrient status than those sampled from the Upland Association. The presence of a montmorillonite clay fraction in dolerite-derived soils (Porter,

Fig. 7.3. : Relative percentage frequency of sightings in eight major habitats for all wildebeest social groups during the study period, with adjustment made for habitat areas. Habitat types are those described in the text, and in the caption to Fig. 7.2..

Fig. 7.2. : Relative percentage frequency of sightings for all wildebeest social groups in nine major communities throughout the study period.

(Acacia nigrescens open woodland; Acacia tortilis open woodland; Acacia nilotica closed woodland; Spirostachys africana closed woodland; Acacia grandicornuta closed woodland; Acacia caffra open woodland; Acacia burkei open woodland; Combretum apiculatum open woodland; and Acacia robusta/Phoenix reclinata riverine community.)

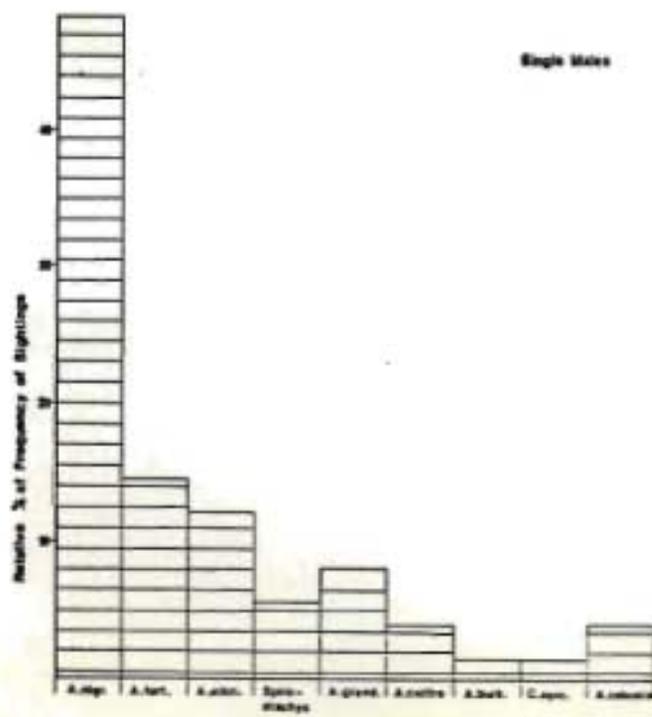
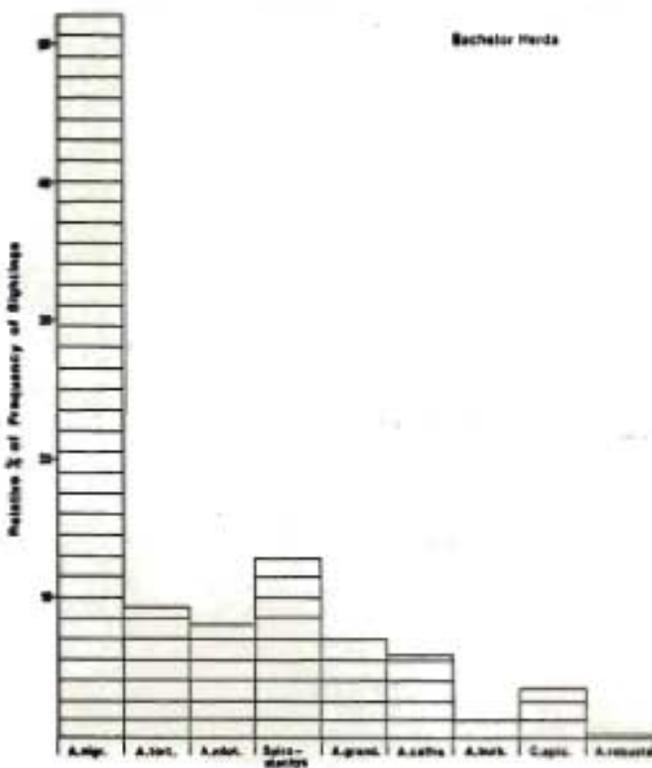
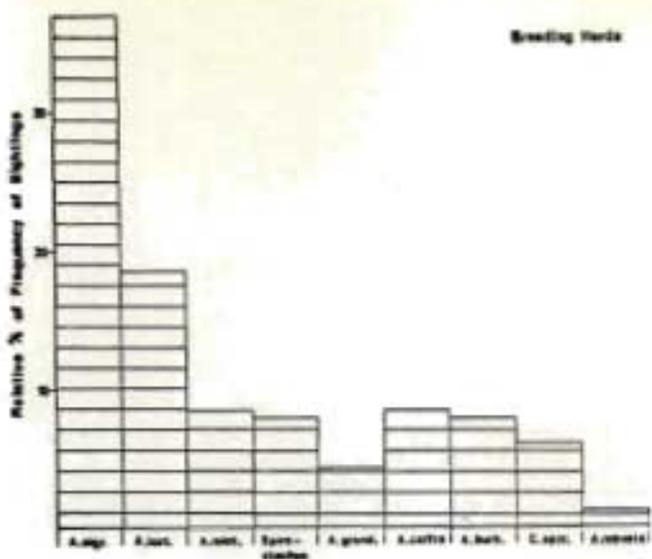


pers. comm.) lends water-binding properties to these soils, and may be instrumental in the rapid recovery of grass communities after rain. Regrowth of short-grass communities represents ideal grazing conditions for wildebeest. Smuts (1972) was able to relate zebra distribution in the Kruger National Park to edaphic factors, and specifically to the presence of dolerite-derived soils.

When the three social groups were considered separately in their utilisation of the nine major communities, significant differences ( $\chi^2$  tests) were found between groups (Fig. 7.4.). Single males differed both from bachelor herds in their selection ( $p < 0,001$ ), and from breeding herds ( $p < 0,001$ ). The differences between bachelor herds and breeding herds was less marked, but still significant ( $p < 0,05$ ). The implication is that resource distribution between social groups is in operation. Such resource distribution has been quantified for impala by Jarman and Jarman (1973). Anderson (1972) has discussed the dispersion of non-breeding impala males into less favourable habitat in HGR, and Estes (1969) maintains that in wildebeest the separation of bachelor herds from breeding herds gives the females and their calves a nutritional advantage.

The high selectivity for A. nigrescens warranted further analysis on a seasonal basis. Fig. 7.5. depicts the relative percentage frequency of sightings in A. nigrescens on a seasonal basis for single males, bachelor herds, and breeding herds respectively. All three groups differed significantly ( $\chi^2$  tests) from each other ( $p < 0,01$ ). Fig. 7.5. suggests that utilisation of A. nigrescens by single, territorial males is greater in the dry season than in the wet season; the peaks in April and August coincide roughly with the first and "second" ruts, but this may be purely circumstantial. The seasonal utilisation appears to be inverse to that of bachelor herds, and suggests that temporal separation of these two social groups may occur with respect to their utilisation of the preferred habitat.

Fig. 7.4. : Relative percentage frequency of sightings for three wildebeest social groups in nine major habitat communities throughout the study period.



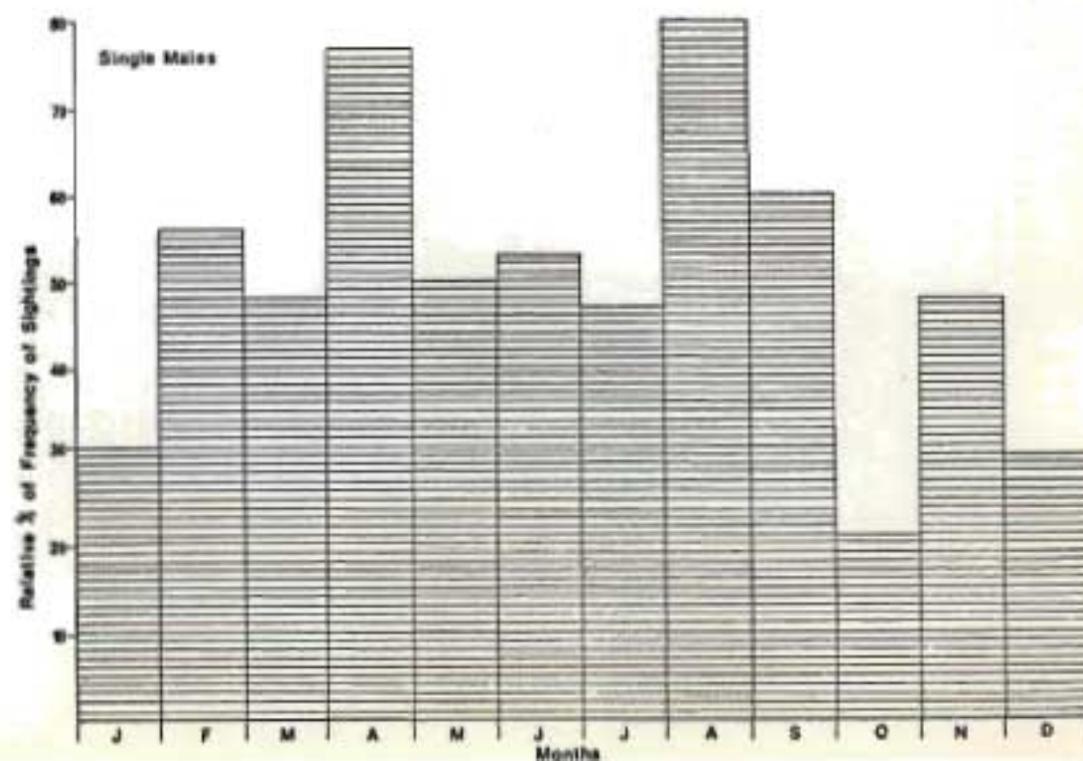
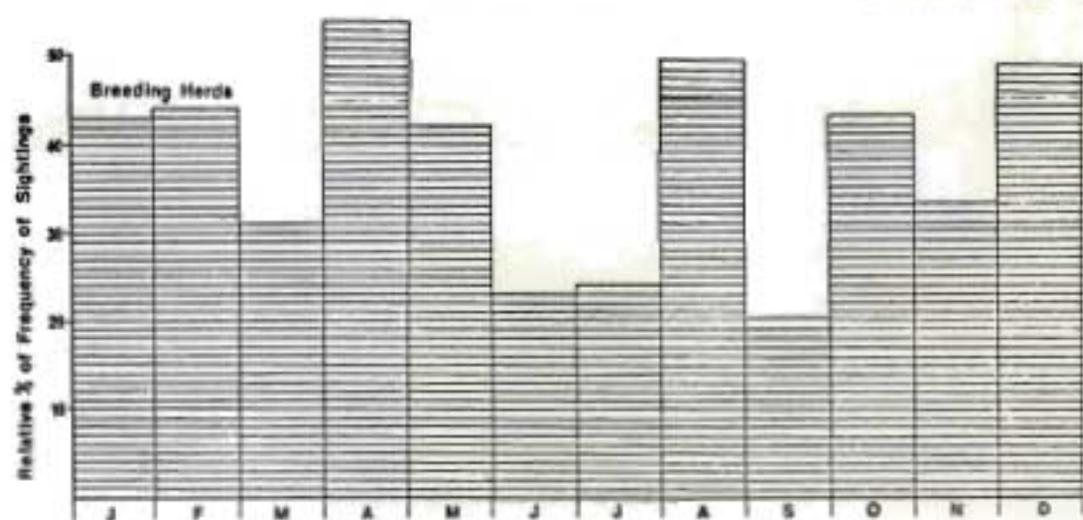
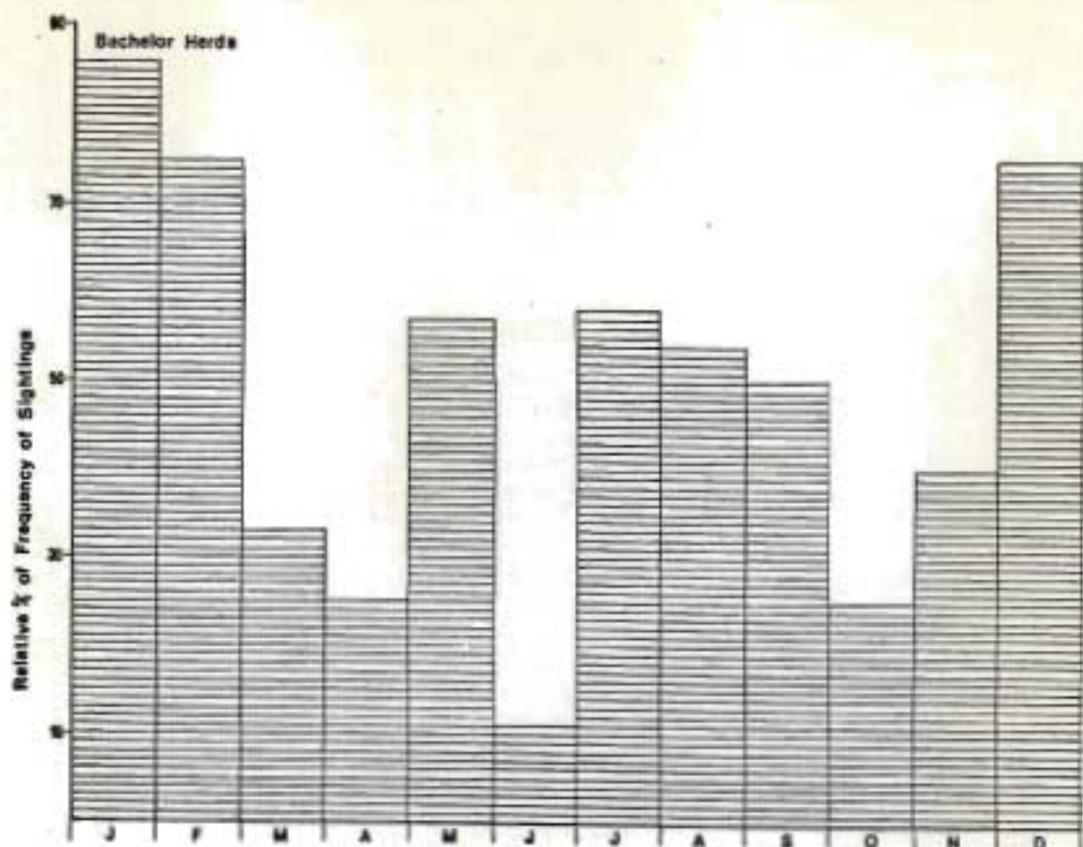
The breeding herd histograms show little apparent change, and differences may be due to sampling error.

The apparent selection by territorial males for preferred habitat raises the question whether the presence of "stamping grounds" (indicative of a territorial male) could be used as an index of habitat selectivity. During the rut, stamping grounds are particularly well marked, usually with a mosaic of interconnecting paths. They are often associated with white rhinoceros middens, usually on the periphery, but occasionally even within the midden itself. The surrounding areas of a stamping ground are heavily overgrazed. Stamping grounds are often sited on hill-sides overlooking valleys, or on the crests of ridges. This is presumably connected with visibility, and behavioural characteristics relating to the defence of a territory, such as "static optic advertising."

Some aspects of seasonal utilisation of habitats did not emerge from this analysis, but are supported by field observations. It was noticeable, for example, that Cynodon dactylon "lawns" (essentially floodplain grassland growing on sandy river banks) were grazed particularly towards the end of the dry season, when other short grass communities are heavily overgrazed. At this time, and in certain areas, it is possible that invertebrate herbivores are providing substantial competition to wildebeest. A potential competitor is the harvester termite, Hodotermes mossambicus.

The results presented in this section must of necessity be regarded as rather crude indices of habitat preference, for it is improbable that the success of sighting animals in different habitats can be completely equalised. Further, the use of a  $\chi^2$  analysis is more suited to distinct presence or absence data than to an essentially dynamic process which is habitat selection.

Fig. 7.5. : Relative percentage frequency of sightings for the three wildebeest social groups in the A. nigrescens woodland community, on a seasonal basis.



## 7.3.2.

RUMEN CONTENT ANALYSIS

The stomach morphology of an ungulate allows classification into three major divisions (Hofmann and Stewart, 1972; Hofmann, 1973):

- 1.) Bulk and Roughage Eaters.
- 2.) Selectors of juicy concentrated herbage.
- 3.) Intermediate feeders.

Both wildebeest and buffalo belong to the first category, which basically includes species with capacious rumens permitting the maximum delay of coarse, fibrous food. A finer structural differentiation (Hofmann, 1973) of stomach morphology allows subdivision of "Bulk and Roughage Eaters" into:

- a) Fresh grass grazers dependent upon water.
- b) Roughage grazers.
- c) Dry region grazers.

Again, buffalo and wildebeest remain unseparated, being placed under "fresh grass grazers dependent upon water."

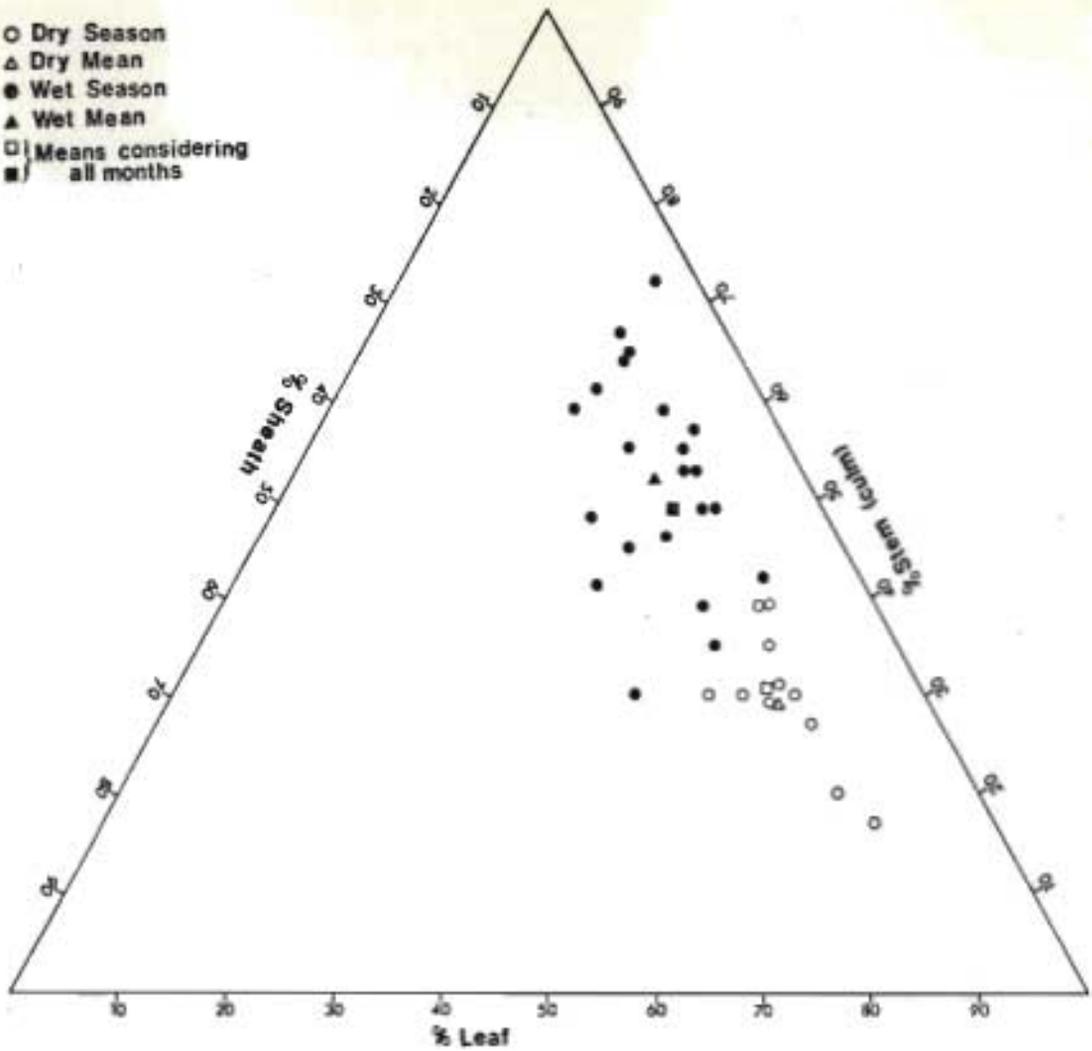
The results of the rumen content analyses showed that both species were almost entirely graminivorous. The wildebeest samples contained other plant material in 4% of the total examined. This non-graminaceous material consisted of negligible amounts of bark or dicotyledon leaves. These results are consistent with those reported by various workers, including Talbot and Talbot (1962), Gwynne and Bell (1968), and Hofmann and Stewart (1972).

An indication of the seasonal differences in rumen grass components is shown for both wildebeest and buffalo in Figs. 7.6. and 7.7. respectively. For wildebeest, only four months in the dry season (June, July, August, September) and four in the wet season (January, February, November, December) have been considered. This was done to prevent overlap of months with "intermediate" rainfall. However, the mean

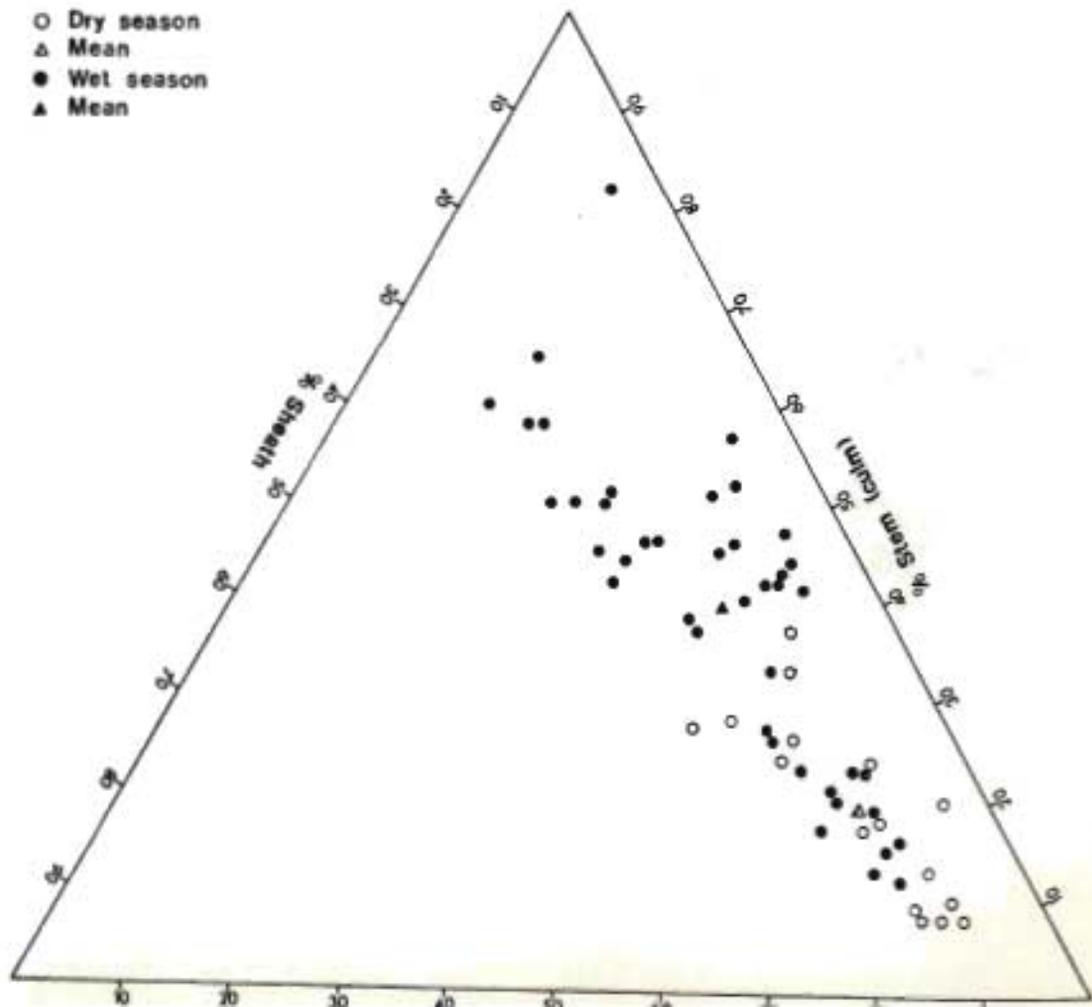
Fig. 7.6. : Frequency of the three principal grass components in the diet of wildebeest. Individual points have been plotted only for the four driest months (June, July, August, September) and for the four wettest months (November, December, January, February) to minimise overlap.

Fig 7.7. : Frequency of the three principal grass components in the diet of buffalo. All months considered. Dry season taken as April to September inclusive; wet as October to March.

- Dry Season
- △ Dry Mean
- Wet Season
- ▲ Wet Mean
- Means considering
- all months



- Dry season
- △ Mean
- Wet season
- ▲ Mean



frequencies of grass components for wet season and dry season were calculated using all months as well (dry: April - September; wet: October - March). The buffalo graph (Fig. 7.7.) includes all samples, and possibly explains why the degree of seasonal overlap is more marked than for wildebeest.

Comparison of the mean seasonal values for the two species is remarkably similar. In both species the percentage sheath is relatively constant. In the wet season, the percentage leaf increases by 23% for both species; and the percentage stem falls by 23% for wildebeest, and by 20% for buffalo. The similarity in dietary components is clear from Fig. 7.8.. It is important to remember that the similarity lies in grass components only, and not necessarily in species. Nevertheless, the similarity raises some interesting problems.

In the first place, the results do not support the findings of Gwynne and Bell (1968), that different species in a grazing succession could be separated on differences in grass dietary components. Either a grazing succession involving wildebeest and buffalo is not apparent (which is unlikely), or there is active selection for the same components, but at different levels in the herb layer. This raises the question of selectivity. An immediate explanation for the similarity in the dietary components is that neither species is selecting at all: the change in components in the diet is merely a reflection of the seasonal changes that occur in grasses. The literature is unanimous as to the status of the wildebeest as a selective grazer, (Talbot and Talbot, 1963; Gwynne and Bell, 1968; Owago, 1975; Sinclair, 1975; and McNaughton, 1976) and the hypothesis regarding non-selection can be justifiably rejected. Further, the ability of buffalo to select for both components and species has been demonstrated by Sinclair and Gwynne (1972).

It is pertinent to compare the feeding methods of buffalo and wildebeest. Buffalo use their tongue and incisors (but not the lips),

which is favourable for plucking whole bundles of grass (Hofmann, 1973). The wildebeest has a characteristic Alcelophine feature: high withers and a caudally sloping back. This postural feature has been interpreted by Hofmann (*ibid.*) as a grazing adaptation "plainsgame" animals. Bell (1969) maintains that the width of the anterior end of the snout determines the rate at which a herbivore can extricate leaf from grass of differing length. An animal like the wildebeest, with a wide snout, is most successful in short leafy mats, but its ability to select leaf falls off rapidly in longer grass types because the leaves are lower in the herb layer, and their angle of insertion on the stem is more acute. It is extremely unlikely that with different feeding adaptations, wildebeest and buffalo are consuming virtually the same components at the same level; the only explanation is that the same components are obtained by different mechanisms at different levels in the herb layer. That the two species differ in their adaptations to the height of the herb layer is well established (Bell 1969, 1970, 1971), and is readily confirmed by the most perfunctory of field observations. The similarity in selection of components is nevertheless surprising, but lends much support to Hofmann's (1973) classification of the two species into one category on the basis of stomach morphology.

Sinclair and Gwynne (1972) also found dietary overlap between wildebeest and buffalo, in the Serengeti. They pointed out that, if the function of food selection is to maximise nutrient intake, then overlap between grazing species would be a reasonable expectation.

The seasonal mean frequencies of dietary components for wildebeest are compared with results from Serengeti (Gwynne and Bell, 1968) in Table 7.3.. Without comparative data as to the availability of dietary components in the two areas, comment is limited; however, the fact that wildebeest in UGR are selecting more leaf in the dry season compared to the Serengeti, and more stem in the wet season,

**TABLE 7.3.** : Comparison of mean seasonal frequency of dietary components of wildebeest from UGR and East Africa. Serengeti data from Gwynne and Bell (1968).

	DRY SEASON		WET SEASON	
	SERENGETI	UGR	SERENGETI	UGR
% leaf	17,2	37,0	61,3	55,2
% sheath	52,7	14,2	28,9	14,3
% stem	30,1	48,8	8,0	30,5

suggests that UGR wildebeest may be utilising taller grass stands than in the Serengeti. If this is so, it may be related to the woodland nature of UGR, as opposed to an open grassland situation in the Serengeti.

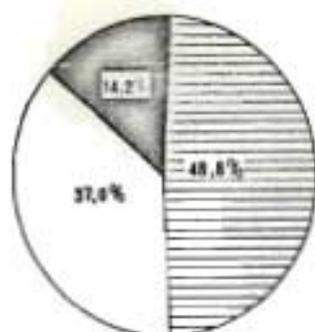
The seasonal changes in frequencies of grass components in the diet are shown for wildebeest and buffalo in Figs. 7.9. and 7.10. respectively. Both species show an expected fall in the leaf component (with a concomitant rise in stem) as the dry season progresses. Similar results (including the relatively constant contribution of the sheath component) for buffalo have been reported by Sinclair and Gwynne (1972). These workers showed that the amount of leaf in the diet was determined by the rainfall. Hoppe, Qvortrup and Woodford (1977) demonstrated a similar relationship for wildebeest. In my study, correlations were performed between percentage leaf and rainfall for that month, and for the month preceding the percentage leaf value. For wildebeest, the same month gave a value of  $r = 0,33$  ( $p < 0,05$ ), compared to  $r = 0,51$  ( $p < 0,001$ ) for the preceding month. The values for buffalo (in the same order) were  $r = 0,40$  ( $p < 0,01$ ) and  $r = 0,37$  ( $p < 0,01$ ). These results indicate that for wildebeest the rainfall of the preceding month was more important in determining the leaf percentage in the diet than was the rainfall of the month in which the rumen contents were collected.

Bell (1969) has explained why the wildebeest is confined to a short herb layer in terms of the animal's nutritional requirements and its feeding mechanism. As a short grass "specialist," the effect of wildebeest grazing on pasture degradation is more critical than that of most other grazers. Conversely, the nutritional status of this preferred short herb layer must impose limitations on the animal itself when environmental factors are ill-disposed. This is best understood in terms of the relative nutritional composition of the grass components. The leaves have the highest ratio of

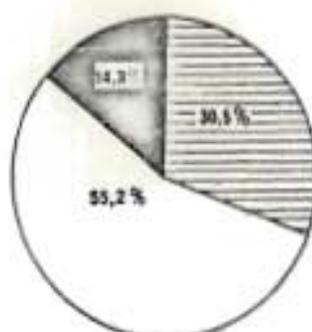
Fig. 7.8. : Diagrammatic representation of seasonal dietary components of wildebeest and buffalo.

Fig. 7.9. : Seasonal changes in mean values (circles, triangles, diamonds) of grass dietary components for wildebeest. Vertical lines indicate  $2 \times S.E.$ ; these have been omitted for leaf component in May and for sheath in January for the sake of clarity. Bracketed means indicate very small sample size.

Leaf  
Stem  
Sheath



Dry Season

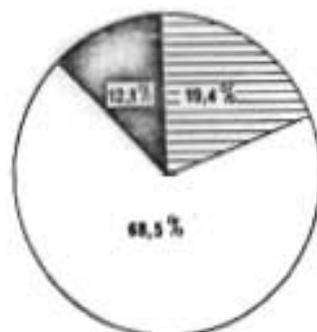


Wet Season

*C. taurinus*

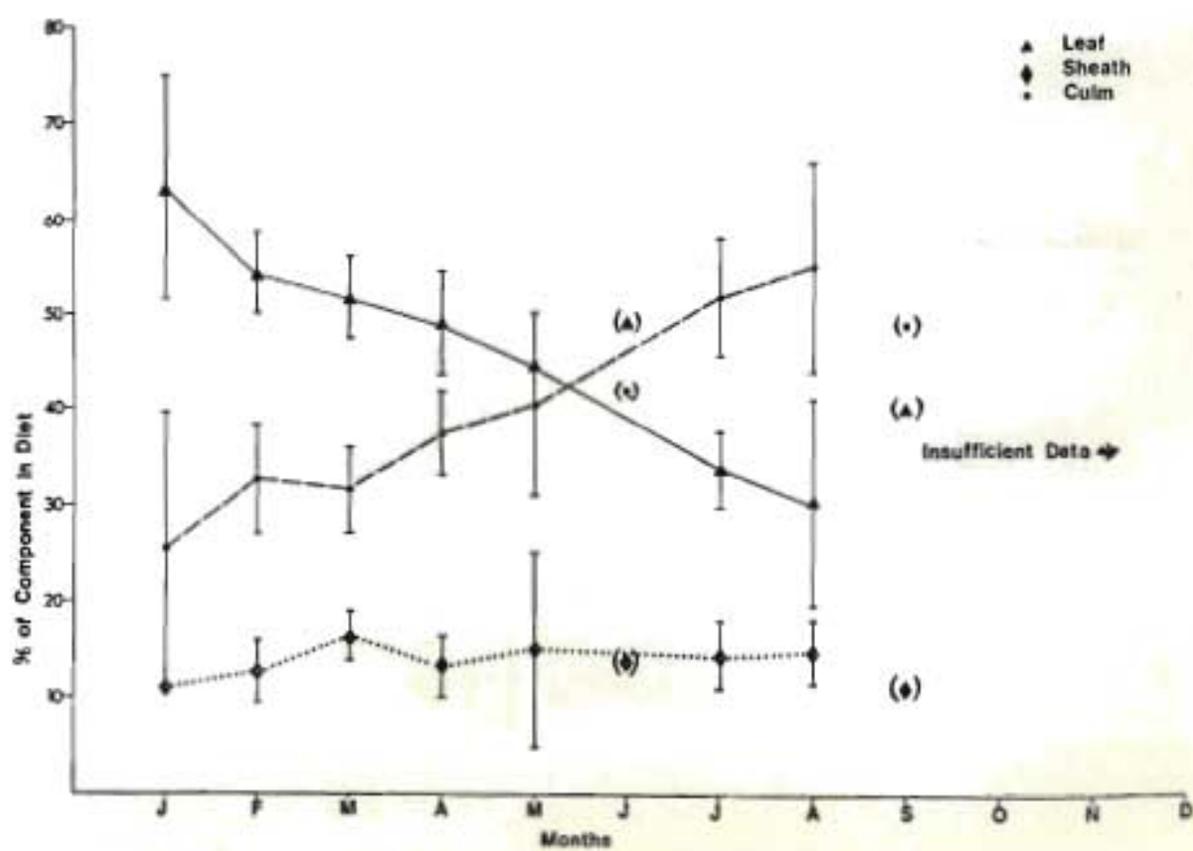


Dry Season



Wet Season

*S. caffer*

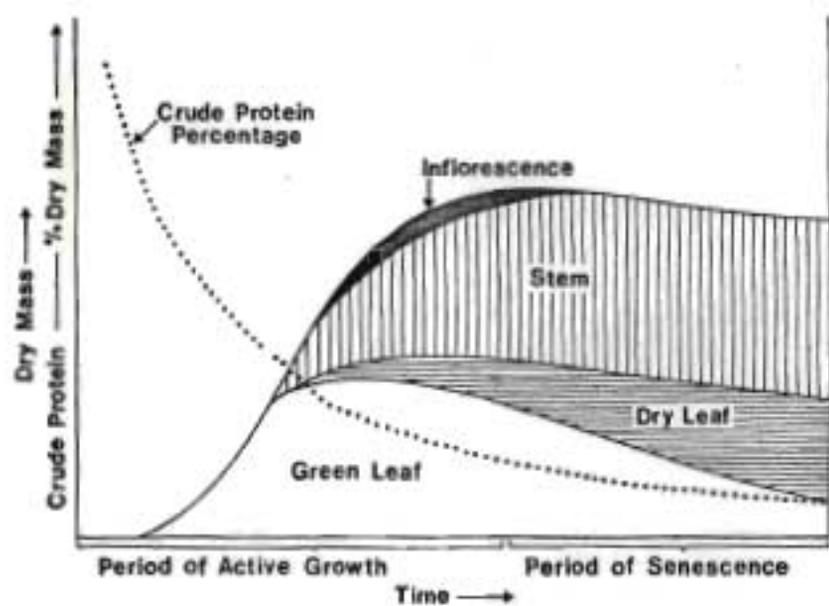
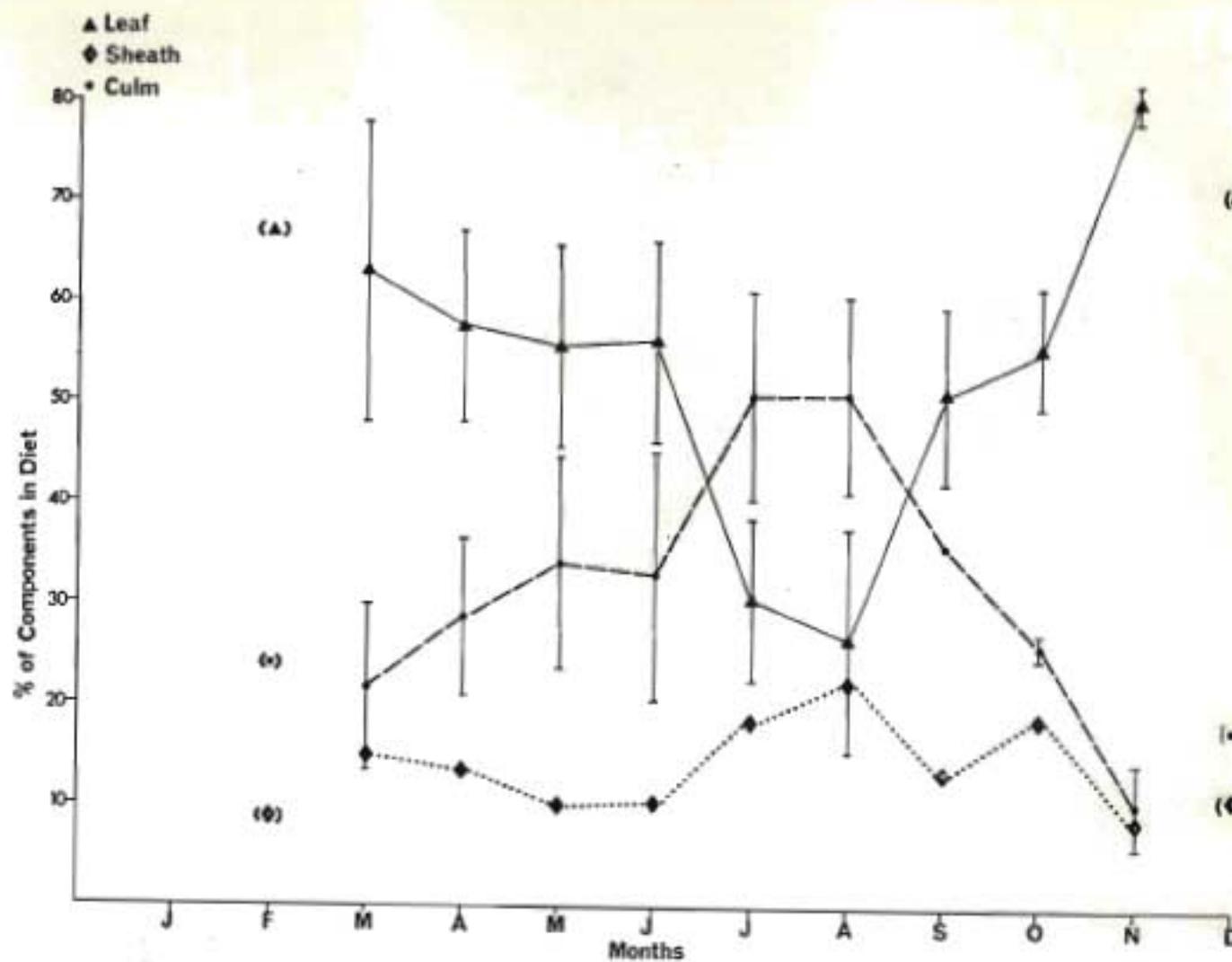


protein and soluble carbohydrates to cellulose; this ratio is lowest in the stem, and intermediate in the sheath (Gwynne and Bell, 1968). The changes in the major grass components together with crude protein levels have been illustrated by Barnes (1969). In Fig. 7.11. it can be seen that the proportion of stem to leaf increases as the plant matures. Both digestibility (measured by the stem component) and crude protein decreases as the shoot develops due to the increase in stem. If grazing is maintained such that growth is prevented beyond the leafy stage (which would occur under optimal wildebeest grazing conditions), the quality of the intake is high, but the yield will be low. But if the defoliation is too close and too frequent, nutrient reserves in the roots are drained in the production of new leaves, with resultant detrimental effects on the pasture. Such a situation arises in UGR with out-of-season rainfall. In July 1973, rainfall of this nature produced a rejuvenation of the growth cycle in short grass swards in UGR. These areas were immediately defoliated by wildebeest (among other grazers), which may well have resulted in utilisation of root reserves several months before the dry season ended. Pratt (1967) maintains that grass subjected to heavy grazing at sensitive periods in the growth cycle may be affected to the extent that yields are drastically altered years later. An added factor in overgrazing is that, along with a reduction of more desirable nutrients in the forage, the digestibility of these nutrients decreases owing to the forced utilization of coarser plant materials (Cook, Taylor and Harris, 1962).

There is evidence that the combined effect of seasonal lows in protein in the leaf together with seasonal lows in leaf proportions may well be a critical factor in the survival of some ruminants during adverse dry seasons (Field, 1968). Sinclair (1975) found in the Serengeti ecosystem that, despite the fact that wildebeest selected as food the more nutritious components of the grass, the quality still fell

Fig. 7.10. : Seasonal changes in mean values (circles, triangles, diamonds) of grass dietary components for buffalo. Vertical lines indicate 2 X S.E.; these have been omitted for sheath means owing to relative constancy of the latter. The September culm 2 X S.E. line has been omitted owing to overlap with leaf S.E.. Bracketed means indicate very small sample size.

Fig. 7.11. : The changes in proportions of grass components and in percentage of crude protein during the growth cycle. (After Barnes, 1969).



to the lowest level necessary for maintenance (this level he determined as 5 - 6% crude protein).

The interpretation of rumen content analyses is subject to pitfalls, particularly with regard to the fact that the contents of the rumen provide an inexact picture of the food ingested (Norris, 1943; Sinclair and Gwynne, 1972; and Owaga, 1975). Different components may have different residence times in the rumen, because forages more resistant to enzymatic activities of rumen micro-organisms will remain in the rumen the longest. Hence the forages that may be least important nutritionally may be most abundant in the rumen.

### 7.3.3.

#### ECOLOGICAL SEPARATION

The univariate F-ratios produced by the multivariate analysis are shown in Table 7.4.. These values select those habitat variables which are capable individually of discriminating between herbivore species. Clearly, variable no. 6 (mean height of the herb layer) has the most discriminatory power in both seasons. Variable 5 (average maximum height of the herb layer) is highly significant in the dry season, and variable 2 (% canopy cover trees) is significant at  $p < 0,05$ , but also only in the dry season. This latter variable shows the least discrimination in the wet season, possibly because during the rains differences between the heights of "beneath-canopy" grasses and those unassociated with trees are far less pronounced than they are in the dry season. A similar, though less marked, relationship between seasons is shown for variables 3 (% aerial cover shrubs) and 4 (mean height shrub layer), possibly for the same reasons.

The analysis further produced three discriminant functions (DF's). The first two accounted for 81,66 and 15,59% respectively of the

TABLE 7.4. : The univariate F ratios with percentage levels of probability for each of the twelve variables.

\* significant at  $p < 0,05$

\*\* significant at  $p < 0,001$

VARIABLE	D R Y   S E A S O N		W E T   S E A S O N	
	UNIVARIATE F RATIO	PROBABILITY %	UNIVARIATE F RATIO	PROBABILITY %
1	0,35	79,16	1,45	23,17
2	3,37	3,31 *	0,14	93,55
3	2,37	9,24	0,28	84,28
4	2,88	5,42	0,02	99,44
5	9,28	0,03 **	2,36	7,56
6	37,83	0,00 **	9,97	0,00 **
7	2,47	8,32	1,57	20,02
8	1,02	39,94	1,43	23,75
9	2,55	7,70	1,80	15,10
10	2,30	9,98	1,41	24,37
11	0,30	83,03	0,77	51,52
12	2,51	7,97	0,73	53,92

overall variance between species for the dry season, and for 67,46 and 29,03% respectively for the wet season. The third DF was not considered on account of its comparatively negligible removal. For the dry season, DF 2 was not significant ( $p > 0,1$ ), but has been included as an indication. The extent of association between each environmental variable and the first two DF's is shown in Table 7.5.. The degree of correlation of the variables with each DF allows that DF to be described in terms of habitat physiognomy. DF 1 suggests a trend from short grass (possibly with bare patches) into tall grass. DF 2 may represent a gradation from open grassland with shrubs into closed woodland.

The distribution of the four species centroids is shown for the dry season in Fig. 7.12. and for the wet season in Fig. 7.13.. The relative position of the centroids represents the extent and nature of the species separation. In the dry season, buffalo are separated by DF 1, and competition is minimised as they appear to move into tall grass areas. DF 1 does not account for separation of the other three species, and it is presumed that they are selecting a herb layer which is very similar in height. The minimal separation that does occur is along the DF 2 axis, with wildebeest showing a tendency for woodland selection, which agrees with the results of 7.3.1..

Ecological separation is minimal (Fig. 7.13.) in the wet season, but food abundance presumably obviates competition. As anticipated, the results show that, except in the case of buffalo, the four herbivores considered possess similar niche dimensions with considerable overlap.

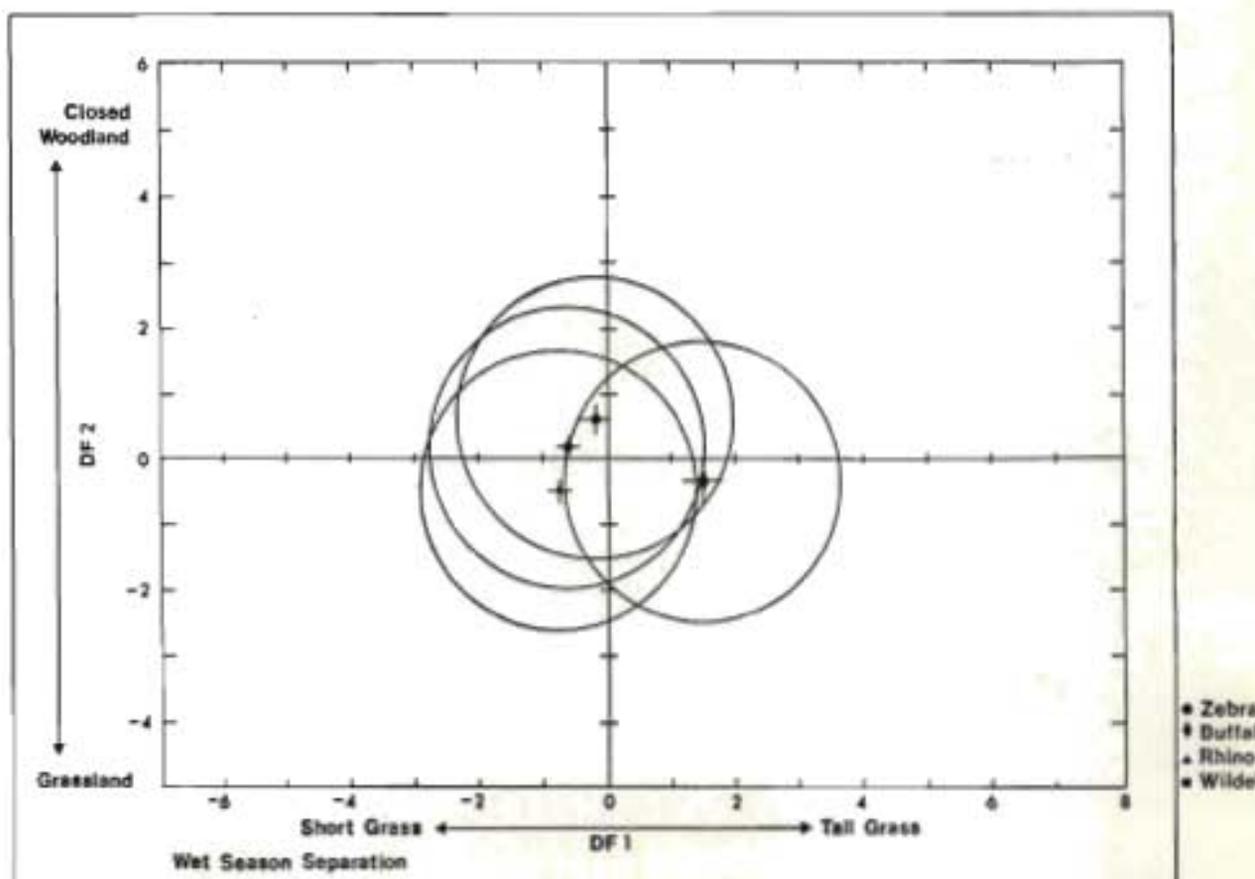
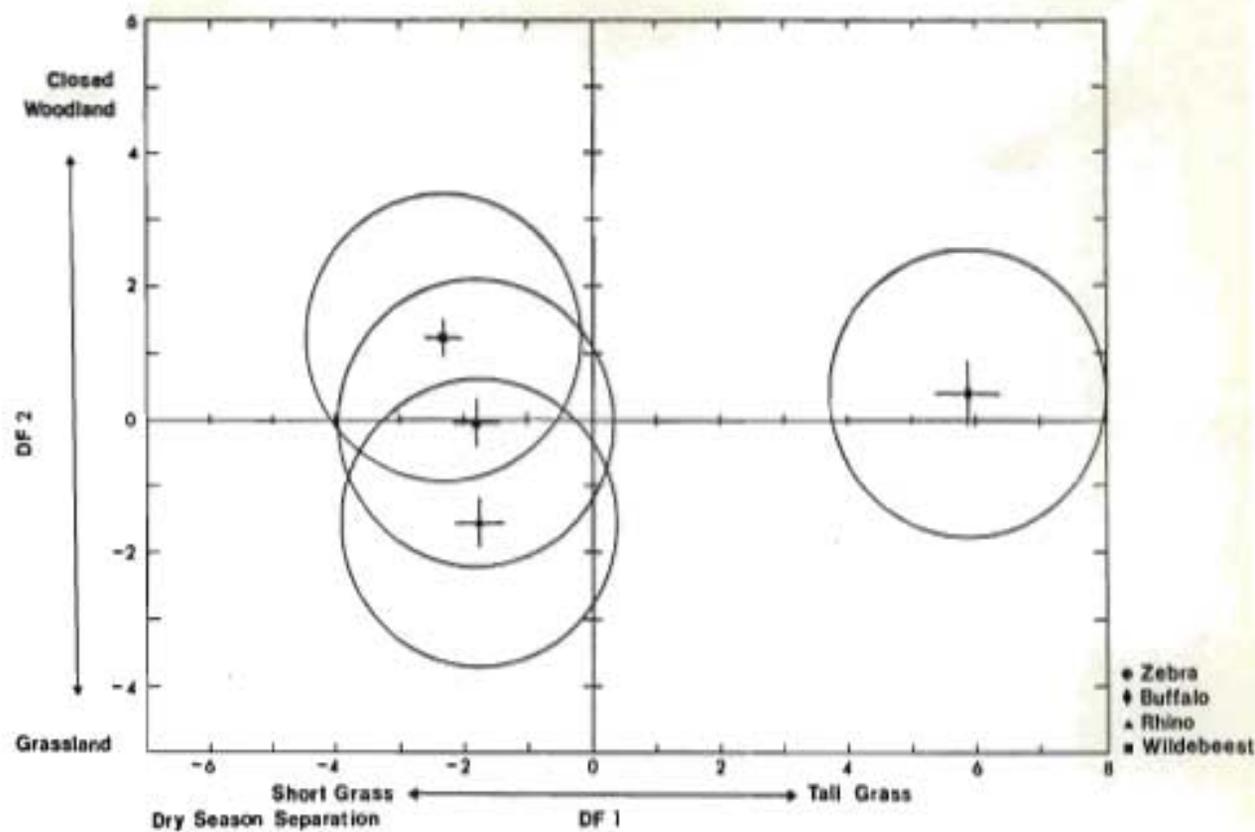
Pielou and Pielou (1967) recognised three types of coexistence: close, separate, and neutral. Close coexistence best fits the mixed herbivore situation where herbivore species are attracted through similar food and environmental requirements. Partial

TABLE 7.5. : Standardised weights for 12 variables from a discriminant function analysis of four species. Those weights with asterisks are those which appear to be strongly correlated with each DF. "Communalities" indicate the total proportion of the variance in each variable which has been accounted for by the three DF's together.

VARIABLE	D R Y S E A S O N			W E T S E A S O N		
	DF 1	DF 2	COMMUNALITIES	DF 1	DF 2	COMMUNALITIES
1	0,022	0,197	0,358	0,118	0,532*	0,091
2	0,152	0,586*	0,079	- 0,093	- 0,078	0,505
3	- 0,277	0,470*	0,162	0,092	0,173	0,300
4	- 0,308	0,499*	0,020	0,033	0,033	0,345
5	- 0,750*	- 0,093	0,402	- 0,407*	- 0,414*	0,573
6	- 0,943*	0,083	0,914	- 0,935*	- 0,113	0,900
7	- 0,465*	0,013	0,185	- 0,419*	0,011	0,318
8	0,278	- 0,085	0,518	0,351	- 0,148	0,208
9	0,295	0,461*	0,431	- 0,083	0,608*	0,337
10	0,196	0,154	0,231	0,295	- 0,373	0,700
11	0,035	0,093	0,100	0,282	0,132	0,115
12	0,437*	0,238	0,136	0,244	- 0,208	0,305

Fig. 7.12. : Disposition of four herbivores with respect to the first two discriminant functions during the dry season. Circles indicate 90% confidence limits. The bars extend for 1 X SE on either side of the species centroids.

Fig. 7.13. : Disposition of four herbivores with respect to the first two discriminant functions during the wet season. Circles indicate 90% confidence limits. The bars extend for 1 X SE on either side of the centroids.



overlap between species is an exceedingly common phenomenon, and close coexistence may only develop into competition if the resources decline below a critical level. However, I am in agreement with Field (1972) who considers that the preoccupation with separation of species may have allowed the possibility of competition to be neglected. The multivariate analysis suggests extreme similarity in the choice of structural aspects of the herb layer for three of the species considered, and the rumen content analyses suggested marked overlap in dietary components for two of the species. This does not necessarily imply competition per se, as two important considerations have not been taken into account. Firstly, the results in this section give no indication of spatial separation; and secondly, niche separation based on the selection of different grass species will not be apparent from the multivariate analysis. Spatial separation has been shown to obviate competition when food overlap occurs: Child and Von Richter (1969) studied three congeneric species with overlapping ranges (Lechwe Kobus leche, puku K. vardonii, and waterbuck), and found that differential habitat preferences resulted in partial spatial separation. Indeed, Hirst (1975) considered that spatial separation of ungulates in the Timbavoti reserve was the main method of avoiding competition. Some indication of spatial separation may be obtained by considering the associations between wildebeest and other herbivores. An analysis of the frequencies with which other herbivores were grazing in the immediate vicinity of wildebeest is shown in Table 7.6.. The numbers of observations were adjusted to account for differences in the numbers of the associated species. Mean values from the 1973 and 1974 helicopter censuses of the Complex were determined to supply ratios to adjust species on an equal number basis. Only the census data for buffalo, white rhino, zebra, and wildebeest can be considered reliable. The adjustments for the other species considered

TABLE 7.6. : Frequency of association of wildebeest with other herbivores. Figures in brackets for single males indicate those observations in which males were moving with the other species as a social unit.

ALL CATEGORIES	BREEDING HERDS	BACHELOR HERDS	SINGLE MALES	SOCIAL CATEGORY	
				NUMBER OF OBSERVATIONS	WILDEBEEST ALONE
422	187	89	146	NUMBER OF OBSERVATIONS	WILDEBEEST ALONE
63,1	72,2	60,9	55,3	% OF TOTAL OBSERVATIONS	
82	35	16	(22) 31	NUMBER OF OBSERVATIONS	WILDEBEEST WITH ZEBRA
12,3	13,5	10,9	(8,3) 11,7	% OF TOTAL OBSERVATIONS	
261,6	111,7	51	(70,2) 98,9	ADJUSTED NUMBER OF OBSERVATIONS	
15,6	19,4	12,9	(10,1) 14,2	% OF TOTAL ADJUSTED OBSERVATIONS	
18	6	4	(4) 8	NUMBER OF OBSERVATIONS	WILDEBEEST WITH WHITE RHINO
2,7	2,3	2,7	(1,5) 3,0	% OF TOTAL OBSERVATIONS	
65,2	21,7	14,5	(14,5) 29	ADJUSTED NUMBER OF OBSERVATIONS	
3,9	3,8	3,7	(2,1) 4,2	% OF TOTAL ADJUSTED OBSERVATIONS	
36	8	6	(14) 22	NUMBER OF OBSERVATIONS	WILDEBEEST WITH IMPALA
5,4	3,1	4,1	(5,3) 8,3	% OF TOTAL OBSERVATIONS	
36	8	6	(14) 22	ADJUSTED NUMBER OF OBSERVATIONS	
2,1	1,4	1,5	(2,0) 3,1	% OF TOTAL ADJUSTED OBSERVATIONS	
52	9	17	(17) 26	NUMBER OF OBSERVATIONS	WILDEBEEST WITH WATERBUCK
7,8	3,5	11,6	(6,4) 9,8	% OF TOTAL OBSERVATIONS	
389	67,3	127,2	(127,2) 194,5	ADJUSTED NUMBER OF OBSERVATIONS	
23,2	11,7	32,3	(18,2) 27,9	% OF TOTAL ADJUSTED OBSERVATIONS	
13	5	3	(5) 5	NUMBER OF OBSERVATIONS	WILDEBEEST WITH WARTHOG
1,9	1,9	2,0	(1,9) 1,9	% OF TOTAL OBSERVATIONS	
43,9	16,9	10,1	(16,9) 16,9	ADJUSTED NUMBER OF OBSERVATIONS	
2,6	2,9	2,6	(2,4) 2,4	% OF TOTAL ADJUSTED OBSERVATIONS	
15	3	4	(4) 8	NUMBER OF OBSERVATIONS	WILDEBEEST WITH KUDU
2,2	1,2	2,7	(1,5) 3,0	% OF TOTAL OBSERVATIONS	
79,5	15,9	21,2	(21,2) 42,4	ADJUSTED NUMBER OF OBSERVATIONS	
4,7	2,7	5,4	(3,0) 6,1	% OF TOTAL ADJUSTED OBSERVATIONS	
4	0	0	(4) 4	NUMBER OF OBSERVATIONS	WILDEBEEST WITH BUFFALO
0,6	0	0	(1,5) 1,5	% OF TOTAL OBSERVATIONS	
8,8	0	0	(8,8) 8,8	ADJUSTED NUMBER OF OBSERVATIONS	
0,5	0	0	(1,3) 1,3	% OF TOTAL ADJUSTED OBSERVATIONS	
27	6	7	(0) 14	NUMBER OF OBSERVATIONS	WILDEBEEST WITH OTHER SPP. (CHIEFLY NYALA)
4,0	2,3	4,8	(0) 5,3	% OF TOTAL OBSERVATIONS	
68,3	15,2	17,7	(0) 35,4	ADJUSTED NUMBER OF OBSERVATIONS	
4,1	2,6	4,5	(0) 5,1	% OF TOTAL ADJUSTED OBSERVATIONS	
669	259	146	264	TOTAL NUMBER OF OBSERVATIONS	
673,9	576,5	393,9	697,6	ADJUSTED TOTALS (INCLUDING ADJUSTED WILDEBEEST).	

can be used as indicators only. Further errors result from the fact that these data are essentially ancillary to the main aspects of the study, and considerable sampling bias may be present.

The results indicate that wildebeest very seldom graze in the same area as white rhino and buffalo in comparison to zebra, and one may infer that white rhino and wildebeest are separated spatially, despite the proximity of their centroids. Wildebeest are most commonly associated with zebra (12,3% of observations for unadjusted numbers), followed by waterbuck. (The waterbuck figures may be biased, as many of the observations making up the Table were made in the Thobothi area, where waterbuck numbers are high.) The association of wildebeest and zebra is a well-established phenomenon. Braack (1973) suggests that the explanation is related more to social than to habitat requirements, while Keast (1965) considers added sensory receptors for predation in addition to the benefits that may result from a grazing succession. Whatever motivates the association, the question of possible separation still remains, even though there exists the teleological danger that separation must follow if competition occurs. Lamprey (1963) showed by analysis of the grass species eaten by the two species that there was little differential preference, and explained separation on the basis of food abundance during the wet season, and spatial separation during the dry. Hirst (1975) was able to separate the species only on the basis of differential soil preference. The selection of different grass components (with zebra taking more sheath and stem) has been demonstrated by Bell (1969) and Owaga (1975). But the results of the multivariate analysis from UGR imply that there is little difference in terms of selection for grass height, and it is grass height which will largely determine the proportion of stem in the diet. Only a comparative rumen analysis of zebra will resolve the finer aspects of separation which are not accounted for by spatial factors.

Walker (1974a) has summarised some of the pitfalls in multivariate research, and shows how invalid results from ecological data may arise. Ferrar and Walker (1974) point out that it is incorrect to place rigorous statistical interpretations on the results, and that these should be interpreted in a qualitative manner. A further consideration that may be a source of error has been discussed by Eisenbeis, Gilbert and Avery (1973). It will be noted that in this analysis, both the univariate F ratios and the association of variables with the DF's provide means of ranking the variables in order of discriminatory power. The above authors point out that different ranking procedures need not give consistent rankings, and consequently it is essential to specify the ranking procedure used.

#### 7.3.4.

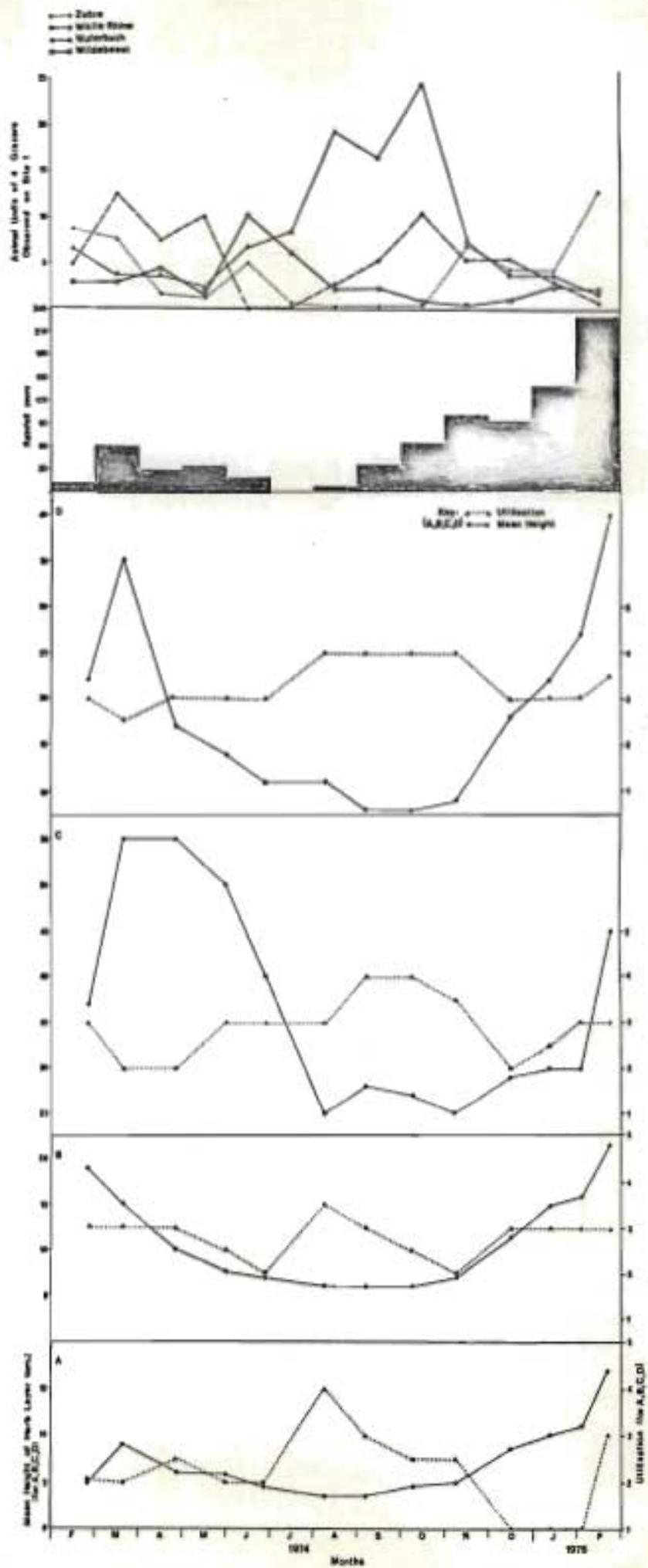
##### THE GRAZING SUCCESSION

As the multivariate analysis showed that the mean height of the herb layer was that variable with maximum discriminatory powers, only that variable has been considered in the seasonal changes on the four plots in Study Area 1. In Fig. 7.14., mean height of the herb layer has been related to season, utilisation, rainfall, and Animal Units of four main grazers.

The change in mean height appears to be related to rainfall, and the relationship is similar to that described for "leaf table height" by Vesey-Fitzgerald (1969). Plate 7.1. compares the herb layer during the dry season (30.9.74) with that during the wet season (22.2.75). Average maximum height of the herb layer is greatest in about February; Porter (1975) used the Board Method to determine standing crop of the grass layer, and his maximum values were obtained between mid-February and late May. Maximum biomass presumably corresponds to the period of maximum growth, or to the end of that period.

Mean height of the herb layer can be considered then to give some

Fig. 7.14. : Seasonal relationships between mean height of the herb layer, utilisation, rainfall, and Animal Units of four main grazers. (Study Area 1).

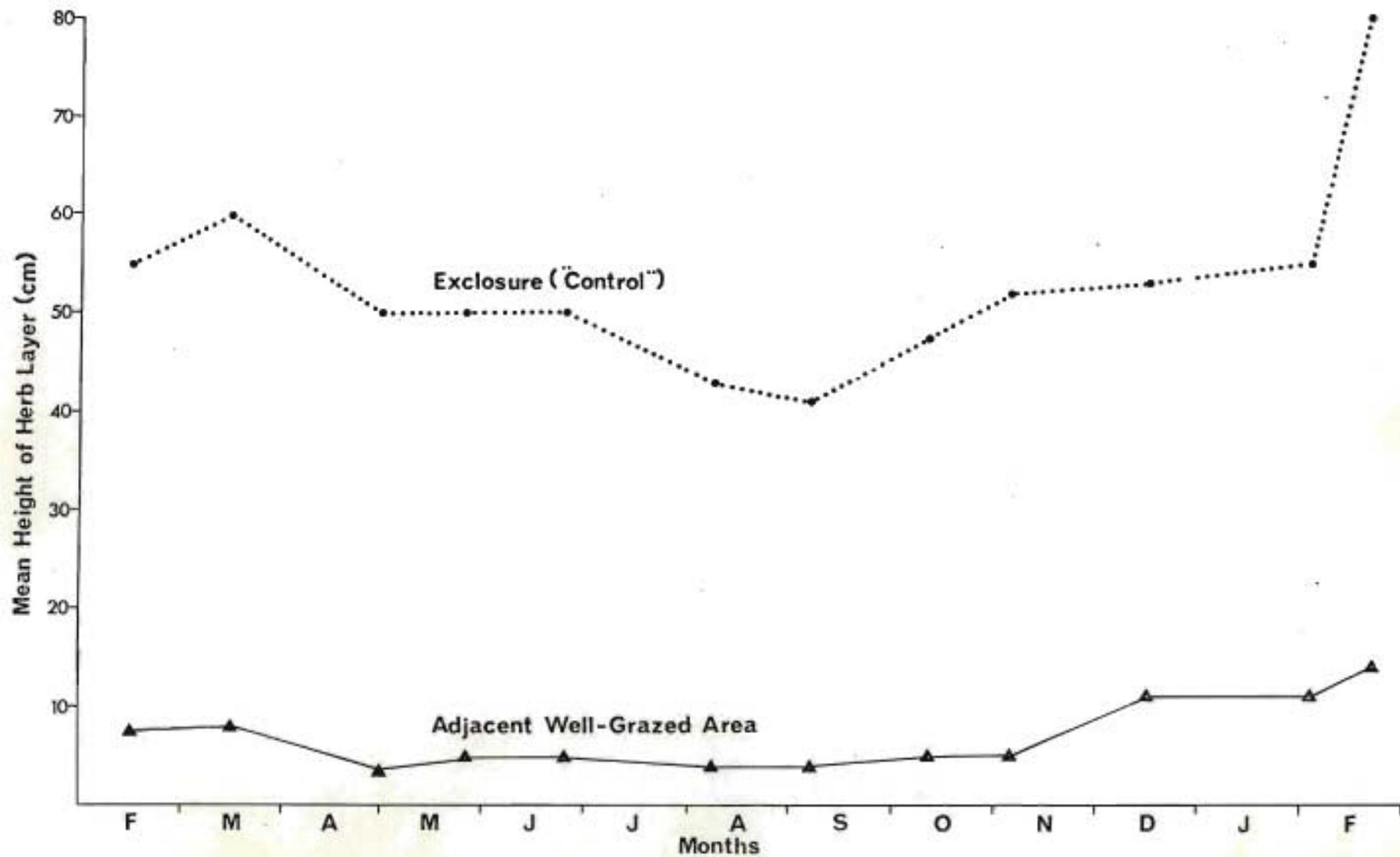


indication of standing crop. Harris and Fowler (1975) estimated that approximately 20% of the net primary production in Mkomazi, Tanzania was consumed by large herbivores. Such a low figure initially suggests that herbivore trophic levels in that region are not food-limited, but Sinclair (1975) has shown that one cannot simply relate primary production with food. Bell (1969) was able to demonstrate that in the Serengeti the carrying capacity of medium to long grass areas increased during the dry season as a result of the activity of grazing fauna in reducing the herb layer structure in the absence of rapid growth. In Fig. 7.14., utilisation is most marked when the herb layer is shortest. This situation in UGR is very similar to that in the Sengwa Wildlife Research Area (Rhodesia), described by Goodman (1975), where the minimum biomass of the herb layer recorded in August and September coincided with maximum utilisation.

These results suggest that Downing's (1974) criteria for conditions of a pasture ideal for conservation purposes are unrealistic. Among other characteristics, Downing (*ibid.*) maintained that the "ideal" pasture would have a grass height greater than 50cm. This value will result in minimal utilisation, and is only attained (in Acacia nigrescens woodland) in the absence of grazing (Fig. 7.15).

The "grazing pressure" of four grazers is included in Fig. 7.14.. Other species were recorded (e.g. impala), but have been omitted for clarity and on account of their low Animal Unit (AU) values. AU values (Mentis and Duke, 1976) have been used in preference to absolute numbers of species, as it was considered that this would provide a more realistic picture of impact on the herb layer. No idea of stocking rate can be arrived at, since no method was devised to estimate the duration of the various species in the Study Area. If a succession occurs, then a suggested sequence for Study Area 1 could be white rhino followed by wildebeest and zebra, followed by waterbuck. The results

Fig. 7.15. : Comparison between mean height of the herb layer in the exclosure plot and in an adjacent well-grazed area.



from Study Area 3 suggested a different sequence: wildebeest and zebra preceded impala, which were followed by white rhino. The implication is that in UGR a grazing succession is not well-defined, and if it is present then the sequence of species is not predetermined, but depends on local concentrations of species in the area under consideration. Waterbuck were consistently found in Study Area 1, and their high numbers might lend bias to a "succession" which is not representative for UGR. The apparently similar temporal utilisation by wildebeest and zebra is somewhat conflicting with the literature, where wildebeest have been recorded as succeeding zebra (Watson and Kerfoot, 1964; Bell, 1969, 1970, 1971). The concept of a grazing succession was originally properly elucidated in the Serengeti (Bell, *ibid.*), where vegetation and topography are associated in an extremely well-defined manner. Such a situation does not exist in UGR, which has a mosaic of habitat types. There is a danger of assuming a succession merely because different grazing species are utilising the same resources. Porter (1975) states that in western UGR, long grass areas are associated with valleys and short grass with hill tops and ridges. He related this situation to a grazing succession, whereby various species progressively moved off the ridges (zebra, waterbuck, and wildebeest, in that order) as the dry season approached. My own observations support the view that the reverse situation is in fact the case i.e. long grass areas predominate on hilltops and short grass areas in the valleys. My conclusion is that a grazing succession is not the rule in UGR, and when it does exist the sequence of animals is far more complex than that described by Bell (*ibid.*) for the Serengeti, and by Porter (*ibid.*) for UGR. Wildebeest are not necessarily the species which utilise areas when the mean height of the herb layer is at its seasonal low.

Further research into the question of a grazing succession in UGR should take into account the occurrence of the pasture mosaic

Plate 7.1. : Comparison between herb layer structure (in Study Area 1, Plot A) observed during the wet season and during the dry season.  
(Dry season photograph taken on 30.9.74; wet season on 22.2.75).

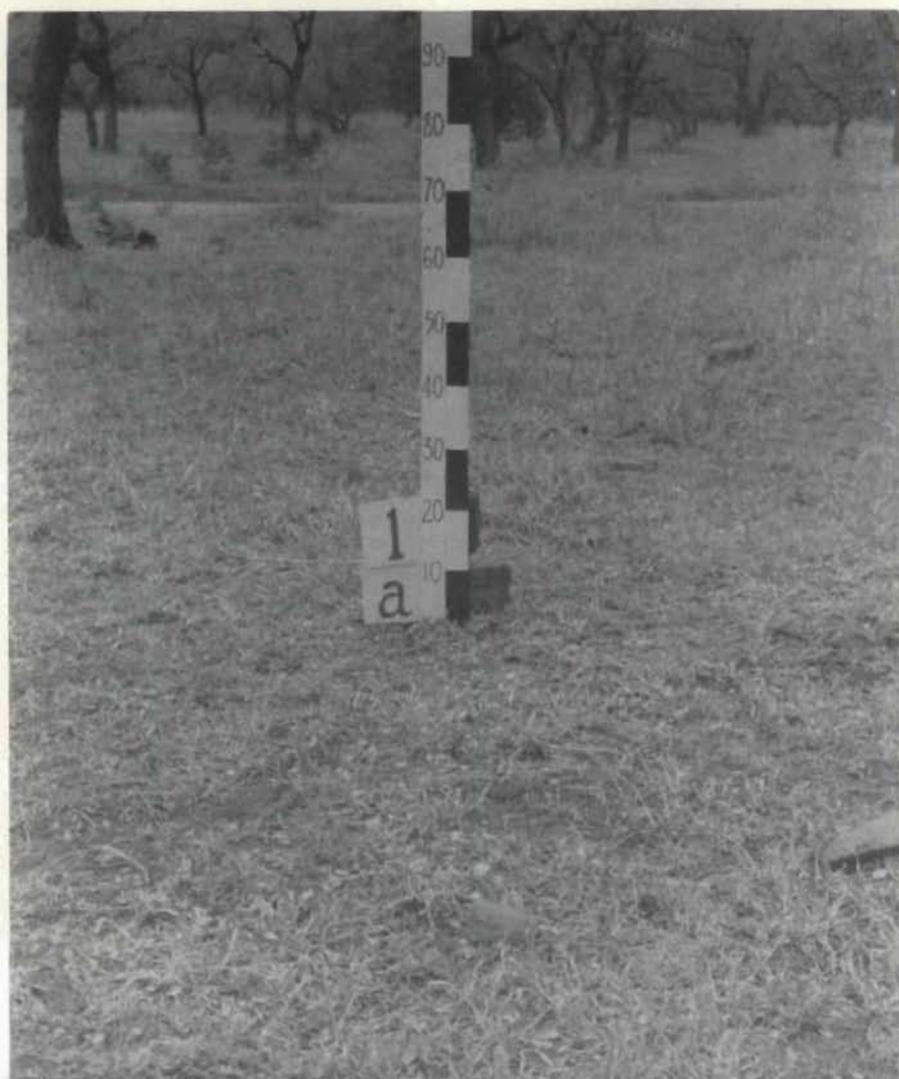
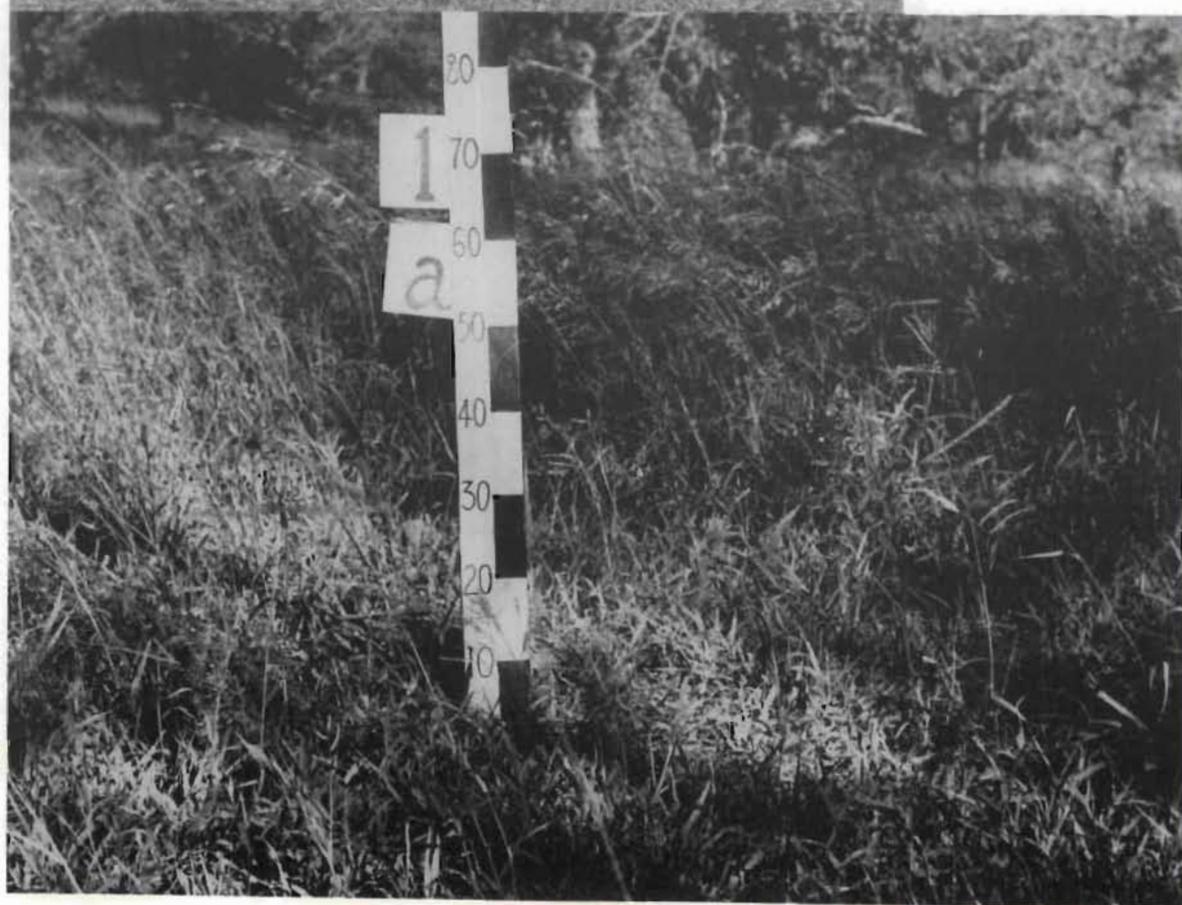


PLATE 7.1



(alternation of long grass and short grass areas). Grazing mosaics have been explained in terms of the accumulative effects of avoidance of less favourable pasture (Vesey-Fitzgerald, 1969), or in terms of soil factors (Talbot and Talbot, 1963). Avoidance of unpalatable grass genera like Bothriochloa and Cymbopogon is certainly a factor in the Complex. The effects of fire may be a further consideration in that some localised patches remain unburnt, especially around termitaria, in areas where harvester termite denudation is marked, or on sandy patches where the annual grass cover has died off.

### 7.3.5.

#### DISTRIBUTION AND MOVEMENT

When fieldwork had been terminated, approval was given for the instigation of a marking program for several species (including wildebeest). Some 60 wildebeest were marked with collars in different areas of the Complex in May, 1975, and subsequent resightings were made from fixed patrols and from an aircraft. In addition, several wildebeest herds were translocated from UGR to HGR, and some of these animals were marked to study movement after translocation. This study of ungulate movement was supervised by Dr. P. M. Brooks, and did not constitute part of my research. The results of the collar-marking program are not considered here, as these will be presented in detail by Brooks (in prep.).

In general, movement is limited and true migration absent. Wildebeest populations in the Complex are relatively sedentary, provided their requirements can be met in the area approximating to their home range. Major factors influencing movement appear to be burns and the provision of pans in upland areas during the wet season. The attraction of wildebeest to burns is well-known (Watson and Kerfoot, 1964; Pratt, 1967), and examples of burn-initiated movement were prevalent during this study. For example, an arson burn in the Corridor in October

1974 resulted in a movement of most animals normally resident in the Seme Flats area of southern HGR onto the Corridor burns. The distance covered was about seven kilometres. The filling of pans in upland areas, coupled with grass regeneration, favours utilisation of such areas during the wet season. Such utilisation may be extremely favourable to pastures readily accessible to wildebeest. The Nqolothi upland area in southern UGR is basically a plateau surrounded by areas which are utilised by wildebeest through much of the dry season. When conditions are favourable, wildebeest are in a position to make immediate use of the "plateau". Consequently this upland region receives favourable grazing treatment: heavy utilisation during the wet season by wildebeest (and other grazers), followed by comparative rest during the dry season on account of the absence of water on the plateau.

The dispersal of wildebeest from HGR into UGR has been discussed in Chapter 2. Eloff (1966) has documented range extension of the species in the Kalahari Gemsbok National Park. It is possible that the spearhead of the dispersal was composed largely of single males, for Smuts (1972) found that in the Kruger Park lone bulls were the first to reach the summer grazing areas. A similar phenomenon has been reported for the range extension of impala (Hitchins and Vincent, 1972). Whatever the mechanism of dispersal into UGR, it can be assumed that dispersal is now complete, as populations have been recorded in the extreme south of UGR for many years.

On the assumption that the siting of previous capture operations would provide an indication of major concentrations in the past, Fig. 7.16. has been prepared. Comparison with Fig. 7.17. implies that a) concentrations have remained largely in the same areas for at least five years, and that b) distribution has been largely unaffected by removal operations.

The dry season or winter distribution is shown in Fig. 7.17, and is

Fig. 7.16. : Locations in the Complex where wildebeest game capture operations took place between 1969 and 1973. It is assumed that capture sites will give some indication of dry season wildebeest concentrations. (Based largely on maps compiled by Densham, and held in the HGR herbarium).



Fig. 7.17. : Distribution of wildebeest in the Complex (based on density expressed in hectares per animal) during the 1974 dry season. Data from helicopter census undertaken in July and August 1974 (Whateley and Brooks, 1974).-



based on the helicopter census of July and August 1974. This distribution is very similar to the results of other censuses, (which have been plotted on maps by Natal Parks Board officers and are held at the HGR herbarium), including those for August 1972, June 1973, and September 1975. The constancy of the distribution is a further indication that dispersal is complete. Although distribution is largely related to habitat, it is sometimes unwise to make direct comparisons between distribution and a habitat map. The Meva basin in the Wilderness Area of UGR will usually reflect high census figures. This area has for years been highly degraded, and the vegetation is dominated by Acacia grandicornuta and Pappea capensis trees. The herb layer shows encroachment by Azima tetra-cantha and Asparagus sp., both of little value to grazers. In some respects, the numbers of wildebeest in the area are related more to movement patterns than to habitat: they utilise the slopes of Tshokolwana and Luthenzezi which contain the Meva basin, and must descend into the Meva to drink from pans, or must pass right through the Meva to drink from the White Umfolozi river when the pans are dry.

Fig. 7.18. depicts those areas which were allocated for game removal in 1974, on the basis of habitat degradation. Although most removal areas overlap the main dry season distribution of wildebeest (Fig. 7.17), little causal relationship can be deduced, as other grazers are involved. Fig. 7.19. (the wet season distribution) was prepared from three fixed-wing flights undertaken in December 1973, and in March and April 1974. As a result the wet season distribution is not as accurate as that for the dry season. The two distributions are similar, except that the Corridor upland areas are utilised more during the wet season.

The conclusion is that summer and winter ranges are not discrete as they are for wildebeest in the Kruger Park (Broack, 1973; Smuts, 1974).

Fig. 7.18. : Areas assigned for game removal in 1974, based on habitat degradation. Based on map compiled by Porter in 1974.

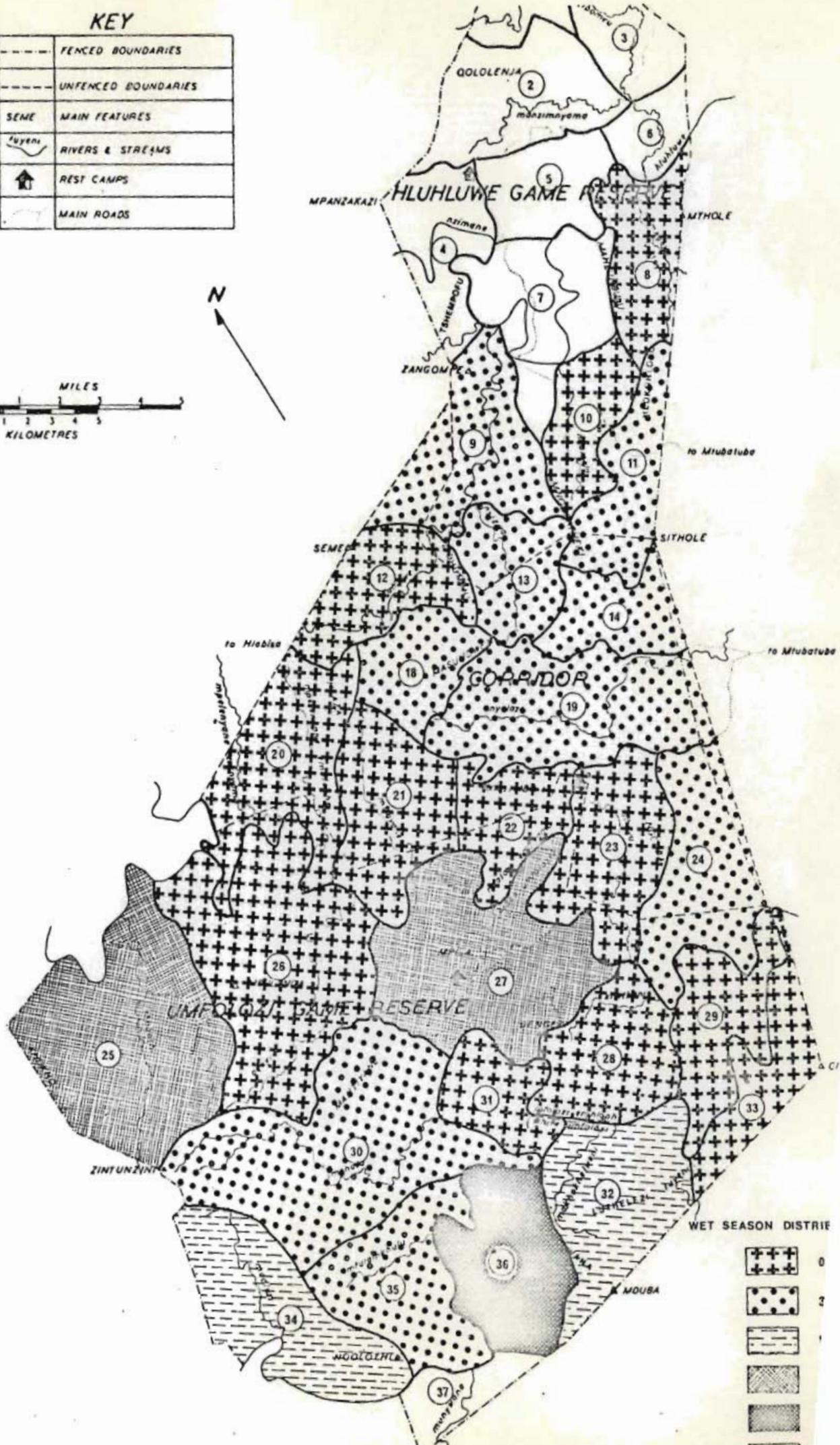
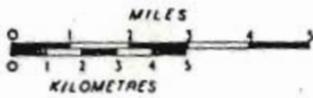


Fig. 7.19. : Rough 1974/75 wet season distribution pattern of wildebeest in the Complex, based on three fixed-wing flights undertaken (14.11.74; 30.12.74; 6.2.75). The key relates the mean number of wildebeest (represented by number classes) to specific numbered regions. These regions are in fact management areas, delimited on the basis of catchment areas and the road network.

Sources of error arise from the fact that any specific numbered region was not necessarily counted on all three flights; further, regions are not of equivalent areas.

# KEY

	FENCED BOUNDARIES
	UNFENCED BOUNDARIES
<b>SEME</b>	MAIN FEATURES
	RIVERS & STREAMS
	REST CAMPS
	MAIN ROADS



WET SEASON DISTRICT

	0
	2
	1

Braack (ibid.) classified wildebeest populations in the Central District of the Kruger Park into those that were fairly sedentary and those which displayed migration in the use of summer and winter ranges. Both migratory and localised populations have also been described from East Africa (Talbot and Talbot, 1963).

The question of the original condition of the species (migratory or sedentary) is not clear. Estes (1976) put forward a model for the evolution of reproductive synchrony in the wildebeest, and this model involved adaptation to a migratory existence. If this is so, then wildebeest are primarily migratory and secondarily sedentary, and resident populations (as are found in the Complex) must represent offshoots of migratory populations. But the persistence of territorial habits in nomadic populations (Watson, 1969) suggests that sedentary habits may represent the original condition of the species, as it is difficult to see how territoriality could evolve as an adaptation to a migratory existence (Estes, 1969). Resident populations in the Complex exactly correspond to Estes' (1976) description of habitat exploitation for "residents": they exploit their small home ranges in basically the same manner as their migratory counterparts, but on a reduced scale, where pasture conditions vary according to slope and drainage.

It is considered that distribution in the Complex is largely related to habitat, and it is unlikely that more subtle factors (like the availability of calcium in the grass, Kreulen (1975)) play an important role.

#### 7.4.

#### CHAPTER SUMMARY

In HGR, some generalisations were made regarding wildebeest habitat choice. A more quantitative approach in UGR showed that Acacia nigrescens woodland was the most favoured habitat. There were indi-

cations of seasonal resource distribution between wildebeest social groups for this habitat.

Analysis of grass structural components from rumen contents revealed similar results for both wildebeest and buffalo. The implications of these results are discussed. In both species, the dietary grass components were related to rainfall.

The mean height of the herb layer was found to be a habitat variable with high discriminatory powers between habitat choice by wildebeest, zebra, white rhino and buffalo. Only the last species showed significant ecological separation based on a multivariate analysis of some habitat variables, although overlap in ecological requirements of the first three species did not take spatial separation into account.

It was suggested that the grazing succession in UGR was more complex than that described from East Africa, and that the sequence of animals in the succession was not always predictable.

Wildebeest populations in the Complex were found to be relatively sedentary, with little seasonal differences in distribution.

## CHAPTER 8

### POPULATION ECOLOGY

#### 8.1.

##### INTRODUCTION

The existence of a population rests on the fact that new matter continually replaces that which it must inevitably lose: this apparently simple concept is complicated by the many factors governing replacement and loss. A population has a birth and death rate, a growth form, density, age structure and numerical dispersion in time and space.

A population study is basically concerned with the causes of fluctuations from year to year, and the factors which determine the magnitude of such fluctuations. Laws (1974), for example, demonstrated how an elephant population decline in Uganda was due to reduced recruitment resulting from deferred mortality, reduced fecundity, and increased calf mortality.

In gregarious bovids, three social classes are universal (Estes, 1974). These are nursery or breeding herds (comprising females with or without young), bachelor herds (all-male), and solitary adult males. The last class usually consists of territorial animals; despite a marked seasonal rutting period, a segment of the wildebeest male

population paradoxically exhibits territoriality throughout the year. Territoriality affects population structure, and through that population reproductive potential. The ecological significance of this behaviour is not entirely clear, although there are sound arguments (Jarman and Jarman, 1973) that displacement of males from the social organisation may result in improved resource flow to females, thus increasing calf production.

I have singled out territoriality, as this is a distinguishing feature of the wildebeest, but it should not be regarded as an over-riding factor in population processes. There is an interplay of numerous factors which govern the trend of any population, and it is fundamental to establish the trend of a population before one may theorise on the factors governing the trend. One approach is to estimate the rate of increase of a population, through the use of the statistic  $r$ . "r" is the observed rate of increase of a population, and is determined by age-specific fecundity and survival, sex ratio and age distribution (Caughley and Birch, 1972). Any change in the environment will change r. In an abstract concept of a population's potential to increase, a stable age distribution is assumed i.e. the life table and fecundity table remain unchanged. A rate of increase so calculated is termed  $r_s$  (Caughley and Birch, ibid.). A special case of  $r_s$  at low density such that the population has maximum rates of survival and fecundity with no limiting resource is  $r_m$ , the intrinsic rate of increase. This statistic is not constant for a species, but relates to a specific environment.

## 8.2.

### MATERIALS AND METHODS

#### 8.2.1.

##### HERD CLASSIFICATIONS

Classifications of herd structure were made both on the ground and

from the air. Classifications varied in accuracy; the more accurate ground classifications were performed by stalking a resting or feeding herd in wooded terrain, and classifying from a tree-top with the aid of binoculars. Such classifications usually allowed for discrimination of 2 - 3 year old animals, but it was often possible only to divide a herd into calves, yearlings, and "adults." Accurate classifications (including sex of 2 - 3 year old animals) were performed during game capture operations, when each animal could be closely observed as it passed through a crush prior to loading onto vehicles.

Ground sampling included a bias in favour of single males, as these are relatively static, and tended to be resampled. This is obviated from an aerial sample, as any particular area is covered once only. Aerial classification enables a good sample to be taken from the entire Complex at one time, whereas the time required for a meaningful ground sample demands a restriction in area. A helicopter is clearly advantageous for ease and accuracy of counting; it also enables one to differentiate between breeding herds without calves and bachelor herds, which is not always possible from a fixed-wing aircraft.

Data collected from aircraft were subject to the following assumptions:

- (i) all single animals were adult territorial males. Solitary females were recorded from ground classifications, but were extremely rare.
- (ii) each breeding herd contained one adult territorial male. Large breeding aggregations may contain more than one such male, but their frequency of occurrence is low.
- (iii) all males in bachelor herds were "adult" (i.e. 2 - 3 years old, or older).

More accurate classifications from the ground (e.g. percentage yearlings

in breeding herds) were combined with aerial data (e.g. percentage breeding herds of sample) to provide levels of accuracy unobtainable by either method alone.

### 8.2.2.

#### LIFE TABLES AND POPULATION MODELS

The female sample (seventy-six animals) from culling operations was used to form an  $l_x$  series for life tables. (Life table symbols are defined in Table 8.7.). The male sample from culling was extensively biased towards territorial males, and was consequently not used. Instead, survivorship curves for both sexes were based on life tables constructed from ninety skulls found in the field (a  $d_x$  series). In both cases, under-representation of younger age classes meant that the first two values in each series were based on field observations.

Comparison was made with life tables prepared from hitherto unutilised data collected from culling operations by Vincent (pers. comm.) in HGR and the northern Corridor in 1967. Vincent's subjective tooth wear classes were related to the infundibular pattern chart (Fig. 3.6.) to estimate absolute ages. The wear classes chosen by Vincent necessitated grouping older animals as follows: 5 - 6,9 years; 7 - 11,9 years; 12 - 13,9 years; 14 + years. The resultant life table (based on 84 females shot) consequently required some "smoothing": this was achieved by taking the mean of groups of three consecutive  $l_x$  values, and ascribing the mean to the second of each group. Vincent's male shot sample appeared to be less biased than my sample, and a male life table (based on 70 shot animals) was constructed for the purpose of comparing survivorship curves between the sexes.

The construction of life tables from shot samples or skulls assumes a stationary age distribution (Caughley, 1966). A stationary age distribution results when a population is constant both in size and in age structure. It is a special case of the stable age distribution

where the population may increase or decrease at a constant rate (Hanks and McIntosh, 1973). The wildebeest population in the Complex (or, indeed, any wildebeest population) does not show a stationary age distribution. Nevertheless, life table information may be used to demonstrate how an unstable population is changing. Spingale (1970) states: "Provided a statement of the purport of a life table is given then there would not seem to be a necessity for a stable age distribution."

In this instance, life tables have been used to construct population models with the object of examining how variation in reproduction and mortality influences the rate of population growth, thereby investigating the factors responsible for natural regulation of the wildebeest population. Different life tables were constructed by varying the mortality rates (particularly during the first year of life), and the age-specific fecundities. Such variation is justified from the literature: Watson (1969) noted that calf mortality in Serengeti wildebeest during the first few weeks varied from 28 to 79%. Buffalo experienced a similar variation (Sinclair, 1974b). Variation in age-specific fecundity ( $m_x$  values) is pronounced in 2 - 3 year old wildebeest: Watson (1969) observed a variation in reproductive success from 25 to 50% for this age class over four consecutive years in the Serengeti.

In all cases where  $l_x$  or  $m_x$  values were varied to provide different life tables,  $r_s$  was calculated according to the method of Andrewartha and Birch (1954). In addition, game removal figures and census data (Natal Parks Board files) were used to calculate a figure for  $r_m$ . The method used was that outlined by Caughley and Birch (1972). This method does not require life tables, and the problem of the stable age distribution does not arise.

### 8.2.3.

#### SUPPLEMENTARY DATA

No emphasis was placed on the collection of behavioural data in this study, as this aspect in the wildebeest has been fully documented (Talbot and Talbot, 1963; Watson, 1969; Estes, 1966, 1969).

Behavioural observations were recorded where they were considered to differ from those described by the above authors.

Data on mortality were extracted from Natal Parks Board files, and were based on monthly reports, chiefly from rangers. Data on herd fluidity were based on the resighting program of collared animals (Brooks, pers. comm.).

### 8.3.

#### RESULTS AND DISCUSSION

#### 8.3.1.

##### POPULATION STRUCTURE

An example of the results obtained from aerial classification is shown in Table 8.1.. The structure corresponds roughly to that attained by the end of winter, when mortality peaks have already been achieved. Comparative results for other months are not presented, as Caughley (1974) has demonstrated that age ratios contain little extractable information: indeed, massive increases or decreases in numbers may go completely unmarked by change in age ratios.

Instead, more relevant parameters of population structure have been compared with other populations. Table 8.2. compares calf percentages for different months and different localities. The 1965/66 calving season in the Complex was the worst recorded, followed by the 1973/74 season. The three months prior to the rut in 1965 received abnormally low rainfall (Table 2.2.), which may have been a factor in

TABLE 8.1. : Population structure of Complex wildebeest population in August 1974, based on aerial classification.

Number of animals sampled	800
Sample as % of population	30%
Number of single sightings	72
% single sightings of sample	9,0%
Number of animals in breeding herds	633
% sample in breeding herds	79,1%
Mean size breeding herd	14,4
Range breeding herds	2 - 40
Number of animals in bachelor herds	95
% of sample in bachelor herds	11,9%
Mean size bachelor herds	5,6
Range bachelor herds	2 - 16
Number of calves counted	123
% of breeding herds comprising calves	19,4%
% sample comprising calves	15,4%
Number of territorial males (single sightings + breeding herds)	116
Territorial males as % of sample	14,5%
Number of "adult" males (territorials + bachelors)	211
"Adult" males as a % of sample	26,4%
Territorial males as a % of "adult" males	55%
Number of territorial males for each breeding herd	2,6
% yearlings in breeding herds (ground classification)	25%
% "adult" males in total breeding herds	6,9%
By subtraction, % "adult" females in breeding herds	48,7%
∴ % "adult" females in sample	38,5%
♂ : ♀	67 : 100
calves : adult females	40 : 100

TABLE 8.2.: Comparative calf percentages.

LOCALITY	DATE	CALF %	SOURCE
Hluhluwe Game Reserve	March-May 1963	27,8	Vincent and Hitchins (1967)
"	May-Sept. 1963	20,3	Anderson (pers.comm.)
"	Feb. 1965	26,7	Estes (1965)
Hluhluwe + Corridor	April-May 1966	11,5	Vincent and Hitchins (1967)
"	June/July 1967	27,3	"
"	Aug. 1974	13,6	Attwell (this study)
Corridor	April 1967	22,1	Hitchins (pers. comm.)
Umfolosi Game Reserve	Jan. 1973	24,7	Brooks (pers. comm.)
"	June 1973	20,6	Attwell } this study
Umfolosi + Corridor	Aug. 1974	14,5	" } this study
Complex	Feb. 1965	20,5	Vincent (1965)
"	Feb. 1974	22,8	Attwell } this study
"	Aug. 1974	15,4	" } this study
Mkuzi Game Reserve	Jan. 1965	19,8	Univ. Natal W.L.Soc Newsletter No. 3
"	May-June 1967	17,3	Anon, NPB. files
"	Apr. 1968	21,2	" " "
"	July 1968	27,5	Univ. Natal W.L.Soc.(1968)
"	July 1973	24,8	Attwell (helicopter)
"	Sept. 1974	26,5	Attwell (hide)
Timbavati Game Reserve Transvaal	April 1967	28,1	Hirst (1969)
Kruger Park, Central) Lindanda) Satara)	after breeding peaks, 1972	30 ) 32 ) 24 )	Braack (1973)
Makarikari, Botswana	March 1965	14,4	Estes (1965)
Wankie Park, Rhodesia	March 1965	22,0	Estes (1965)
"	Aug-Oct. 1966	11,2	Anderson (1967)
Serengeti Mara, Kenya	Jan. 1959-61	29 )	Talbot and Talbot (1963)
"	Oct.-July 1959-61	19 )	
Tarangire Reserve, Masailand	July-Oct. 1962	10,6	
Athi-Kapiti Plains, Kenya	March 1971	20,3)	Petersen and Casebeer (1972)
	October 1971	4,8)	

reduced conception rates. The 1974 low figure almost certainly results from heavy calf mortality (See 8.3.4.). Calf mortality in Mkuzi during 1974 was negligible in comparison to that in the Complex (September figures for Mkuzi show 26,5% calves compared to 15,4% for the Complex). The high percentages shown by Kruger Park may be due to the greater contribution to productivity from yearlings (Braack, 1973) and to minimal calf mortality. Braack (*ibid.*) noted no calf loss between February and July in Kruger Park, while the loss of yearlings during the same period was high. This is suggestive more of a disease factor than of predation, because it is unlikely that predation would favour calves and not yearlings.

The calf : adult cow ratio is a product of conception rates and mortality. Table 8.3. shows the realised natality of different populations, expressed by a calf : cow ratio. Comparison with other populations implies that conception rates are high in the Complex (as seen by the February 1974 ratio), and that calf mortality must account for the marked change by August.

Comparative sex ratios for adults (including 2 - 3 year olds) are tabulated in Table 8.4.. The preponderance of females is common to almost all populations. Mentis' figure of 131 ♂ : 100 ♀ was derived from a nagana campaign shot sample, and is unlikely to reflect the true ratio, for the following reasons: during culling operations, territorial males are shot far more frequently than females. Solitary territorial males are reluctant to leave their territories, and are thus easier to shoot than females. When in a breeding herd, their territorial posture again singles them out. Males are further selected for aesthetic reasons, and for the fact that, being larger than females, they are more desirable for ration distribution to Game Guard camps. From 1959 to 1964, the 5010 adults shot were in the ratio of 133 ♂ : 100 ♀ (Vincent, 1965), and must have resulted in considerable depression of the male segment. During 1973 and 1974

TABLE 8.3. : Realised natality as expressed by a calf : cow ratio.

LOCALITY	DATE	No. CALVES:100 Ad.♀♀	SOURCE
Hluhluwe Complex "	Feb.1965 Feb.1974 Aug.1974	53 69,5 40	Estes (1965) Attwell (this study) " "
Makarikari, Botswana	Mar.1965	32	Estes (1965)
Wankie, Rhodesia	Mar.1965	40,7	Estes (1965)
Masai-Mara ) " ) Tarangire Reserve	1959-61 1962	49 (Jul-Oct.) ) 67 (peak) ) 18	Talbot & Talbot (1963) Lamprey (In: Talbot & Talbot, 1963).
Ngorongoro Athi-kapiti Plains "	Jan.1965 Aug.1970 Mar.1970	70,4 52 ) 58 )	Estes (1965) Petersen and Casebeer (1972)

TABLE 8.4. : Comparative sex ratios (adults).

LOCALITY	DATE	♂	♀	LEVEL OF SIGNIFICANCE	SOURCE
Umfolozzi Game Reserve Complex HGR - UGR	1929-30 1974	131 67	100 100	$p < 0,001$ $p < 0,001$	Mentis (1970) Attwell (this study)
Mkuzi Game Reserve	1972-73 1973-74	67 47	100 100	$p < 0,001$ $p < 0,001$	Brooks (pers. comm.) Attwell (this study)
Kruger Park Central District	1968 1972	37 45	100 100	$p < 0,05$	Braack (1973)
Makarikari, Botswana	1965	43	100	$p < 0,001$	Estes (1965)
Wankie, Rhodesia	1965	30	100	$p < 0,001$	Estes (1965)
" "	1966	38	100	$p < 0,001$	Anderson (1967)
Tarangire	1961	49	100	*	Lamprey (In: Talbot & Talbot, 1963).
Serengeti - Mara	1959-61	108	100	*	Talbot & Talbot (1963)
Ngorongoro	1965	67	100	$p < 0,001$	Estes (1969)
Athi-Kapiti Plains	1970-71	50	100	$p < 0,001$	Petersen & Casebeer (1972)
Serengeti	"over 5 years"	100	100	*	Watson (1967)
Nairobi National Park	1966	82	100	NS, $p > 0,1$	Foster & Kearney (1967)
" " "	1968	50	100	*	Modha (1969) In: Petersen & Casebeer, 1972)

\* raw data unavailable.

culling took place in an even more biased ratio of  $544\sigma^{\text{r}}: 100\text{q}$  ; however, it is considered that this biased cull did not affect the sex ratio overmuch, because since 1967 the ratio has been balanced by Game Capture operations, which remove primarily breeding herds. Of 152 adults sexed from game capture during the study period, 138 were female (  $10\sigma^{\text{r}}: 100\text{q}$  ).

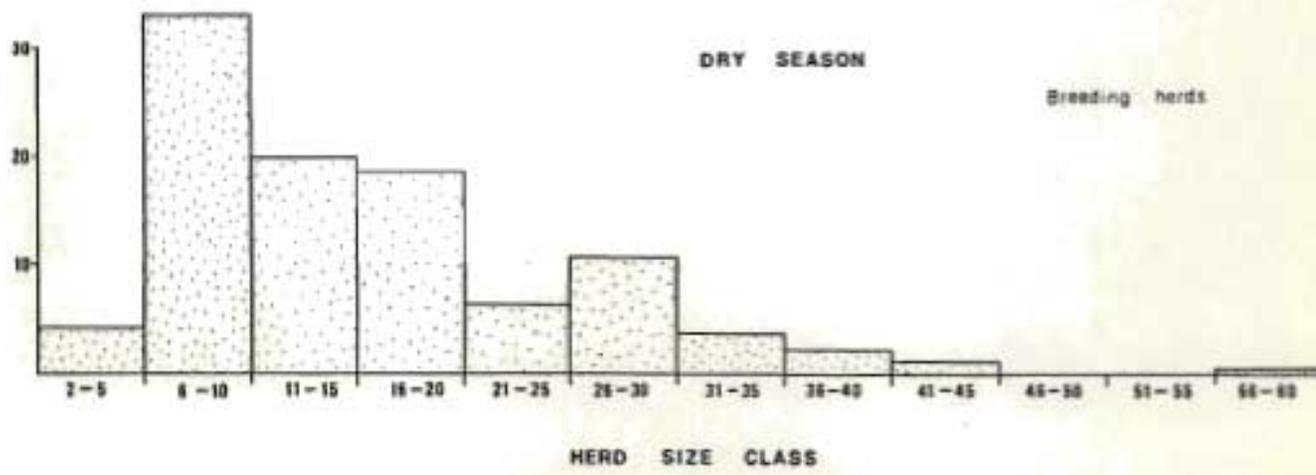
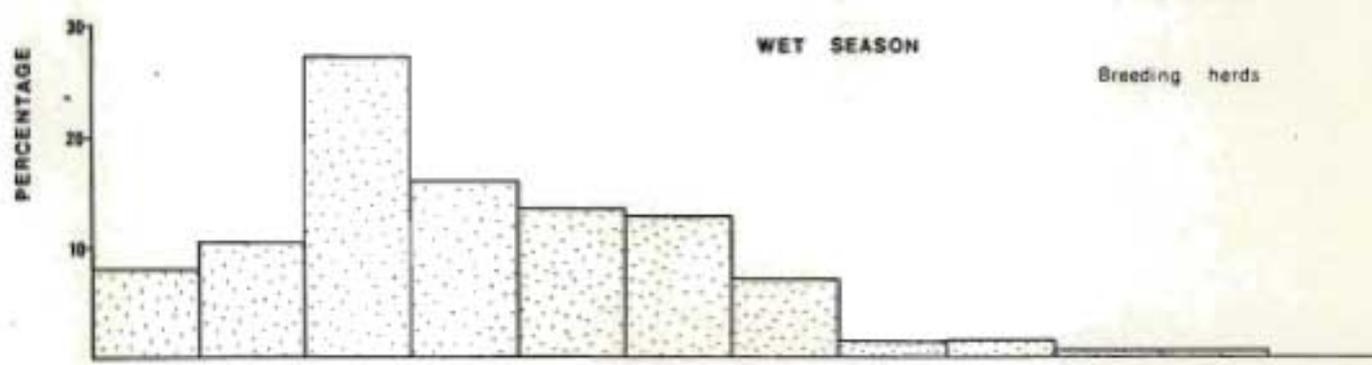
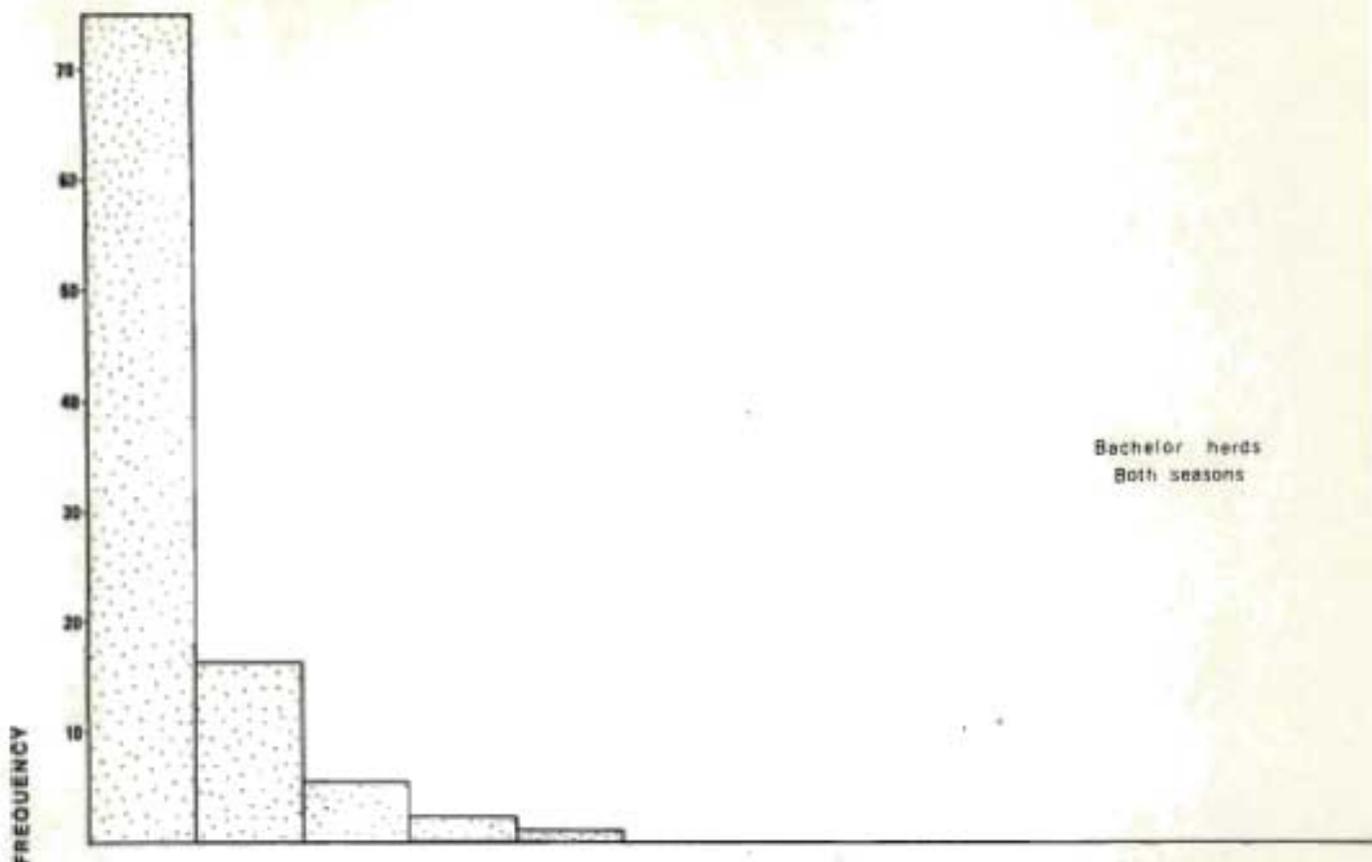
Since pre-natal sex ratios are close to parity, differential mortality must take place at the expense of males. Surprisingly, this is not borne out by significant differences between sexes of skulls found in the field or from records of mortality in the Complex (see 8.3.4.). It is unlikely that the differential sex ratio in the Complex results solely from early male-biased culling, as the present ratio is comparable with other populations in Africa. The comparison with other populations leads one to assume that the female-favoured ratio is a natural condition, and is indeed found in most territorial antelope. Whatever reasons there are for the failure of mortality returns and found skulls to reflect differential mortality between the sexes, one cannot escape the fact that such mortality is real. Depression of the sex ratio may result from differential responses to various socially and environmentally induced stress factors (Brooks, 1975). In wildebeest, such factors might involve expulsion of experienced sub-adult males from the breeding herd nucleus (see 8.3.2.) during the rut; the use of marginal habitat by bachelor herds; the susceptibility of territorial males to predation; and the loss of condition and lowered vigilance during the rut.

Jewell (1973) has commented that the persistence of a ratio close to parity at birth is puzzling, as this appears to be biologically uneconomical, since a single male may serve some twenty females. The explanation may lie in the fact that when predation favours females, the male segment acts as a buffer. In addition, males may act as agents of dispersal, either through the adoption of new

territories, or through the use of less favourable habitat by bachelor herds.

Since the male and female segments of the population are largely separated by the existence of breeding and bachelor herds, it follows that the sizes of these herds might affect various population parameters. Percentage frequency of herd size classes (number of herds sampled from the air = 785) is shown in Fig. 8.1.. An analysis of variance showed a significant difference ( $p < 0,01$ ) between wet and dry seasons for breeding herds only; bachelor herds did not differ significantly ( $p > 0,5$ ) between seasons, and are consequently not depicted according to season. Bachelor herds are notably small in the Complex, and never attain the sizes recorded in East Africa. Petersen and Casebeer (1972) noted bachelor herds of over 100 on the Athi-Kapiti plains in Kenya. There is a tendency for breeding herds to be larger during the wet season (Fig. 8.1.); this phenomenon was also observed in the Serengeti by Talbot and Talbot (1963). A similar seasonal pattern in mean herd size occurs in buffalo populations (Sinclair, 1974a). A possible explanation is related to food requirements - it is advantageous to be in a small herd during the dry season, because the larger the herd the further and more often it has to travel to find fresh grazing. An additional determinant of herd size is predation. Jarman (1974) has proposed that predation is the pressure inducing many antelope to associate in herds, while dispersion and availability of food items limit the maximum size that these herds can achieve. Smuts (1976a) found that family group size in zebra was higher in areas in the Kruger Park where lion populations had been reduced: hunting success of predators was an important factor limiting group size. Structure of the habitat may also influence group cohesion. With respect to zebra, Smuts (*ibid.*) maintains that large family groups are an indication of prime habitat conditions. If, as Eisenberg (1966) suggests, adaptation to





HERD SIZE CLASS

open habitats favours group formation, then the relatively small herd sizes in the Complex may reflect an adaptation to woodland. This may occur at the expense of increased calf predation (see 8.3.4.). Reference to Table 8.5. shows that the mean size of breeding herds at the same month in the Complex appears not to have altered since at least 1963. The higher figures for Wankie suggest the availability of more open habitat. Mean figures for Serengeti are not available, but descriptions of migrations (Grzimek and Grzimek, 1960) confirm that such figures would be well in excess of any noted in Table 8.5..

Breeding herds make up a relatively constant percentage of the population (at least during the study period), of about 80%. Braack (1973) found a similar situation in the Kruger Park, with no apparent seasonal variation in the percentage of animals in the three social groups.

Data from the resighting program of marked animals in the Complex (Brooks, pers. comm.) indicate that a breeding herd is not a cohesive unit, but that considerable fluidity exists (Table 8.6.). This conflicts with the findings of Estes (1966, 1974) in East Africa, where wildebeest breeding herds tended to have a fixed membership over at least five months after the calving season. Other species which may display consistency of herd structure are buffalo (Sinclair, 1974a) and zebra (Smuts, 1974). Where strong cohesive bonds exist, a high degree of inbreeding may result. Osterhoff, Young and Ward-Cox (1970) even suggest that inbreeding in buffalo herds in the Kruger Park may result to the extent that certain abnormalities could conceivably retard population growth. Although gross morphological abnormalities (e.g. twinning of foreleg hooves) were noted in this study on two occasions, one of which has been described by Keep (1974), it is unlikely that these result from inbreeding. The only genetic constraint that I can envisage acting on the Complex population would

TABLE 8.5. : Comparison between mean breeding herd size of different populations.

LOCALITY	DATE	MEAN BREEDING HERD SIZE	SOURCE
HGR + N. Corridor Complex "	March/April 1963 March 1974 August 1974	20 19,3 14,8	Anderson (pers. comm.) Attwell (this study) " "
Mkuzi Reserve	1973/74	17,8	Attwell (this study)
Kruger National Park Wankie National Park Ngorongoro	1971/73 January 1968 "year round average"	20 28,5 10	Braack (1973) Higgins (1969) Estes (1969)

TABLE 8.6. : Resightings of a marked adult female ("White I") in UGR, illustrating fluidity in herd composition.

<u>DATE OF SIGHTINGS</u>	<u>HERD SIZE</u>
6. 8.75	11
14. 8.75	22
21. 8.75	12
4. 9.75	23
11.10.75	27
14.10.75	21
5. 2.76	30 +
10. 2.76	55
21. 2.76	23
9. 3.76	19
17. 3.76	12
1. 4.76	37
4. 4.76	16
10. 4.76	31
22. 4.76	25
27. 5.76	17

be that resulting from the consistent removal of territorial males from culling operations. The male that ultimately becomes territorial will have a very much larger number of offspring than any contemporary female. As a result, he is the more effective agent of rapid genetic and evolutionary change (Jewell, 1973).

### 8.3.2.

#### TERRITORIALITY AND BEHAVIOURAL CONSIDERATIONS

Mention has already been made regarding some aspects of the contribution of the male segment to population ecology. Territorial males may aid in preventing overutilization of any one part of the range by breaking up concentrations into small units and spacing them out. Further they promote efficiency in reproduction, as chaos would result from contending males of equal rank congregating around an oestrous female (Estes, 1974).

The male segment, and in particular territorial animals, is considered in this separate section, owing to suggested behavioural and reproductive deviations from those observed in other populations. Adult males made up between 20 and 25% of the Complex population during the study period. This percentage compares favourably with other populations in Africa (Petersen and Casebeer, 1972; Braack, 1973). About half of the adult males are territorial, though this figure will vary depending on the time of the sample, for Estes (1969) has described a 25% increase in the number of territorial animals at the time of the rut. Although the percentage of territorial males in the adult male segment is within, and sometimes above, the range shown by other populations, the number of territorial males per breeding herd (2,6) is low in comparison to Estes' (1969) figure of 5 - 10 in Ngorongoro. Despite this, there is no evidence to suggest that the low value for the Complex (if indeed it is a low value, as there is only one comparable figure) influences age-specific fecundity.

In Section 5.3.6., evidence was presented that not all calves are born within a restricted birth season, and that these out-of-season calves coincided with a secondary peak. Fig. 8.2. depicts the change in percentages of solitary animals in the population recorded from the air. The peak in April and May corresponds to the true rut, but an equally pronounced peak occurs in August. The values for May, June and August may justifiably be considered "peak" values, because the July value of 7,5% was found to be significantly different ( $p < 0,005$ ) from the May, June and August values of 9%, by using the Normal Approximation to Binomial with mean = 9%. This peak should be regarded as real, for Estes (1974) states that the territorial drive tends to wane at the end of the dry season i.e. despite the effects of low rainfall, the peak is apparent. Further, evidence from Section 5.3.6. suggested that some conceptions were taking place at this time. Anderson (pers. comm.) distinguishes between a "Secondary breeding peak" and a "false rut." Both are separated from the main rut by at least two months, but the former is distinguished by some conceptions, whereas in the latter, although typical rut behaviour occurs, conceptions are absent or rare. Unless one defines "rare" the distinction is not wholly clear-cut. Certainly, the survival of out-of-season calves would be very low, and far fewer would be seen than were actually born. With this in mind, one may tentatively state that wildebeest in the Complex experience a "secondary breeding peak." Anderson (pers. comm.) suggests that vegetation phenology is an important cue in determining the "intensity" of the second rut. Where food is relatively consistent in nutritional value throughout the year, a seasonally breeding species will react to both increasing and decreasing daylength by producing bimodal breeding peaks of roughly equal intensity. But where habitat is marginal, and feeding strategy less successful, the secondary peak will be evident as a false rut only.

In Fig. 8.2., the February 1975 peak is probably related to rainfall. Estes (1969) has described how a secondary peak may result from the restoration of abandoned pastures after the first rains, when bulls leave bachelor herds to set up territories on restored pastures. This peak, according to Estes, has no obvious link with sex.

Wildebeest in Zululand are somewhat anomalous in their territoriality when compared to the classic behaviour described by Estes (1969). He showed how breeding herds were accompanied by a territorial male only when the breeding herd happened to be, or was confined on, that male's territory. Applying this to the Complex situation, one would expect frequently to record "unescorted" herds, when herds are not on territories. Estes showed that if a male accompanies a herd outside his territory he will cease to show territorial behaviour; yet in the Complex breeding herds without males displaying territorial characteristics are rare. Estes (in litt.) explains this apparent anomaly by assuming that there is not a complete territorial network, i.e. that some territories have no communal boundaries with others. This is indeed the case in the Complex, and probably arises from the fact that the favoured habitat (Acacia nigrescens woodland) is fragmented and not continuous. What appears to happen is that the "bull's sphere of territorial dominance tends to extend outward until it encounters an equal contrary force from another wildebeest." (Estes, in litt.).

A further deviation from the classical behavioural patterns described by Estes (1969) involves the age at which sub-adult males are expelled from breeding herds to form bachelor herds. Estes (ibid.) described how in East Africa males joined bachelor herds as yearlings. Despite being weaned at seven or eight months, the majority of calves observed by Estes remained attached to their mothers right up to the next calving season, i.e. when they achieved yearling status. The

continual interference of the old calf aroused hostility in its mother, causing her to reject it in favour of the newborn offspring. The distressed behaviour of the rejected yearling attracted the attention of the territorial bull associated with the breeding herd, which culminated in constant chasing of the yearling until expulsion took place.

My data from the Complex showed that the presence of yearlings in a bachelor herd was exceptional, and that it was in fact the 2 - 3 year old males who were expelled from breeding herds. These males tended to appear in bachelor herds after the calving season, and I propose an alternative explanation to that described by Estes above. Watson (1969) observed bulls attempting to mount cows just about to produce calves, and he suggested that this may be related to some olfactory stimulant in the amniotic fluid. This theory received added support from Estes' (1969) observations of bulls displaying sexual interest in post-parturient females. Yearlings would not presumably be subject to this sexual interest, as spermatogenesis only takes place at about two years of age (see 6.3.). The 2 - 3 year old males may "compete" with territorial males in their attentions to parturient females, thus providing a basis for their expulsion at the time of calving. This explanation must remain hypothetical, as such behaviour was not observed in the field.

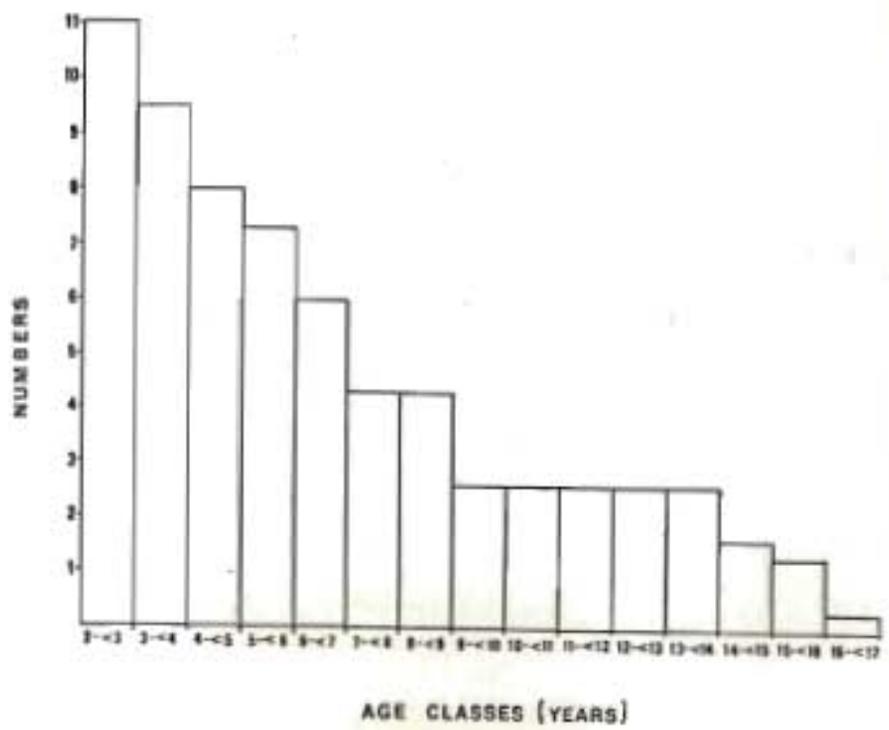
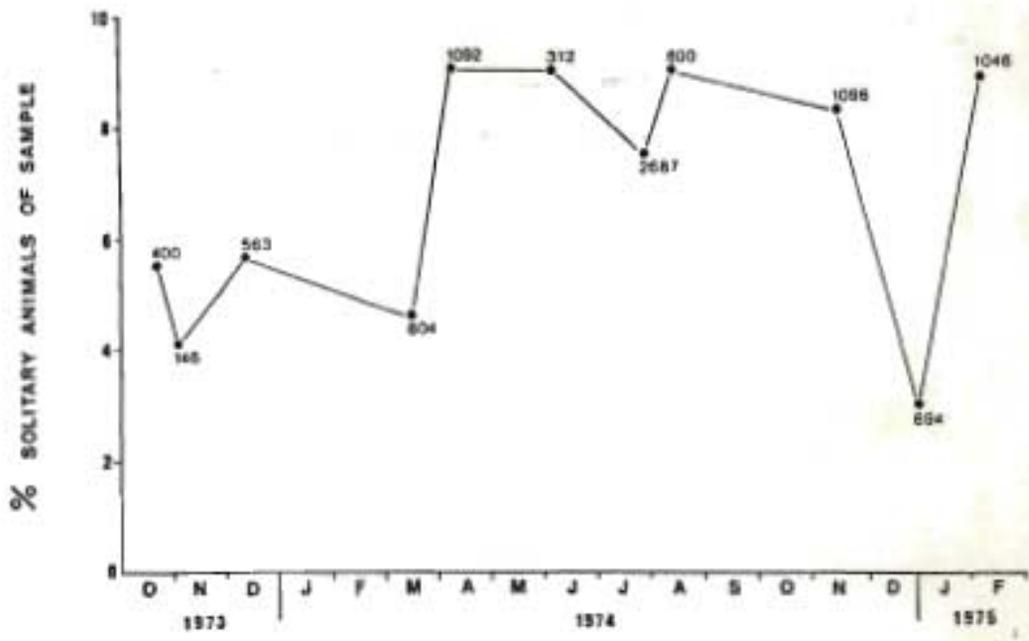
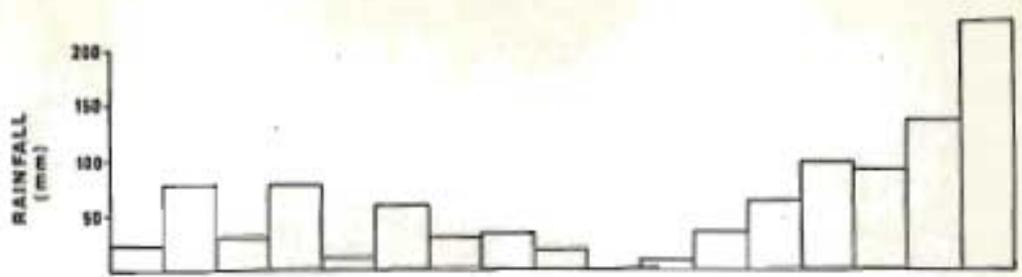
Estes (ibid.) described the adoption of territoriality in males at the end of their third year; Watson (1969) maintained that no males younger than five years took part in the rut. In the Complex, territoriality is assumed at about four years of age.

### 8.3.3.

#### LIFE TABLES AND POPULATION MODELS

The numbers of females shot in each age class are shown in Fig. 8.3. - this is the "smoothed" shot sample, giving a progressive decrease in





numbers with increasing age (a pre-requisite for the construction of a life table). The  $l_x$  values for calves and yearlings were derived from field observations, as they were under-represented in the shot sample. In February 1974, there were 69,5 calves to 100 adult females. By August, this ratio had been reduced to 40 : 100. From the life table (Table 8.7.), the total mortality for females three years and older is 17,2% per year. The period under consideration (February to August) was only six months, and I have thus assumed adult mortality during this period to be 8,6%. Of 100 adults alive in February 1974, 91,4 then would have survived to August. These had  $x$  calves, such that:

$$\frac{100}{40} = \frac{91,4}{x}$$

$$\therefore x = 36,6$$

$$\begin{aligned} \text{Calf mortality was then } & \left( \frac{69,5 - 36,6}{69,5} \right) \cdot 100\% \\ & = 47\% \end{aligned}$$

If one assumes a constant calf mortality rate, then the rate per month would be 7,8% i.e. by the time calves enter yearling status three months later, a further 23,4% mortality would have taken place, giving a total of 70,4% over the first year of life. A linear relationship between calf mortality and time is unlikely, as there appear to be two peaks in mortality (see 8.3.4.), one after calving and the other towards the end of the dry season. To detract from the errors resulting from assumption of a linear rate, I have set the figure for calf mortality in Table 8.7. as 60%. The  $m_x$  values are derived from conception rates (see 5.3.5.). Small sample size prevented designation of age-specific  $m_x$  values for adults. 22% of yearlings were found to conceive during the study period; thus, 11% of the 2 - 3 year olds will have female calves, assuming equal sex ratios at birth.

**TABLE 8.7.** : Life-table for female wildebeest using 60% calf mortality; other mortality rates are derived from the shot sample. Symbols as in standard demographic notation, viz.

$l_x$  = fraction of females surviving at time  $X$ . This is the probability at birth of an individual surviving to age  $X$ .

$q_x$  = mortality rate. The fraction that died during the interval  $X$  and  $X + 1$ , expressed as a fraction of those alive at age  $X$ .

$m_x$  = the mean number of female offspring born per female of age  $X$ . As the foetal sex ratio is equal when 86% of adult females conceive,  $m_x$  will be 0,43 for adults.

Age ( $X$ )	$l_x$	$q_x$	$m_x$	$l_x m_x$	$X l_x m_x$
0	1,000	0,60	0,00	0,000	0,000
1	0,400	0,15	0,00	0,000	0,000
2	0,340	0,13	0,11	0,037	0,074
3	0,296	0,16	0,43	0,127	0,381
4	0,249	0,10	0,43	0,107	0,428
5	0,224	0,18	0,43	0,096	0,480
6	0,184	0,26	0,43	0,079	0,474
7	0,136	0,00	0,43	0,058	0,406
8	0,136	0,41	0,43	0,058	0,464
9	0,080	0,00	0,43	0,034	0,306
10	0,080	0,00	0,43	0,034	0,340
11	0,080	0,00	0,43	0,034	0,374
12	0,080	0,00	0,43	0,034	0,408
13	0,080	0,40	0,43	0,034	0,442
14	0,480	0,17	0,43	0,021	0,294
15	0,040	0,80	0,43	0,017	0,255
16	0,008	1,00	0,43	0,003	0,048

The calculation of  $r_s$  from Table 8.7. is as follows:

$$R_0 = \sum l_x m_x = 0,773$$

where  $R_0$  = the number of times the population doubles itself per generation.

$$T_c = \frac{\sum x l_x m_x}{R_0} = \frac{5,174}{0,773} = 6,6934$$

where  $T_c$  is the generation length - the mean time from birth of the parent to birth of the offspring.

$$r_s = \frac{\log_e R_0}{T_c} = \frac{-0,2575}{6,6934} = -0,038$$

i.e. the population is decreasing at 3,8% per year.

Using adult mortality rates derived from the shot sample (i.e. as in Table 8.7.), I have calculated the probable maximum rate of increase of the Complex population, assuming the most favourable environmental conditions. Minimum calf mortality would be about 25%, and adult age-specific fecundity might increase to 100% under prime range conditions ( $m_x = 0,5$ ). Using these figures, and by the same method as above,  $r$  was calculated to be 8%. A higher figure could be realised if the age structure (i.e. mortality rates of adults) was altered more favourably, but there is no sound basis on which a more "favourable" structure can be proposed.

The effects of a different  $l_x$  series may be illustrated by using a series based on a shot sample from HGR and the Northern Corridor, obtained in 1967 (Vincent, pers. comm.). Vincent (1965) estimated the mortality in wildebeest in the Complex in 1965 to be 20% over the first three years of life. I consider this unrealistic, and have attributed 20% mortality to calves alone. The remaining  $l_x$  and  $q_x$  schedules in Table 8.8. are based on the smoothed shot sample provided by Vincent. From his own data (pers. comm.), I

TABLE 8.8. : Life table and calculation of  $r$  based on shot sample collected in 1967 (Vincent, pers. comm.) from the Complex, with  $m_x$  values obtained at the time. See Table 8.7. and text for explanation of symbols.

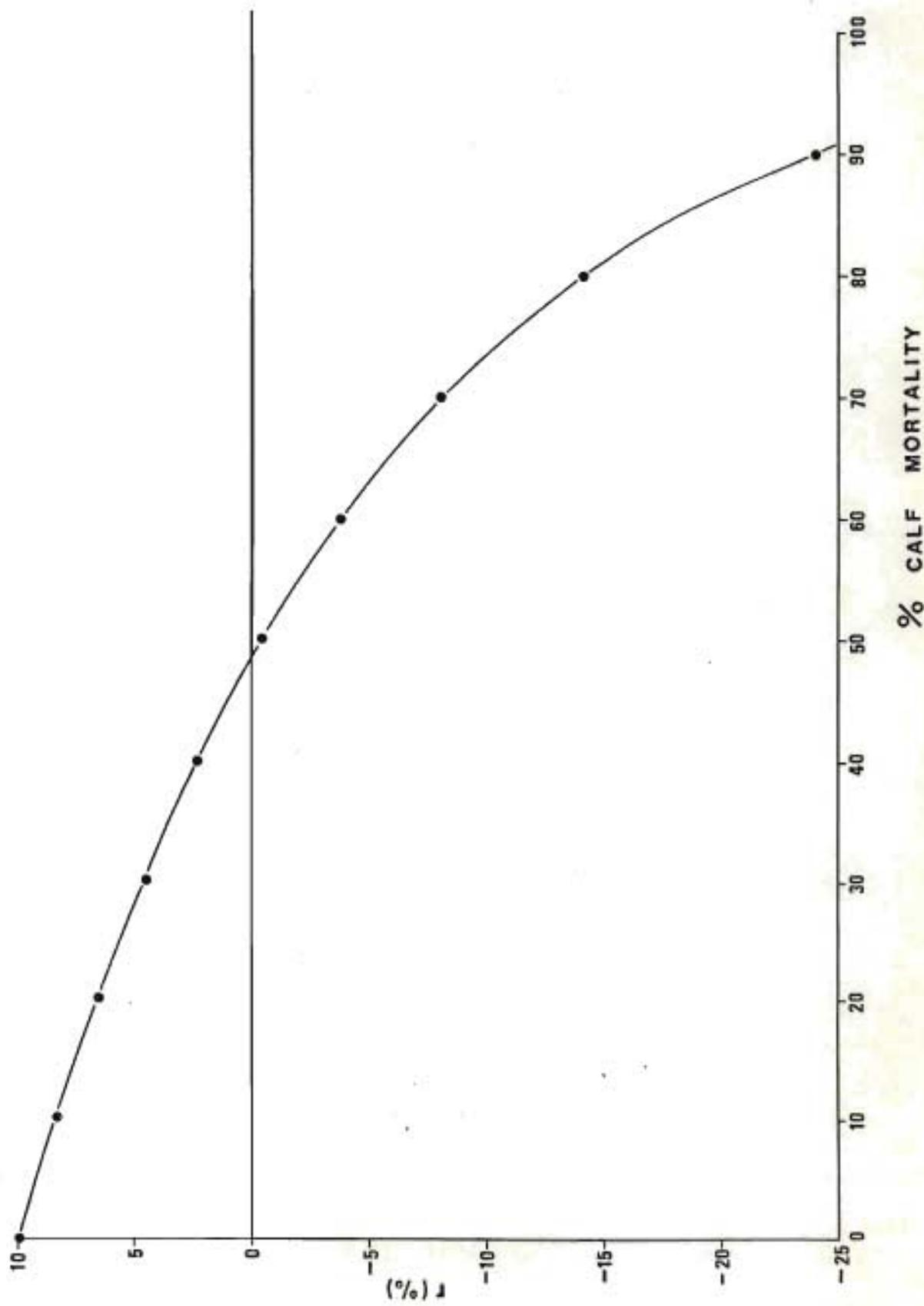
X	$l_x$	$q_x$	$m_x$	$l_x m_x$	$X l_x m_x$
0	1,00	0,20	0	0	0
1	0,80	0,12	0	0	0
2	0,70	0,10	0,11	0,077	0,154
3	0,63	0,09	0,46	0,290	0,870
4	0,57	0,28	0,46	0,262	1,048
5	0,41	0,24	0,46	0,189	0,945
6	0,31	0,26	0,46	0,143	0,858
7	0,23	0,26	0,46	0,106	0,742
8	0,17	0,17	0,46	0,078	0,624
9	0,14	0,00	0,46	0,064	0,576
10	0,14	0,14	0,46	0,064	0,640
11	0,12	0,25	0,46	0,055	0,605
12	0,09	0,33	0,46	0,041	0,492
13	0,06	0,17	0,46	0,028	0,364
14	0,05	0,20	0,46	0,023	0,322
15	0,04	0,50	0,46	0,018	0,270
16	0,02	1,0	0,46	0,009	0,144
$R_0 = \sum l_x m_x = 1,447$					
$T_c = \frac{\sum X l_x m_x}{R_0} = \frac{8,654}{1,447} = 5,9806$					
$r = \frac{\log_e 1,447}{5,9806} = 0,0617$					

calculated an adult pregnancy rate of 91,5% - this gives  $m_x$  values of 0,46 for adults. The same yearling conception rate (22%) as in my study has been assumed. The resultant value of  $r$  is 6%. Allowing for the assumptions and inaccuracies inherent in the method, one may guardedly state that over seven years the population in the Complex has changed from an increase of 6% per annum to a decrease of almost 4%, and that this decrease is due largely to changes in age structure and calf mortality.

Watson (1969) also calculated an  $r$  value from life tables for Serengeti wildebeest, but arrived at a totally unrealistic figure of 46,63%, in that he did not divide  $\log_e R_0$  by  $T_c$ . Using his own data, I calculated an  $r_s$  value of 7,3%, which is close to the maximum  $r_s$  values that could be attained by the Complex population.

Hanks and McIntosh (1973) found that variation in elephant neo-natal mortality was the most important factor operating as a population controlling mechanism. Fluctuations in fertility rate of buffalo have been shown by Sinclair (1974b) not to be a major factor in regulation of the population. On the basis of studies such as the above, I have changed calf mortality while keeping age-specific fecundity values constant, to provide a hypothetical relationship between rate of increase and calf mortality. Apart from the calf values ( $X = 0$ ), age-specific mortality rates ( $q_x$  series) have been retained as from my shot sample (Table 8.7.). The results of the models are shown in Fig. 8.4.. This approach lacks the sophistication of a computerised model like that of Starfield, Smuts and Shiell (1976), whose results suggested that a decline in the wildebeest population of the Kruger National Park could have been precipitated by cropping. Nevertheless, Fig. 8.4. does indicate that, with the  $l_x$  series derived from the 1973/74 shot sample, calf mortality at levels greater than 50% will lead to a decline in the population.

Fig 8.4. : The influence of calf mortality on the rate of  
increase of the Complex wildebeest population.



The 1973 census figure for the Complex was 3429 (Table 1.2.). After the census was performed in July, 203 animals were removed up to and including December. Applying the rate of decrease (3,8%) derived from Table 8.7. to the remaining 3226 animals, the projected population for 1974 would be 3103, without making allowance for game removal in that year. 391 animals were removed before the August 1974 census: this gives a corrected projection of 2712 animals. The actual 1974 census figure was 2687 animals i.e. the projected figure based on a rate of increase with 60% calf mortality was within 0,9% of the actual census figure. It does not follow that my value for "r" is accurate, and the close agreement of real and projected population figures may be circumstantial, as a calf mortality figure derived from one year cannot be used in a projection for that year (it will only be several years later that a low cohort resulting from high calf mortality will enter the breeding pool.) Rather, the close agreement suggests that the population has been subjected to calf mortalities of a similar magnitude for some years.

Brooks (1973) laid down limits of accuracy for helicopter counts, by which figures in consecutive years could be checked. An increment rate is applied to the census figure of the previous year (as in the projection above), and an estimated census error of 10% for wildebeest is allowed. Should the projected figure fall outside 10% either side of the actual census figure, Brooks suggested that the accuracy of the census should be brought into question. He assumed an 8% increment figure for wildebeest; my results suggest then that census figures could be discarded on the grounds of "inaccuracy" when in fact it is the assumed increment rate itself which is inaccurate. It is clear that rates of increase are constantly changing, especially during game removal operations, and it appears injudicious to ascribe limits of accuracy for census data based on rates of increase, unless a recent and reliable estimate of r is available.

The weakness of life tables lies in the mutual biological dependence of their age-specific statistics (Caughley, 1970a). For example, any change in the mortality rate of a given age will affect a large number of entries in the table. The chief errors arising in my results probably result from a small (i.e. unrepresentative) sample, and from the effects of smoothing. Moreover, Caughley and Birch (1972) maintain that  $r_s$  is a statistic having little relevance to the problems that a field study is usually expected to solve, and that an estimate of  $r_m$  is more important, particularly for implementation of sustained-yield harvesting, as it is required to estimate how fast a population will build up after being reduced to any particular level (Caughley, 1972).

The method of estimation of  $r_m$  involves fitting a curve to the pattern of growth of a population after its density has been artificially reduced, and extrapolating it backwards to minimal population size (Caughley and Birch, 1972). If one assumes that the pre-reduction total was asymptotic, and that growth is approximately logistic,  $r_m$  may be estimated by regression from the equation:

$$\log_e \frac{K - N}{N} = a - r_m t$$

where  $K$  = pre-reduction population level ("Asymptotic")  
 $N$  = subsequent total  
 $t$  = year (time)  
 $a$  = y intercept for the linear equation.

I assumed the high 1970 census figure (see Table 1.2.) of 6363 to approximate  $K$ . The population is assumed to fluctuate around  $K$  until it is reduced artificially. The recovery after this reduction is derived as follows (refer to Table 8.9.) : after the 1970 census of 6363, 1512 animals were removed - this is the artificial reduction. The population was thus reduced to 4851 for the year 0 in 1971. The 1972 census figure was 3509, but this had been reduced

TABLE 8.9. : Tabulation of data used in the estimation of  $r_m$ .  
See text for explanation of symbols.

YEAR (t)	NUMBER (N)	K - N	$\frac{K - N}{N}$	$\log_e \frac{K - N}{N}$ (= y)	ty
(1971) 0	4851	1512	0,3117	- 1,1658	0
(1972) 1	5185	1178	0,2272	- 1,4819	- 1,4819
(1973) 2	5405	958	0,1772	- 1,7305	- 3,4610

by 1676 before the census. Compensating for the removal, the "true" 1972 figure would be  $3509 + 1676 = 5185$ . Similarly, for 1973, "true" census =  $3429 + 1676 + 300$  (compensating for 2 years of removal). I have calculated the regression for the three years only, owing to the inherent inaccuracy of there being no allowance made for the contribution to productivity of those fractions which had been removed.

The regression formula is given by:

$$r_m = \frac{\sum ty - (\sum t)(\sum y)/n}{\sum t^2 - (\sum t)^2/n}$$

$$n = 3, \quad \sum t = 3, \quad \sum t^2 = 5$$

$$\sum t^2 - \frac{(\sum t)^2}{n} = 5 - \frac{9}{3} = 2$$

$$\sum y = -4,3782 \quad \sum ty = -4,9429$$

$$\sum ty - (\sum t)(\sum y)/n = -4,9429 + 4,3782 = -0,5647$$

$$\therefore -r_m = \frac{-0,5647}{2} = -0,2823$$

$$\therefore r_m = 0,2823$$

This value of  $r_m$  is clearly very approximate, owing to the many assumptions and approximations. The simplest model of sustained-yield harvesting (Caughley, 1972) shows that the harvest rate should be half  $r_m$ , when the density is to be maintained at about half that of carrying capacity. For example, in a population of 1000 at  $K$ , with  $r_m = 20\%$ , the MSY (Maximum Sustained Yield) will be 50 (10% of 500) removed per year. At this harvesting rate, the population should theoretically decline until it reached 500, where it would stabilise indefinitely. Applying this model to the 1970 census figure, the harvest rate should be  $\frac{28,23}{2}\%$  of  $K/2$  i.e. 14,11% of 3081  
= 435 animals.

This figure is well below the actual figure removed, even allowing for the fact that the value for  $r_m$  is probably excessively high. Natal Parks Board policy has not been based on an MSY, but rather on lowering what were considered to be overpopulations in certain areas; nevertheless, if one wished to maintain the population at about 3000 head, the removal figures have been excessive. Consequently, game removal may have been a factor in causing the negative value for  $r_s$  obtained from life tables.

#### 8.3.4.

#### DISCUSSION ON REGULATION OF THE POPULATION

The 1976 wildebeest census figure in the Complex of 2689 was almost identical to that of 1974 (2687). No game removal was undertaken in 1974, 1975 or 1976. There are several factors in regulation which warrant studies of their own. In particular, one may only speculate at this stage on the effects of resource limitation. Sinclair (1975), from work on the Serengeti ecosystems, deduced that resource limitation alone could limit herbivore trophic levels. Klein (1970) considered that deer populations in North America were limited not by predation but by a direct interaction with the quantity and quality of food.

The function of territoriality in the regulation of numbers was originally considered to be an important factor (Wynne-Edwards, 1964). More recent work by Spingale (1974) on waterbuck suggests that territorial behaviour is not the ultimate factor regulating population numbers. He writes: "In territorial studies we have been rather carried away by the part of the male ..... but it is clearly the female which must supply the clue to a limiting factor to population increase, if there is such a factor, for she is biologically more active." Previous higher rates of increase in the Complex at higher levels of numbers indicate that territoriality

is not a major factor limiting wildebeest populations.

More concrete data are available on mortality and predation. Section 8.3.3. introduced some aspects of the effect of calf mortality on the rate of increase. Watson (1966) maintains that to some extent the size and structure of the existing population reflects the various calf mortality fluctuations of the previous ten to twelve years. There is no doubt that calf mortality was high during the study period (8.3.3.) - some 25% of the breeding herds sampled by helicopter in August 1974 were without calves. The rate of increase will be sensitive to the various density-dependent mechanisms governing mortality and reproduction, in some cases instantly so, and in other cases after a considerable time lag (Watson, 1969). This time-lag effect is particularly noticeable when a low calf cohort is followed through sexual maturity. With respect to productivity, the important increment is that number of females able to conceive added to the "breeding pool" of the population each year. Specifically in wildebeest, this is the 2 - 3 year old age class. An estimate of the percentage of this age-class in the population may be arrived at as follows: In February 1974, it was estimated that "adult" females comprised 32,8% of the population (this includes 2 - 3 year olds). Pregnancy rates indicated that 14% did not conceive i.e. 4,6%. Calves made up 22,8% of the population for that month. If one assumes that an equivalent number of females three years and older produced these calves, then the actual percentage of such females would be  $22,8 + 4,6 = 27,4\%$ . By subtraction from 32,8%, the percentage of 2 - 3 year olds would be 5,4%. From Vincent's report (1965), disregarding a 1 : 1 adult sex ratio which he assumed, and employing conception rates (91%) calculated from his data collected in 1967, I determined by the same method that the female 2 - 3 year old segment made up 15,2% of the population. Errors in the method will be apparent:

no allowance is made for calf mortality, but this will to some extent be compensated for by the fact that no allowance is made for the contribution (albeit small) to calf numbers from the 2 - 3 year old age class itself. But as the same assumptions have been made for both calculations, and since they are both based on data collected at the same month (but at different years), it is considered that the results are comparable. If this is so, then over nine years the vital 2 - 3 year old increment has suffered a threefold decrease, from 15,2% to 5,4%. Computerised population models for wildebeest in Kruger Park (Starfield, Smuts and Shiell, 1976) indicated that the population decline could have been precipitated by cropping, in that the reserve breeding population was removed. It is reasonable to suppose that cropping coupled with increasing calf mortality were major factors leading to stabilisation of the Complex population.

It is unwise to base an estimate of calf mortality on a single measure of the calf crop towards the end of the year. Kruuk (1972) presents data to show that almost all variation in wildebeest calf production (crop) in East Africa is caused by variation in the fecundity of yearlings. If fecundity varies to this extent in the Complex, then it is essential to compare figures obtained after the calving season with those towards the end of the year, otherwise a low calf crop with low mortality might be interpreted as an average crop with high mortality.

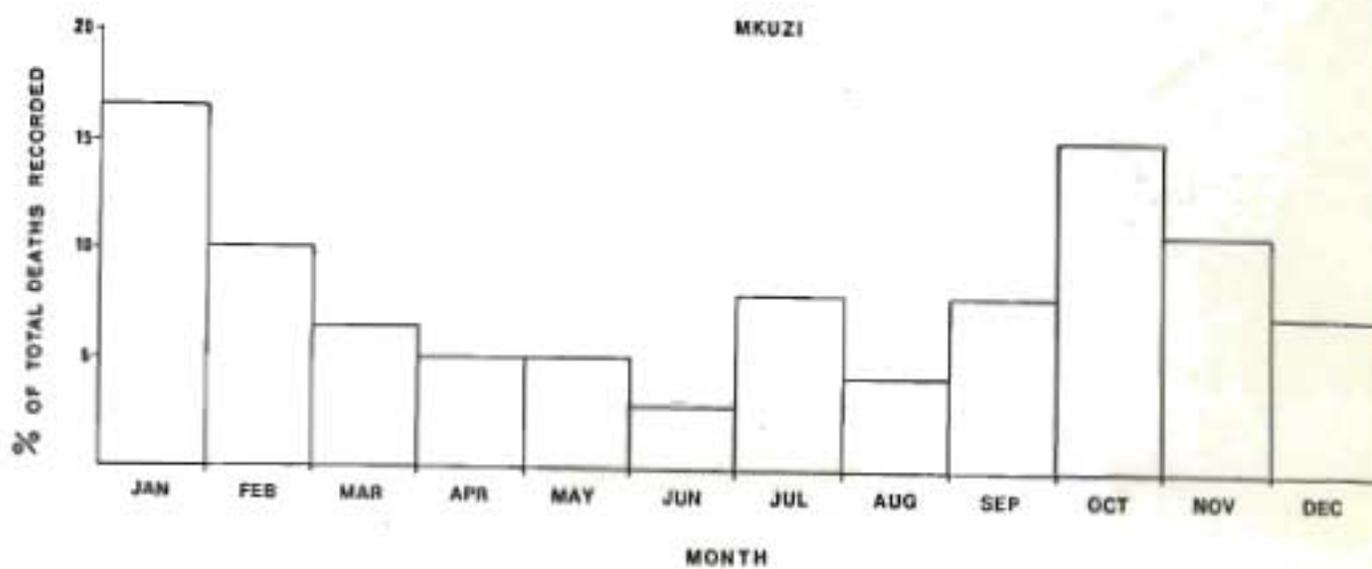
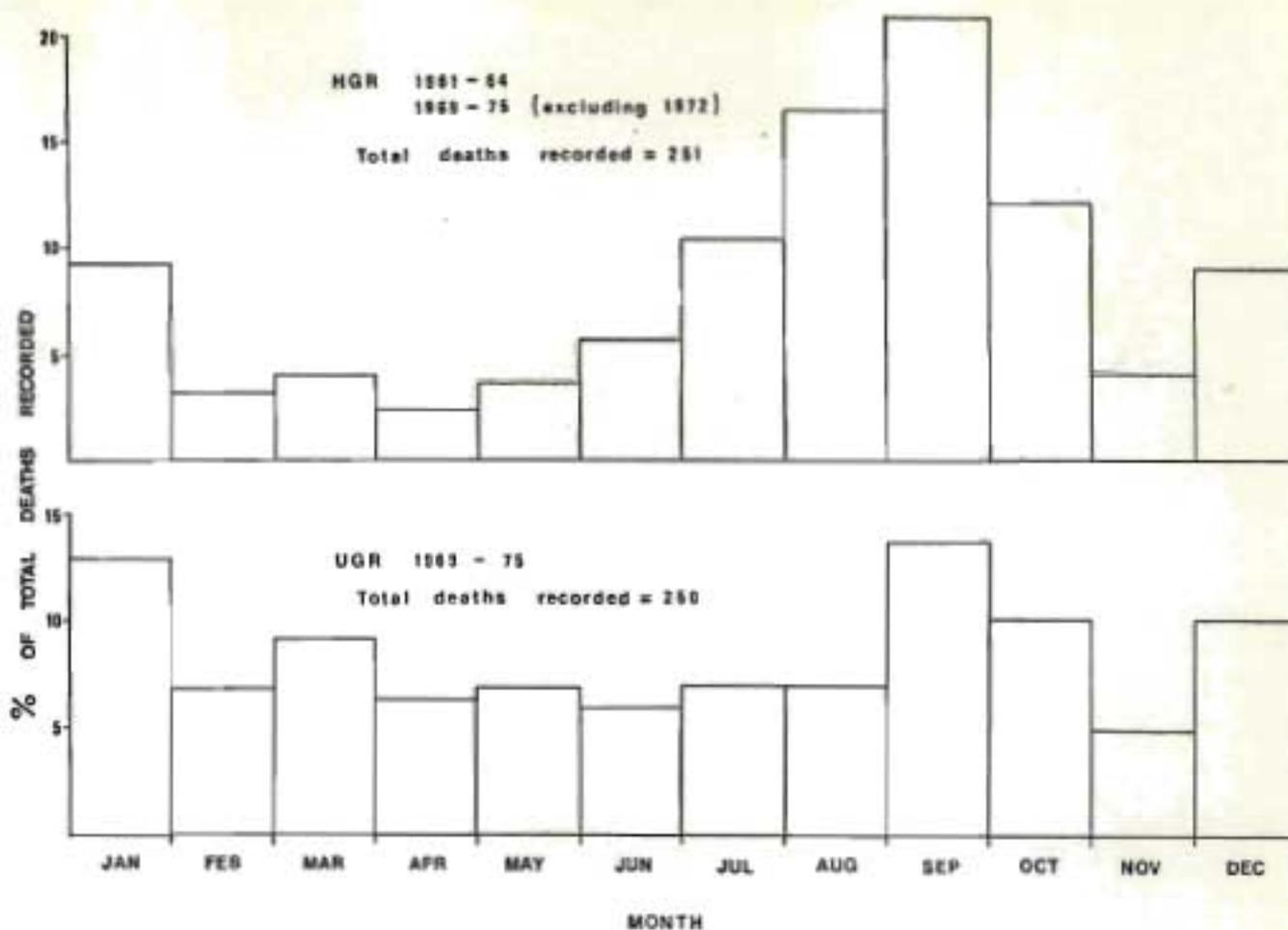
Calf mortality in the Complex is a function of several factors which require further research; the problem is complicated by the speed at which predators and scavengers remove any calf that dies. In particular, the role played by hyaena predation is unclear. Estes (1976) has described how calf mortality in Ngorongoro is a function of herd size: those wildebeest accustomed to a more sedentary existence suffered far greater mortality than those populations which tended to form larger aggregations. In Ngorongoro, wildebeest recruitment is

of the same order of magnitude as hyaena predation (Kruuk, 1972). Figs. 8.5. and 8.6. compare the monthly patterns of recorded deaths of wildebeest in the Complex and Mkuzi Game Reserve. Both areas show peaks after the calving season and at the end of the dry season. Both areas contain hyaena, but only the Complex has lion populations. The inference is that hyaena may then be responsible for the post-calving mortality peak in the Complex, rather than lion. But reference to Table 8.2. suggests that levels of calf mortality in Mkuzi are substantially lower than they are in the Complex. If the hyaena hypothesis is correct, then one must assume that the status of the hyaena populations differs considerably between the two areas. The whole question remains unclear, and points towards an hyaena research programme, and possibly towards investigation of disease factors amongst calves.

Whatever the reasons, calf mortality is clearly a major factor in the current stabilisation of the population. Preliminary work by Melton (pers. comm.) on waterbuck in UGR also suggests that calf survival is crucial to the decline that that population is presently experiencing. The important point is that if juvenile mortality is density - independent (as would be the case with hyaena predation), then high mortality of pre-reproductives could well follow a poor calving season, with extremely deleterious effects on the population. Adult mortality is a further factor that must be considered, particularly in the light of the comparatively recent impact of lion predation. Natural mortality histograms (Fig. 8.5.) are for animals of all ages. Adult females as well as calves contribute to the January peak, as some adults die during parturition. The September peak probably results from loss of condition after the dry season; I suggest that the peak is more marked in HGR owing to the lower temperatures recorded at this time in HGR. Ferrar and Kerr (1971) found that in Kyle National Park (Rhodesia) a drop in temperature

Fig. 8.5. : Cumulative monthly percentages of natural deaths of wildebeest recorded over several years for UGR and HGR.

Fig. 8.6. : Cumulative monthly percentages of natural deaths of wildebeest recorded in Mkuzi Game Reserve from 1969 to 1974. Total number of deaths recorded = 138.



was the trigger to mortality in reedbuck Redunca arundinum in poor condition.

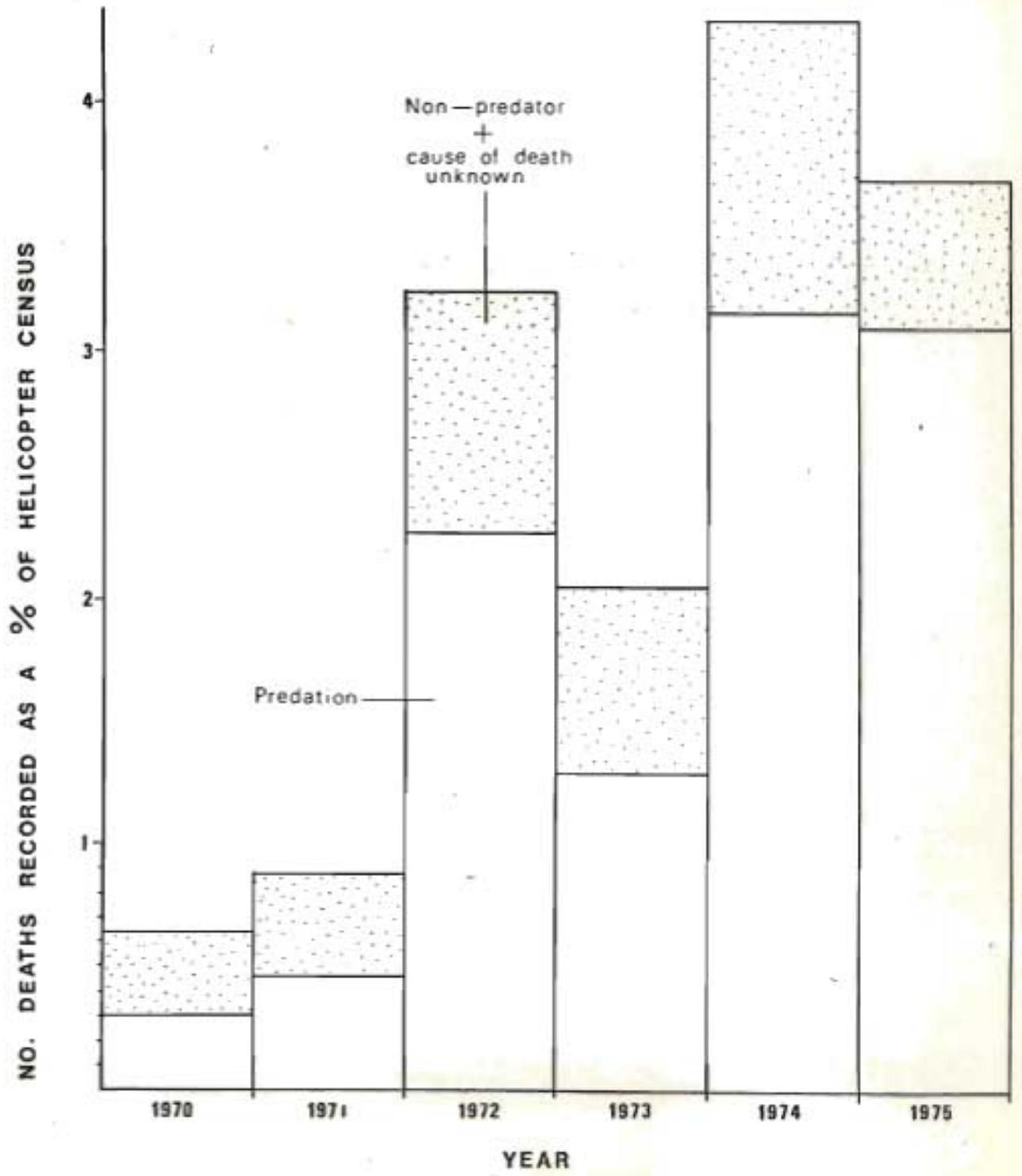
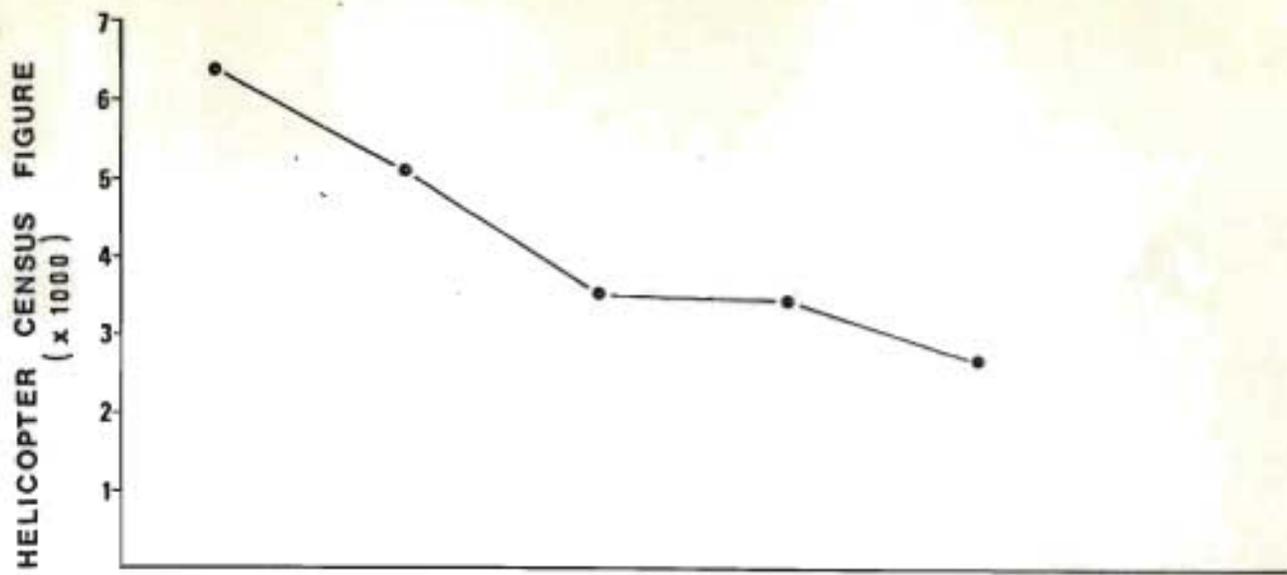
From 1961 to 1975 (excluding 1965-1968 and 1972 for HGR, for which no records were to be found) the sex of animals from natural mortality was recorded in 413 cases, in the ratio of 202 ♂♂ to 211 ♀♀.

There is no significant bias towards either sex (Chi-squared test;  $p > 0,5$ ). This ratio differs markedly from the observed live sex ratio of 67 ♂ : 100 ♀ ( $p < 0,001$ ). A similar result was found with skulls collected in the field (40 ♂ : 32 ♀), in that there was no sexual bias ( $p > 0,1$ ), although the ratio differed significantly from the observed live sex ratio ( $p < 0,001$ ). It is possible that differential rates of destruction between skulls of males and females may occur, but I consider this unlikely. Horn sheaths may well disappear differentially, but it is still possible in most cases to determine sex from the size of the underlying bone.

Watson (In : Kruuk, 1972) found that in the Serengeti 77,5% of the field skulls were male, which he attributed to a higher rate of destruction of female skulls. If this was the case in the Complex, the real ratio would be closer to parity, making the deviation from observed live ratios more puzzling.

The wildebeest is indisputably an important prey species of lion in Africa, although in some cases the selectivity is a measure of its abundance (Wright, 1960; Kruuk and Turner, 1967; Hirst, 1969; and Pienaar, 1969a). Fig. 8.7. differentiates between predation and other factors in records of natural deaths from UGR. (Lion kills were recorded in HGR only in 1973). The 1969 histogram has been omitted, as the census figure for that year was quite unrealistic. The predation portion of the histograms is largely due to lion (95,1%). Predation took place in the ratio of 91 ♂ : 84 ♀ (of those animals for which sex was recorded), again with no sex selection ( $p > 0,5$ ). Of the above, 151 were lion kills in the ratio

Fig. 8.7. : The relationship between natural wildebeest mortality (for six consecutive years in UGR) and population size. The helicopter census figures in the top section of the figure are for the Complex as a whole - no total was available for 1975. In the lower section, mortality figures are expressed as a percentage of the UGR helicopter census results.



79 ♂ : 72 ♀ (no significant difference from a 1 : 1 ratio;  $p > 0,5$ ).

Assuming that there has been an equal efficiency in reporting game deaths from year to year, then one may deduce from Fig. 8.7. that mortality, and specifically predation, has increased with a decreasing population i.e. predation appears to be density-independent. Melton (pers. comm.) has determined a Preference Index for lion kills in the Complex from 1970 to 1975, using an adjustment for population size for eight prey species. The general trend over this period shows a preference in this order: waterbuck, nyala, kudu, wildebeest, warthog/zebra, buffalo, and impala. Data collected by Smuts (1975b) indicate that in the Kruger National Park, predation pressure by lions has recently shifted from one group of species to another. This may be related to a change in vulnerability of one group of prey animals, possibly on account of increase in grass cover. In the Central District of Kruger, Smuts (*ibid.*) calculated that the rate of lion predation was sufficient to stabilise the wildebeest population. In this area, lion density was 12,7 per 100km<sup>2</sup> (all ages), and 9,0 per 100km<sup>2</sup> (for adults and sub-adults only).

Anderson (pers. comm.) has provided estimates of lion numbers in UGR and the Complex. From these figures, I calculated that in the last quarter of 1975 there were 16 lions of all ages per 100km<sup>2</sup> in UGR. After lion reduction by shooting, the density in October 1976 for UGR and the S. Corridor was 10,2 animals/100km<sup>2</sup> (6 adults + subadults/100km<sup>2</sup>). These figures are very similar to the Kruger situation, where stability of the wildebeest population was being maintained.

It is certain that some percentage of natural mortality returns (see Fig. 8.7.) recorded as "cause of death unknown" results from predation. The extent of hyaena predation on adults is a further

unknown. Hirst (1969) recorded adult wildebeest as hyaena prey in the Transvaal, and Kruuk (1972) considers the hyaena to be eminently suitable for a role of adjusting ungulate numbers to range conditions without large fluctuations in numbers, as any animal in poor condition would be cropped.

In the preparation of survivorship curves, I have considered adults only, as calf mortality is so variable. Fig. 8.8. compares curves for adult males and females, based on skulls found in the field - the  $l_x$  values have been derived from a time-specific life table. I have used Vincent's 1967 shot sample as a further comparison, because his male sample appeared less biased than mine: the results are presented in Fig. 8.9.. In both cases, females tend to live longer, similar to the situation in impala (Jarman and Jarman, 1973). Caughley (1966) states that we do not know enough about mortality patterns to justify the construction of any system of classification, but the generally "convex" pattern is disturbed in Fig. 8.9. by a lowered plane of mortality between about seven and twelve years in both sexes. This could well be a reflection of the use of subjective age classes based on wear employed by Vincent, as described earlier, and probably does not relate to a significant ecological phenomenon.

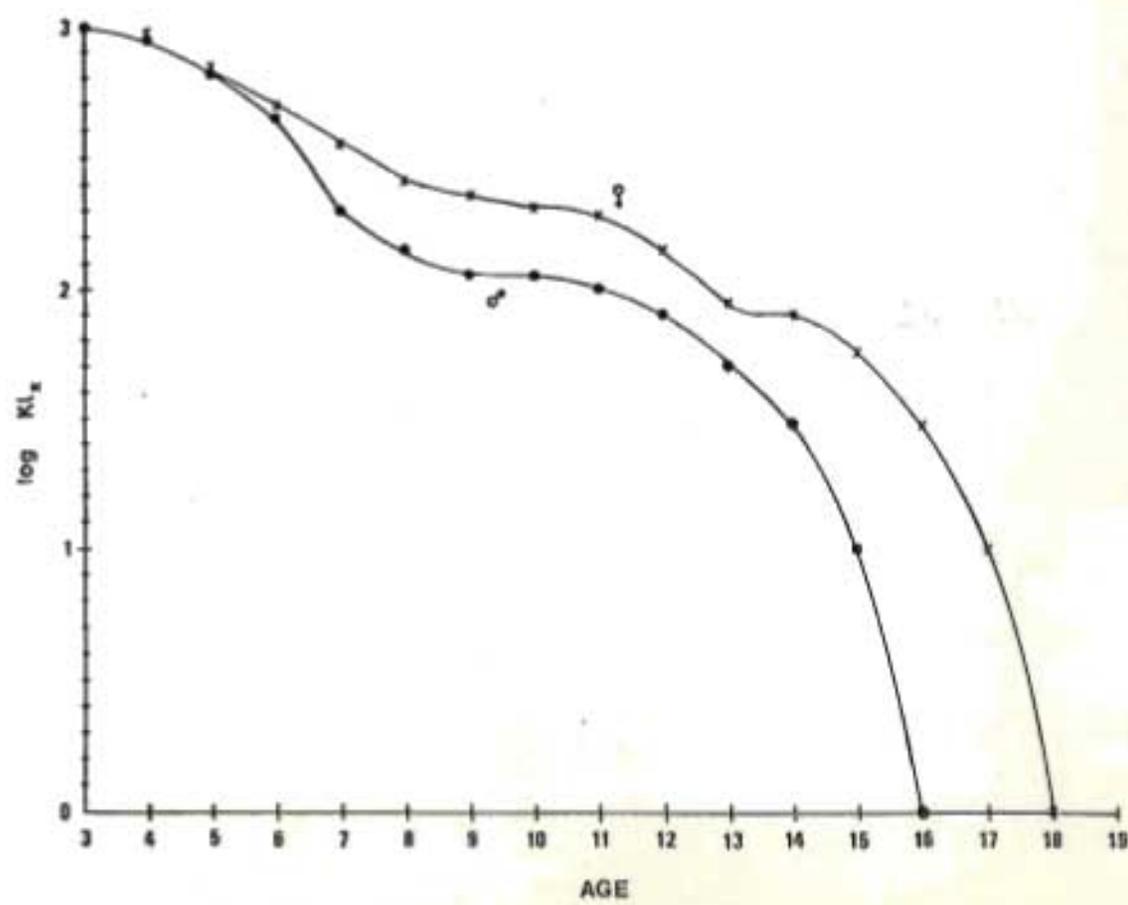
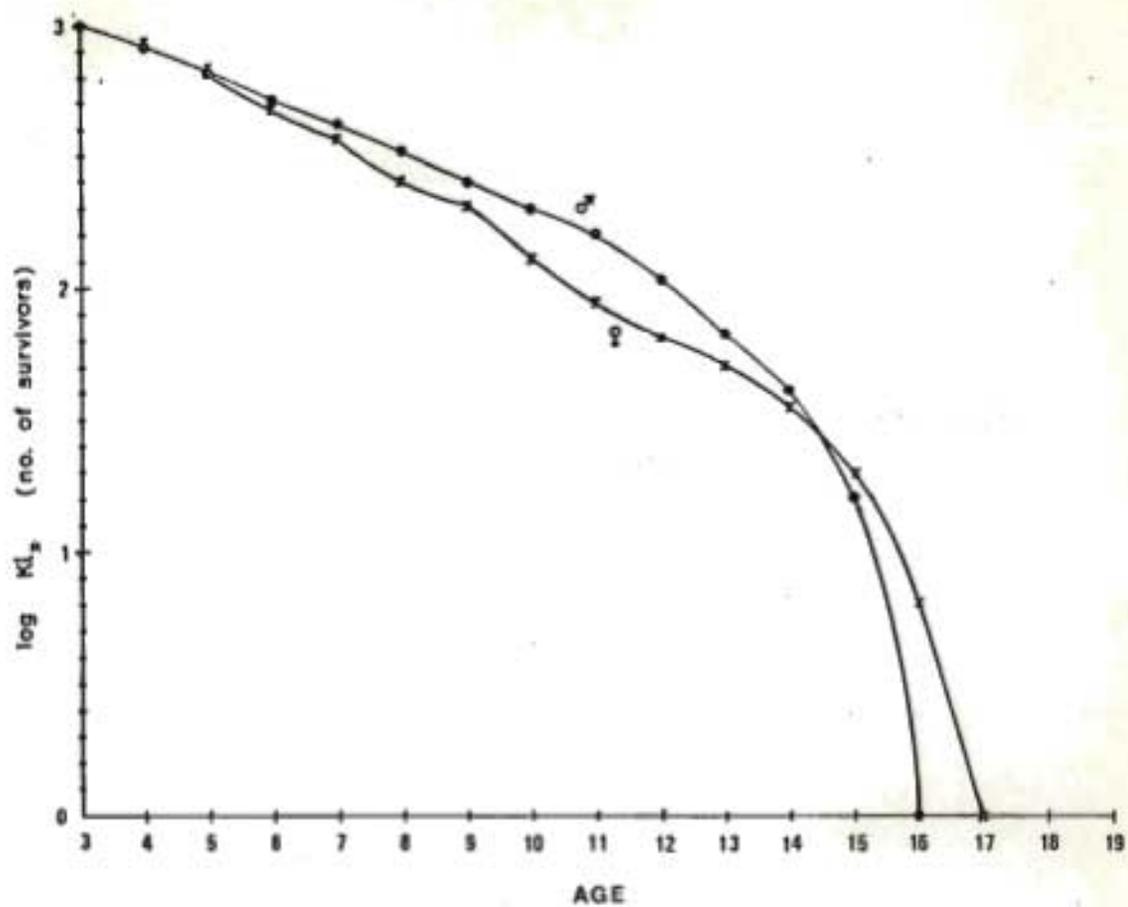
#### 8.4.

##### CHAPTER SUMMARY

Data on various parameters of population structure were collected and compared with those from other wildebeest populations in Africa. The differential sex ratio was found to generally agree with ratios from other populations: it was surmised that early male-biased culling had been balanced by game capture operations which concentrated on breeding herds. Breeding herds were significantly larger during the wet season, and were unstable in terms of membership.

Fig. 8.8. : Survivorship curves for adults based on skulls collected in the field.

Fig. 8.9. : Survivorship curves for adults based on shot sample collected by Vincent (pers. comm.) in 1967.



Seasonal changes in the percentage of territorial males provided further evidence that the species experiences a secondary breeding peak. The significance of territorial behaviour, and its deviation in the Complex from published findings, is discussed.

Population models were constructed from life tables based on shot samples. The probable maximum potential rate of increase of the Complex wildebeest population was determined as 8% per annum, but during the study period the population was estimated to be decreasing by 3,8% per annum. By varying life table parameters (chiefly mortality), results suggested that the population would decrease at levels of calf mortality exceeding 50%. Calf mortality during the study period may have been as high as 70%. Secondary factors in the stabilisation and decline of the population appeared to result from a combination of the game removal programme and an increasing lion population.

Two sets of survivorship curves were constructed, the one based on a shot sample, and the other on skulls found in the field.

## CHAPTER 9

### MANAGEMENT CONSIDERATIONS

#### 9.1.

##### THE NECESSITY FOR MANAGEMENT

Management of wildlife areas becomes essential where such areas are considered as vignettes of the past, and where all surrounding land has undergone ecological degradation (Harris and Fowler, 1975; Dasmann, 1976). This situation is particularly marked in the Complex, where the size precludes the possibility of the area functioning as a self-contained ecological unit. Some attempt must be made to channel or limit ecological processes within the framework set by the management aims laid down for the area.

#### 9.2.

##### THE AIMS OF MANAGEMENT

The primary aim of management (as set out in the HGR management plan) is: "to maintain as nearly as possible those conditions which are likely to have prevailed within the reserve before man substantially modified it; also to preserve the cultural and historical values associated with the reserve".

With respect to wildlife, the aim is "to maintain, modify and/or improve (where necessary) the habitat diversity presently found in the area and thus ensure the perpetuation and natural existence of all species of fauna and flora indigenous to the proclaimed area".

### 9.3.

#### PRIMARY CONSIDERATIONS FOR WILDEBEEST

In the light of both clauses above, the primary consideration with respect to wildebeest management is the maintenance of suitable habitat both for wildebeest and for other species, leading in turn to considerations of the levels at which the population should be maintained.

The notoriously difficult question of "carrying capacity" and "stocking rate" arises from the extreme complexity of the interactions between the food requirements of different populations and the food supply of the habitat. In a wildlife context, carrying capacity may be regarded as the maximum stocking rate which the habitat can support in the long term without habitat deterioration. This differs from the agricultural concept, where in some circles carrying capacity is held to be that stocking rate providing the maximum sustained yield.

In 1974, the stocking rate for the Complex was 33,4 ha per wildebeest. Using the mean mass of one wildebeest derived in Chapter 4 (174,05kg), the 1974 census figure of 2687 was equivalent to a biomass of 4,97 kg/ha. Broock (1973) arrived at a value of 69 ha per wildebeest for the Central District of the Kruger Park, which was reduced to 48,3 when considering only those areas utilised by wildebeest. In the Complex, concentrations of wildebeest may reduce the area available to values in the order of 8 ha per wildebeest (Seme Flats, HGR, 1974).

Generally, comparative figures of density or biomass for a single species may be of little value, in that consideration is not given

to the interactions with other populations. An approach in overcoming this and other problems in calculating stocking rates is to estimate the relative energy requirements of various species so as to equate species of differing size (Mentis and Duke, 1976). The results are expressed in Animal Units (AU) per hectare. With average range conditions, AU should be apportioned between unselective grazers, selective grazers and browsers in a fairly fixed ratio. This may be in the order of: 40% unselective grazers, 40% selective grazers, and 20% browsers (Mentis, 1976). Mentis and Duke (*ibid.*) have provided factors for the conversion of absolute numbers of different species into AU, thus enabling one to assign desired numbers for each species under consideration. Using data from Mentis (pers. comm.), I have estimated that during the study period the stocking rate (expressed in AU/ha) in the Complex was roughly in the following proportions: 35% unselective grazers, 55% selective grazers, and 10% browsers. There is increasing justification (Mentis, pers. comm.) for being conservative about the percentage of selective grazers; game removal in the Complex should consequently be directed towards the selective grazing component, in particular impala, wildebeest and warthog. Mentis (pers. comm.) considers that a stocking rate of 1AU/7,2 ha is permissible in the Complex (for all ungulates considered together), but that the total biomass should be maintained below this level (as it is at present) on account of habitat deterioration and the undesirably high contribution of selective grazers. In addition, nutritional crises are unlikely when a population's demand for food is below the level where that demand might tax supply by the habitat.

Although the above suggests that a reduction of the wildebeest population is justified, there are other factors which indicate that removal of wildebeest in the Complex should not be undertaken at present. Chapter 8 suggested that natural regulation of the population had

taken place over the last few years. The fact that regulation is occurring at population levels well below former figures implies that the regulating factor (or factors) have only very recently (in terms of management history) come into operation, or that the magnitude of operation of this factor has undergone a sudden increase.

It is consequently recommended that the population be monitored carefully before it is subjected to any further removal. Smuts (1975b) has shown that once wildebeest populations reach a certain critical low level, they are unable to absorb normal rates of predation, and will continue to decline until predation pressure is reduced. It is inadvisable to cull a population which is experiencing high levels of calf mortality; in attempting to reduce the population to a desired level under such circumstances one must guard against the possibility of a population crash. It is suggested that:

- a) calf mortality in particular be monitored, by methods outlined in Chapter 8.;
- b) selected tissues and organs (as advised by a veterinarian) be removed from calves found dead in the field, for the investigation of pathogens;
- c) the hyaena research programme be regarded as a priority, particularly in regard to predation on calves of all species;
- d) an annual check be made on the Preference Indices of lion, in order to ascertain whether predation pressure on adults is increasing in a population already suffering high calf mortality.

#### 9.4.

##### SECONDARY CONSIDERATIONS FOR WILDEBEEST

Those management recommendations unrelated to reduction of the population may be regarded as secondary.

Attention should be directed towards the encroachment of Themeda triandra grassland by Acacia caffra scrub. Considerable attention

has been paid to the problem of scrub encroachment in many parts of Africa, and it is not the place here to advocate methods of scrub eradication. The A. caffra/T. triandra habitat in UGR was found (Chapter 7) to be of importance to the wildebeest despite its small area. Other encroaching species (e.g. Euclaea schimperi, E. divinorum, Maytenus senegalensis, and Dichrostachys cinerea) are recognised as a problem in the Complex; these species also play a role in the reduction of desired wildebeest habitat. Caution should be exercised in the reduction of buffalo populations, as the grazing and trampling pressure of this species is a major natural factor in the production and maintenance of favourable pastures. Advice should be obtained from persons experienced in elephant feeding behaviour and habitat interactions in order to assess the probable effects of introducing elephant into the Complex (this assumes ab initio that fencing is adequate).

Localised overgrazing is a problem which may be approached without resorting to removal, particularly as it was found during this study that culling had little effect on inducing movement away from a favoured area. Consistently high numbers of wildebeest were associated with Dengezi hill and its environs in UGR during the study period; continuous culling in the area served only to make the animals harder to shoot.

Ayeni (1975) has shown that the provision of waterholes may be used as a management tool to distribute wildlife more evenly. Water availability is a crucial parameter in determining carrying capacity (Western, 1975). It is suggested that consideration be given to the provision of artificial water sources during the dry season, particularly in the Corridor. This step should not be taken unless it forms part of a research project, for Weir (1970) has documented the diversity of effects which may result from the creation of additional water supplies. The reactions of both animal populations and habitat are unpredictable in this regard.

In some respects, the major ecological management problem of the Complex is one of animal movement rather than overstocking. A more direct approach than the provision of artificial water supplies is the translocation of herds from overgrazed areas to underutilised terrain. The results to date from the wildebeest collar-resighting programme suggest that such a measure may be employed on a seasonal basis only i.e. there is a tendency to return to the original capture site, but the time taken for the return may be sufficient to allow protection to areas from overgrazing at critical periods.

## 9.5.

### GAME REMOVAL PROCEDURE

This section discusses some approaches that may be undertaken when it is considered desirable to re-instate game control for wildebeest.

#### 9.5.1.

##### REMOVAL SOLELY TO REDUCE BIOMASS OR TO DECREASE RATE OF INCREASE

Before initiating a cropping programme, it is essential that some estimate of the current rate of increase be arrived at. No cropping should be undertaken if the estimate of  $\underline{x}$  is negative. Starfield, Smuts and Shiell (1976) have shown the possibly drastic effects of cropping a decreasing wildebeest population. Should cropping be undertaken in a stationary or increasing population, it is recommended that the status of the population be monitored at intervals not exceeding one year. Smuts (1975b) maintains that should it be necessary to crop wildebeest drastically during times of drought, then concomitant predator cropping should be undertaken, irrespective of their numbers at the time. In the absence of computer simulation, an estimate of the rate of exploitation necessary to stabilise the population may be arrived at by equating female mortality with the annual female recruitment (Kimball and Wolfe, 1974). The various contributory

components of total annual mortality are not directly additive, but correspond to the following relationship (Ricker, 1958, quoted by Kimball and Wolfe, *ibid.*):

$$a = m + n - mn$$

where  $a$  = total annual mortality rate

$m$  = cropping mortality

$n$  = other mortality.

Solving for  $m$  will provide the required theoretical rate of harvesting. In order to arrive at an estimate of  $n$ , it is suggested that the collection of field skulls be continued in order to determine whether female mortality rates alter radically from the patterns shown in Chapter 8. Rapid age determination from the tooth wear-age chart (Fig. 3.6.) will allow construction of a  $d_x$  based life table, and hence mortality rates.

The selection of sex and age in harvesting is a matter of some conjecture; the effects of any particular policy can be resolved only by computer simulation. The functions of the male segment have been discussed in Chapter 8, and there are grounds for protecting territorial males to preserve genetic viability. However, the fact that the sex ratio of wildebeest in the Complex does not appear to deviate markedly in favour of females when compared to other populations (Table 8.4.) after years of male-biased culling, suggests that male-biased culling has not been overtly deleterious to the population. Further, the rapidity with which males may leave bachelor herds to set up territories after rainfall (Fig. 8.2.) indicates that the bachelor herd segment of the population functions in an efficient manner as a reservoir of territorial males. If possible, selection for culling should not heavily favour either sex. Alternatively, different sexes could be selected in different years (Walters and Bandy, 1972). It is dubious whether selection should be aimed at the most productive segment of the population (2 - 3 year old females), as has previously

been recommended on occasions (Natal Parks Board Files) in the Complex, as this policy may affect the population's age structure adversely for many years after. Rather, offtake should be distributed among the separate subunits of the population.

### 9.5.2.

#### REMOVAL ON A SUSTAINED-YIELD BASIS

Dasmann (1976) has pointed out that those who are most affected by the presence of a proclaimed area must fully share in its benefits, otherwise they will await the change of government permitting deproclamation. This premise is particularly pertinent to the Complex, which lies in an area demarcated by the South African government as a homeland (KwaZulu).

Should the wildebeest population attain a status where its viability warrants cropping on a sustained-yield basis, then provision should be made to market the yield locally. Clearly, this would involve major changes in the management aims for the Complex (9.2.), but this may become imperative in the light of political developments.

The simplest model of sustained yield likely to approximate cropping of large mammals assumes that the population, if reduced to a very low density, would climb back to carrying capacity along a logistic curve (Caughley, 1972a). The maximum sustained yield (MSY) is harvested from a density corresponding to the steepest part of the curve. A random crop with respect to sex and age is then given by:

$$MSY = \frac{1}{2} r_m \cdot \frac{1}{2} K$$

(symbols defined in Chapter 8.)

Caughley (1972a, 1972) has outlined the optimal strategies in harvesting specific age classes and sexes. Sex-selective harvesting of males may almost double the MSY obtained unselectively. Beddington (1974) provides a basic model to investigate which age groups to

crop, and what sex ratio to aim for. His model suggests that, for both sexes, two age classes at the most should be harvested; the one group should be partially cropped and the other completely removed.

Maximum productivity can be realised by considering the time of harvesting as well: disturbance during the rut should be reduced as much as possible, as stress may affect both conception and implantation (Skinner, Van Zyl and Oates, 1974). Clearly, the population should not be culled during the calving season, as this may induce abortions. In terms of meat productivity, the optimal age to cull would be at about the end of the first year. Culling need not be annual, as Walters and Bandy (1972) have shown how higher yields may be obtained by harvesting once every several years.

An additional source of income would accrue from the involvement of safari clients in a culling programme. Provided this sphere of culling is closely supervised and restricted to certain areas (e.g. the Corridor), there is no reason why the wildebeest should not be regarded as a trophy resource. Good "heads" in wildebeest appear to be the result of genotype and not longevity. Spinage (1969a) raises the problem of the continued removal of animals with horns in the trophy category. Asymptotic horn spread in males is attained at about 3,5 years, and the basal circumference asymptote about a year later (both these parameters contribute directly to what constitutes a desired "head"). If all "big heads" are selectively removed from an area, and further "big heads" are shot as they are recruited (i.e. when they reach about 4,5 years), then they will be unlikely to have passed on the genotype unless it is a recurrent mutation. Spinage (*ibid.*) suggests that all mandibles from trophy hunting be submitted to research staff so as to monitor the ages of animals so removed. If too many young animals are being shot, then trophy hunting should be restricted for several years to allow young animals to pass into full territorial status, in order that the genotype may be continued.

9.6.

CONCLUSIONS ON MANAGEMENT

Since 1973, game removal has been confined to removal areas (Porter, 1976). Removal areas are mapped on the basis of veld assessments, and constitute those areas with degraded or deteriorating habitat. Expected incremental rates are applied to the census figures derived from a helicopter census undertaken in late winter, thus providing bases for "guesstimates" of animal removal rates. This procedure has been somewhat facilitated by Porter's (1975) findings (substantiated by this study) that the maximum standing crop of grass occurs between mid-February and May after good rains. This allows NPB staff to arrive at a decision (usually before April) as to whether the standing crop is adequate for specific populations for the following six months. Porter (1975) advises that, should the standing crop be considered inadequate, game removal should take place early in the capture season to minimise losses of animals in poor condition.

Despite accumulating biological data, management procedures are still essentially on a trial-and-error basis. To obtain real insight into management of any species, a computer systems model is essential. One requires answers to the following question: "How would a situation that presently exists be altered if we modified the mechanism of population regulation within ranges of values that we know from other studies are realistic?" (Watt, 1968; italics mine). I consider that we presently have sufficient biological data on the major mammals in the Complex to consider simulation modelling.

The following points underline the need for computer simulation:

- a) single and multiple species simulation models provide the only real method of predicting the effects of cropping under different conditions (Smuts, 1975b). Offtakes of each species are dependent not only on their own standing crop, but also on those of other species.

- b) the effects of predator cropping, or the cropping of prey species in the absence of predator control, can only be fully investigated through simulation.
- c) the complex task of assigning stocking rates would be greatly facilitated through simulation. This study has highlighted the extreme similarity in choice of structural aspects of the herb layer and of grass dietary components by several species. Data of this nature could be incorporated with models of varying ratios of selective grazers, unselective grazers, and browsers.

#### 9.6.1.

##### MANAGEMENT IN PERSPECTIVE

It cannot be overemphasized that the problem of exponentially increasing human populations in the face of finite resources cannot be countered by increasing the efficiency of utilisation of these resources. No amount of efficiency in resource management will ever cater for the needs of KwaZulu (or for the needs of humanity) unless such management and exploitation coincides with an immediate and continuing programme of human population control.

### THESIS SUMMARY

Justification exists for the conservation of wildlife on both economic and ecological grounds, but the limited areas of game reserves demand that species within such areas be managed on a scientific basis. To base management of blue wildebeest (Connochaetes taurinus taurinus) populations in the Umfolozi Reserve - Corridor - Hluhluwe Reserve Complex on scientific grounds, data were collected in the field for two years from 1973.

Determination of age is a pre-requisite for any mammalian investigation into reproduction and population ecology. A tooth eruption calendar was arrived at to provide a reliable method of age determination for wildebeest up to 3,5 years. In adult animals, the cementum layers in the teeth were used to determine age; the changes in molariform infundibular patterns were related to "cementum age" to provide an age-wear chart, which was considered adequate for life-table data.

Mass and measurement data were incorporated into growth curves and equations, based on the growth theory of Von Bertalanffy (1938). In this manner, the age of attainment of the asymptotic value for specific morphometric parameters were determined. Such information is of use in the cropping of wildebeest on an economic basis.

Seasonal changes in wildebeest condition were investigated using the Kidney Fat Index (KFI) and the percentage of fat in the bone marrow. The interpretation of KFI values was found to be complicated by the

fact that kidney mass itself showed significant seasonal variation. Bone marrow fat was mobilised only after body fat, and significant marrow fat mobilisation probably occurred only in females.

Reproduction in the female was discussed with an emphasis on ovarian relationships. By using foetal mass data, the peak of the rut was found to be in April, and the parturition peak in December. Abnormally high rainfall preceding the rut may cause this event to occur earlier in the year. Evidence was presented to suggest that out-of-season calves were conceived over a specific period, and that such conceptions might occur in yearlings which had failed to conceive at the "true" rut in April.

In the male, onset of spermatogenesis occurred at about two years of age, when the mean testis mass was about 20g, the seminiferous tubule diameter about 116  $\mu\text{m}$ , and body mass about 160kg. At least 2,5 years elapsed between the initiation of spermatogenesis and active breeding. Despite the fact that seasonal changes took place in testis mass, epididymal mass and tubule diameter, both spermatogenesis and conceptions took place at seasonal "lows." Some doubt was cast on whether the male wildebeest (in addition to other ungulates) experiences a true sexual cycle, as the seasonal changes in reproductive organs may be related merely to nutrition.

Acacia nigrescens woodland was found to be the habitat of choice in Umfolozi Game Reserve (UGR). There were indications of seasonal resource distribution between wildebeest social groups within this habitat. Analysis of grass structural components from rumen contents revealed similar results for both wildebeest and buffalo, and the implications of these results were discussed in terms of dietary competition.

A multivariate discriminant function analysis was performed on some habitat variables which were considered important in the ecological separation of wildebeest, white rhino, zebra and buffalo. The mean

height of the herb layer was found to be that variable with maximum discriminatory powers. Only buffalo showed significant ecological separation determined in this manner, possibly because overlap in ecological requirements of the other three species did not take spatial separation into account.

It was suggested that the grazing succession in UGR was more complex than that described from East Africa, and that the sequence of ungulates in the succession was not always predictable.

Wildebeest populations in the Complex were found to be relatively sedentary, with little seasonal differences in distribution.

Data on various parameters of population structure were collected and compared with those from other wildebeest populations in Africa. Breeding herds were significantly larger during the wet season, and were unstable in terms of membership. Seasonal changes in the percentage of territorial males provided further evidence that the species experiences a secondary breeding peak. The significance of territorial behaviour, and its deviation in the Complex from published findings, was discussed.

Population models were constructed from life-tables based on shot samples. During the study period, the population was estimated to be experiencing a rate of decrease in the order of 3,8% per annum. By varying life-table parameters (chiefly age-specific mortality), results suggested that the population would decrease at levels of calf mortality exceeding 50%. A figure of 70% for calf mortality was arrived at during 1974. Two sets of survivorship curves were constructed, the one based on a shot sample, and the other on skulls found in the field.

Management recommendations were based on the above findings, and it was suggested that careful monitoring of the population should take place before the wildebeest population in the Complex is subjected

to further culling or game capture. The impact of hyaena predation on calf mortality requires further investigation.

Encroachment of undesirable plant species onto favoured wildebeest habitat was discussed. Mention was made of the possibility of providing sources of artificial water to combat problems of localised overgrazing.

Recommendations were made on approaches that should be taken when it is considered desirable to re-instate game control for wildebeest. Two strategies were described: the first for removal solely to reduce biomass or to decrease the rate of increase, and the second for removal on a sustained-yield (i.e. economic) basis.

The need for computer simulation modelling for management purposes was emphasized.

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APPENDIX I : HISTOLOGICAL PROCESSINGEMBEDDING

<u>STATION</u>	<u>TIME</u>
1. 50% alcohol	2 hours
2. 70% alcohol	2 hours
3. 80% alcohol	2 hours
4. 90% alcohol	2 hours
5. 95% alcohol	2 hours
6. 95% alcohol	2 hours
7. Absolute Alcohol	2 hours
8. Absolute Alcohol	3 hours
9. Xylene	2 hours
10. Xylene	2 hours
11. Wax	2 hours
12. Wax	1 hour
13. Vacuum Infiltrator	1 hour

STAINING

<u>STATION</u>	<u>TIME</u>
1. Xylene	4,5 minutes
2. Absolute Alcohol	4,5 minutes
3. 90% Alcohol	4,5 minutes
4. 70% Alcohol	4,5 minutes
5. Meyer's Haematoxylin	10 minutes
6. Water	3 minutes
7. Water	3 minutes
8. Alcohol Eosin	5 minutes
9. 70% Alcohol	5 minutes
10. 90% Alcohol	5 minutes
11. Absolute Alcohol	5 minutes
12. Xylene	5 minutes

APPENDIX II : HISTOLOGICAL PROCESSINGEMBEDDING

<u>STATION</u>	<u>TIME</u>
1. 70% Alcohol	3 hours
2. 80% Alcohol	2 hours
3. 90% Alcohol	2 hours
4. Absolute Alcohol	2 hours
5. Chloroform	1 hour
6. Chloroform	2 hours
7. Wax	6 hours

STAINING

<u>STATION</u>	<u>TIME</u>
1. Xylene	5 minutes
2. Absolute Alcohol	5 minutes
3. 90% Alcohol	5 minutes
4. 70% Alcohol	5 minutes
5. Haematoxylin	10 minutes
6. Water	3 minutes
7. Water	3 minutes
8. Eosin	2 minutes
9. 70% Alcohol	5 minutes
10. 90% Alcohol	5 minutes
11. Absolute Alcohol	5 minutes
12. Xylene	5 minutes