T AN OUTLINE OF THE ECOLOGY AND BEHAVIOUR

OF THE RED LECHWE (KOBUS LECHE LECHE GRAY, 1850)

by

A

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Submitted in partial fulfilment of the requirements for the
degree of Doctor of Philosophy in the Department of Zoology,
University of Natal, Pietermaritzburg.

P Pietermaritzburg: 1979. PP Univ of Natal,

NT Thesis (Ph. D. ; Zoology)-University of Natal, Pietermaritzburg, 1980

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.

D.T.WILLIAMSON ....

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ABSTRACT

In a number of publications serious concern has been expressed about the status of lechwe in the Kwando/Linyanti/Chobe system. Concern has also been expressed about the effects of possible water extraction from the Okavango Delta on the habitat of lechwe in the delta. This study was motivated by this concern and was undertaken to provide information that would facilitate the conservation and management of lechwe in Botswana.

Continuous field work on the western edge of the Linyanti Swamp began in January 1975 and ended in May 1977. Follow-up visits were made in February/March and September/October 1979.

Data were collected on the following: variation in water levels, physiognomic and floristic characteristics of lechwe habitat, age determination, food habits, habitat use, distribution,condition, growth, reproduction, non-social behaviour, social behaviour and organization and population status.

From data collected it was concluded that, although there was no indication of a drastic population decline, the prevailing high water levels in the system were causing a downward trend in the population by pushing the animals into poorer quality habitat. The decline in the quality of the habitat available to the population was reflected by high juvenile mortality and reduced fecundity of young females.

On the basis of the findings of this study a strategy for the conservation and management of lechwe in the Linyanti Swamp is proposed.

ACKNOWLEDGEMENTS

This study was supervised and administered by Prof. J.A.J.Meester. I am grateful to Prof. Meester for his efficient administration of the project and for his meticulous criticism of drafts of this thesis. Dr. Wolfgang Von Richter acted on behalf of the Department of Wildlife, Botswana in setting up the project and gave help and encouragement during the field work. His assistance is acknowledged with thanks.

Field work was financed by a generous grant from the South African Nature Foundation. I am extremely grateful to the Foundation. The Department of Wildlife, Botswana provided the use of an aircraft for aerial survey work and this dissertation was partly written up while I was employed in the Department. I am grateful to the Director of Wildlife for the assistance given to me and for permission to do field work in Botswana. The Okavango Wildlife Society provided financial assistance with the preparation of this report, for which I express sincere thanks.

Mr. Peter Smith of Maun and the staff of the Rhodesian National Herbarium, Salisbury provided essential help with the identification of plant specimens. Prof. J.Hanks, while Chief Professional Officer, Natal Parks Board, generously made available to me the Board's excellent library and laboratory facilities and gave invaluable guidance with histological and other matters. Ms A. Ludbrooke gave indispensable tuition and assistance with histological processing. Ms C. Melton did the serum cholesterol determinations of lechwe sera . Ms E.A.Roy provided invaluable assistance with reference material. Ms C. Hammond and Mr R. Scholes helped with the computer analysis of plant utilization data. Ms A. Waterhouse provided much help with photographic material. I am very grateful to all the people and institutions mentioned here.

A number of people provided help with collection and/or analysis of data and made constructive criticisms of various aspects of this thesis. In this respect I should like to thank particularly Prof. J. Hanks, Drs J.L.Anderson, C.A.M.Attwell, N.Dräger, L.P.Fatti and M.Jorgenson and Messrs A.Graham and D.Kreulen. For assistance in the field I thank Tigwe, Patrick, !agwa(Silas), Yaya and Tarrapan.

This thesis could not have been produced without the assistance of my wife Jane, who typed drafts and manuscript, drew figures, proof read and collated the manuscript. For her unstinting help and for her support and companionship I am immeasureably grateful.

For hospitality and assistance while I was working in the field I am grateful to Jeff Steen, Shushuke Minato, Peter Smith, Ted Watt, the directors and staffs of Hunters Africa (Pty) Ltd and Micheletti Bates (Pty) Ltd, Tony and Felicity Ziegler, and particularly to Megan Biesele.

In Pietermaritzburg Basher and Pam Attwell gave me a room in their house and treated me with great kindness and generosity, for which I am extremely grateful to them. My mother and sister, Joan, in Johannesburg and my parents-in-law, Bim and Margaret Dowle, in Pietermaritzburg, provided warm hospitality during visits to South Africa from Botswana, for which I would like to record my sincere thanks.

Over the years my interest in wildlife has received vital encouragement and support, for which I would like to thank in particular Prof. Archie Mossman, Mr C.J. McBride and his son Chris and the Johannesburg Consolidated Investment Company Limited.

CHAPTER 1

INTRODUCTION

1.1

BACKGROUND

There are two lechwe (Kobus leche) populations in Botswana, one in the Okavango Delta and one in the Kwando/Linyanti/Chobe system. This study was proposed by the Department of Wildlife, National Parks and Tourism because of concern for the survival of lechwe in the face of impending water extraction schemes in the Okavango Delta (Von Richter, pers. comm.*). The threat of major developments in the Okavango Delta has receded, at least for the time being (United Nations Development Programme, 1977) but grave concern has been expressed about the status of the Chobe lechwe population (Child & Von Richter, 1969; Child, 1975; Sheppe & Haas, 1976). In view of the improved prognosis of Okavango lechwe and the apparently perilous situation of the Chobe lechwe, it seemed appropriate to change the emphasis of the study and to concentrate on the latter population.

Because the study was done under the auspices of the Department of Wildlife, National Parks and Tourism, its design was influenced by the need to accommodate the Department's priorities. These priorities reflect both the prevailing socio-economic conditions and the status of wildlife conservation in Botswana. To provide a context within which the objectives of the study can be evaluated, a brief outline of Botswana's environmental and socio-economic conditions and the status of wildlife conservation will be presented.

1.1.1

The Environment of Botswana

Botswana extends from 18°S to 27°S and from 20°E to 28°E (Figure 1.1). The country is landlocked and has an area of 570 000 square kilometres, which is about the same as that of Kenya or France. Situated in the middle of the Southern African Plateau, it has a mean altitude of about 1 000 metres above sea level and is separated from the oceans by higher plateaux and mountain ranges.

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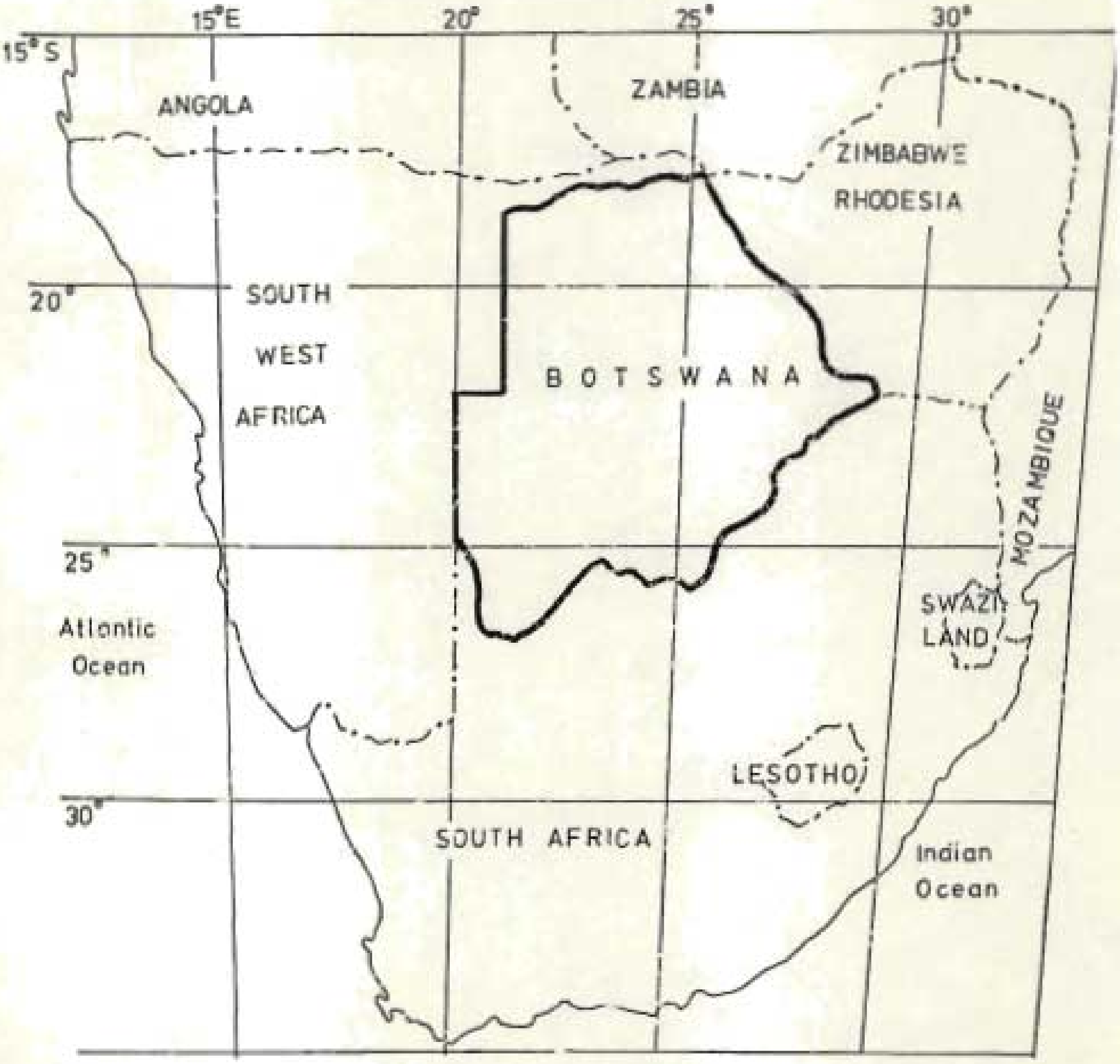


Figure 1.1: Geographic location of Botswana

Much of the country is covered by a mantle of Kalahari sand and has a flat and almost featureless topography. The climate over most of the country is semi-arid and varies seasonally between a hot, moist summer and a cool, dry winter. Rainfall is erratic in time and space. Permanent surface water occurs only in the north in the Okavango Delta and in the Kwando/Linyanti/Chobe system.

Soils in Botswana are mostly poor (Child, 1971). The drier areas support shrub and tree savanna. More heavily wooded areas occur in the wetter eastern and northeastern part of the country (Wild & Fernandes, 1967). The wetlands of the north are dominated by swamp grasses and sedges and fringed by woodland on ridges and islands of higher ground. The diverse habitats of Botswana support a varied and prolific fauna (Smithers, 1964 and 1971; Jubb & Gaigher, 1971; Bell-Cross, 1972).

Pristine patterns of large mammal distribution and abundance began to be seriously disrupted during the 1950's with the erection of veterinary cordon fences (Falconer, 1971), which interfered with the seasonal movements of large herbivores. New fences and expanding human settlement are steadily increasing the level of disruption.

1.1.2

Socio-economic Conditions

The 1971 census estimated the human population of Botswana at 630 000, but it is growing rapidly (Fosbrooke, 1971 and 1973) and is now about 800 000 (Field, 1977). In addition to population growth, there is rapid economic growth, including a substantial expansion and commercialization of the livestock industry (Central Statistics Office, 1976). These factors have combined to produce pressures on the land in the form of deteriorating range conditions and mounting demands for the opening up to development of what are now primarily wildlife areas.

During 1975 the Government responded to these pressures with the announcement of the National Policy on Tribal Grazing Lands. The objectives of this policy are:

"(a) To make grazing control, better range management and increased productivity possible .....

(b) To safeguard the interests of those who own only a few cattle or none at all".

The primary means by which these aims are to be implemented is through the zoning of all land into Commercial Farming Areas, Communal Grazing Areas and Reserved Areas. It is only in the Reserved Areas that provision is made for land use practises other than stock raising, such as mining, cultivation or wildlife utilization.

The process of zoning is currently underway and it has profound implications for the future of wildlife in Botswana. It means that the era of untouched wilderness is over. It also means that where it is sought to reserve land for wildlife it will in future be necessary to demonstrate that wildlife industries can bring economic benefits to the non-stockholders of the area. In the latter regard it is highly significant that where attempts have been made to document the contribution of wildlife to the country's economy (Von Richter, 1970; Von Richter & Butynski, 1974; Fleming, 1976) it has emerged that it is the utilization of wildlife through traditional and safari hunting that has contributed most to the local economy.

Contributions to the economy by different wildlife-related activites are detailed in Table 1.1 below.

The importance of utilization is further emphasized by another recent estimate of the contribution of wildlife to the economy which was made in the Rural Incomes Distribution Survey (Central Statistics Office, 1976). This survey estimated that the utilization of wildlife contributed a mean of 111 Pula (one Pula is approximately equal to one Rand) to 95% of rural households. This represented 48% of the income of the poorest 10% of households, 17,6% of the median household income and 10,2% of the mean household income (75% of households had incomes lower than the mean).

1.1.3

Wildlife Conservation and Management

The conservation and management of wildlife in Botswana is the responsibility of the Department of Wildlife, National Parks and Tourism. A systematic conservation policy and programme were first introduced in 1966 (Campbell, 1973). During the first phase of this programme, National Parks and Game Reserves totalling 80 000 square kilometres, or 14% of the country (Figure 1.2), were established and traditional and safari hunting were organized along rational lines. During

TABLE 1.1: INCOME FROM WILDLIFE-RELATED ACTIVITIES (after Fleming, 1976)

Activity	Amount (Pula)	% of total
A: Hunting based		
(i) Traditional hunting	1 212 000	32,3
(ii) Trophies and curios	927 000	24,7
(iii) Safari hunting	685 000	18,2
B: Tourism based		
(i) Catering for tourists	906 000	24,1
(ii) Departmental camps and guides for tourists	28 000	0,7
TOTALS:	3 758 000	100,0

Figure 1.2: Botswana: sketch map showing important conservation areas and areas of maximum human impact (after Campbell, 1973).

this phase the emphasis was on preservation and law enforcement.

Because of the socio-economic pressures described in the previous section, the Department has been obliged to change its priorities. The change has been towards an emphasis on utilization. This has now been clearly spelt out in the National Development Plan 1976-1981: "The principles of sustained utilization and co-ordinated management, rather than the narrower concepts of preservation and enforcement, will characterize Departmental policies in the future."

The significance of this change in priorities is that there are large wildlife populations outside the National Parks and Game Reserves whose survival will depend on the success of the utilization policy. The Department seeks to implement the policy of utilization through the concept of wildlife management areas. It is proposed that in these areas wildlife management should be the primary land use, but that other compatible land uses should be tolerated. The Government has accepted this idea in principle but insists that its practical viability must be demonstrated before the proclamation of management areas can be considered.

1.2

TAXONOMY

Ansell's (1971) taxonomic treatment of the Order Artiodactyla was adopted for this study. He recognized three subspecies of Central African lechwe:

Subspecies	Present distribution
1. Red lechwe, *Kobus leche leche* Gray, 1850	Upper drainages of Kafue, Zambezi and Lualaba rivers, Okavango Delta and Kwando/Linyanti/Chobe system.
2. Kafue lechwe, *Kobus leche kafuensis* Haltenorth, 1963	Kafue Flats only.
3. Black lechwe, *Kobus leche smithemani* Lydekker, 1900	Bangweulu basin only.

The validity of a possible fourth subspecies, *Kobus leche robertsii*, Rothschild, 1907, is uncertain (Ansell, 1971). This subspecies apparently used to occur in Zambia, along the Luongo River in the Kawambwa District, but none survive today. It may have been an intermediate form between the red and the black lechwe (Ansell, *op. cit.*; Grimsdell & Bell, 1975).

This study relates to *Kobus leche leche*. An adequate description of this subspecies is provided by Dorst and Dandelot (1970) (see also Roberts, 1951).

Other members of the genus *Kobus* are the waterbuck (*K. ellypsiprymnus*), the Nile lechwe (*K. megaceros*) , the Uganda kob (*K. kob*) and the puku (*K. vardoni*).

The genus *Kobus* A. Smith, 1840 is classified as follows:
Order Artiodactyla, Suborder Ruminantia, Infraorder Pecora, Family Bovidae, Subfamily Reduncinae, Genus *Kobus*.

1.3

DISTRIBUTION AND STATUS

Lechwe occur only in wetland areas and their distribution reflects this specialized habitat requirement.

Original and present distribution, briefly outlined below, are described by Ansell (1971). Original distribution was: Botswana; from the Boteti River and Lake Ngami northwards; Caprivi Strip, Kwando/Linyanti/Chobe system; eastern and southeastern Angola, perhaps as far northwest as the Luano/Cuanza confluence area, approximately 10°22'S, 16°30'E; Zambia in the upper Zambezi, Kafue, Chambeshi and Luapula drainages and Mweru Marsh; southeastern Zaire in the upper reaches of the Lualaba and Lufira rivers and their tributaries to about as far north as 06°S.

Present distribution is not well known in either Angola or Zaire. In Botswana, because of reduction of habitat by desiccation, the species no longer occurs south of about 20°S (Smithers, 1971). Ansell (1971) infers from Hanks (1969) that lechwe have been exterminated in several areas in Zambia, although I am unable to draw the same inference from the reference given, as Hanks makes no claim to have surveyed the whole country.

Figure 1.3 shows the approximate distribution of K. leche in Zambia. Figure 1.4 shows the present distribution of K. leche leche in Botswana and the Caprivi Strip.

There are no numerical data available on lechwe populations in Angola and Zaire and nothing is known about trends in these populations. The numerical status of all known lechwe populations in Zambia and Botswana has been investigated during the present decade. Data published or available are given in Table 1.2.

Two of the populations studied have been described as either threatened or declining. Sayer and Van Lavieren (1975) predict that the Kafue Flats population will decline with the raised flood level in the Flats resulting from the Iteshi-teshi and Kafue Gorge dams. Child (1975) expresses the opinion that the population in the Kwando/Linyanti/Chobe system is declining rapidly.

1.4

THE PURPOSE OF THIS STUDY

The objectives of this project were determined primarily by the data needs of the Department of Wildlife, National Parks and Tourism with regard to lechwe. In view of the apparent decline of the Chobe lechwe it was clearly necessary to provide data on which steps to ensure the conservation of this population could be based. Also, because of the Department's commitment to utilization, it was necessary to collect data that would enable sustained utilization of the species to be planned when the population's survival had been assured. Thus the broad objectives of the study were to provide data that would facilitate the conservation and ultimate utilization of lechwe in Botswana.

Various writers (e.g. Geist, 1971) have stressed that conservation and management of a species should be based on a knowledge of its total biology, including behavioural adaptations. For this reason it was decided not to study any single aspect in great detail or depth, but rather to try and gather data that would provide the basis for a general description of the species' ecology and behaviour.

Another factor influencing the planning of the study was the availability of data from other studies on lechwe. A certain amount of information on lechwe ecology was available from Zambia (e.g.Allen, 1963; Robinette

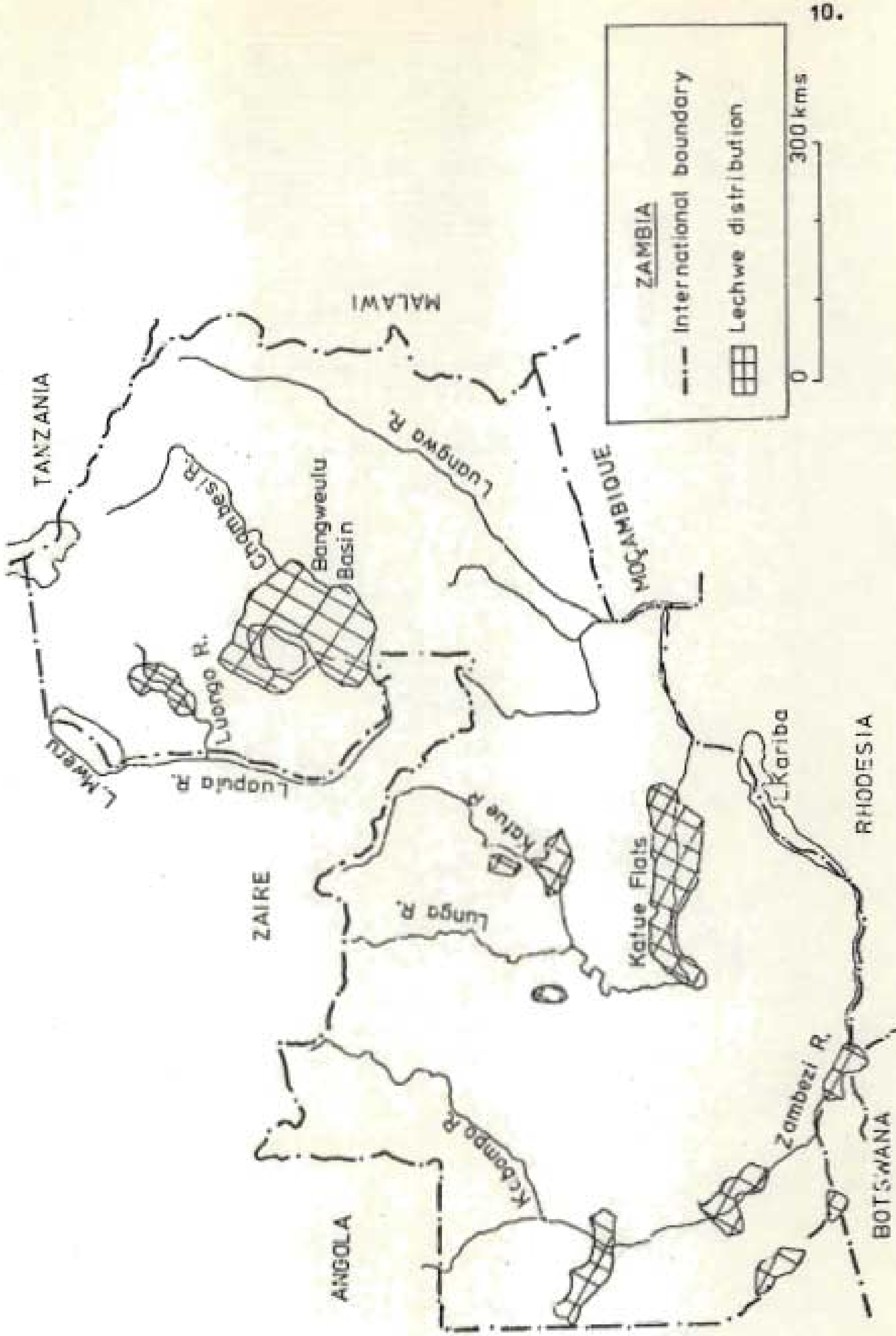


Figure 1.3: Zambia: distribution of lechwe (after Grimsdell and Bell, 1975).

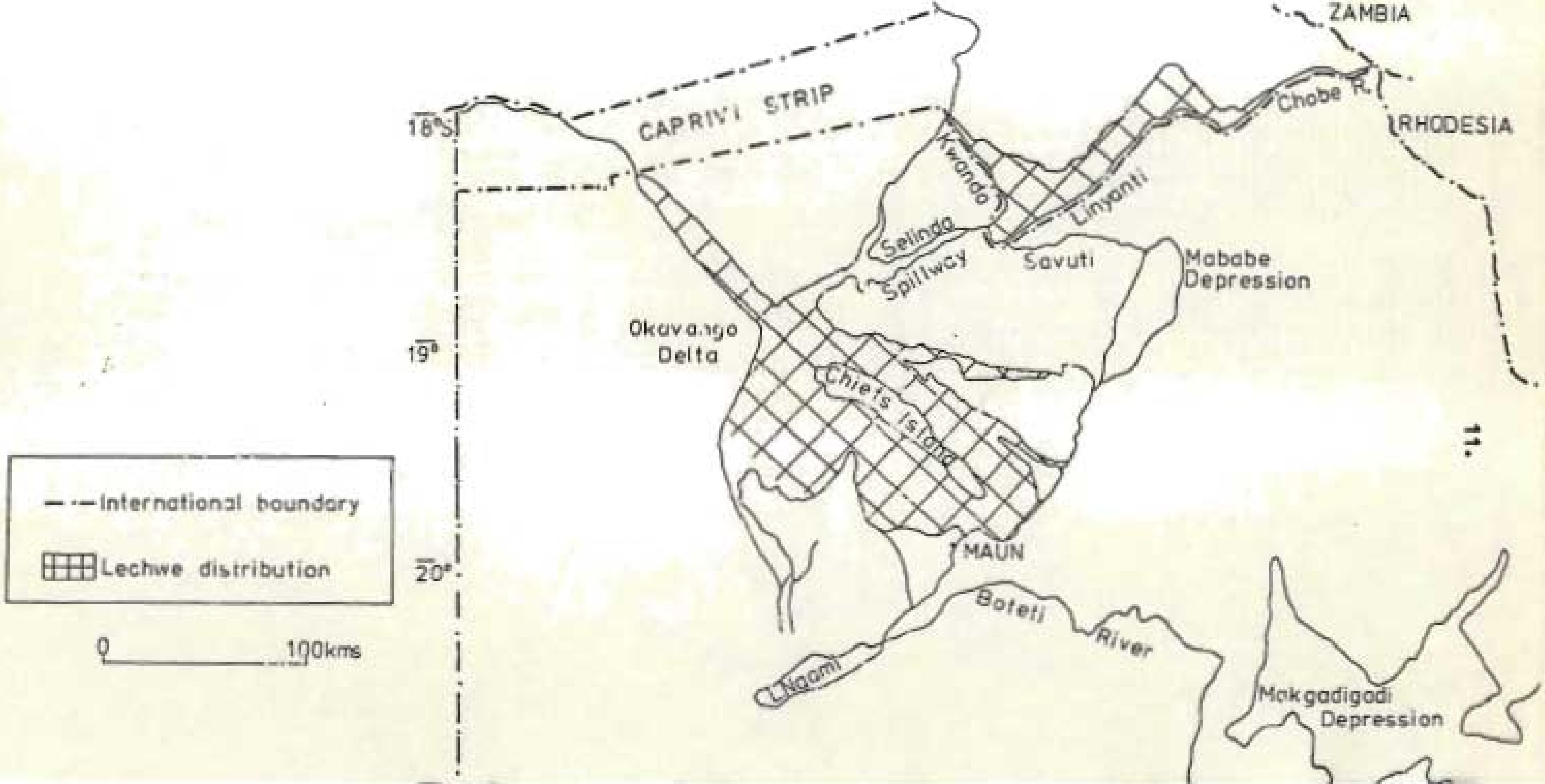


Figure 1.4: Northern Botswana (after Tinley, 1966).

TABLE 1.2: LECHWE POPULATIONS IN ZAMBIA AND BOTSWANA

SUBSPECIES	LOCATION	ESTIMATE OF NUMBERS	SOURCE
K.l.leche	Okavango	30 - 40 000	U.N.D.P. (1977)
K.l.leche	Linyanti/Chobe	10 - 15 000	This study
K.l.leche	Buanga Plain	± 3 000	Bell & Grimsdell (1972
K.l.kafuensis	Kafue Flats	± 90 000	Bell *et al.*, 1973
K.l.smithemani	Bangweulu Basin	± 20 000	Grimsdell & Bell (1975

& Child, 1964; De Vos & Dowsett, 1966), but all these studies related to subspecies other than the red lechwe and were rather limited in scope and duration. Preliminary investigations on certain aspects of the ecology and behaviour of the red lechwe had been carried out in Botswana, Child & Von Richter (1969) and Lent (1969) but these studies were again limited in scope. It was concluded that all the findings reported in the literature needed to be augmented and it was decided that data collection should aim at providing descriptions, quantitative where possible, of the following:

(a) lechwe habitat, in terms of water regime and the physiognomic and floristic characteristics of the vegetation;
*(b) habitat selection and food preferences;
*(c) growth;
*(d) reproduction;
*(e) condition;
(f) population parameters and population dynamics;
(g) non-social behaviour;
(h) social organization and behaviour.

For several reasons it was not practical to work in the Chobe National Park on the section of the Chobe population that was studied by Child and Von Richter (1969). This may well have been an advantage as the Chobe population is migratory and probably subject to considerable human disturbance.

An alternative study area was located on the Kwando, or western side of of the Linyanti Swamp. The next chapter describes this area.

Continuous fieldwork began in January 1975 and ended in May 1977. Follow up visits to the study area were made in February/March (three weeks) and September/October 1979 (two weeks).

CHAPTER 2

STUDY AREA

2.1

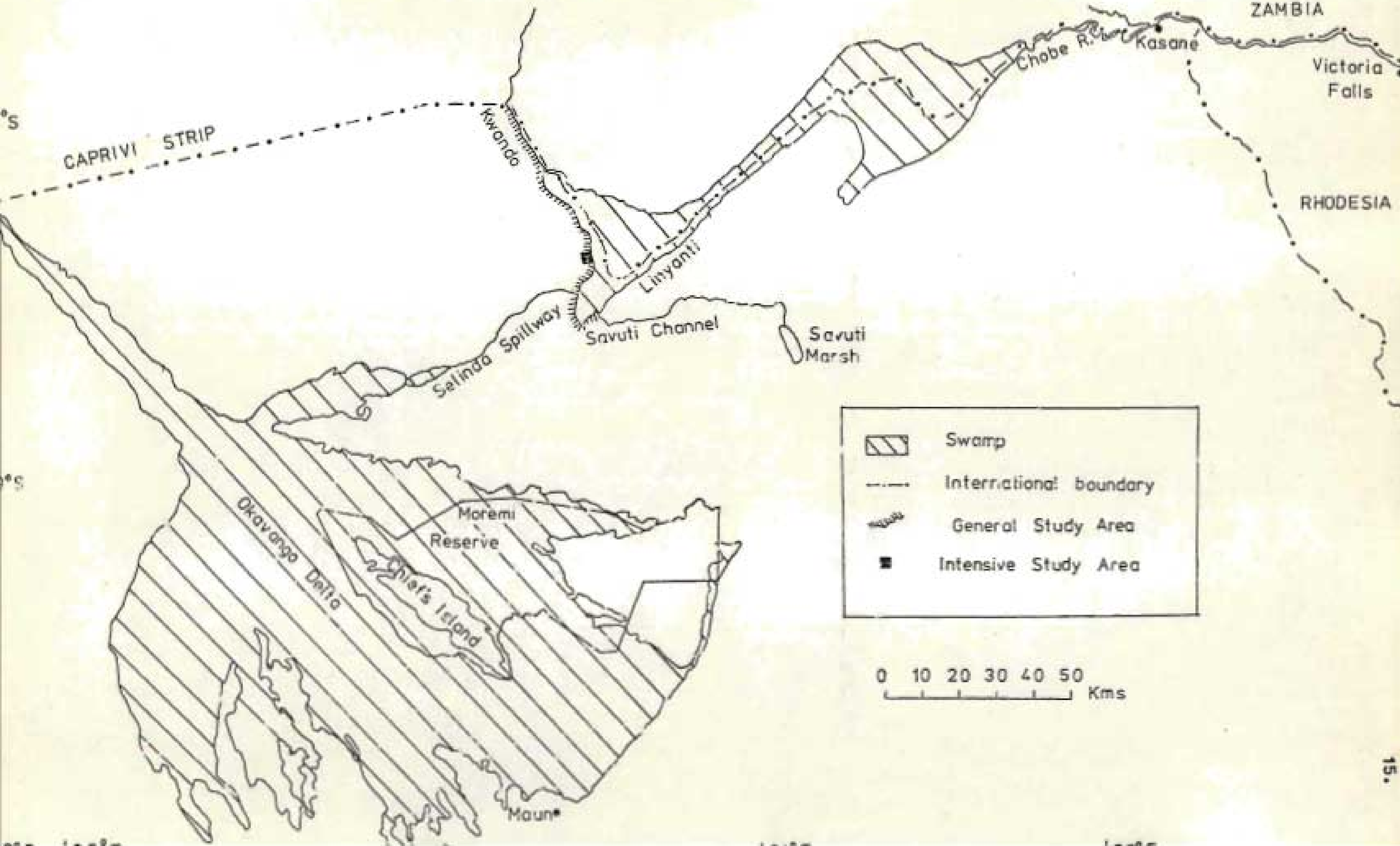
INTRODUCTION

During this study some data were collected over a fairly large area, referred to as the general study area, while other data were collected in a small, selected area, referred to as the intensive study area.

The general study area included that part of the west bank of the Kwando River which is in Botswana, the western edge of the Linyanti Swamp and the eastern edge of the swamp, as far as about 60 kilometres northeast of the Savuti Channel (Figure 2.1). Over this area the following types of data collection were made:
aerial counts;
ground counts, to establish the sex and age structure of the population;
collection of shot sample;
miscellaneous observations on distribution and behaviour;
general observations on vegetation and flood regime.

The intensive study area was about six square kilometres in area and centered on 18°22'S and 23°32'E. In this area data were collected on the following:
social organization and behaviour;
non-social behaviour;
habitat utilization;
structure and composition of floodplain vegetation;
flood regime.

The following study area description refers, for the most part, to both the general and the intensive study areas. Where the vegetation, soils and flood regime of the intensive study area are specifically described, this is made clear in the text.


ZAMBIA
Kasane
Chobe R.
Victoria Falls
RHODESIA
CAPRIVI STRIP
Kwando
Linyanti
Savuti Channel
Savuti Marsh
Selinda Spillway
Okavango Delta
Moremi Reserve
Chief's Island
Maun
Swamp
International boundary
General Study Area
Intensive Study Area
0 10 20 30 40 50
Kms

2.2

TOPOGRAPHY

The study area lies at an elevation of about 1 000 metres above sea level and is characterized by the extreme flatness of the topography. Where the Kwando enters Botswana in the north there is a calcrete ridge with an altitude of perhaps 50 metres. Apart from this, the only relief features are drainage lines and low sand ridges.

2.3

GEOLOGY AND GEOMORPHOLOGY

The study area lies within the Kalahari sand-covered plain of the Tertiary system. The sands are wind- and water-borne and vary in thickness from 30-360 metres, with a maximum thickness of perhaps 1,5 kilometres in the Caprivi Strip (Reeves, 1971). The older geological formations are almost completely masked by these sand deposits. Indirect geophysical methods and limited bedrock exposures have enabled investigators to make inference about the hardrock geology of the region. On this basis Hutchins *et al.*, (1976) suggest that Karroo sediments underlie the study area.

It is possible that faulting along a northeasterly axis gave rise to the Linyanti Swamp. The water of the swamp appears to back up against the extension of the Gomare fault which forms the southeastern edge of the swamp. At present northeastern Botswana is experiencing seismic activity (Reeves, 1972) and it has been suggested (Scholz *et al.*, 1975) that the trend of this activity and of existing faults may mark an incipient arm of the East African Rift system. Unlike the situation in the Okavango Delta, there is no evidence that this seismic activity is influencing the hydrology of the Linyanti Swamp.

2.4

SOILS

Soils in the study area are predominantly Kalahari sands, re-sorted by alluvial action. These sands are fine-grained and uniform. Studies as far apart as the Okavango region (United Nations Development Programme, 1977) and western Zambia (Verboom & Bunt, 1970) have found very similar distributions of grain size. In the Okavango, median grain size is about 0,25 millimetre (United Nations Development Programme, 1977). Clay content is generally low so that although porosity is high, water retention tends to be low. In general, structure is poorly developed and fertility low.

Of particular interest in terms of lechwe habitat are floodplain soils. These are of riverine alluvial origin and in the study area appear to conform to the Molapo Series of Siderius (1972). This series develops where seasonal flooding occurs. Its texture varies from sandy clay loam to sandy clay and drainage is poor. It has a Melanic A horizon, overlying a gley horizon, which develops as a result of periodic inundation. Pockets of halomorphic soil occur within this floodplain type. These are characterized by a surface deposit of salt and often support uniform grass cover of Sporobolus species.

Within the intensive study area soil samples were collected along a gradient of increasing dryness/decreasing moisture and from halomorphic pockets. Tables 2.1 and 2.2 give the results of analyses of these samples. In zone 3 soils are permanently moist and often flooded; in zone 4 soils are flooded 3-6 months in most years; in zone 5 soils are flooded for less than 3 months and often not at all. The results in Table 2.1 indicate that along the gradient of increasing dryness soils become more acidic bacause of leaching, and poorer in exchangeable cations.

2.5

HYDROGRAPHY

The Kwando River rises on the central Angolan plateau, flows through the Caprivi Strip and enters Botswana at 18°10'S and 23°20'E. It meanders in a southeasterly direction along the Caprivi/Botswana border for about 25 kilometres before entering the Linyanti Swamp, the main body of which has the shape of an inverted triangle with a base of about 50 kilometres and a height of approximately 35 kilometres. The Kwando continues as a clearly discernible channel which flows along the western edge of the swamp until it reaches the extension of the Gomare fault referred to in section 2.3. Here the channel makes a right angle and

TABLE 2.1: PARTIAL ANALYSIS OF SOILS FROM INTENSIVE STUDY AREA

Soil	pH	Elect. Cond. mmhos/cm	Potassium me %	Sodium me %
Halomorphic	8,1	2,5	5,2	16,0
	9,4	3,6	7,4	18,0
Zone 3	8,9	3,6	2,4	7,0
	8,6	0,92	3,4	10,0
Zone 4	7,2	0,085	0,28	0,6
	7,3	0,10	0,24	0,4
Zone 5	5,6	0,06	0,09	0,05
	6,4	0,07	0,14	0,20

TABLE 2.2: ANALYSIS OF SALT

Sodium	Potassium	Chlorine	CO_3	HCO_3	SO_4	Sand
46%	4%	2%	3%	10%	7%	4%

flows to the northeast.

The point where the channel changes direction forms the apex of the swamp. At this point there are several lake-like bodies of open water. Also at this point the Selinda Spillway flows into the system from the Okavango Delta and the Savuti Channel flows out of the system to terminate in the Savuti Marsh of the Mababe Depression. Neither the input of the Selinda Spillway, which flows only in years of high flood in the Okavango, nor the outflow along the Savuti Channel have been measured.

After turning to the northeast the channel continues in that direction along the southeastern edge of the swamp. This edge of the triangle is about 40 kilometres long and extends out of the main body of the swamp as an arm of swamp about 10 kilometres wide which continues into the vicinity of Lake Liambezi. The channel flows along this arm of swamp into the lake. The river that emerges from the lake is known as the Chobe and it flows northeast through a relatively narrow floodplain until it joins the Zambezi near Kasane.

During this study the level of the swamp was monitored by means of a gauge post in the main channel in the intensive study area. Gauging data are presented in Figure 2.2. This figure illustrates two important important aspects of the flood regime. Firstly, changes in the flood level are slight, less than 10 centimetres over the entire two year period. This is probably due to the fact that flood waters spread over a large area. It is somewhat misleading in the sense that small changes in level have important consequences. On four occasions (July 1975, March 1976, August 1976, March 1977) a rise in the water level of between 3-5 centimetres resulted in the inundation of all seasonally flooded areas.

The second noteworthy feature of the flood regime that is illustrated by Figure 2.2 is that there are two annual peaks in the level of the swamp. Between June and August a peak is reached as flood waters from rainfall in the Angolan highlands arrive. This peak subsides relatively slowly. Between February and April a peak occurs as a result of local rainfall. This peak subsides relatively rapidly.

The occurrence of a June/August peak is partly corroborated by Curson (1947), who reports a peak in June in the eastern Caprivi.

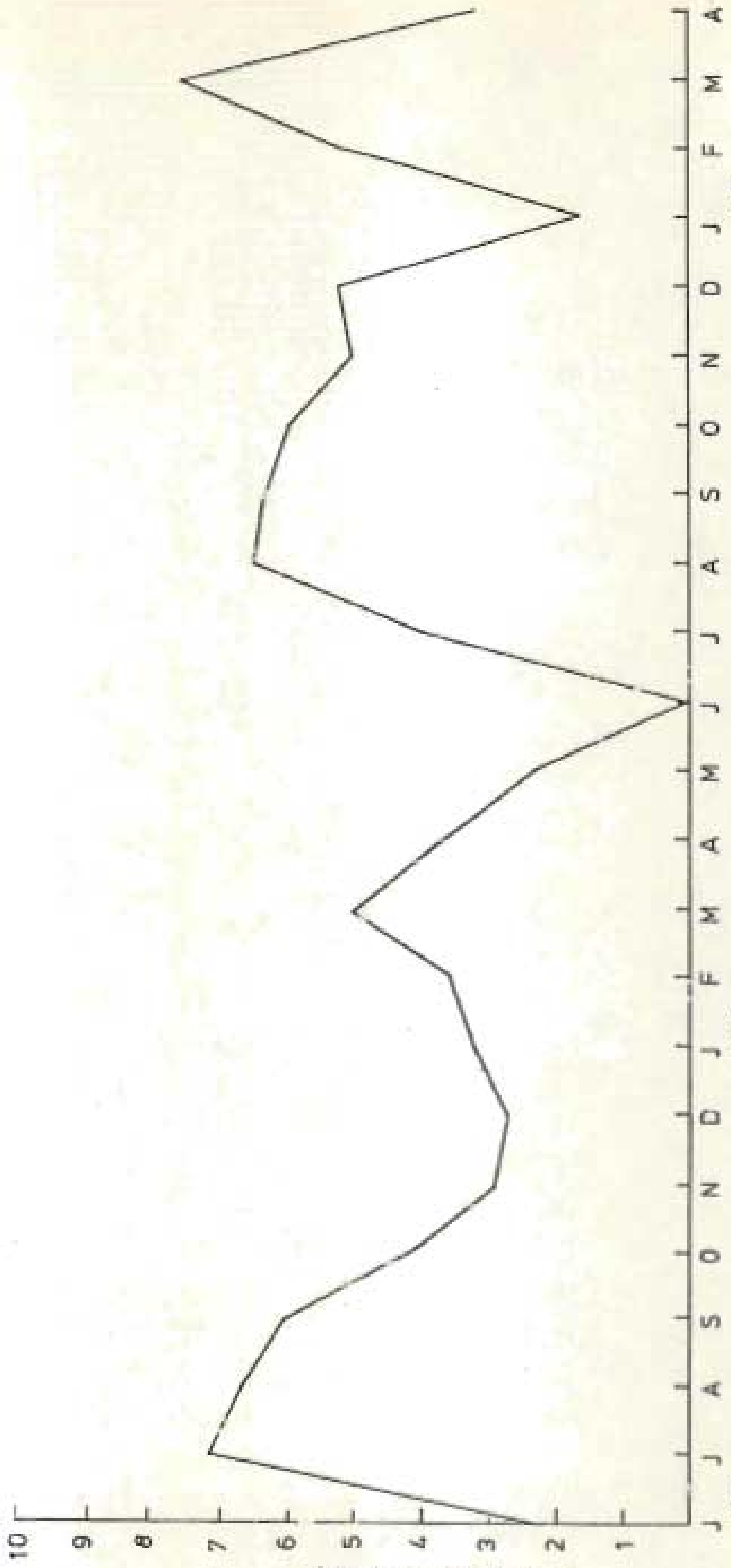


Figure 2.2: Height (cm) of water level above lowest level (June 1976) recorded at gauging station in intensive study area.

It was established by examining aerial photographs from 1925, 1944, 1962, 1974 and 1977 and satellite images from 1972, 1975 and 1976 that in addition to fluctuations in water levels within the year, there are differences in flood regime between the years. There appear to be high and low flood cycles. It was found, for example, that areas which were dry during 1962 and 1972 were flooded for all or part of 1975, 1976 and 1977. During 1978 flood levels were the highest that have ever been recorded (P.A.Smith, pers. comm.*). The flood regime thus appears to have been in a high cycle during the study period. From the aerial photographs it appeared that high and low cycles affected the extent of the seasonally flooded areas and the semi-perennial swamp but not the extent of the perennial swamp.

On all satellite images a boundary can be seen about 5 kilometres west of the existing edge of the swamp. It is possible that this boundary once formed the edge of the swamp and that the swamp has diminished in size since that time.

2.6

CLIMATE

For purposes of this study three seasons were recognized:

(i) the rains: the period during which rain occurs, generally from November/December to March/April;

(ii) the cool, dry season: the period when temperatures are lower and little or no rain occurs, generally May to August;

(iii) the hot, dry season: the period with high temperatures and no rain, generally September to November/December.

No climatic data are available for the study area, but the salient features of the climate can be illustrated with data from meteorological stations within the region.

2.6.1

Temperature and Insolation

Figures 2.3 and 2.4 show seasonal trends in mean monthly maximum and minimum temperatures recorded over a period of 48 years at Maun and over a period of 16 years at Shakawe. Figure 2.5 presents temperature data given by Curson (1947) for one year in the eastern Caprivi. A similar seasonal trend is evident.

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* P.A.Smith, Agricultural Research Officer, P.O.Box 107, Maun, Botswana.

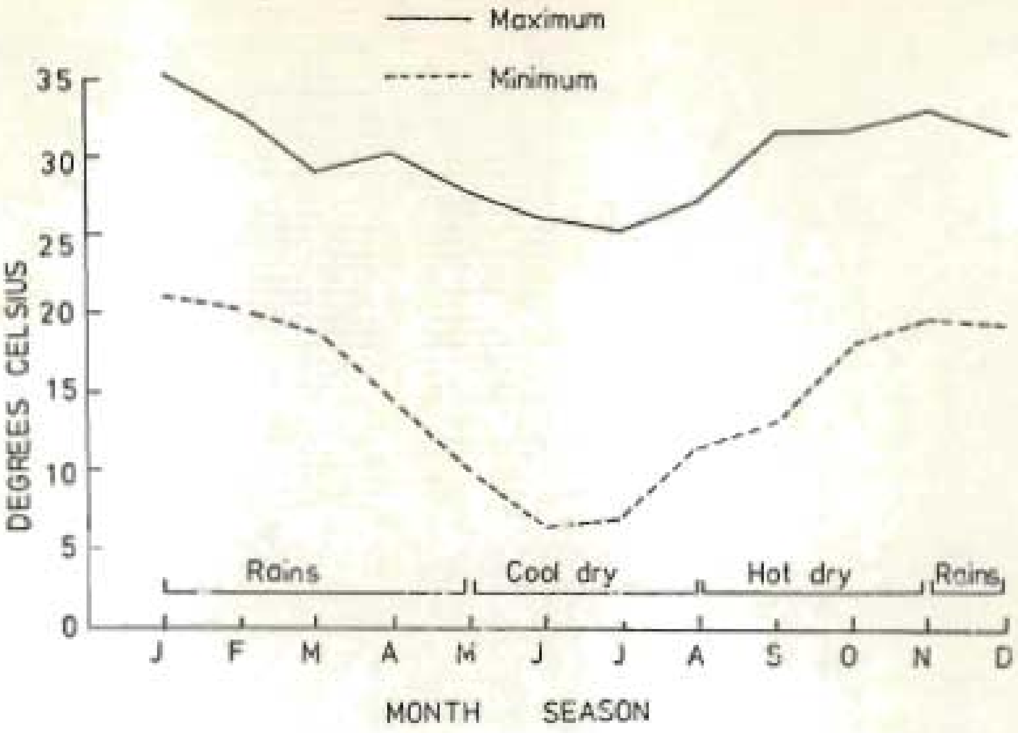

Figure 2.3: Mean monthly maximum and minimum temperatures at Maun (Weather Bureau, Gaborone, 1978).

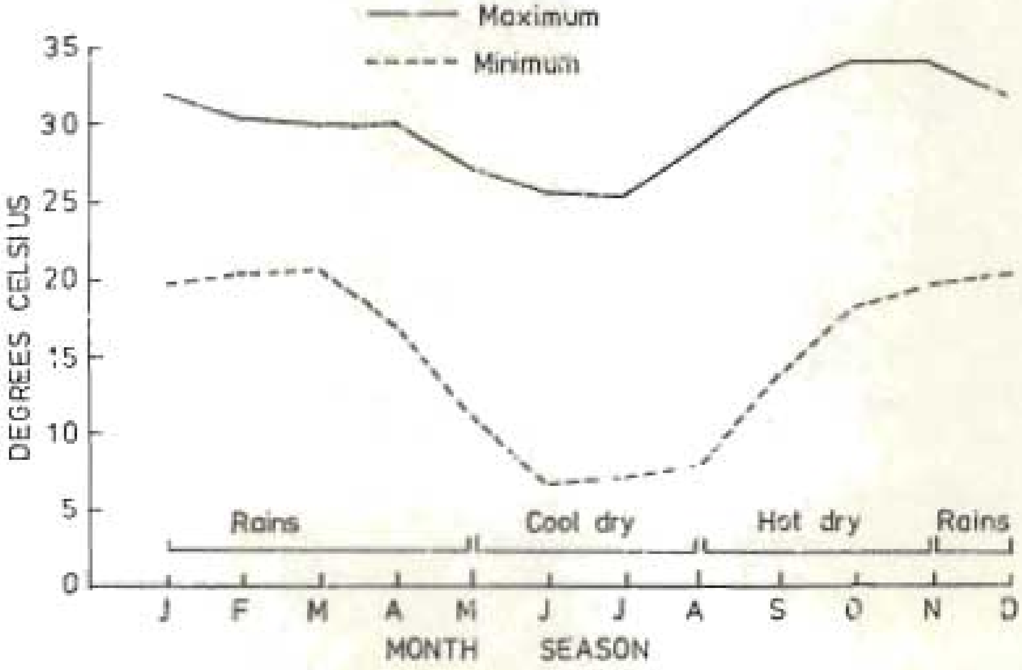

Figure 2.4: Mean monthly maximum and minimum temperatures at Shakawe (Weather Bureau, Gaborone, 1978).

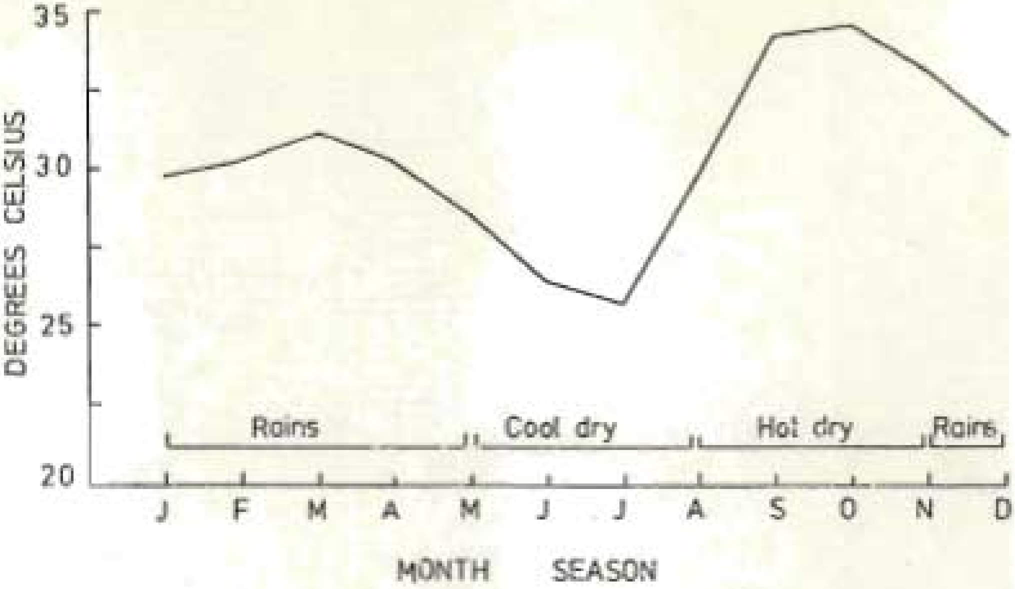

Figure 2.5: Monthly maximum temperatures in the Eastern Caprivi (Curson, 1947).

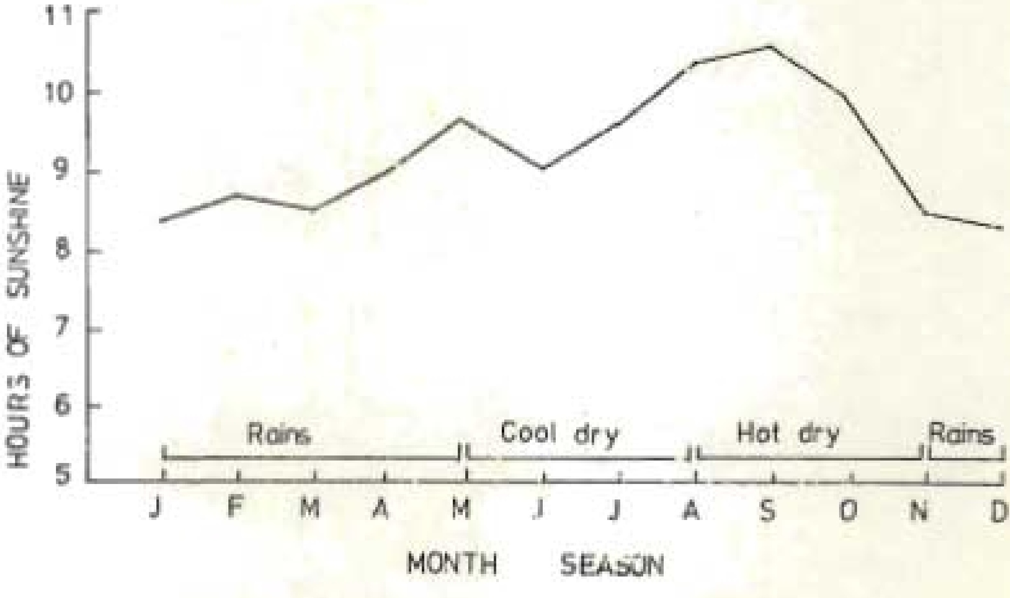

Figure 2.6: Mean daily hours of sunshine at Maun (SWECO, 1976).

Data are available from Maun on radiation and the mean daily hours of sunshine per month. Mean daily incoming radiation is 2076 joules/ cm^2/day (SWECO, 1976). Data on mean hours of sunshine per day are presented in Figure 2.6, from which seasonal trends can be readily observed.

2.6.2

Humidity

Figure 2.7 illustrates seasonal variation in relative humidity. It can be seen from the figure that relative humidity never approaches saturation levels.

2.6.3

Rainfall

Pike (1971) places the study area between the 600 millimetre and 700 millimetre isohyets. Rainfall figures given by Curson (1947) for one year in the eastern Caprivi (Figure 2.8) are consistent with this estimate, which is compatible also with figures from the nearest meteorological stations (Table 2.3), having regard to the existence of a gradient of increasing rainfall along a northeasterly axis.

92,5% of rainfall precipitates between November and March. The dry season varies in length from 2-8 months, with a mean of 4,3 at Kasane (Sommerlatte, 1976). Seasonal distribution of rainfall is illustrated by data from Shakawe, set out in Table 2.4. The ranges given in Table 2.4 show the great variability in rainfall. This variability is reflected also in the range of total annual rainfall. At Kasane the range is from 340-1400 millimetres. At Maun 245 millimetres were recorded during the 1972/1973 rainy season while during the 1973/1974 season rainfall was 1195 millimetres, the highest ever recorded at this station.

2.6.4

Other Climatic Factors

Evaporation exceeds rainfall for most of the year, as illustrated by Figure 2.9. The high evaporation, variability of rainfall and high temperatures make for a much less favourable environment for plant growth than the mean annual rainfall figures indicate.

Dew and mist occurred occasionally during the cool, dry season but never on more than a few nights or early mornings. Frost was never observed in the study area and the lowest temperature recorded during

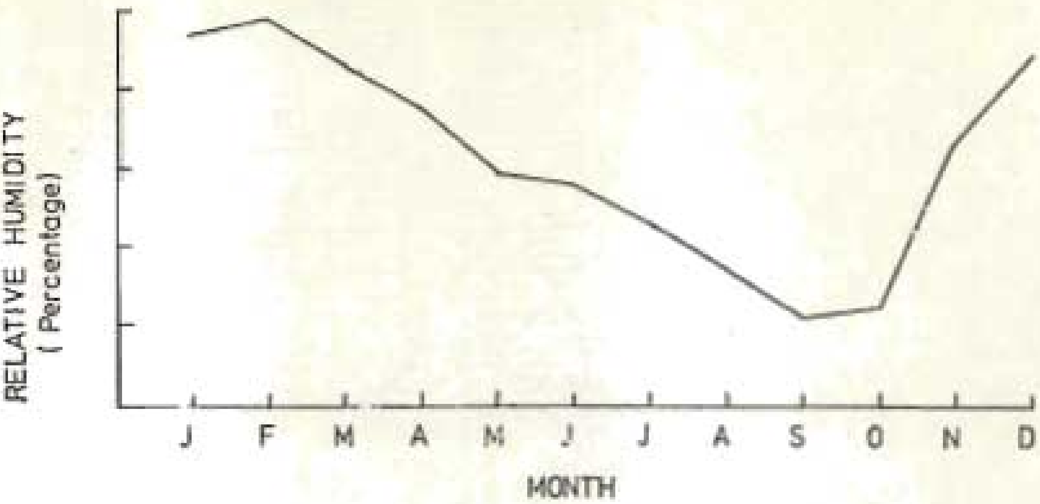

Figure 2.7: Relative Humidity at Maun (SWECO, 1976)

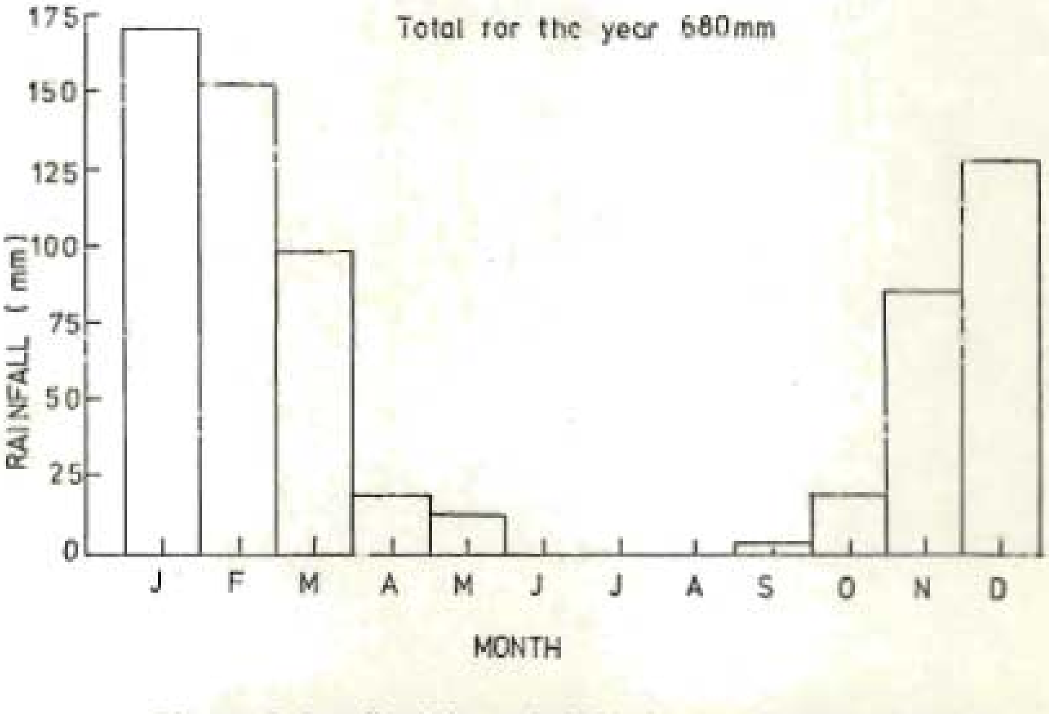

Figure 2.8: Monthly rainfall in the Eastern Caprivi (Curson, 1947)

TABLE 2.3: RAINFALL AT STATIONS NEAREST TO GENERAL STUDY AREA

Place	Air distance from camp	Mean annual rainfall (mm)	Rainfall 1974/75 (mm)	Rainfall 1975/76 (mm)	Rainfall 1976/77 (mm)
MAUN	175 km	477,5	605,2	387,5	505,7
SHAKAWE	175 km	577,2	434,9	473,7	606,5
KASANE	190 km	707	783,5	774,6	744,6

TABLE 2.4: MEAN MONTHLY RAINFALL AT SHAKAWE (SWECO, 1976)

Month	Mean rainfall (mm)	Range	No. of days with rain
January	134,8	53,7 - 352,4	15
February	137,0	12,4 - 292,1	12
March	79,4	5,0 - 185,7	10
April	35,7	0 - 134,3	4
May	2,7	0 - 17,8	1
June	0,7	0 - 11,3	0
July	0,1	0 - 2,0	0
August	0,2	0 - 2,3	0
September	3,8	0 - 35,9	1
October	13,6	0 - 66,5	3
November	66,4	0 - 291,5	9
December	101,6	29,2 - 229,0	11

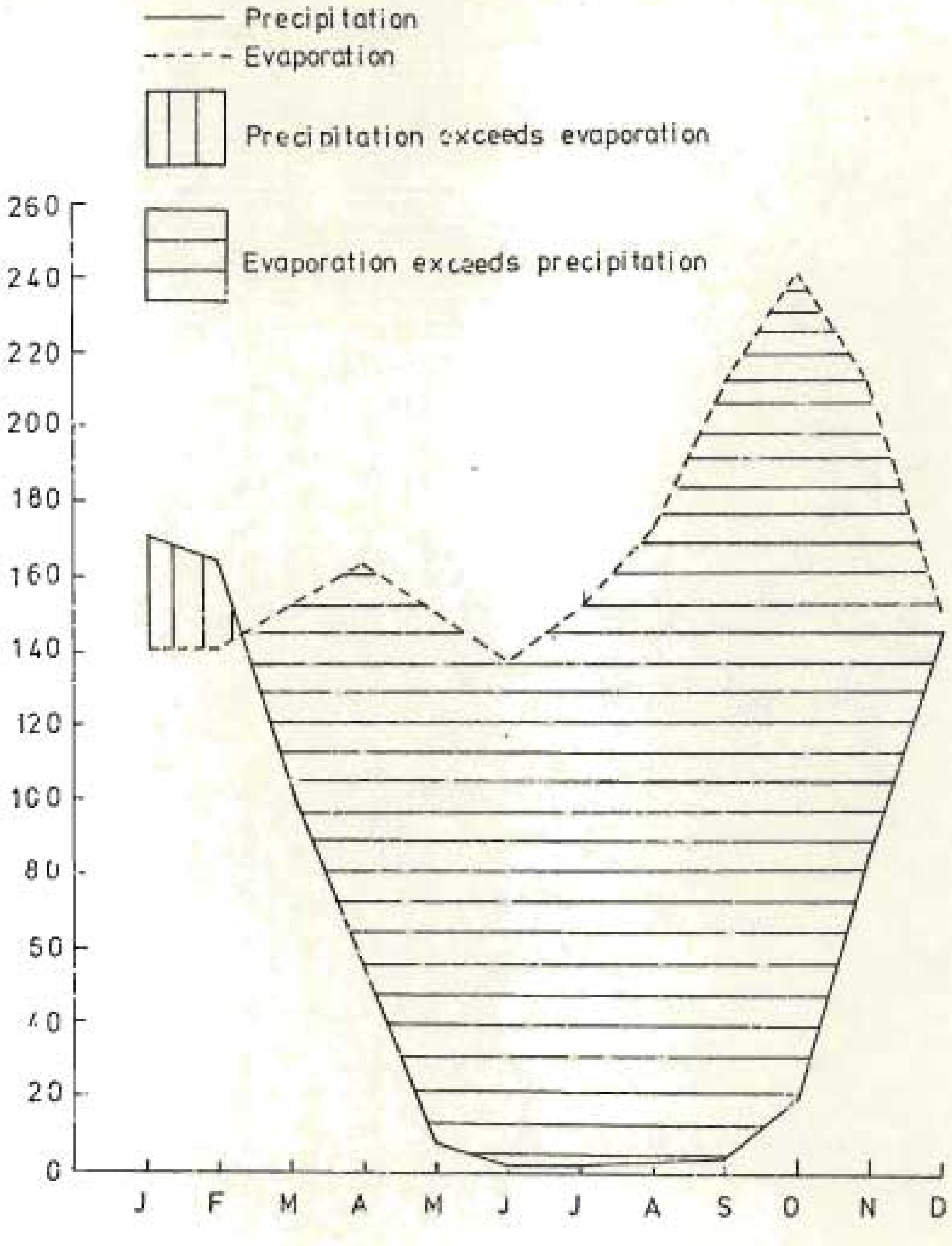

Figure 2.9: Mean monthly precipitation and evaporation at Kasane (Sommerlatte, 1976).

this study was 5° Celsius.

The prevailing winds were southeasterly, easterly and northeasterly. Strong winds occurred most frequently during August and September.

2.7

VEGETATION

Apart from plant collections by P.A.Smith (pers. comm.*) no fieldwork has been done on the vegetation of the Kwando area. The present study was concerned with the ecology of the lechwe and attention was necessarily directed to those plant communities which are of importance to this species. The number of communities actively used by lechwe is limited but, for the sake of completeness, a brief outline of the vegetation of this area will be given before lechwe habitat is described.

2.7.1

Broad Vegetation Types

On the basis of water regime the area can be broadly divided into aquatic, transitional, riparian and dry-land vegetation types. These broad types are made up of a mosaic of different communities. Those most widely observed within each vegetation type in the study are listed below.

Aquatic vegetation types (largely after United Nations Development Programme, 1977)

Open channel fringe: these fringes may be up to 10 metres wide and are usually dominated by *Cyperus papyrus*, although also in some places *Phragmites* spp.

Vegetated channel: these are essentially backwaters and support a wide variety of rooted, floating and emergent vegetation. Common species include *Nymphaea* spp., *Potamogeton* spp. and *Utricularia* spp.

Lediba: this is a lake-like body of open water, varying in size from less than one hectare to several hundred hectares. Open water vegetation, where it occurs, is similar to that found in vegetated channels, fringe species are similar to those along the channel fringes.

Islands: higher and drier islands support trees; *Phoenix* sp. and *Syzgium* sp. dominate small islands, while larger islands support, in addition, species such as *Diospyros mespiliformis*, *Garcinia livingstonei*, *Lonchocarpus capassa* and *Acacia nigrescens*. The lower, wetter islands

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* P.A.Smith, Agricultural Research Officer, P.O.Box 107, Maun, Botswana.

are grass covered, common species including *Panicum repens*, *Cynodon* dactylon, *Sporobolus spicatus* and *Eragrostis inamoena*. Islands are strictly speaking riparian communities but they are described here because they form part of the aquatic mosaic.

Perennial swamp: these communities are permanently inundated and, depending on water depth and variation in water depth, may be dominated by *Cyperus papyrus*, *Phragmites* sp. or *Miscanthidium* sp.

Semi-perennial swamp: these communities are liable to drying out temporarily in years of low flood. They are dominated by species such as *Cyperus articulatus*, *Nymphaea* sp., *Potamogeton* sp., *Oryza longistaminata* and other aquatic grasses.

Transitional vegetation types

Swamp margins: these are flooded to a depth of 20-30 centimetres during high flood and vary in width from 10 metres to hundreds of metres. *Panicum repens* is the dominant plant in these communities.

Low floodplain: this community is flooded for 3-8 months annually depending on the flood cycle. It is dominated by grass species such as *Cynodon dactylon*, *Eragrostis* spp., *Setaria* spp.

High floodplain: this community is flooded for about three months of the year but not at all during low flood cycles. It is dominated by grass species such as *Cymbopogon excavatus*, *Imperator cylindrica*, *Eragrostis* spp., and *Aristida* spp.

Riparian vegetation types

These occur in a great variety of combinations along the edges of swamps and floodplains and on islands in the swamps and floodplains. Trees are the dominant plants and common species include *Acacia nigrescens*, *Acacia luederitzii*, *Diospyros mespiliformis*, *Lonchocarpus capassa*, *Garcinia livingstonei*, *Kigelia africana*, *Combretum imberbe*, *Croton megalobotrys*, *Ficus sycomorus*, *Sclerocarya birrea*, *Albizia versicolor*, *Hyphaene* sp. and *Phoenix* sp. Common shrubs include *Diospyros lycioides*, *Euclea divinorum* and *Grewia* spp.

Dryland vegetation types

Acacia woodland: this community occurs as open and closed woodland dominated by *Acacia* species and usually having a good ground cover. Common species include *Acacia erioloba*, *A. hebeclada*, *A. tortilis* and *A. fleckii*. Other species are *Dichrostachys cinerea*, *Lonchocarpus nelsii*, *Zizyphus mucronata* and *Grewia* spp.

Terminalia sericea woodland: this community encompasses open and closed woodland and shrubland with good ground cover and dominated by T. sericea. It occurs on sandy soils.

Mopane woodland and shrubland: this community usually occurs on claypan soils, and has a high density of woody plants dominated by Colophospermum mopane and has less ground cover than other woodland communities.

Mixed woodland: is a complex of the above three types.

Grassland: occurs in areas that are waterlogged during the rains. Species composition is highly variable.

2.7.2

Lechwe Habitat

Within the intensive study area an effort was made to describe lechwe habitat in more objective and quantitative terms. All grasses and sedges encountered in this area were collected and sent for identification to the National Herbarium, Salisbury. The more common dicotyledonous plants were also collected for identification. A systematic list of the plants collected is given in the Appendix.

On the basis of water regime five zones were recognized. In zones 2-5 ten of the transects designed by Walker (1976) were run in each zone. No transects were run in zone 1 because of the physical difficulty of doing so and the presence of hippo (Hippopotamus amphibius) and crocodile (Crocodylus niloticus). The starting point of each transect was randomly located.

In addition to the Walker transects, 20 of the transects designed by Riney (1963) were run in the intensive study area and a further 20 of these transects were run in areas outside the intensive study area, for comparative purposes. The Riney transects were subjectively located within each zone.

Data relating to the physiognomy and status of the vegetation in the various zones are presented in Tables 2.5 and 2.6. The flood regime and vegetation of each zone are described below. Brief comments are also made on the use of each zone by lechwe, but the main discussion of habitat utilization will be found in Chapter Four.

TABLE 2.5: DATA FROM TRANSECTS IN DIFFERENT VEGETATION ZONES (after Walker, 1976)

Vegetation zone	2	3	4	5
Cover/abundance	26,8%	35,1%	54,9%	70,6%
Maximum plant height	1,8 m above water	0,191 m	1,400 m	1,700 m
Moribund grass	-	8,9%	16,6%	13,9%
Proportion of forbs	2,9%	0,04%	2,1%	1,2%
Litter	-	5,3%	5,0%	7,4%
Proportion grazed	1,0%	29,6%	7,0%	1,1%

TABLE 2.6: RESULTS OF TRANSECTS IN DIFFERENT VEGETATION ZONES (after Riney, 1963)

Zone	Area	No. of Transects	Ground % Strikes	Litter % Strikes	Grass % Strikes	Grass Height (m)	Tree/ Shrub % Strikes	Tree/Shrub Height (m)	Overall trend
3	Intensive study area	7	37	20	43	0,062	0,2	0,50	stable
3	General study area	9	26	23	53	0,062	0,3	0,037	stable
3	Combined	16	32	21	48	0,062	0,3	0,269	stable
4	Intensive study area	9	24	28	48	0,416	1,1	0,30	stable
4	General study area	5	6	25	69	0,444	0,4	0,375	stable
4	Combined	14	15	27	59	0,430	0,8	0,338	stable
5	Intensive study area	5	28	20	50	0,705	2,2	0,20	declining
5	General study area	7	4	24	71	0,816	0,6	0,248	stable
5	Combined	12	16	22	61	0,761	1,4	0,224	slightly down

Zone 1: is equivalent to the perennial swamp in 2.7.1. It was permanently inundated and water depth was up to two metres. In the study area it was dominated by *Phragmites* sp. Lechwe used it as escape cover and in transit.

Zone 2: is equivalent to the semi-perennial swamp in 2.7.1. It was inundated throughout the study period but aerial photographs clearly showed that much of this zone dried out during July 1962 and December 1974. Water depth seldom exceeded 1–1,5 metres. The most important species of this zone are listed in Table 2.7. Lechwe did a limited amount of feeding in this zone and also used it as escape cover.

Within zone 1 there occur islands which are heavily used by lechwe for feeding, resting and seclusion of neonates. Most of the islands in the intensive study area were heavily wooded. Islands visited in other parts of the swamp were grass covered, the most common species being *Panicum repens*, *Sporobolus spicatus*, *Cynodon dactylon* and *Eragrostis inamoena*.

Within zone 2 there are similar islands and also numerous termitaria. Within the intensive study area most termitaria were small and covered with grass, commonly *Panicum repens* at water level and *Cynodon dactylon* above the water level. Slightly larger termitaria support shrubs such *Achyranthes aspera* and *Commicarpus africanus*, which were heavily browsed by sitatunga (*Tragelaphus spekei*) and perhaps by lechwe as well. Large termitaria support trees, commonly *Lonchocarpus capassa*, *Acacia nigrescens* and *Acacia erioloba*.

Zone 3: is equivalent to the swamp margins in 2.7.1. It is never deeply flooded but its soil remains permanently moist. Its width varies greatly depending on base levels. Important species in this zone are listed in Table 2.8. This zone was very heavily used by lechwe for a wide range of activities.

Zone 4: is equivalent to low floodplains in 2.7.1. It is flooded for 3–8 months of the year, depending on the flood cycle. Water depth seldom exceeds one metre. The most important species of this zone are listed in Table 2.9. Lechwe made use of this zone to varying degrees, males more so than females.

TABLE 2.7: ZONE 2 SPECIES COMPOSITION, PERCENTAGE CONTRIBUTION TO BIOMASS (after Walker, 1976)

Species	% Contribution	Grass	Sedge	Dicot.
Cyperus articulatus	51,3		X	
Nymphaea caerulea	16,8			X
Potamogeton thunbergii	15,0			X
Pycreus flavescens	6,9		X	
Panicum repens	5,1	X		
Oryza longistaminata	1,9	X		
Scirpus uninodus	1,3		X	
Sacciolepis typhura	1,1	X		
Cyperus denudatus var. *denudatus*	0,4		X	
Rhynchospora holoschoenoides	0,2		X	
Paspalidium platyrrhachis	0,1	X		

<u>TABLE 2.8</u>: <u>ZONE 3, SPECIES COMPOSITION, PERCENTAGE CONTRIBUTION TO BIOMASS</u> (after Walker, 1976)

Species	% Contribution	Grass	Rush/ Sedge	Dicot.
Panicum repens	62,2	X		
Scirpus uninodus	14,0		X	
Cyperus denudatus	8,4		X	
Sporobolus spicatus	6,8	X		
Cynodon dactylon	2,5	X		
Juncus rigidus	1,8		X	
Mariscus squarrosus	1,5		X	
Pycreus flavescens	1,3		X	
Eragrostis inamoena	1,2	X		
Vetiveria nigritana	0,1	X		
Fuirena umbellata	0,1		X	

TABLE 2.9: ZONE 4, SPECIES COMPOSITION, PERCENTAGE CONTRIBUTION TO BIOMASS (after Walker, 1976)

Species	% Contribution	Grass	Sedge	Dicot.
Eragrostis lappula	35,2	X		
Setaria anceps	16,2	X		
Eragrostis trichophora	14,9	X		
Cynodon dactylon	6,5	X		
Paspalum orbiculare	5,2	X		
Trachypogon spicatus	4,2	X		
Aristida pilgeri	3,6	X		
Panicum repens	2,3	X		
Fuirena umbellata	1,7		X	
Nicolasia sp.	1,6			X
Panicum dregeanum	1,5	X		
Cyperus longus	1,1		X	
Cyperus denudatus	1,0		X	
Cyperus articulatus	1,0		X	
Cymbopogon excavatus	1.0	X		
Eragrostis inamoena	0,9	X		
Sorghastrum friesii	0,8	X		
Heliotropium ovalifolium	0,6			X
Fimbristylis sp.	0,5		X	
Indigofera astragalina	0,2			X
Fimbristylis ferruginea	0,1		X	

Zone 5: is equivalent to high floodplain in 2.7.1. It is flooded for less than three months of the year in normal years and not at all in years of low flood. The most important species of this zone are listed in Table 2.10.

Comparison of Tables 2.7 to 2.10 shows striking differences between the wetter and drier areas in the relative contributions to plant biomass by grasses, sedges and dicotyledonous plants. These differences are shown graphically in Figure 2.10.

2.7.3

Dynamics

Short and long term fluctuations in flood regime were documented in 2.5 above. It is likely that these fluctuations, together with the variability of rainfall, have an effect on the vegetation through their influence on soil moisture.

It was possible to detect some short-term changes by subjective observations. At the end of the rains grasses in zones 4 and 5 dried off rapidly. With the coming of the floods in the cool, dry season the amount of herbage available in zones 3 and 4 was reduced by the raised water levels. The overall affect was that in the drier areas the quality of the vegetation declined, while in the wetter areas the quantity of available forage was reduced. It is likely that by the end of the dry season these changes result in a period of nutritional stress for lechwe.

An attempt was made to monitor forage quality in zones 3, 4 and 5. Grass clippings were made in each zone in each season. These clippings were air-dried and later analysed for apparent crude protein content. The results of the analyses are presented in Table 2.11. These results go some way towards confirming the subjective observations presented here, but the number of replicates is small and the results for the hot, dry season are somewhat anomalous. This is partly due to the fact that some light rain fell during the season when the clippings were made and this may have improved conditions for plant growth.

The overall means for each zone are significantly different and this may be one of the factors influencing habitat selection (Chapter 8).

TABLE 2.10: ZONE 5, SPECIES COMPOSITION, PERCENTAGE CONTRIBUTION TO BIOMASS (after Walker, 1976)

Species	% Contribution	Grass	Sedge	Dicot.
Cymbopogon excavatus	29,3	X		
Imperatar cylindrica	12,2	X		
Eragrostis lappula	11,1	X		
Trachypogon spicatus	10,0	X		
Aristida pilgeri	5,7	X		
Brachiaria dura	4,2	X		
Hyperthelia dissoluta	4,2	X		
Pogonarthria squarrosa	3,2	X		
Schizachyrium jeffreysii	3,0	X		
Eragrostis pallens	2,6	X		
Aristida congesta	2,4	X		
Eragrostis trichophora	2,3	X		
Setaria sphacelata	2,1	X		
Elionurus argenteus	2,1	X		
Sorghastrum friesii	1,8	X		
Panicum dregeanum	1,0	X		
Setaria anceps	0,6	X		
Rhynchelytrum repens	0,6	X		
Trichoneura grandiglumis	0,5	X		
Eragrostis echinochloidea	0,4	X		
Brachiaria humidicola	0,2	X		
Aristida meridionalis	0,2	X		
Sporobolus ioclados	0,1	X		
Cyperus denudatus	0,1		X	
Phyla nodiflora	0,1			X

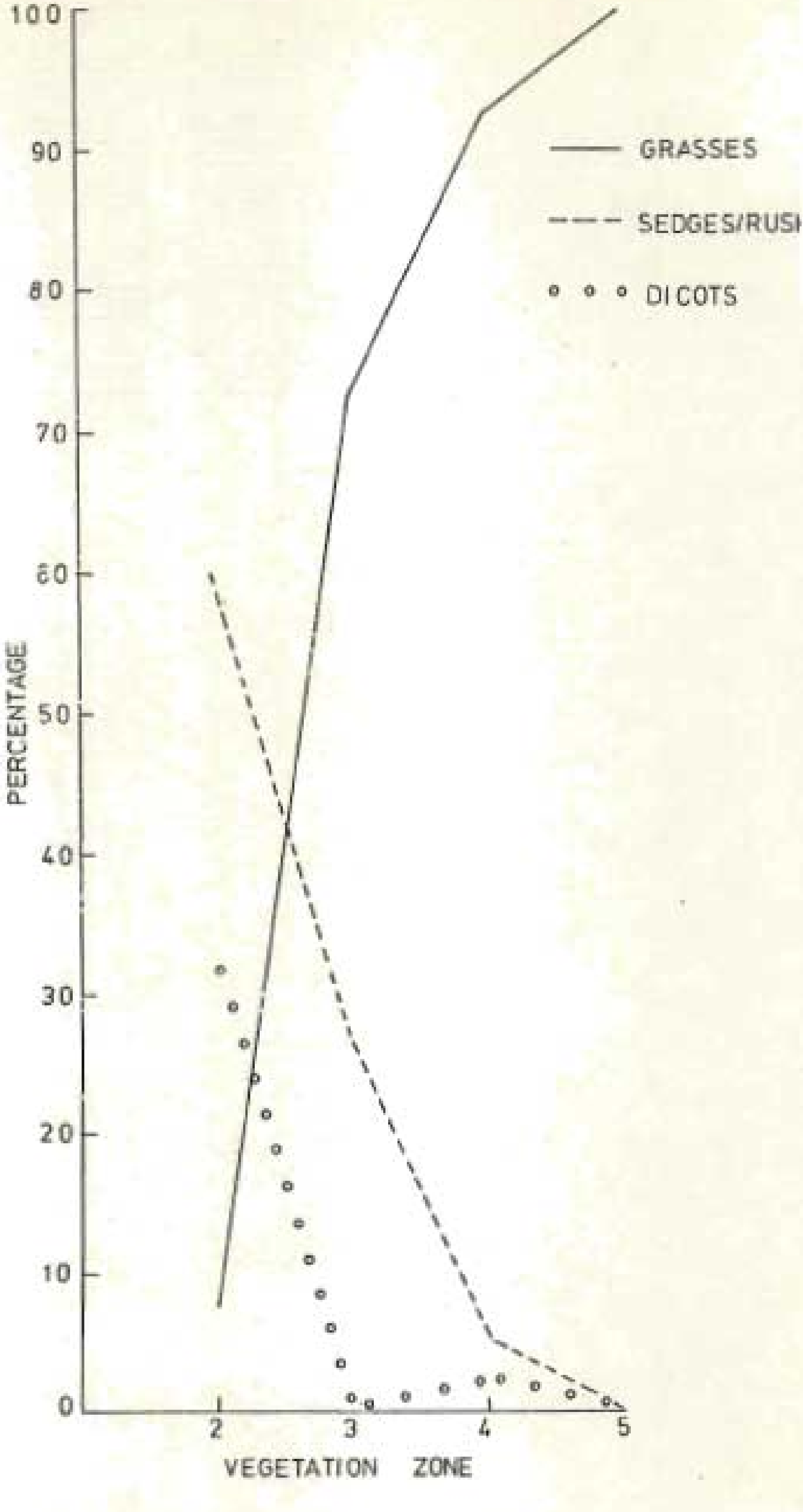

Figure 2.10: Percentage contribution to biomass of grasses, sedges/rushes and dicotyledonous plants in the vegetation zones of the intensive study area.

TABLE 2.11: SEASONAL VARIATION IN APPARENT CRUDE PROTEIN PERCENTAGE OF FLOODPLAIN GRASSES

Season	Zone	Mean % crude protein	95% C.I.	Number of replicates
Rains	3	5,2	5,0 - 5,4	31
Rains	4	4,1	3,9 - 4,3	26
Rains	5	3,3	3,2 - 3,4	25
Cool, dry	3	4,5	4,2 - 4,8	16
Cool, dry	4	3,9	3,6 - 4,2	16
Cool, dry	5	2,9	2,6 - 3,2	15
Hot, dry	3	5,2	4,9 - 5,5	12
Hot, dry	4	3,6	3,3 - 3,9	12
Hot, dry	5	3,5	3,1 - 3,9	11
Total	3	5,0	4,7 - 5,3	59
Total	4	3,9	3,6 - 4,2	54
Total	5	3,2	3,1 - 3,4	51

Longer term vegetation changes, in terms of floristics and physiognomy, may be inferred from the long term flood cycles which are clear from aerial photographs, satellite images and such field signs as the presence of termitaria in areas that are now flooded.

During high flood cycles transitional types will evolve towards aquatic communities. This trend was clearly observed during the present study. Areas that were bare ground in January 1975 were flooded during March 1975 - and by March 1979 had evolved from open water to dense stands of *Cyperus articulatus* with patches of *Typha* sp. beginning to appear.

During low flood cycles transitional types will evolve towards terrestrial as opposed to flood plain communities. Neither extreme favours lechwe and it seems likely that these changes influence the population ecology of lechwe on the Kwando by altering the amount of favourable habitat that is available to them.

2.8

LARGE MAMMAL STATUS

The fauna of the study area is varied and prolific. Over 50 mammal species were encountered. Elephant (*Loxodonta africana*), black rhino (*Diceros bicornis*), hippo, zebra (*Equus burchelli*) and 17 bovid species, ranging from gemsbok (*Oryx gazella*) to sitatunga, contribute the bulk of the biomass. No data on the status or trend of populations are available. The Order Carnivora is represented by lion (*Panthera leo*), leopard (*Panthera pardus*), cheetah (*Acinonyx jubatus*), spotted hyena (*Crocuta crocuta*), wilddog (*Lycaon pictus*), blackbacked jackal (*Canis mesomelas*), side-striped jackal (*Canis adustus*) and numerous smaller predators.

2.9

LAND USE HISTORY

P.A.Smith (pers. comm.*) reports that until the 1930's the west bank of of the Kwando was inhabited by Bushmen and Bayei people. During the late 1930's these people were apparently moved into the Eastern Caprivi because of the prevalence of sleeping sickness. The area has since been uninhabited and few obvious signs of habitation remain.

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The area is at present used only for safari hunting. This activity has little influence on animal numbers but it does affect behaviour. Animals are noticeably more wary of vehicles and people than they are in protected areas. The widespread burning that is practised by hunters to improve visibility and movement through the bush probably affects the vegetation, but this is difficult to assess in the absence of base line data.

CHAPTER 3

AGE DETERMINATION

3.1

INTRODUCTION

3.1.1

Review of Importance and Methodology of Age Determination

Age determination is a sine qua non for studying the population ecology of large mammals. Because an insight into the population ecology of a species is essential for its conservation and management, the importance of a methodology of age determination is manifest. This importance is reflected in the copious literature on the subject, but, unfortunately, it is still true to say that "no wholly reliable method for African mammals has yet been demonstrated " (Spinage, 1973).

The broad subject of age determination has been reviewed by Morris (1972) and Spinage (1973). There would seem to be no purpose in embarking on a detailed repetition of these reviews. In order to provide a background for the section below on the selection of methods, the relevant available techniques and their merits and demerits will be outlined. The outline follows Morris' review and is preceded by a few general introductory remarks.

Two aspects of relevance to all methods of age determination are the desirability of having access to known-age material and the problem of individual variability. Known-age material is essential for calibration, no matter what technique is used. Individual variability introduces an inevitable and, in wild populations, usually measurable margin of error.

Morris (1972) divides the available techniques into two broad categories: methods of determining relative age and methods of determining absolute age. The former is a comparative process, the age of one animal being assessed in relation to the state of development of another. Where age needs to be determined in terms of years and months, it can be assessed only by comparing one specimen with another of known age or relating some kind of measurement to a growth curve or regression line previously prepared from known-age material. Individual variability may seriously impair the reliability of these comparisons, particularly with older animals. Methods of determining absolute age allow the age of an animal to be expressed in precise units of time, usually years with larger animals. These methods are based mostly on the counting of incremental lines, in teeth or bones, which reflect changes in the rates of physiological processes.

(a) Methods of Determining Relative Age

(i) Age determination based on increase in size

Body mass: mass is quickly and easily determined except with very large animals. But the value of the method is limited because of the overlapping between age classes once the asymptotic mass is reached and because factors other than age have a marked influence on mass.

Linear dimensions: linear measurements are easily made but they are variable in accuracy because of the extensibility of muscles and soft parts. Further, as with mass, once asymptotic dimensions are reached, overlapping between age classes occurs.

Dry weights of eye lenses: dry weights of lenses have been successfully used to determine the ages of medium-sized animals, for example rabbits. With larger animals it has been found that there is considerable overlapping between adult age classes (Child et al., 1965; Rautenbach, 1971; Smuts, 1974; Howells & Hanks, 1975).

(ii) Age determination based on structural degradation

Tooth wear: tooth wear has been widely used as a means of age determination, but it has been shown to be subject to large margins of error (e.g.Szabik, 1973). The rate of tooth wear is affected by diet and the hardness of the teeth, leading to individual and regional differences in the rate of wear. Subjective estimates of wear may produce highly variable results (Keiss, 1969). Several workers have used measurements on teeth to quantify and render more objective age determination from tooth wear (e.g.Spinage, 1972; Grimsdell, 1973; Hall-Martin, 1976). Hall-Martin (op. cit.) used linear regression and correlation analysis to demonstrate a highly significant correlation between lingual crown height and the number of cementum lines and occlusal width and the number of cementum lines.

(iii) Age determination based on growth changes

Tooth succession: the sequence of loss and replacement of deciduous teeth offers a quick and simple method of age determination up to the stage at which full permanent dentition has erupted. Problems of individual variability have been mentioned by a number of workers, for example Steenkamp (1975) and Caughley (1977). Steenkamp asserts that "in critical studies on age determination, tooth eruption alone cannot be regarded as a reliable measure of age ". He does accept that "the chronology of tooth eruption is acceptable as a crude measure of age".

Other changes in teeth: after eruption changes continue to occur in the tooth. For example, the pulp cavity is gradually occluded by the growth of secondary dentine. Changes of this nature perhaps offer potential methods of age determination but they have been little tried. Where they have been tried, they have been found to be very crude indices of age (Hall-Martin, 1976).

Changes in bone marrow: the stages by which haemopoietic tissue in young animals is replaced by fat with increasing age allow approximate age distinctions to be made between subadult and adult animals. The utility of the method is limited because adult age classes are indistinguishable and because it may be invalidated by the effects of nutritional status.

Fusion of epiphyses: the presence of unfused epiphyses allows a distinction to be made between adults and younger animals in which growth is occurring. Again, adult age classes are indistinguishable.

Accumulation of insoluble lens proteins: biochemical methods of estimating age, based on the accumulation of insoluble lens proteins, have been used to determine age accurately in small animals (Otero & Dapson, 1972; Dapson & Irland, 1972; Birney *et al*, 1975). At present these techniques do not seem to be practical for large mammals because of the need to process the specimens while they are fresh (Ludwig & Dapson, 1977).

External features: external signs of aging, for example changes in pelage colour and horn size and shape, may be used as indicators of age. Age classes based on these features may be useful in the field classification of wild populations.

(b) Methods of Determining Absolute Age

(i) Incremental lines in dentine and cementum

These lines may be studied in either facial sections of bisected teeth (e.g.Mitchell, 1967), in undecalcified sections (e.g.Smuts, 1974) or in stained, decalcified sections (e.g.Hall-Martin, 1976). The use of stained, decalcified sections is often regarded as the most accurate available method of age determination, but the method is laborious, expensive and often involves an unavoidable element of subjective interpretation (e.g.Hall-Martin, *op. cit.*).

(ii) Incremental lines in bone

Incremental lines are found in bone and these have been used to determine age in mammals (Klevezal & Kleinenburg, 1967). There may be advantages in using bone as opposed to teeth, particularly in the greater thickness of appositional bone and the consequent clearer separation of annual lines (Morris, 1972). The use of this technique in Africa has not been reported.

3.1.2

Previous Work on Age Determination in Lechwe

Three previous studies on lechwe, all in Zambia, have directed attention to the subject of age determination.

Robinette & Child (1964) drew up a rough schedule of tooth eruption and of horn length related to age. The data on horn length and age are of limited relevance to studying lechwe in Botswana as the subspecies occurring there has strikingly shorter horns.

Sayer & Van Lavieren (1975) established nine age classes on the basis of tooth eruption and wear. They report having obtained their criteria for age determination from personal communication with Grimsdell.

Grimsdell & Bell (1975) used three methods to assign absolute ages to tooth eruption and wear classes. Firstly, they used data from 62 known-age animals in a captive herd at Chilanga to establish tooth eruption and wear classes. In doing so they assumed that age criteria for Kafue and black lechwe were similar.

Secondly, because black lechwe are seasonal breeders, discrete age groups can be identified in the field up to at least three years of age. Hence, it was possible to correlate tooth wear and eruption with age in samples of young lechwe caught in the field.

Thirdly, incremental layers in the cementum of first molars were investigated both in stained decalcified sections and in facial sections of bisected teeth. Ultimately stained, decalcified sections were abandoned in favour of facial sections of bisected teeth because interpretation of the former was difficult while preparation of the latter was far less time-consuming, although the technique often (55% of teeth examined) gave inconclusive results.

On the basis of these methods, Grimsdell and Bell produced a tooth eruption schedule (reproduced as Table 3.1) and four photographic plates illustrating 13 classes of maxillary and mandibular tooth eruption and wear.

Grimsdell and Bell also produced field age determination criteria for males and females. They used horn length and the number of horn ridges to distinguish between at least three male age classes (calves, yearlings, 2-3 year olds) and they used shoulder height and body length to distinguish between female calves, yearlings and animals over two years old.

3.1.3

Factors Influencing Choice of Methods

The choice of methods was influenced by two factors peculiar to this study. These were, firstly, the type of material that was available and, secondly, the objectives which were formulated in view of the nature of this material.

The most important consideration relating to the available material was that it proved to be impossible to gain access to known-age material. This precluded conclusive calibration and age determination, thus rendering pointless any attempt to contribute to the development of methods of age determination. Accordingly the objectives adopted were:

(a) determining as accurately and efficiently as possible the age of each animal in my shot sample;

(b) assessing the reliability of the techniques used by testing the level of agreement between the various methods.

TABLE 3.1: TOOTH ERUPTION STAGES FOR THE MANDIBLE

(after Grimsdell & Bell, 1975)

Group	Age	I_1	I_2	I_3	C	Pm_2	Pm_3	Pm_4	M_1	M_2	M_3
Group 0 (0 - 1 year)	birth	D	(D)	(D)	(D)	(D)	(D)	(D)			
	1 week	D	D	D	D	D	D	D			
	3-4 months	D	D	D	D	D	D	D	(P)		
	6 months	D	D	D	D	D	D	D	P		
	9 months	D	D	D	D	D	D	D	P	(P)	
	1 year	D	D	D	D	D	D	D	P	(P)	
Group 1 (1 - 2 years)	14 months	D	D	D	D	D	D	D	P	P	
	18 months	D	D	D	D	D	D	D	P	P	(P)
	2 years	D	D	D	D	D	D	D	P	P	P
Group 2 (2 - 3 years)	2,5 years	D/(P)	D	D	D	(P)	(P)	D	P	P	P
	2,75 years	P	P	P	P	P	P	(P)	P	P	P
Group 3 (2 - 3 years)	3 years	P*	P*	P*	P*	P	P	P	P	P	P

D = Deciduous tooth

P = Permanent tooth

( ) = Tooth still in process of eruption

( ) = Tooth only just visible above bone or gum

* = Incisors showing very little wear

Other factors which influenced the choice of methods were the results of previous work on age determination in lechwe and results generally obtained by other methods, as reported in the literature.

The lack of known-age material and the fact that Grimsdell and Bell (1975) had established a schedule of tooth eruption and wear made it obligatory to use these methods. The results of their investigation of cementum lines made me decide to count annuli on facial sections of bisected teeth, but to check these results against a representative sample of stained, decalcified sections.

The methods chosen in the light of previous work on age determination in in lechwe were thus:

(a) tooth eruption and wear;

(b) counting annuli on facial sections of bisected teeth;

(c) checking the results of (b) by counting annuli on a representative sample of stained, decalcified sections.

The choice of (a) was obligatory and the other two methods were probably the most rigorous available under the circumstances. In view of the stated objectives of age determination, it seemed unnecessary to go beyond these methods and they were duly adopted as the basis of age determination in this study.

3.2

MATERIALS AND METHODS

3.2.1

Source of Material

The material for this study was obtained from a shot sample of 231 animals of both sexes and all age classes. These animals were all collected in the Linyanti Swamp, within a radius of 30 kilometres of the centre of the general study area.

3.2.2

Field Examination of Material

Immediately after collection, skulls were cleaned as thoroughly as possible and the following procedures carried out:

(a) horns of males were measured for

- (i) length along the front curve,

(ii) basal circumference;

(iii) distance between horn tips;

(b) maxillary and mandibular teeth were carefully examined and the stage of tooth eruption or wear determined by reference to the schedule and photographs of tooth eruption and wear prepared by Grimsdell & Bell (1975);

(c) Vernier calipers (accurate to 0,05 millimetre) were used to make two sets of measurements:

(i) heights of left and right first incisors from the tip of the tooth to the gum line;

(ii) length of tooth row from the anterior edge of PM_2 to the posterior edge of M_3:

in both cases the mean of the two values was used;

(d) the mandible length was measured with a steel tape (to 1,0 millimetre) from the tip of the mandibular symphysis to the posterior edge of the angle, on the buccal side only;

(e) each mandible was photographed from a vertical position for record purposes;

(f) M_1 and M_3 were extracted from the mandible for further study.

3.2.3

Additional Measurements and Cementum Line Counts

Because it was the first permanent tooth to erupt, M_1 was selected for study.

Before sectioning two measurements were made with Vernier calipers (accurate to 0,05 millimetre).

(i) The shortest length between buccal cusps and the root "saddle" (Spinage, 1972). I will hereafter refer to this measurement as "buccal height".

(ii) The maximum lingual crown height measured from the level of the root saddle to the highest point on the lingual crown. I will hereafter refer to this measurement as "lingual height".

After these measurements had been made the teeth were sectioned longitudinally along the antero-posterior axis using a lapidary saw with a 0,5 millimetre blade. After sectioning, the maximum infundibular depth was measured with calipers and the sections were polished on a fine electric grindstone. The cementum was then examined with a binocular dissecting microscope (12,5 - 25x) under reflected light.

I counted the darker, narrow bands in the cementum and ignored the bands at the dentino-cemental interface. In adopting the latter practice I followed Grimsdell (1973) and adopted the logic of Attwell (1977) who argues that such lines reflect physiological processes related to eruption and bear no relation to season.

The literature reveals some confusion about the number of dark lines laid down per year. Spinage (1976) asserts that in areas of bimodal rainfall, two dark bands per year will be laid down and that in areas of unimodal rainfall, one dark line per year will be laid down. Hall-Martin (1976) concurred with the latter assertion, but Simpson & Elder (1969), Simpson (1973) and Grimsdell (1973) all found two dark lines per year in areas of unimodal rainfall. This confusion made it necessary to attempt to determine how many lines were laid down per year in the population under consideration.

To determine the number of dark lines laid down per year, the correctness of Grimsdell and Bell's tooth eruption schedule was assumed and animals whose ages were determined by tooth eruption were regarded as known-age animals. The number of dark lines found in this known-age sample was used to determine the number of lines laid down annually.

In order to check the estimate of the number of dark lines laid down annually, after sectioning and polishing, the cementum of a small sample of third mandibular molars was examined. It was assumed that as M_3 erupted at a different time to M_1 there would be a consistent difference in the number of dark lines counted in the cementum of M_1 and M_3. Because the difference in eruption times was known, the expected difference in the number of cementum lines could be calculated. It was assumed that if the actual difference was the same as or close to the expected difference, this would tend to confirm the estimate of the number of dark lines laid down annually.

Linear regression and correlation analyses were used to investigate the relationship between the number of dark lines in the cementum of M_1 (determined from facial sections of bisected teeth) and the following variables:

(i) the number of dark lines in the cementum of M_1 as determined from stained, decalcified sections;

(ii) the number of dark lines counted in the cementum of M_3;

(iii) age estimated on the basis of tooth eruption and wear;

(iv) buccal height;

(v) lingual height.

3.2.4

Counting Cementum Lines on Stained, Decalcified Sections

After the number of cementum lines had been determined from facial sections of bisected teeth, a representative sample from all age classes was selected. These bisected teeth were further divided so that the face to be sectioned included at least half of the cementum pad and the cementum of the root. These specimens were fixed in 10% formalin for approximately seven days. Thereafter they were decalcified in a 5% solution of nitric acid for four to seven days. The process of decalcificatio was deemed to be complete when the tissue had acquired a rubbery consistency as determined by palpation. After washing, the specimens were dehydrated, cleared and routinely embedded in paraffin wax. Sections, 5-10 μm thick, were cut on a rotary microtome with a high angle blade tilt. It was found that cooling the face of the block with ice facilitated the sectioning process. Sections were attached to marked slides and routinely stained with Erlich's Haemotoxilin. After staining, sections were mounted in Canada Balsam and allowed to dry.

Counting was performed by projecting an enlarged image of the slide onto a piece of white paper with a standard 35 millimetre slide projector. A clear image is readily obtainable and the lines can be traced on the paper to investigate their continuity.

Linear regression and correlation analyses were used to investigate the relationship between the number of dark staining lines seen in stained, decalcified sections and:
(i) age determined by tooth eruption and wear;
(ii) lingual height;
(iii) buccal height.

3.2.5

Estimation of Ages in the Shot Sample

The age of all animals in the shot sample was determined by either tooth eruption or wear (16,8% by eruption, 83,2% by wear). The ages of 80,2% of the specimens were also determined by cementum line counts from facial sections of bisected teeth. A further age determination was done on 22,1% of the sample by cementum line counts from stained, decalcified sections. This means that two different methods were used to determine the ages of many animals and that the ages of a substantial sample were determined by three different methods. The determinations by each different method were done on separate occasions and in a random order so that the results from one method would not prejudice those from another.

Inevitably there were cases where two methods gave different results. There were even cases where three different results were reached. It was felt that it would be undesirable to resolve these conflicts by subjective judgements and a hierarchy of 'reliability' was therefore adopted, which was derived essentially from the weight of opinion in the literature.

Because it was used to calibrate the cementum line counts, it was a logical necessity to rank the tooth eruption sequence as the most reliable method.

Several workers, for example Robinette et al.,(1957); Keiss (1969); Kerwin & Mitchell (1971), have demonstrated substantial inaccuracies in the use of tooth wear as a means of age determination. On the other hand, a number of workers, for example Miller (1974), Hall-Martin (1976), Turner (1977), have shown that counting cementum annuli from stained, decalcified sections is an accurate method of age determination. Several workers have successfully used cementum line counts from facial sections of bisected teeth to determine age (Mitchell, 1967; White, 1974; Aitken, 1975; Grimsdell & Bell, 1975; Attwell, 1977; Anderson, 1978). Grimsdell & Bell (1975) in fact preferred this method for practical reasons, but in my opinion, its validity has not been as widely demonstrated as that of the use of stained, decalcified sections and I therefore ranked its reliability below that of the use of decalcified sections. The hierarchy of reliability that was established on the basis of the literature was thus: tooth eruption, stained, decalcified sections, facial sections of bisected teeth, tooth wear.

There were occasions when the cementum line counts gave obviously anomalous results. For example, there were a few cases where males that were somatically mature by criteria derived from more reliably aged animals showed only one or two annuli under reflected light. In these cases it was necessary to accept the estimate of age based on tooth wear.

3.3

RESULTS AND DISCUSSION

The results of age determination by the different methods used are presented and discussed in the order that seems logical.

3.3.1

Tooth Eruption

The ages of all animals that did not have fully erupted permanent dentition were determined by the reference to the eruption schedule prepared by Grimsdell & Bell (1975). The lack of known-age material and the fact that births in the Kwando population, although peaking seasonally, occur throughout the year, made it impossible either to detect differences in the eruption calender of the Zambian or Kwando populations or to measure the variation in age at each stage of eruption.

It was inferred that there was variation in age at eruption because a number of workers have shown that such variation does occur. For instance, Roettcher & Hoffman (1970), with impala, and Attwell (1977), with wildebeest, both reported differences in the eruption calender of discrete populations of the same species. Caughley (1965) and Steenkamp (1969) both found that the age at which a tooth erupted was dependent on the age at eruption of the preceding one, and that variability in eruption increased the later the tooth emerged. Steenkamp (1970, 1975), with cattle, has shown further that the timing of eruption is also influenced by the crowding of teeth and the plane of nutrition. He maintains that "tremendous variation occurs between individuals of similar age, sex and breed".

Clearly, age determination by tooth eruption is subject to a margin of error. It was not possible to make an objective estimate of the magnitude of this margin of error but the work of Sowls & Phelps (1968) gives an indication of the degree of variability that can occur. In bushpig (Potamochoerus porcus Linn.) they found that differences in the eruption times of individual temporary teeth varied from two to six weeks, while the differences in the eruption times of individual permanent teeth varied from three to 12 weeks.

3.3.2

The Relationship between Age and the Number of Cementum Layers

The number of dark lines laid down annually in the cementum was established by examining subadult teeth whose age had been determined by reference to the tooth eruption schedule. Teeth damaged during extraction were not included in this sample, which meant that not all subadult teeth were examined for this purpose. The results of this examination are presented in Table 3.2.

My interpretation of these results is that one dark line is usually laid down annually and that the first line is present by the end of the first year of life. Thus, if, for example, a tooth had three dark lines in the cementum, I would estimate the animal's age as being between three and four years old.

Table 3.2 indicates that this is not always the case; some animals had either one less or one more line than indicated by my interpretation. The exceptions are possibly explained by departures from the eruption schedule.

This understanding was based on examination of the cementum of M_1. The results of checking the validity of the interpretation by counting cementum lines in M_3 are shown in Figure 3.1.

It will be seen that there is good correlation between the number of annuli found in the two teeth. There is an interval of about 18 months (Table 3.1) between the eruption of M_1 and M_3. Because M_3 erupts at the end of the second year, one would expect the difference in the number of lines in the two teeth to be variable. If M_3 erupts early it will have one less line, if it erupts late it will have two fewer lines than M_1. A difference of one or two lines was found in 13 tooth pairs (81% of the sample). The equation for the regression line was:

$$y = 0{,}87\ x - 1{,}24 \quad (r = 0{,}906;\ \ p < 0{,}001)$$

On the basis of these results it was assumed that one dark line is laid down in the cementum each year.

TABLE 3.2: THE RELATIONSHIP BETWEEN AGE ESTIMATED ON THE BASIS OF THE TOOTH ERUPTION SCHEDULE OF GRIMSDELL & BELL (1975) AND THE NUMBER OF CEMENTUM LINES IN M$_1$

Age by tooth eruption (years)	No. of lines under reflected light	No. of lines histologically
0,25 (Pm$_4$ examined	0	-
	0	-
	0	-
	0	-
0,5	0	-
	0	-
0,75	0	-
	0	-
	0	-
	1	1
1,0	1	1
	1	1
1,25	1	-
	1	-
	-	1
1,5	-	1
	2*	1
	1	-
2,0	1*	2
	-	2
2,5	1*	2
	2	-
	2	2
	2	-
	2	-
	3	-
2,75	2	2
	2	2

- : signifies that tooth not examined by this method or no clear count possibl

* : conflict between line counts

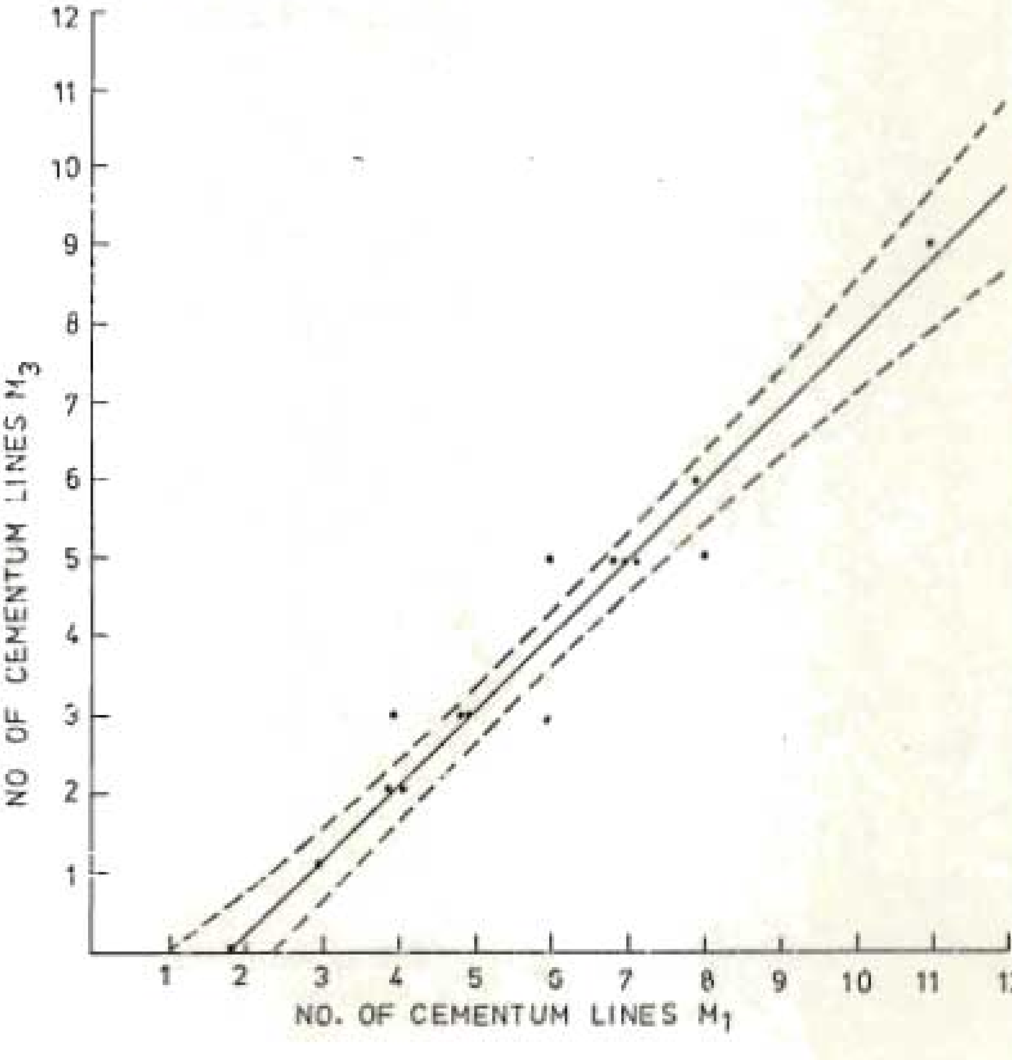

Figure 3.1: The relationship between the number of cementum lines counted in M_1 and the number of cementum lines counted in M_3. Solid line is the regression line. Dashed lines indicate 95% confidence limits.

3.3.3

Cementum Line Counts from Facial Sections of Bisected Teeth

A total of 183 first mandibular molars was sectioned for age determination purposes. It was found that it was necessary to inspect the entire length of the cementum when looking for annuli. These were found in almost all teeth, although their clarity varied substantially. On different specimens annuli were visible at various points along the entire length of the cementum but on no single specimen were they continuous or consistent.

The cementum layer for each year consisted of a broad, pale band and a narrower, darker band, the latter being used for counts in this study. The first light band was usually noticeably broader than subsequent bands and it was commonly found that with increasing age annuli became compressed. Splitting of annuli was common as was the presence of accessory lines. These two phenomena were particularly prevalent in the pad between the roots of the tooth.

The occurrence of discontinuous and split and accessory lines created considerable difficulties with the counting of bands. The causes of these phenomena are not well understood. Attwell (1977) suggests that discontinuities may reflect the fact that "accretion of cementum occurs simultaneously in different zones, but that there is a possible physiological mechanism preventing continuity between the zones". It has further been suggested (R.Jeffery, 1978) that the deposition of cementum is not even, being thickest in the pad between the roots and in the root apices, and that it does not necessarily occur consistently in the same plane. All of these factors could account for discontinuities in annuli which are viewed in a section in one plane.

If discontinuities were the only problem and if the suggested explanations are correct it would be logical to accept the highest line count in the pad or root apex as the correct one. But split and accessory lines made it impossible to do this with lechwe teeth. If the causes of split and accessory lines were known, it might be possible to make sense of them but I have not been able to find a satisfactory explanation of them in the literature. If Smuts (1974) is correct about the existence of a causal relationship between cementum annuli and nutrition, one could envisage that accessory lines might be caused by short term nutritional stresses, for example, summer droughts during which forage quality declines significantly. But this hypothesis is purely speculative and the causation of split and accessory lines remains an unsolved problem.

The relevance of discontinuities in annuli and split or accessory lines is that they introduce an inescapable element of subjectivity into the counting of cementum bands. To ameliorate this problem a consistent, if arbitrary, approach to the counting of annuli was adopted. Experience showed that the clearest and most consistent lines were found on the inside of the root in the upper section adjoining the pad between the roots. It was assumed that the maximum number of distinct annuli here was the "true" number. When lines were not visible here,I counted the maximum number visible at the point along the cementum where the lines were clearest. As far as possible split and accessory lines were disregarded, although it was not always easy to identify these as such.

Two further possible complications in counting annuli are the resorption of cementum and the exposure of the cementum pad at the occlusal surface in cases of very heavy wear.

Resorption occurs in old animals, beginning at the roots, and has been recorded in waterbuck (Spinage, 1967) and buffalo (Grimsdell, 1973). The occurrence of resorption means that the counting of cementum annuli will give only a minimum age and that the accuracy of age determination by this method will decline with increasing age (Sergeant & Pimlott, 1959; Simpson & Elder, 1969; Lockard, 1972).

The second complication did not arise in this study as none of the teeth examined showed exposure of the cementum pad at the occlusal surface.

The accuracy of cementum line counts will be discussed further at the end of the following section.

3.3.4

Cementum Line Counts from Stained, Decalcified Sections

Sections from 51 first mandibular molars were examined. All sections, except those from animals less than one year old, showed dark staining narrow lines and pale broad bands. The sections from animals less than one year old showed only broad pale bands.

The dark lines were found along the entire length of the cementum but the ease with which they could be counted and interpreted varied from place to place. All of the difficulties of interpretation listed by Hall-Martin (1976) were encountered in this study. Split and accessory lines were particularly confusing in the pad between the roots and in the root apices. The number of lines in the pad was up to three times the number in the roots and was often obviously in excess of the possible longevity of the species. In general, the upper inside part of the root adjoining the cementum pad proved to be the most satisfactory site for counting.

The difficulty of interpreting cementum lines in histological sections is exemplified by the statement of Smuts et al., (1978) that "there is little doubt that incremental cementum lines in the teeth of the African lion are more difficult to count than those of animal species from cold temperate zones in general. Had known age material not been available for the present study, interpretation of the pattern of cementum apposition could not have been achieved". Similarly, in this study, I found it impossible to interpret the lines on histological sections without first learning to do so by studying a sample of sections from animals whose age had been estimated by cementum line counts from facial sections of bisected teeth and by tooth wear. Once I had learned to interpret the lines, counting was not difficult but there must have undoubtedly been an unknown amount of error in the results.

Because it was impossible to make independent age determinations from histological sections it seemed logically necessary to reconsider the established hierarchy of reliability. As the interpretation of annuli on facial sections of bisected teeth was less problematic than interpreting histological sections, the former method was accepted as the more reliable in cases where conflicts between cementum line counts by the two methods occurred.

The lack of known-age material precluded the possibility of objectively assessing the accuracy of age determination by cementum line counts. It could be argued that calibration by means of the tooth eruption sequence is sufficient to establish the reliability of the method, but there are indications that this may not be so. Tooth eruption is complete before or at the time when animals reach somatic maturity and it is possible that events largely confined to adult life influence the rate of cementum deposition. That this possibility exists is suggested by the fact that a number of teeth from adult females showed appreciably more cementum lines, both on facial sections and histologically, than anticipated on the basis of age determined by tooth wear. Anderson (pers. comm.*) found a similar discrepancy in nyala. This may mean that additional lines are laid down at some point in the reproductive cycle. Where this discrepancy occurred the hierarchy of reliability was adhered to, despite misgivings about consequent inaccuracies, because of the valid doubts several studies have raised about age determination on the basis of tooth wear (e.g.Kerwin & Mitchell, 1971; Szabik, 1973).

An attempt was made to assess the reliability of cementum line counts by doing a linear regression and correlation analysis of the relationship between the number of lines counted by the two methods. The logic of this procedure is that if the number of lines counted is the same, this indicates that the counts are reliable. The results of this analysis are illustrated in Figure 3.2. The equation for the regression line is:

$$y = 0{,}0904x + 0{,}192 \quad (r = 0{,}923; \; p < 0{,}001)$$

It should perhaps be pointed out that the term "confidence limits" in the caption to Figure 3.2 (and in all subsequent figures showing confidence limits) is used <u>stricto sensu</u>. These confidence limits give a band within which there is a 95% probability that the mean or expected value of "y" will be found, given a particular value of "x". The calculation of these confidence limits is based on the formula:

$$SD_{yx} = s\sqrt{\frac{1}{n} + \frac{(x - \bar{x})^2}{\leq (x - \bar{x})^2}} \qquad \text{(Steele \& Torrie, 1960)}$$

(s = the residual standard deviation of the regression line)

This approach differs from that used, for example, by Hall-Martin (1976) and Attwell (1977). Those workers used what is more correctly called a prediction interval (L.P.Fatti pers. comm.**). This gives the interval within which 95% of all values of "y" corresponding to a given "x" value would be expected to fall. Calculation of these confidence limits is based on the formula:

$$SD_{yx} = s\sqrt{1 + \frac{1}{n} + \frac{(x - x)^2}{\leq (x - x)^2}} \qquad \text{(Steele \& Torrie, 1960)}$$

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** P.Fatti, Applied Maths, Wits University, Johannesburg, 2001.

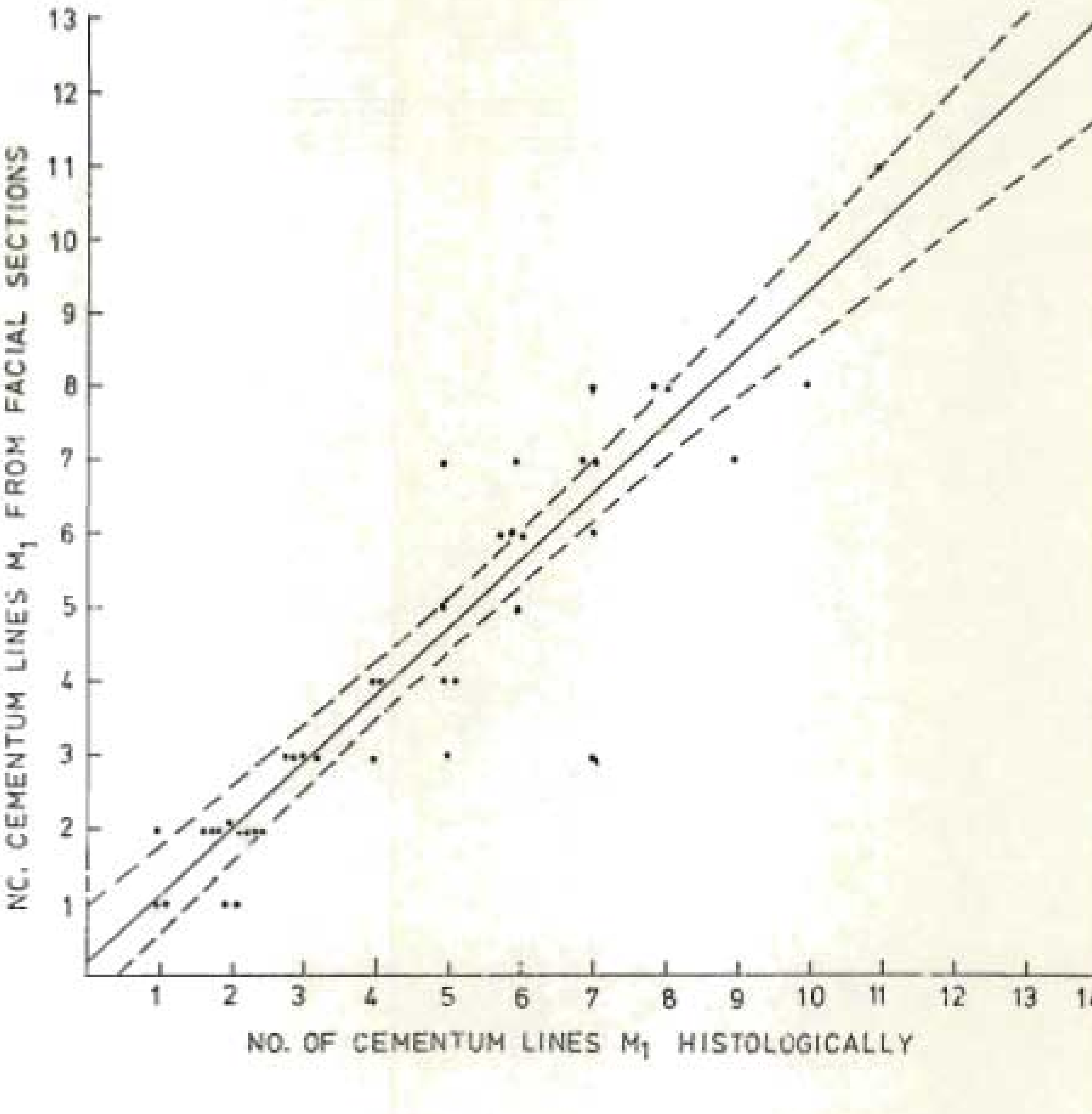


Figure 3.2: The relationship between the number of cementum lines counted on facial sections of bisected teeth and the number of cementum lines counted on histological sections. The solid line is the regression line. The dashed lines show the 95% confidence limits.

The first formula was used because, for the purposes of the comparisons being made, it was the expected values that were of particular interest.

In Figure 3.2 68% of the counts are in complete agreement and 90% are within ± one line. Thus most of the cementum line counts would give age estimates within ± one year of each other when the two different methods of counting are used.

An attempt was made to establish whether or not it is the same lines that are seen in facial sections of bisected and in histological sections. It proved impossible to resolve this question because I was never completely sure that I was looking at the same portion of the cementum on both kinds of section. It would have helped if the sections for histological processing had been photographed and marked before preparation but this idea only occurred to me after the histological work had been completed.

3.3.5

Comparison of Age Estimates by Tooth Wear and Cementum Line Counts

The ages of all animals with fully erupted permanent dentition were estimated on the basis of tooth wear. Lack of known age material again prevented accurate assessment of the reliability of the estimates. In the absence of alternative methods of assessment, the reliability of age estimates on the basis of tooth wear was investigated by comparison with age determinations on the basis of cementum line counts.

Using Grimsdell and Bell's (1975) photographs of tooth wear patterns, each animal was put into an age class, for example, 3-4 years old. For the purpose of calculating regression the upper limit of each age class was used. Thus a 3-4 year old animal would be recorded as being four years old. This had the effect that the expected number of cementum lines was one less than the tooth wear age of the animal. A 3-4 year old animal would be expected to have three cementum lines.

The results of regressions calculated for tooth wear ages and the number of cementum lines counted, are illustrated in Figures 3.3 and 3.4.

Figure 3.3 shows a significant correlation between age estimated by tooth eruption and wear and the number of cementum lines counted on facial sections of bisected teeth. The equation for the regression line was:

Figure 3.3: The relationship between age determined by tooth eruption and wear and the number of cementum lines counted in facial secti of M_1. The solid line is the regression line. The dashed lin shows the 95% confidence limits.

$y = 0{,}821x + 1{,}491 \quad (r = 0{,}787; \; p < 0{,}001)$

58% of the teeth examined contained the number of cementum lines that were anticipated in the basis of age estimated by tooth wear. There was appreciable scattering of points, particularly in the older age classes. These data indicate that, as postulated by Morris (1972) and found, for example, by Attwell (1977), the reliability of age determined by tooth wear decreases with age. The picture presented by Figure 3.3 may be exaggerated in that some of the scattering may by attributable to:

(a) the large number of age classes based on the eruption calendar for which there could not possibly be matching numbers of cementum lines;

(b) the fact that all determinations of the number of cementum lines are shown, including several that were disregarded in favour of other criteria.

Inspection of Figure 3.2 suggested that scattering was particularly bad beyond six cementum lines. An alternative regression was calculated for animals with six or fewer cementum lines. The equation for this regression was:

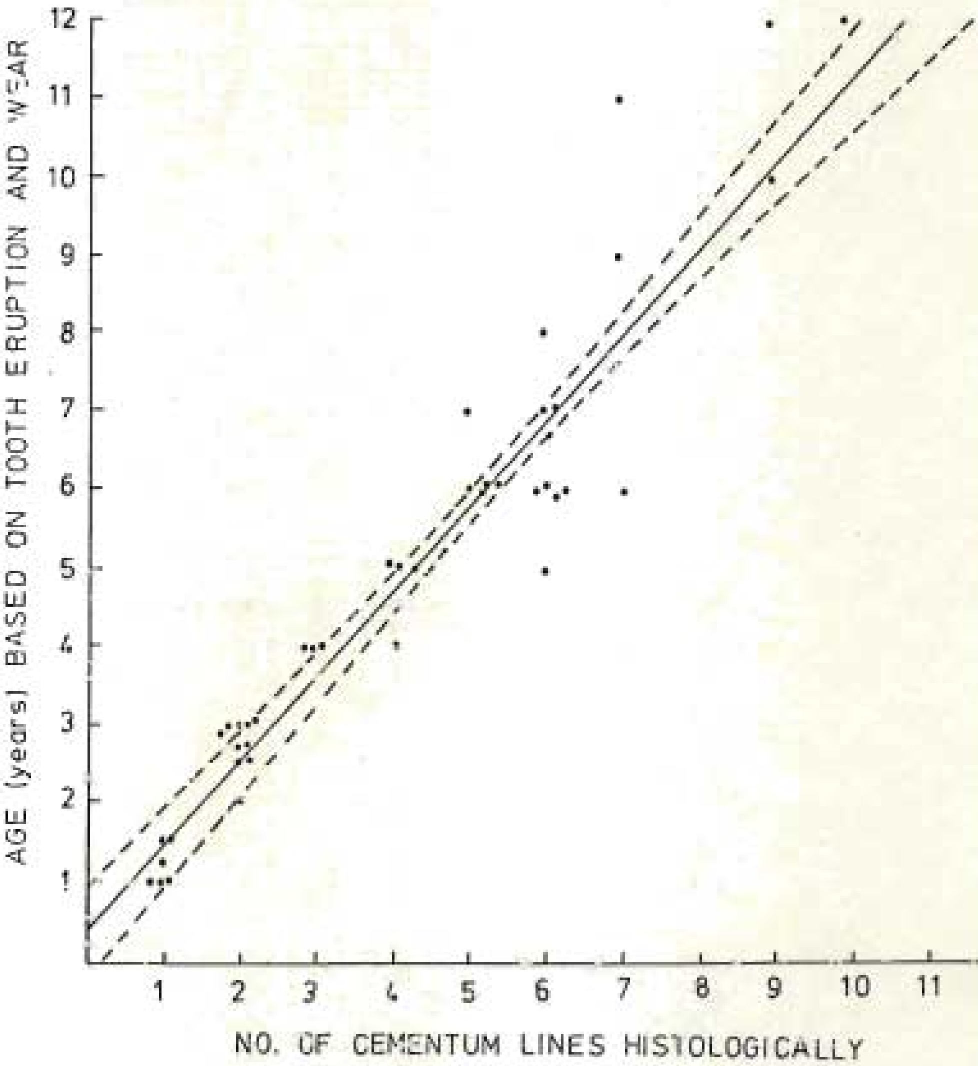
$y = 0{,}797x + 1{,}467 \quad (r = 0{,}839; \; p < 0{,}001)$

Up to the point of six cementum lines the correlation between tooth wear age and the number of cementum lines counted is thus fairly good and it is highly significant. In view of the level of agreement between the two methods of age determination it seems reasonable to conclude that, at least up to seven years of age (six cementum lines), the accuracy of age determination by these methods approximates the standard implicit in the assertion of Spinage (1973) that "for general population studies age determination to the nearest year is often sufficient".

This contention is to some extent supported by the results illustrated in Figure 3.4. There is a high degree of correlation between age determined by tooth eruption and wear and the number of cementum lines counted on stained, decalcified sections. The equation for the regression line was:

$y = 1{,}084 + 0{,}404 \quad (r = 0{,}960; \; p < 0{,}001)$

69% of the teeth examined contained the number of cementum lines that was expected on the basis of age estimated by tooth wear. These results



<u>Figure 3.4</u>: The relationship between age determined by tooth wear and eruption and the number of cementum line counted in histological sections of M_1. The soli line is the regression line. The dashed lines sh the 95% confidence limits.

are biased because teeth were selected for histological processing primarily because there was good agreement between the other methods of age determination. Thus the level of agreement shown in Figure 3.4 may well be artificially high.

For comparative purposes the results obtained by Grimsdell & Bell (1975) are reproduced. Figure 3.5 shows the theoretical relationship between age determined by tooth eruption and wear and cementum line counts. Figure 3.6 presents graphically the results of the linear regression and correlation analysis to which their data was subjected. This demonstrates that similar levels of agreement between the two methods of age determination were found in both studies.

The level of agreement that was found between age estimated by tooth eruption and wear and by cementum line counts is also within the range found in the various studies quoted by Spinage (1973). This range was from 38-88% , most workers finding levels of agreement from 50-70%. These findings tend to support Morris' (1972) contention that tooth wear on its own can allow only approximate estimates of age.

3.3.6

Measurements of Tooth Row and Mandible Length

The results of measurements of tooth row and mandible are presented in Table 3.3. There are differences with age in subadult animals, but in these classes age is more reliably determined by tooth eruption.

The relationships between the four measurements of tooth wear and estimate age are shown graphically in Figures 3.7 - 3.10.

In Figure 3.7 incisor height is plotted against estimated age. A large overlap between age classes is apparent and the pattern of wear does not conform obviously to the negative exponential curve postulated by Spinage (1973).

Two factors may have contributed to these results:

(a) errors in age determination;

(b) the fact that some measurements were made after gum shrinkage had occurred, making it difficult to locate the gum-line precisely.

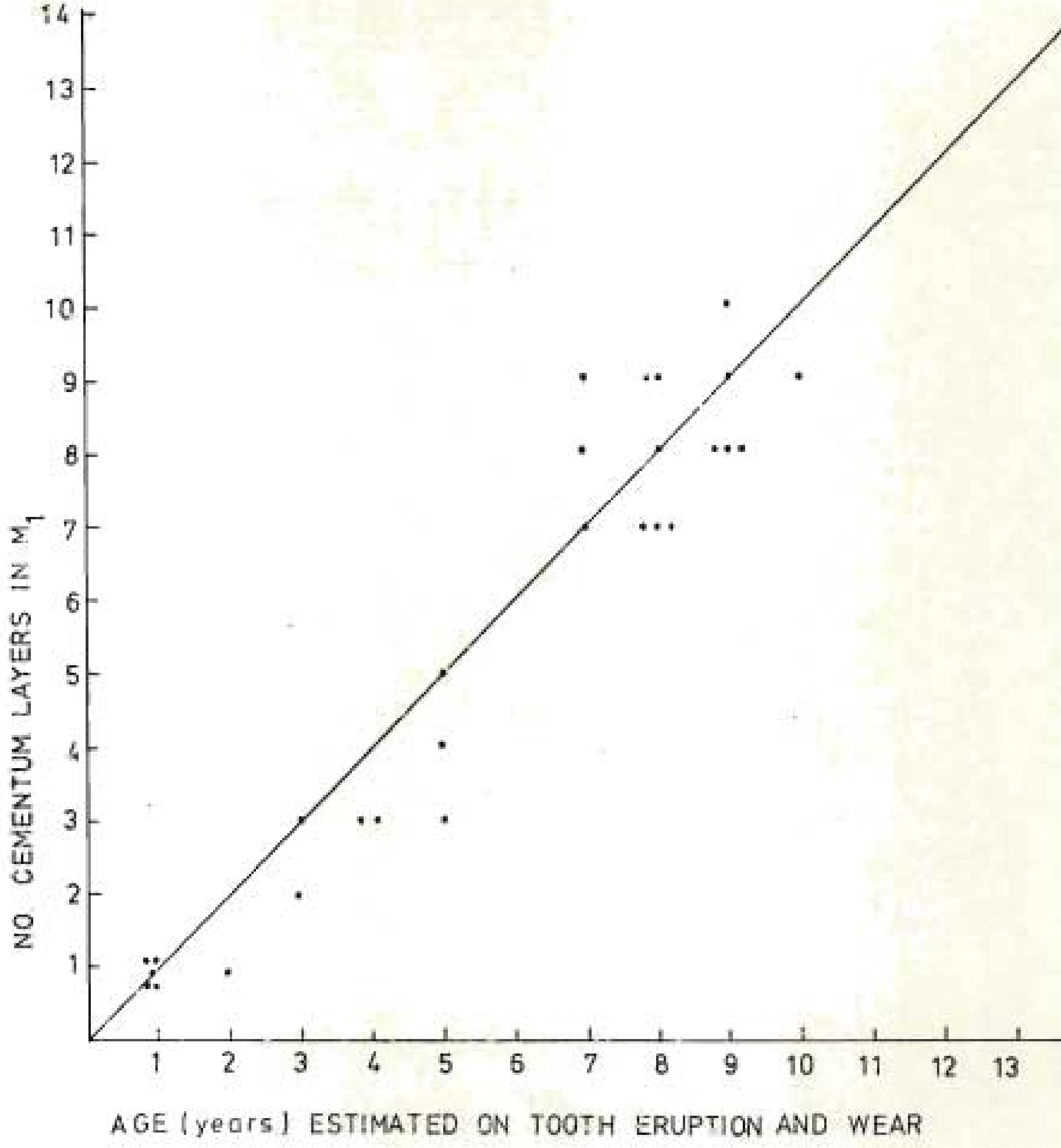


Figure 3.5: Theoretical relationship between age estimated by tooth eruption and wear and the number of cementum layers in M_1 (Grimsdell & Bell, 1975).

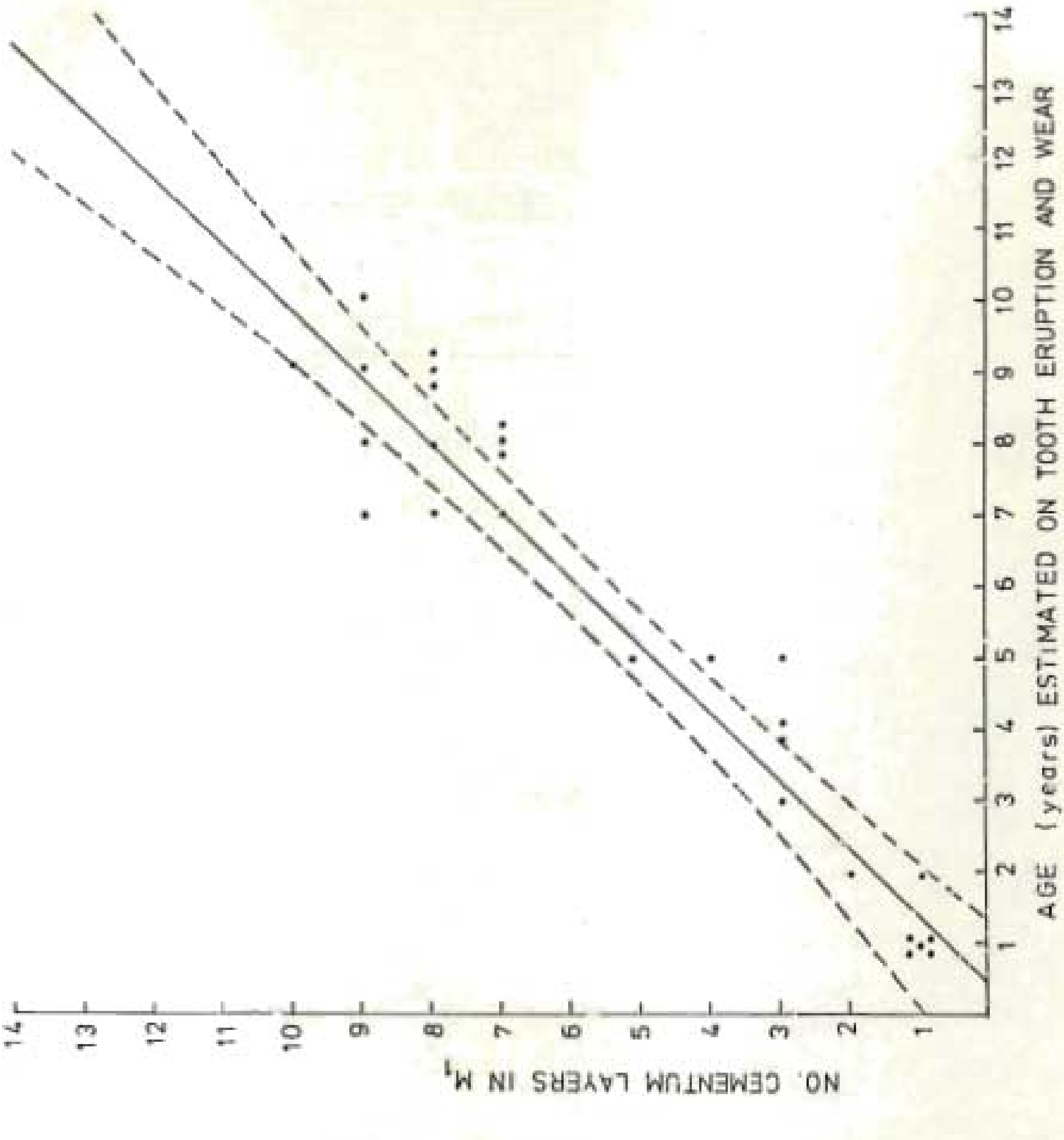


Figure 3.6: Regression calculated from Grimsdell & Bell's (1975) data on the relationship between age determined by tooth eruption and wear and the number of cementum layers in M_1. ($y=1,06x - 0,40$: $r=0,920$, $p< 0,001$). The solid line is the regression line. Dashed lines show the 95% confidence limits.

TABLE 3.3: CHANGES WITH AGE IN THE LENGTHS OF THE TOOTH ROW AND MANDIBLE (AGE ESTIMATED BY TOOTH ERUPTION AND CEMENTUM LINE COUNTS)

AGE	TOOTH ROW (cm)			MANDIBLE (cm)		
	Mean	S.E.	Range	Mean	S.E.	Range
0,25	3,7	0,1	3,3-4,1	14,1	0,1	13,8-14,3
0,5	4,7	0,1	4,5-4,8	17,2	0,1	16,8-17,5
0,75	5,3	0,1	4,9-5,8	18,3	0,2	17,9-18,9
1,0	5,6	0,2	4,2-6,3	18,4	0,3	17,7-19,3
1,25	6,1	0,1	5,9-6,4	19,1	0,1	19,0-19,3
1,5	7,0	0,2	6,2-7,4	20,1	0,6	19,3-21,7
2,0	7,1	0,2	6,6-7,4	20,0	0,1	19,9-20,0
2,5	7,8	0,1	6,9-8,2	20,7	0,2	20,1-21,6
2,75	7,8	0,1	7,4-8,3	21,2	0,4	20,6-22,4
3,0	7,6	0,5	7,3-8,1	21,1	0,3	19,7-22,0
3< 4	7,5	0,03	6,9-8,1	22,0	0,1	20,0-24,4
4< 5	7,4	0,02	6,8-7,8	22,3	0,1	20,8-24,0
5< 6	7,2	0,03	6,6-7,8	22,6	0,2	21,0-24,6
6< 7	7,3	0,1	6,4-8,0	22,6	0,2	20,9-24,0
7< 8	7,2	0,1	6,6-7,8	22,2	0,3	21,2-23,7
8< 9	5,8	0,2	6,3-7,5	22,3	0,7	21,6-22,9
9< 10	6,9	0,1	6,7-7,0	22,5	0,4	22,2-23,3
10+	7,1	0,1	6,9-7,5	22,3	0,2	22,0-22,6

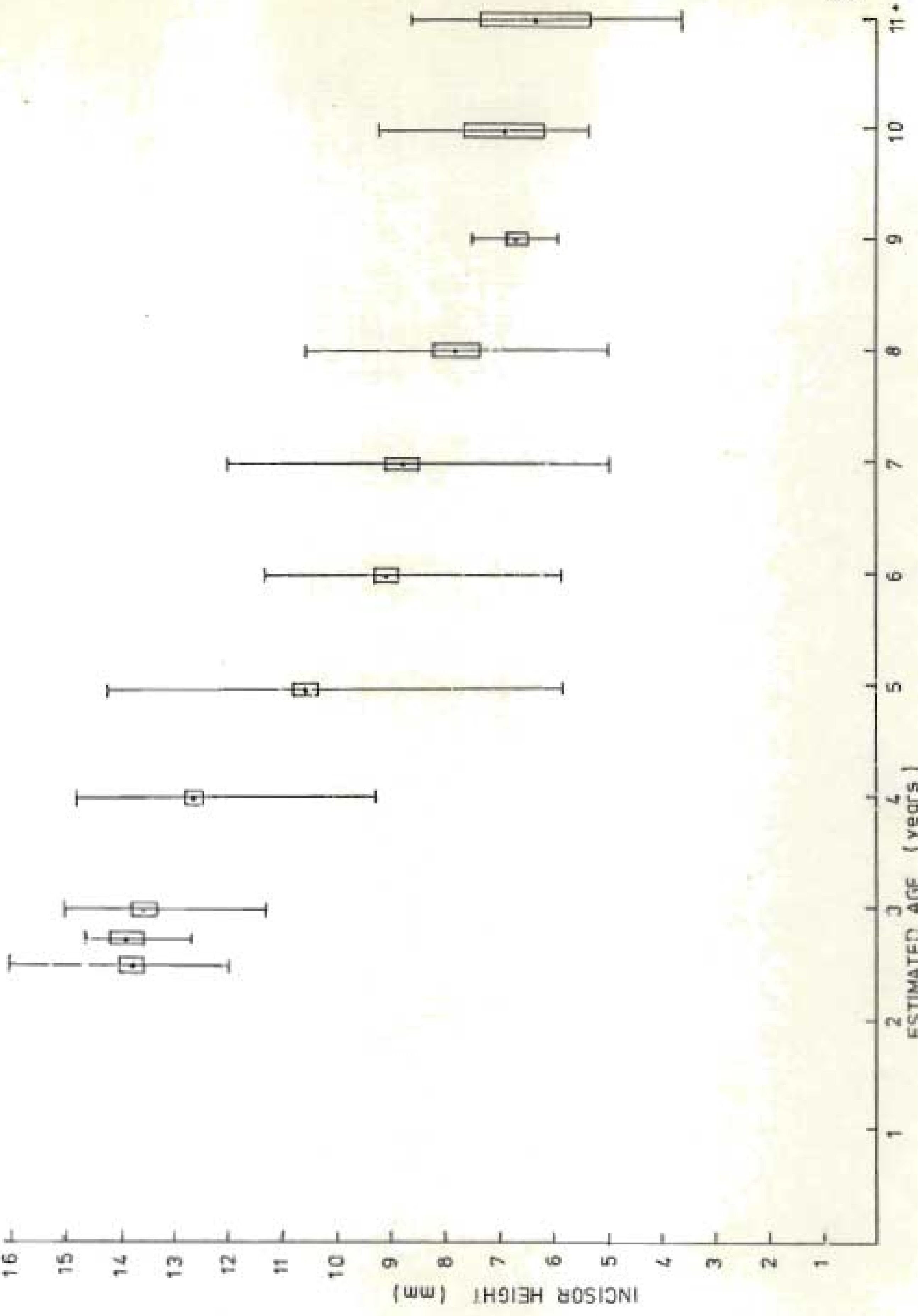


Figure 3.7: The relationship between incisor height (I_1) and estimated age. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges.

In Figures 3.8 – 3.10 a similar overlap between age classes is obvious, but here a curvilinear relationship between age and wear is more apparent. This coincides with the findings of Grimsdell (1973).

Figures 3.11 and 3.12 show graphically the results of regression and correlation analyses of the relationship between the number of cementum lines determined from stained, decalcified sections and the lingual and buccal heights of M_1. Although the correlation is good it is not as good as that found for giraffe by Hall-Martin (1976). Slightly lower correlation coefficients resulted when the same analyses were done with the number of cementum lines determined from facial sections of bisected teeth. The range of variability found here means that the predictive value of these measurements is limited. This conclusion applies generally to the measurements of tooth wear made in this study and corroborates the statement of Spinage (1973) that: "The use of measurements is pseudo-objective; it may remove the observer bias, but it cannot correct for varying rates of wear".

3.3.7

Conclusions Relating to Laboratory Age Determination

A critical aspect of age determination in this study was the use of the tooth eruption schedule of Grimsdell & Bell (1975) both for the actual age determinations and for calibrating cementum line counts. Caughley (1977) reports enormous variation in the eruption of permanent incisors, but the same need not necessarily be assumed with regard to the eruption of, for example, molars which are not preceded by deciduous teeth. Sowls & Phelps (1968) found that twelve weeks was the largest difference that occurred in the eruption times of individual molars in bushpigs.

No direct method of estimating variability in the time of eruption was available to me, but the relationship between age estimated by eruption stage and the number of cementum lines (Table 3.2) is such that it seems unlikely that the eruption calendar could be much more than 6-12 months in error. Of 28 teeth examined only 4 (14%) showed anomalous results or conflicts between the two methods of counting cementum lines. On this basis it was assumed that ages estimated by tooth eruption stage are accurate to within about six months.

For animals whose permanent dentition was fully erupted, there was fairly good agreement between ages estimated by cementum line counts and by tooth wear, at least up to about seven years of age. As suggested

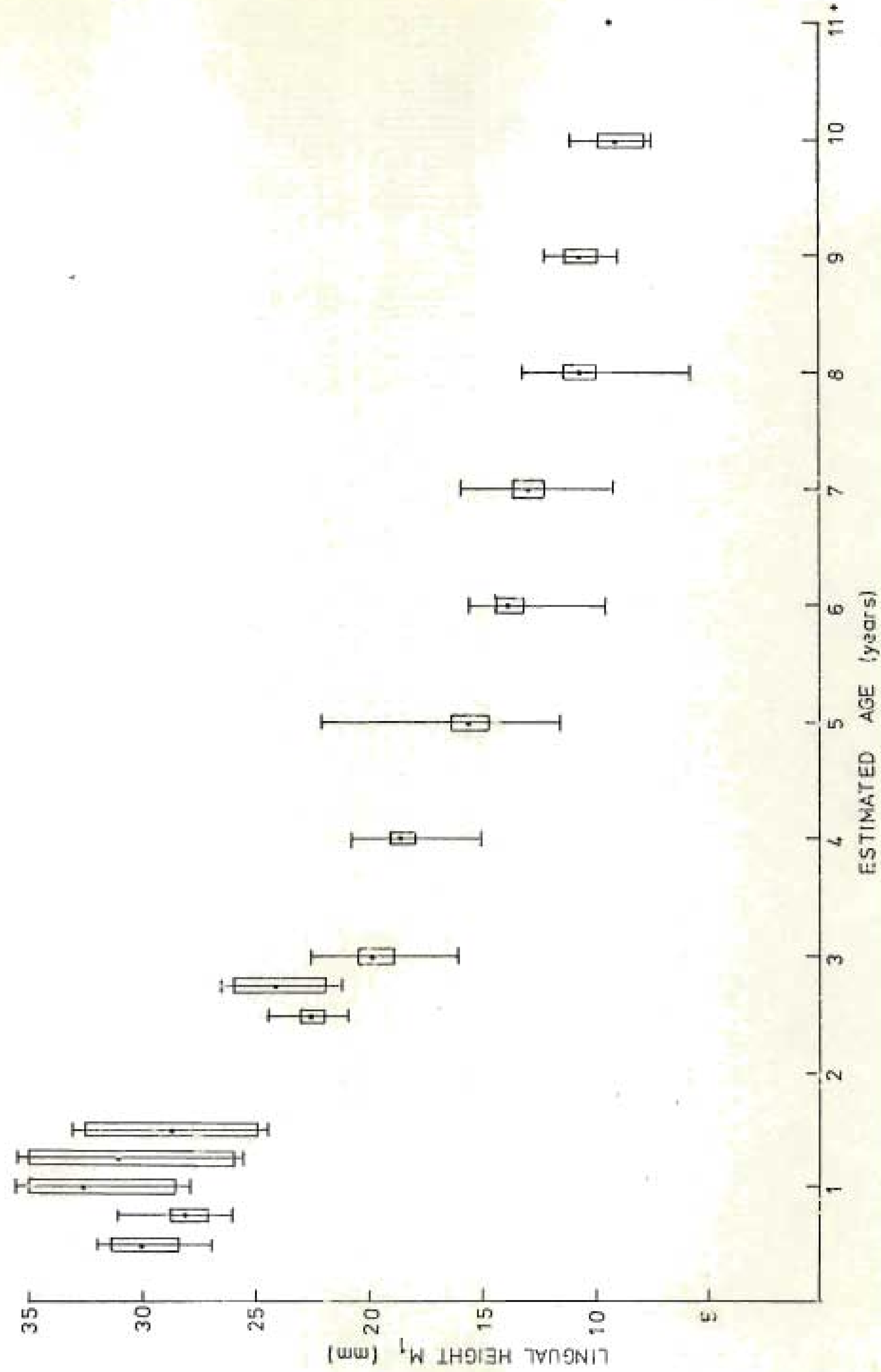


Figure 3.8: The relationship between lingual height of M_1 and estimated age. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges.

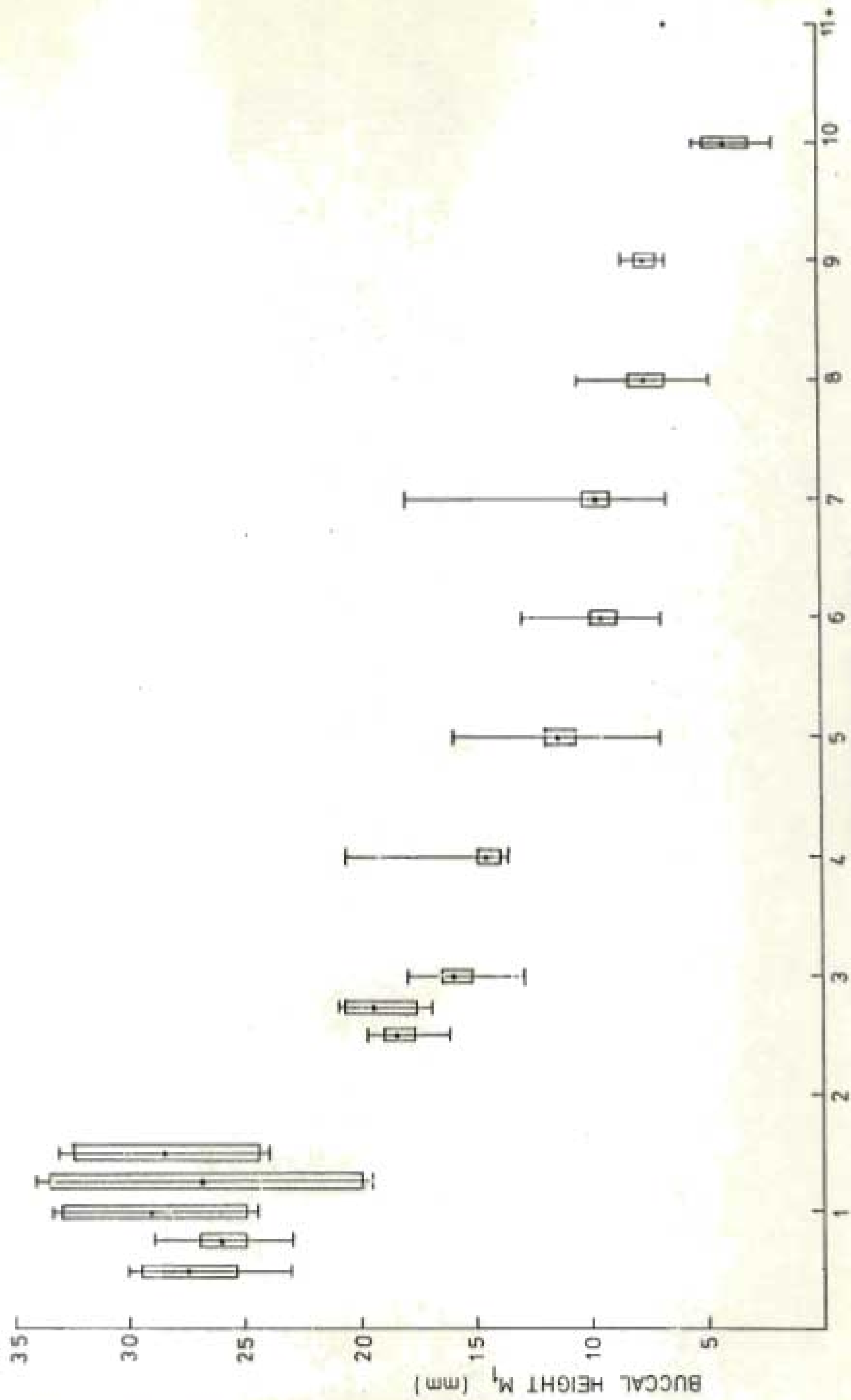
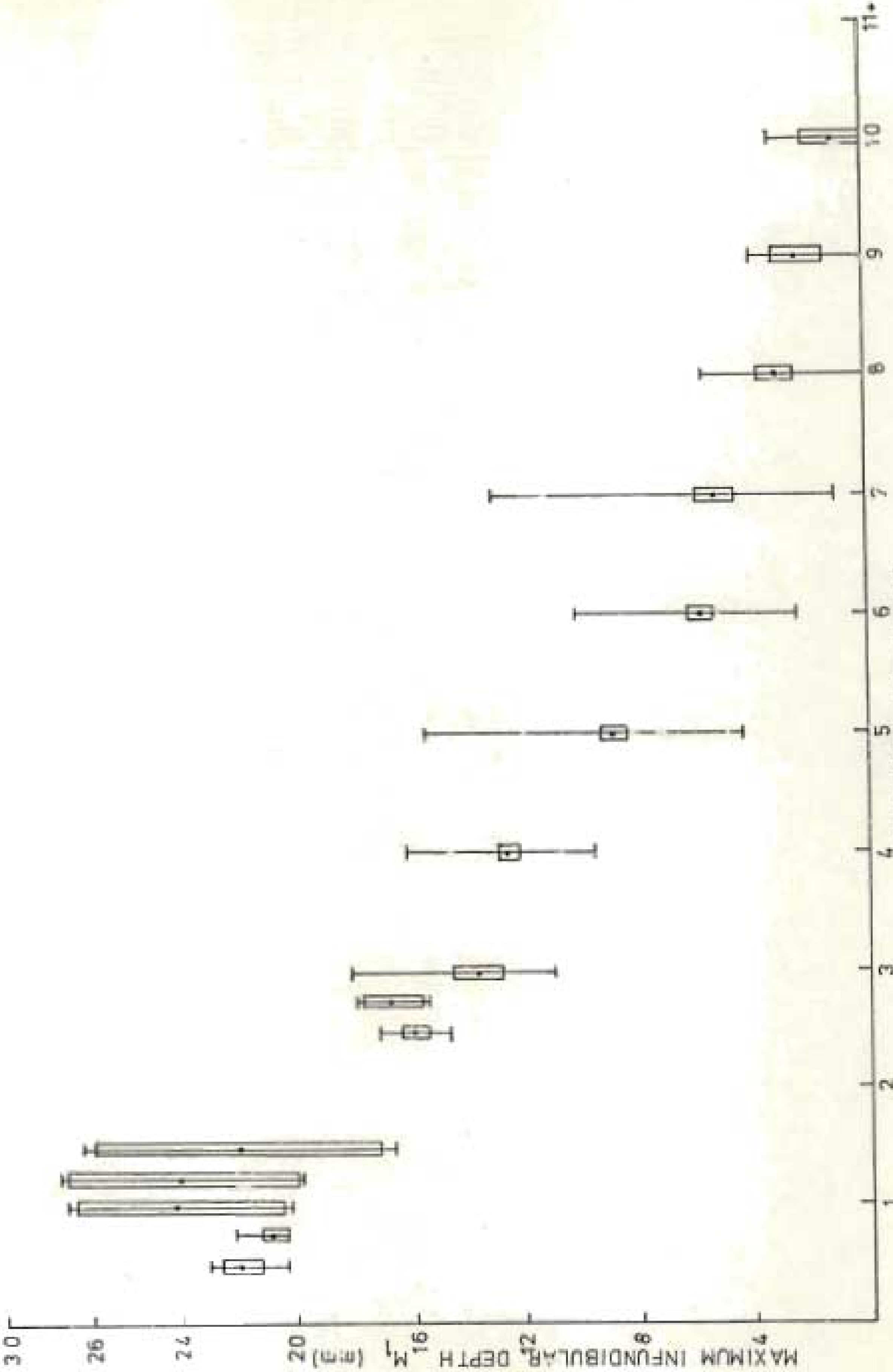


Figure 3.9: The relationship between buccal height M_1 and estimated age. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges.



<u>Figure 3.10</u>: The relationship between maximum infundibular depth M_1 and estimated age. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges.

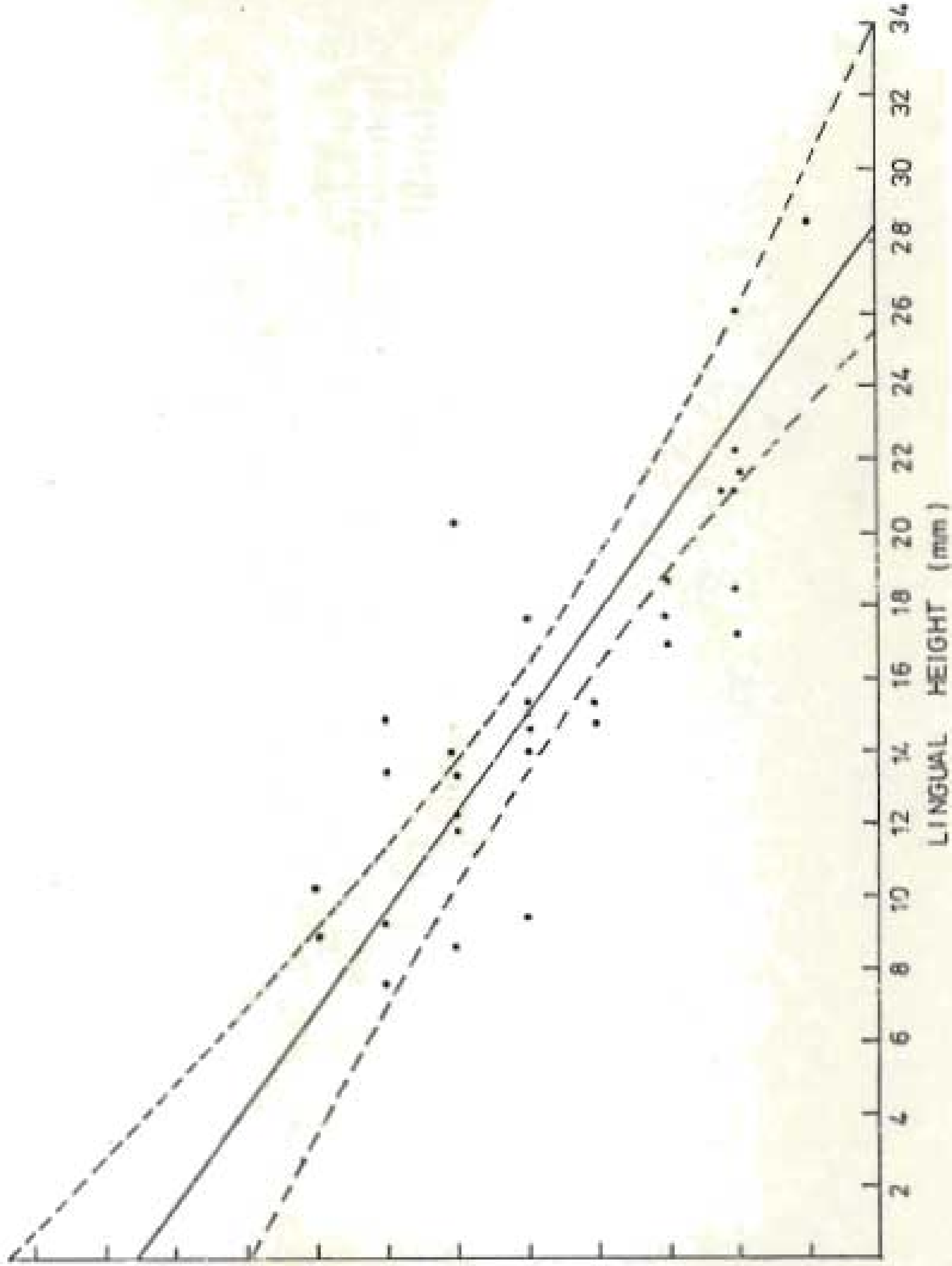


Figure 3.11: The relationship between the number of lines histologically and lingual height M_1. ($y = -0{,}37x + 10{,}63$, $r = 0{,}820$, $p < 0{,}001$) The solid line is the regression line. Dashed lines show the 95% confidence limits.

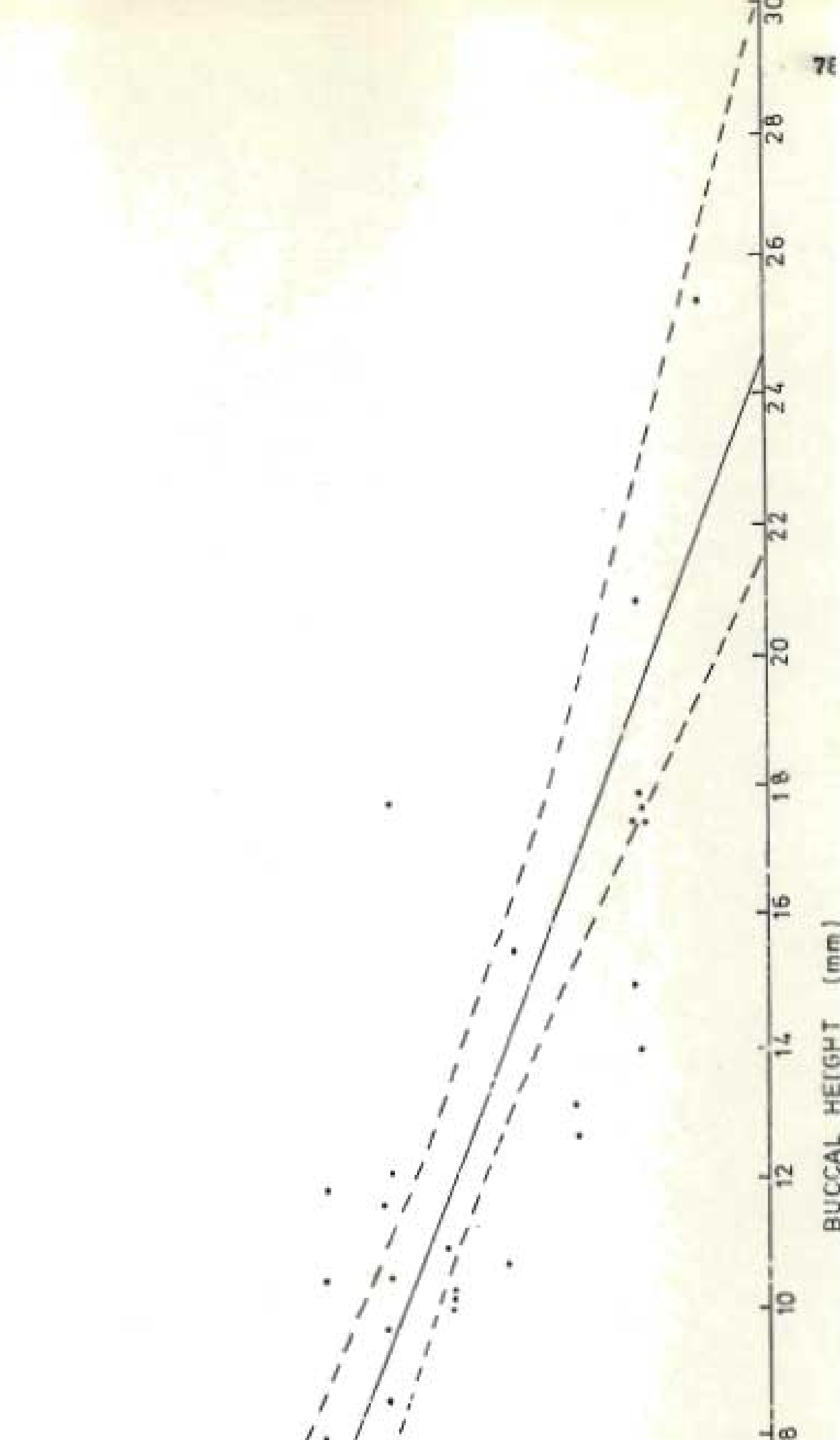


Figure 3.12: The relationship between the number of cementum lines histo
logically and buccal height M_1 ($y = -0,40x + 9,73$; $r = 0,6$
$p < 0,001$). Solid line is the regression line. Dashed line
show the 95% confidence limits.

in section 3.3.5, it seems reasonable to assume that up to this point, ages were probably accurate to within about one year. In this context, Smuts (1974) makes a point about age determination in zebra which applies with equal force to lechwe: "The value of accurate age classes up to four and half or five years of age is extremely important in zebra, since it is within this period that major physiological and psychological changes effecting reproduction and mortality take place". Thus in the critical stages of the life cycle age determination in this study was probably satisfactory for the purposes of conservation and management.

I believe that these results were the best that could reasonably by obtained under the circumstances, but it must be acknowledged that they cannot provide the basis for any definitive conclusions. All the findings relating to growth, reproduction and mortality that are based on these results must necessarily be regarded as first approximations.

3.3.8

Anomalies in Dentition

Few obvious anomalies were seen. In one case supernumerary premolars were found on the buccal sides of the mandible. These teeth were not operative. In one case the mandibular second premolars were absent. In one case the mandibular fourth premolars were absent and there were pronounced gaps in the tooth rows.

3.3.9

Field Age Determination

On the basis of ages estimated by laboratory methods, criteria for field age determination were established. These criteria make it possible to distinguish eight male age classes and three female age classes.

(a) Neonates: these were sufficiently small to be able to stand under the dam's belly and have a distinctive brown pelage. They lack the black stripe on the front of the leg.

(b) 3-4 months: pelage is closer to the adult reddish brown, but the black stripe has not yet appeared on the front of the leg. Appreciably larger than neonates.

(c) 6-9 months: males in this class can be recognized by their newly emerged horn spikes.

(d) Under one year: males in this class are recognizable by their short, straight horns and general body size. Females are approximately two thirds the size of an adult female and can be fairly reliably recognized when a comparison of size is possible.

(e) Yearlings: males are recognizable by the length and spread of horns and general body size.

Grimsdell and Bell (1975) were able to recognize females in this class on the basis of shoulder height and body length. I found that recognition was not sufficiently easy and reliable for field use of this class. Figure 3.13 shows that by 1,5 years female shoulder height is already within 5% of the female's asymptotic height. Figure 3.14 shows a similar situation with regard to body length.

Although a similar situation applies to males, the adult males are so much heavier in build that they are easily distinguished and, of course, there are also substantial differences in horn size and shape.

(f) 2-3 years: males are recognizable of the basis of the length and spread of horns and general body size.
(g) 3-4 years: males are recognizable by their horn length and spread which is generally less than that of adults. Where doubt exists on this basis the thickness of the neck provides a very clear diagnostic character. In animals of this age it is still noticeably thinner than in adult males. This is obvious from Figure 3.15 in which the relationship between neck girth and age is graphically presented.
(h) Over four years: males have by 4-5 years developed the thick neck and generally heavy build of adulthood and horns have reached adult length and spread.

The data on the length and spread of male horns are summarized in Table 3.4.

3.4

CHAPTER SUMMARY

A brief outline of the available methods of age determination is given and the choice of methods for this study is explained.

Four methods of laboratory age determination were used:
tooth eruption;
tooth wear;
cementum line counts from facial sections of bisected teeth;
cementum line counts from stained, decalcified sections.

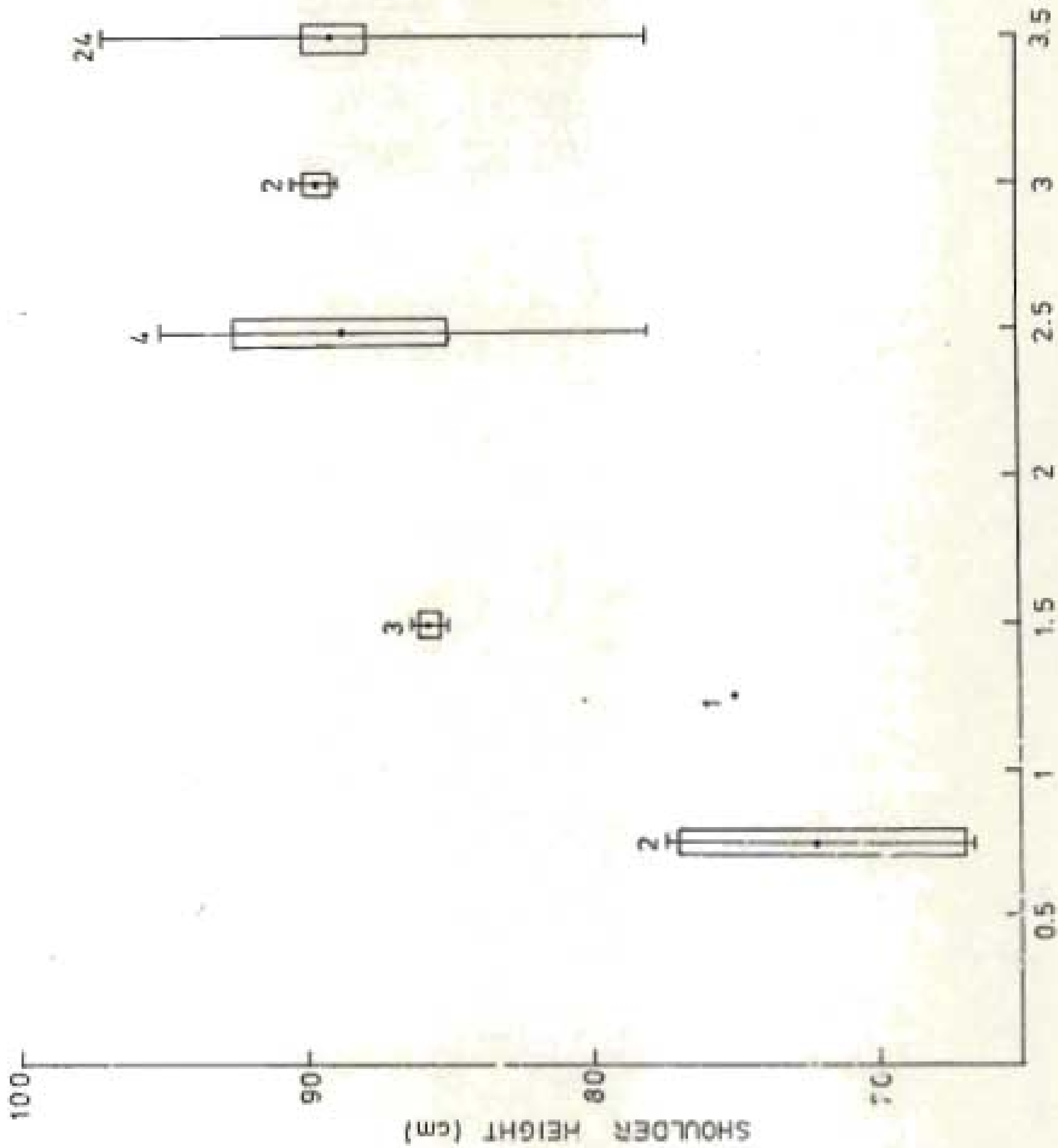


Figure 3.13: The relationship between age and shoulder height in lechwe females. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges; numbers are sample size.

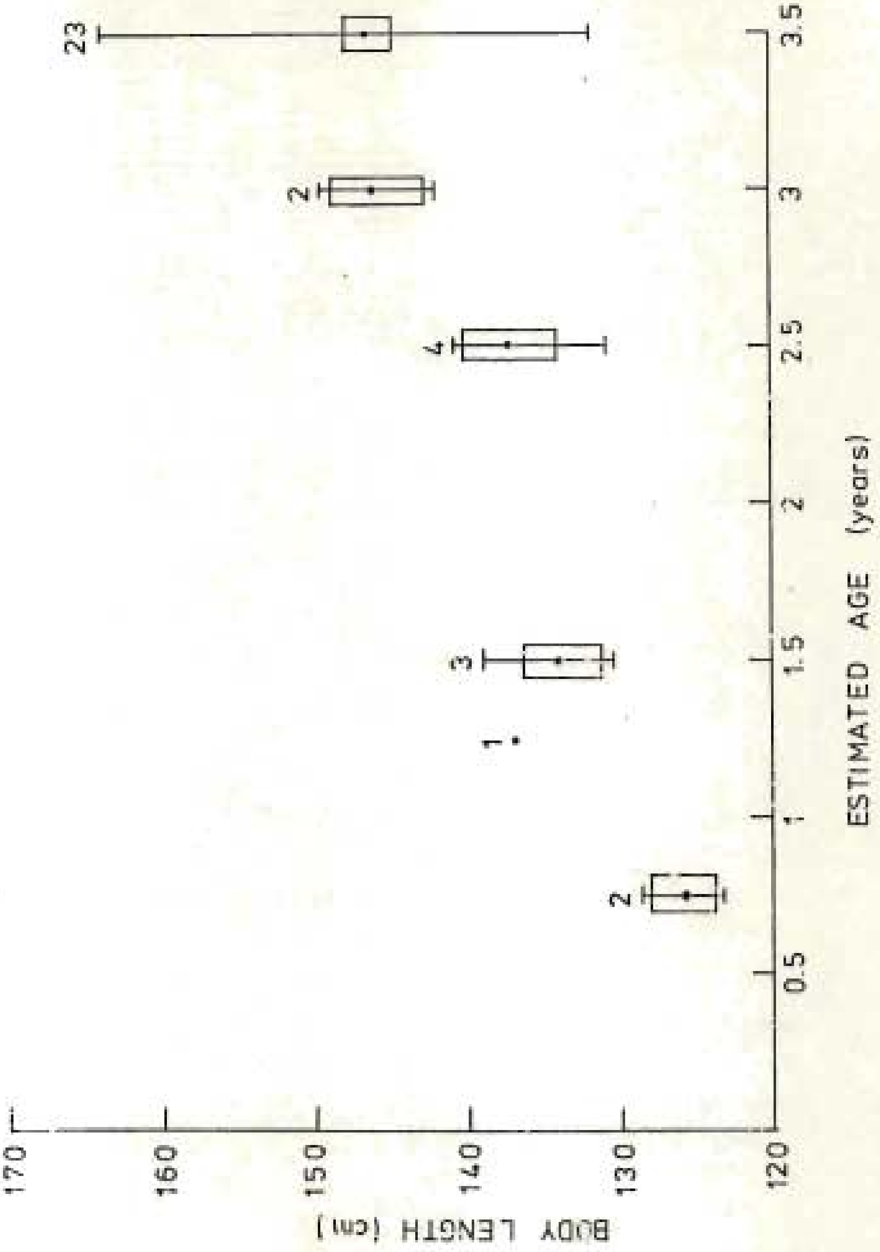


Figure 3.14: The relationship between age and body length in lechwe females. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges; numbers are sample size.

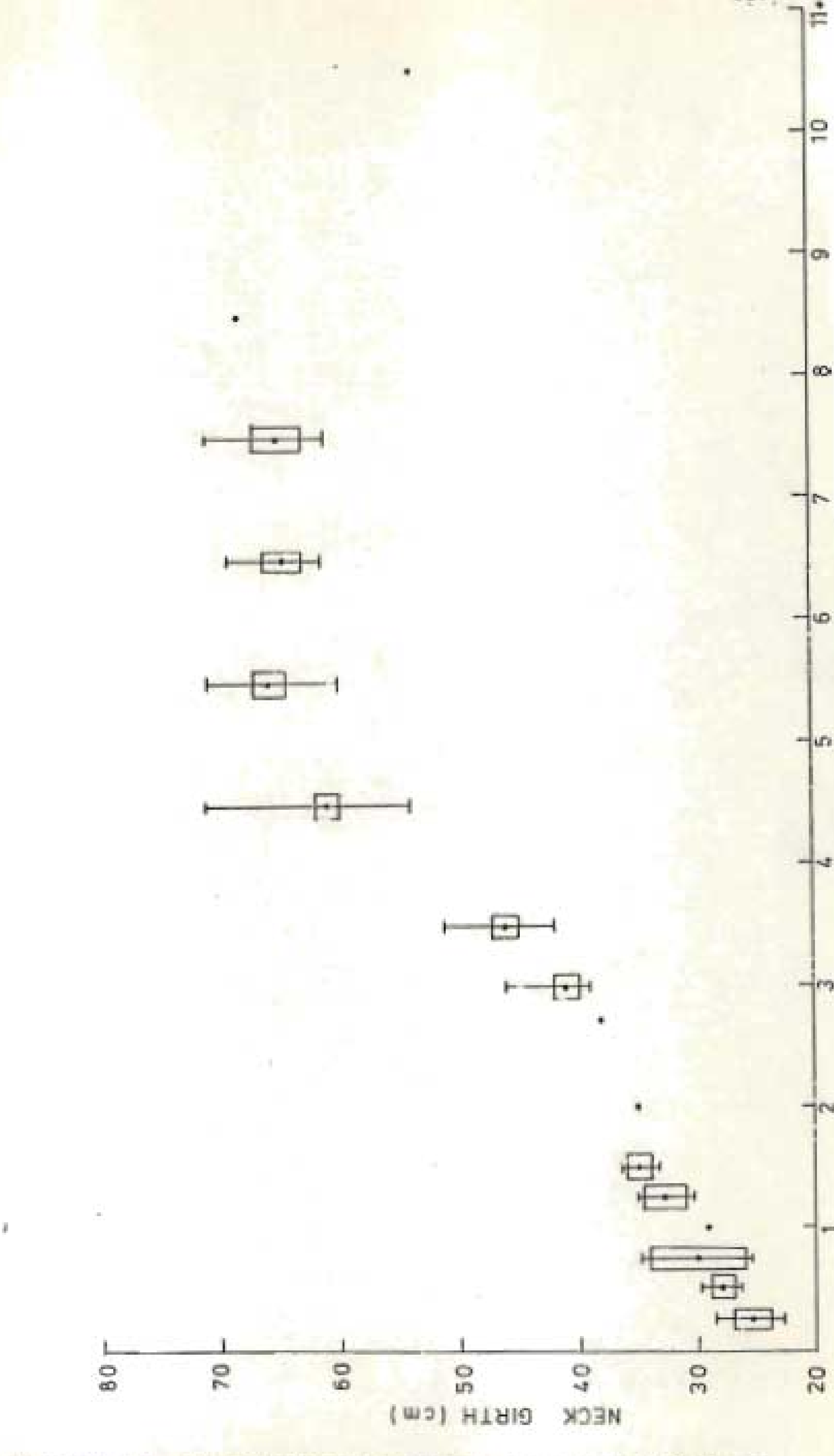


Figure 3.15: The relationship between age and neck girth in lechwe males. Points show means; rectangles show ± 1 S.D.; vertical lines show ranges.

TABLE 3.4: HORN GROWTH RELATED TO AGE

AGE years	Horn Length			Tip-Tip			Horn Length/ Ear Length
	Mean	S.E.	Range	Mean	S.E.	Range	
0,75	6,5	1,2	5,0-8,0	12,9	0,2	12,5-13,5	0,5:1
1,0	9,4	1,4	7,0-12,0	14,3	0,5	13,5-15,0	0,7:1
1,25	21,0	0,4	20,0-21,7	18,2	0,2	18,0-18,3	1,6:1
1,5	24,8	0,3	24,3-25,5	13,2	1,9	11,3-15,0	1,8:1
2,0	33,9	1,4	32,5-35,2	15,5	-	-	2,4:1
2,75	37,1	1,7	34,0-40,5	21,3	9,3	12,0-30,5	2,7:1
3,0	41,4	2,2	30,5-50,8	14,2	2,1	6.5-19,0	3,0:1
3- 4	54,0	1,3	42,6-65,0	20,9	3,1	19,0-37,0	3,7:1
4- 5	60,1	0,5	54,0-66,0	34,6	1,5	19,7-43,0	4,1:1
5- 6	56,8	0,9	51,5-64,9	32,5	2,4	15,7-41,3	3,7:1
6- 7	57,6	0,9	53,0-62,0	39,2	3,5	29,5-50,5	3,5:1
7- 8	54,8	1,6	50,2-62,3	36,2	2,9	27,8-41,1	3,7:1
8- 9	55,3	0,3	55,0-55,5	37,5	-	-	3,7:1
9- 10	54,0	1,5	52,5-55,5	35,0	-	-	3,5:1
10+	53,2	0,2	53,0-53,3	35,0	-	-	3,6:1

The tooth eruption schedule and tooth wear classes employed were those developed by Grimsdell & Bell (1975). Tooth eruption stage was assessed by reference to the eruption schedule and tooth wear was assessed by subjective comparison with photographs of the various age classes and by measurements of molar and incisor height and maximum infundibular depth.

The number of cementum lines laid down annually was established by regarding animals whose age was determined by tooth eruption as "known age" animals.

The relationships between the results of the different methods of age determination were investigated by linear regression and correlation analyses. In general it was concluded that the results obtained were probably satisfactory for the purposes of management and conservation but it was thought that they were not a reliable basis for definitive conclusions.

Field age determination criteria were established for eight male age classes and three female age classes.

CHAPTER 4

HABITAT USE, FOOD SELECTION AND DISTRIBUTION

4.1

INTRODUCTION

4.1.1

Background

It is widely recognized that a precondition for the conservation of an animal is the protection of its habitat. In order to protect an animal's habitat it is obviously essential to have an understanding of its patterns of habitat use. Food selection is a particularly important aspect of habitat use because nutrition affects many aspects of a species' biology.

Approaches to the study of habitat use range from an historical survey of distribution (Joubert, 1973) to a detailed statistical analysis of the relationship between site occupancy by an animal and various environmental measures (Hudson et al., 1976). The former approach is descriptive, the latter attempts to "probe ... the basic determinants of habitat selection" (Hudson et al., op. cit.). Other techniques for studying habitat use include pellet group counts (Anderson et al., 1972), recording of sightings along transects (Lamprey, 1963), mapping the occupancy of different habitat types from an aircraft (Sinclair, 1974; Grimsdell & Bell, 1975), studying the movements of marked animals, radio-tracking of collared individuals (Leuthold & Sale, 1973) and multivariate analysis of feeding site characteristics to investigate niche differentiation (Farrar & Walker, 1974; Attwell, 1977).

For the most part studies of the food habits of African ungulates have been descriptive. Many workers have produced lists of food plants taken by different species (for example, Talbot & Talbot, 1962; Goddard, 1968 and 1970; Leuthold, 1970 and 1971; Bigalke, 1972). Selection of individual plants and of plant parts (Gwynne & Bell, 1968) has been demonstrated but the factors which actually determine food selection are by no means fully understood. Field (1976) had shown correlations between food preference and a number of physical and chemical characteristics of plants, but correlation does not establish causation (Grimsdell, 1978). The factors which determine food selection are doubtless complex and a complete causal explanation of food selection would probably require experimental work. Lack of time and financial constraints make an analytical approach to food habit studies impractical in most field studies and in any event data from descriptive studies are probably adequate for the purposes of conservation and management. If an animal's food habits have been studied in one area it is not unreasonable to assume that it will select similar foods in other similar areas.

4.1.2

Previous Work on Lechwe Habitat Use and Food Selection

It has long been recognized that lechwe are swamp or floodplain animals (for example, Selous, 1881) and aspects of habitat use have been considered in a number of studies involving lechwe. Allen (1963) provided a general description of lechwe habitat in the Bangweulu Swamp. Robinette & Child (1964) described lechwe habitat on the Kafue Flats, made some general observations on habitat use and used pellet group counts to assess the intensity of use in some areas. Child & Von Richter (1969) assessed habitat use on the Chobe River by noting, during road counts, the frequency of occurrence of lechwe in different habitat types. Lent (1969) made a few general remarks about lechwe habitat in the Okavango Delta. Sayer & Van Lavieren (1975) on the Kafue Flats and Grimsdell & Bell (1975) in the Bangweulu Swamp used aerial surveys to monitor seasonal changes on the occupancy of different habitat types. Biggs (1979) described the physiognomic and floristic characteristics of lechwe habitat in the Okavango Delta and made general observations on habitat use.

Several aspects of lechwe feeding ecology have been reported in the literature. Vesey-Fitzgerald (1965) described lechwe pastures in the Bangweulu Swamp qualitatively in terms of common species in the various plant communities. Child & Von Richter (1969) studied feeding preferences of lechwe on the Chobe River and provided a list of plant species taken at different times of the year. Von Richter & Osterberg (1977) found that feeding preferences were correlated with the nutritive value of the major food plants. They suggested that the animals showed a preference for the plants highest in crude protein content. Grimsdell & Bell (1975) studied the vegetation of the Bangweulu Swamp in terms of its function as a food supply for lechwe. They used digestible crude protein content as an index of potential carrying capacity and found that the existing lechwe population was apparently well below the potential carrying capacity of the area. Handlos, Handlos and Howard (1976) used analysis of rumen contents to study food selection by Kafue lechwe and found a seasonal variation in plant species selected.

Much the most comprehensive work on lechwe feeding ecology has been done by Rees (1976, 1978 a, b and c). Her work includes a description of the food supply of Kafue lechwe in terms of floristics, chemical composition and digestibility and she describes the seasonal variation in the quantity of herbage removed from different plant communities by lechwe. She has also shown seasonal variation in the quality of herbage harvested by free ranging animals and has attempted to determine the quantity of the herbage taken in by a free ranging animal.

In addition to studies specifically of lechwe feeding behaviour, this aspect of the species' biology has been considered in the context of two broad schemes for classifying the food habits of African ungulates. Leuthold (1977), following the criteria of Hofmann & Stewart (1972) and Hofmann (1973) (in neither of which works lechwe are discussed), classifies lechwe as bulk and roughage feeders (grazers) which graze fresh grass and are dependent on water. The basis of this classification is stomach morphology. The system is of interest in that it has been incorporated into a method of assessing the carrying capacity of African rangelands (Mentis, 1977; Mentis & Duke, 1976).

Jarman (1974) grouped African ungulates on the basis of feeding style and includes lechwe in his Group C - "species which feed on a range of grasses and browse, rather selectively, in a range of vegetation types within a fairly large home area. The diet changes seasonally as does their preference for vegetation types." This system of classification is relevant in the context of social organization.

4.1.3

Objects of this study with respect to Habitat Use, Food Selection and Distribution

The purpose of studying habitat use was to identify the habitat types in my study area that were most important to lechwe.

For practical reasons I adopted a largely descriptive approach to studying food habits and my primary objects were to:

(a) determine to what extent lechwe in my study area conformed to previous classifications of their feeding style or behaviour;

(b) to identify the major food supply of lechwe in my study area.

I felt that if these objectives were met the data gathered would be satisfactory for the purposes of conservation and management.

Because "distribution is often an excellent and accurate index usable in the diagnosis of food ... and cover questions" (Leopold, 1933) observations on distribution were made to check findings in relation to habitat use. It was assumed that changes in distribution would reflect changes in habitat use and that the magnitude of changes in distribution would be an index of variability in habitat use.

4.2

MATERIALS AND METHODS

4.2.1

Habitat Use

A method similar to that of Croze (1974) was used to study habitat selection because it was simple and produced quantitative results that were amenable to statistical analysis. In the intensive study area a circuit was established which sampled each vegetation zone more or less equally. This circuit was walked regularly and sightings of undisturbed groups of lechwe were recorded (I tried to collect sightings from every hour of the day). Each record included the following details: date, time, location, activity, group size and composition in terms of sex and age (adult male, adult female, subadult male and juvenile).

At least 500 sightings were collected in each season after the first cool, dry season, during which the method was developed and the circuit established.

Each sighting was later allocated to its appropriate vegetation zone on the basis of its location. The area of each zone was calculated by tracing its outline onto mm^2 graph paper and counting the number of squares occupied. The null hypothesis that no vegetation zone was selected was tested with a chi-squared analysis (chi-squared with *a priori* hypothesis, Scheffler, 1969).

The results of this analysis were compared with those of pellet group counts inside and outside the intensive study area and an analysis of sightings of lechwe outside the intensive study area.

During 1976/1977 determinations were made seasonally of the crude protein content of grasses in zones 3, 4 and 5 in the intensive study area (Table 2.11). A regression of the frequency of sighting in each zone on the percent crude protein of grass in that zone was calculated from data collected contemporaneously in order to test the idea that habitat use was related to the quality of the food supply.

4.2.2

Food Habits

Data on feeding style were collected by direct observation of free ranging animals and by examination of the rumen contents of 231 animals shot in the general study area. The fresh mass of ingesta was determined for each animal shot and the proportion of mono- and dicotyledonous plant material in the rumen was estimated after a careful examination of the rumen contents.

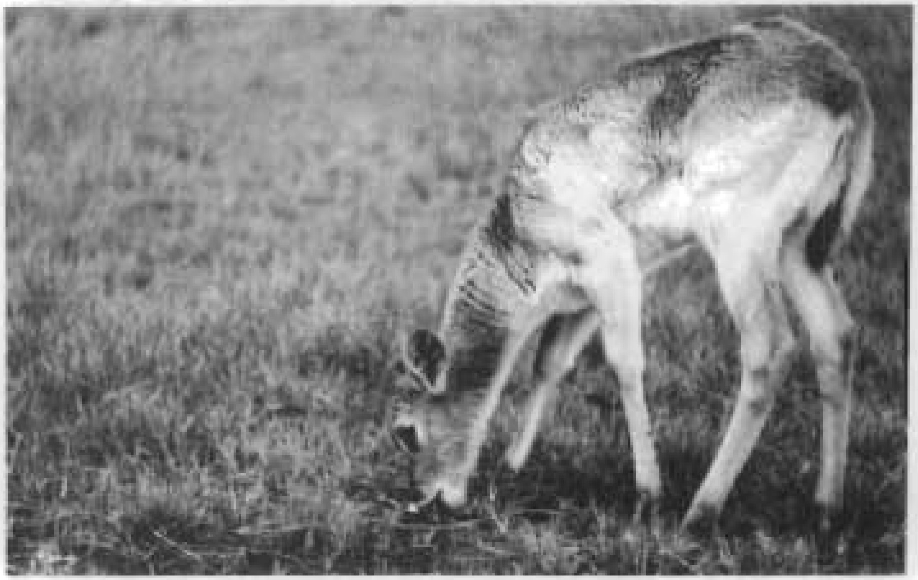
Data on the food supply utilized by lechwe were collected by direct observation and from randomly located transects along which utilization was measured by the method of Walker (1976).

Direct observations were made mainly from two hides in the intensive study area (Plate 4.1). From these hides feeding animals could be observed at close quarters (Plate 4.2), and with binoculars (Zeiss 8x56) it was easy to see individual plants on which animals were feeding. While watching animals under these conditions I tried to note not only the species of plant being fed on but also its growth stage.

Walker's (1976) method entails the examination of a 100 rooted grass plants along a 50 metre transect, one on each side of the line at one metre intervals. The following details were recorded for each plant: species, size of tuft, percentage damaged, percentage grazed and growth stage (vigorous, senescent or dead). Data from these transects were analysed by an updated version of Walker's (1976) computer programme. A total of 30 utilization transects was done at the end of the 1976/1977 rains, 10 each in vegetation zones 3, 4 and 5 (Chapter 2).

It was difficult to do these transects properly in flooded areas. In zone 2, 10 transects were completed for the purpose of providing a quantitative description of the vegetation (Chapter 2) but grass plants were far too sparsely distributed to allow use of the standard sampling interval (one metre) for assessing utilization. Nevertheless every

4.1



4.2

grass plant encountered along a transect was examined for signs of utilization.

In zone 1 water depth made it difficult and in places dangerous to do transects. In this zone subjective assessment of utilization was made on the basis of what I saw in transit through it.

Data on the drinking behaviour of lechwe were collected by direct observation during work on activity budgets.

4.2.3

Distribution

For aerial surveys (Chapter 10) on the Kwando edge of the Linyanti Swamp, 1:40 000 scale aerial photographs were used for navigation. During survey flights the location and size of lechwe groups sighted were noted directly on the photographs. Distribution maps were prepared from these sighting records. Additional information on distribution was obtained from ad hoc observations made in the course of regular ground coverage of most of the general study area.

4.3

RESULTS AND DISCUSSION

4.3.1

Habitat Use

Table 4.1 gives the proportions of the different vegetation zones in the intensive study area. Table 4.2 shows the results of a chi-square analysis of the frequency of lechwe sightings in each vegetation zone. Most of the data in Table 4.2 come from the circuit mentioned in section 4.2.1, but some data from brief vehicle excursions through the study area are included because the vehicle track passed through nearly all vegetation zones (if anything observations were biased towards the drier areas).

Zone 1 is not included in Table 4.2 because it was usually impossible to see animals in this zone. Lechwe do use this zone as escape cover and in transit but it was difficult to quantify this use. There were obvious signs of grazing in zone 1 but it was impossible to determine whether this was by lechwe or sitatunga.

TABLE 4.1: THE APPROXIMATE AREAS AND PERCENTAGES OF THE TOTAL AREA OF THE DIFFERENT VEGETATION ZONES IN THE INTENSIVE STUDY AREA

Zone/Type	Area ha.	% Total
1	116,8	19,5
2	68,5	11,4
3	134,9	22,5
4	119,0	19,8
5	68,5	11,4
Woodland	92,3	15,4

BLE 4.2: THE RESULTS OF A CHI-SQUARED ANALYSIS OF THE OBSERVED AND EXPECTED FREQUENCIES OF SIGHTING LECHWE IN THE DIFFERENT VEGETATION ZONES OF THE INTENSIVE STUDY AREA (chi-squared with *a priori* hypothesis, Scheffler, 1969)[1]

eason/Year and ample size	ZONE 2		ZONE 3		ZONE 4		ZONE 5		Chi-squared	P
	% sightings[2]	$\frac{(O-E)^2}{E}$	% sightings	$\frac{(O-E)^2}{E}$	% sightings	$\frac{(O-E)^2}{E}$	% sightings	$\frac{(O-E)^2}{E}$		
ool dry 1975 (n = 252)	10,3	0,945	66,6	173,337	15,5	4,368	7,5	4,883	183,553	$< 0,001$
ot dry 1975 (n = 690)	3,5	37,598	73,9	810,776	21,3	0,811	1,3	61,142	910,327	$< 0,001$
ains 1975/1976 (n = 528)	1,3	45,933	74,8	637,817	18,9	0,193	4,9	18,704	702,652	$< 0,001$
ool dry 1976 (n = 503)	5,6	14,250	73,6	582,232	18,3	0,563	2,6	33,197	630,242	$< 0,001$
ot dry 1976 (n = 536)	3,5	28,234	81,5	822,647	11,6	17,851	3,4	29,611	898,343	$< 0,001$
ains 1976/1977 = 592)	5,2	19,592	87,0	1100,047	4,6	68,464	3,1	36,033	1224,136	$< 0,001$

: By this method chi-squared = $\sum \frac{(O-E)^2}{E}$ (see also Bishop, 1971; Steel and Torrie, 1960)

: Percentage frequency is shown here to facilitate comparisons between zones and between seasons. The chi-squared analysis was performed with the raw data i.e. the actual numbers of sightings.

Table 4.2 shows clearly that lechwe habitat use was selective. Zone 3 was heavily favoured, zone 4 was used roughly in proportion to its size, while zones 2 and 5 were used less than expected.

Seasonal variation in habitat use was neither great nor consistent. In all seasons zone 3 was heavily favoured and from season to season no clear consistent pattern was apparent in the way in which the degree of use of each zone varied.

It is suggested that habitat selection by lechwe can largely be explained by the attractiveness of the food supply and the availability of escape cover. The value of each vegetation zone as a food supply for lechwe is discussed in detail in section 4.3.3 and it is there concluded that the vegetation of zone 3 is the most important food supply for lechwe. Further, the grasses in zone 3 consistently had the highest crude protein percentage (Table 2.11) and the regression of frequency of sighting against percentage crude protein of grass showed a strong positive correlation between these parameters. The regression equation was:

$$y = 41{,}60x - 136{,}56 \quad (n = 9; \; r = 0{,}911; \; p < 0{,}001)$$

where y = frequency of sighting; x = % crude protein of grass

In the light of the preference for zone 3 (Table 4.2), the evidence of its importance as a food supply and the correlation between frequency of sighting and percentage crude protein of grass, there appears to be little doubt that attractiveness as a food supply is one of the factors explaining habitat use.

There is indirect evidence indicating that availability of escape cover also has an important effect on lechwe habitat use. Robinette & Child (1964), Lent (1969) and Sayer and Van Lavieren (1975) have noted that lechwe are seldom found far from water and emergent vegetation and that there are areas of habitat apparently suitable in terms of vegetation that are never used by lechwe. I found a striking example of the latter situation in the Khwai drainage on the eastern Okavango Delta. In one area there were luxuriant stands of Panicum repens, the dominant species in zone 3 in my intensive study area, which were obviously completely untouched. This area was dry when visited and the nearest water was a considerable distance away. This and similar observations lead me to suggest that an attractive food supply is not on its own a sufficient inducement for the use of an area by lechwe. It is probably also essential that there be escape cover available in the form of water and emergent vegetation.

Pellet group counts inside and outside the intensive study area (Table 4.3; relative frequencies are given because two different plot sizes were used) confirm that zone 3 is heavily favoured. An analysis of sightings of undisturbed lechwe groups outside the intensive study area (Table 4.4) also confirmed the preference for zone 3 and showed that other zones were used to about the same extent inside (Table 4.2) and outside the intensive study area.

The study of habitat use in the intensive study area was continued over a period in excess of two years and after this length of time it became possible to make inferences about the impact that lechwe have on the vegetation in the areas that they use. The impact of other grazing ungulates on the floodplain vegetation was known to be slight (see section 4.3.3) and it became clear that lechwe have a marked impact on the structure of the grasses they graze. Zone 3 (Plate 4.1) has the appearance of a lawn and is kept short by lechwe grazing (Table 2.5). In March 1979 I found that much of zone 4 (see Table 2.5) had also been grazed down to a few centimetres in height and I believe that this was probably because extremely high floods during 1978 (P.A.Smith, pers. comm.*) forced animals to move out of zone 3.

The fact that lechwe have a clear impact on the vegetation in areas they use heavily made it possible to assess lechwe habitat use in most of the general study area. There were clear signs of lechwe use in many parts of this area and from this and Tables 4.3 and 4.4 I inferred that the general patterns of use indicated by Table 4.2 are applicable throughout the general study area, even for the large areas of perennial swamp. In these areas lechwe occur only on islands which are in effect patches of dryland habitat and are zoned in a very similar way to the floodplain. On all islands visited or seen from the air, a similar pattern of use of the vegetation, mostly grasses and sedges, to that obtaining in the intensive study area was observed.

Further analysis of the data summarized in Table 4.2 allows some slight refinements to be made of the broad picture of lechwe habitat use presented above.

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TABLE 4.3: THE RELATIVE NUMBER OF PELLET GROUPS/PLOT FOUND ALONG TRANSEC

INSIDE AND OUTSIDE THE INTENSIVE STUDY AREA

Area	Intensive study area						Outside intensive study area		
Season	Hot dry 1975			Rains 1976/77			Hot dry 1975		
Zone	3	4	5	3	4	5	3	4	5
Relative no. pellet groups/plot	26	7	1	22	2	1	27	8	1
No. plots	180	120	120	250	250	250	180	100	140

TABLE 4.4: LECHWE SIGHTINGS IN AREAS OUTSIDE THE INTENSIVE STUDY AREA, SHOWING SEASONAL CHANGES IN THE FREQUENCY OF SIGHTING IN DIFFERENT VEGETATION ZONES

Zone	COOL DRY		HOT DRY		RAINS	
	Number of sightings	% total	Number of sightings	% total	Number of sightings	% total
1	2	1,2	0	0	0	0
2	19	11,8	8	6,6	4	4,4
3	106	65,8	90	73,8	71	78,0
4	29	18,0	21	17,2	12	13,2
5	5	3,1	3	2,5	4	4,4

As might be expected the amount of time lechwe spent feeding in shallow water was related to flood levels. These were high during both the cool, dry season and at the end of the rains; at the end of the rains they subsided rather quickly. Data on the frequency of lechwe sightings in the water are given in Table 4.5. There is a preponderance of sightings in the water during the cool, dry season. The decline of sightings in the water during the cool, dry season in 1976 is probably due to the fact that part of the floodplain was burned early in the dry season and many lechwe spent extended periods feeding on the green flush, which lasted the whole of the dry season.

Table 4.5 also shows that the proportion of sightings on termitaria was consistently high, despite the relatively small area occupied by these features (in Table 4.2 these sightings were allocated to the vegetation zone within which they occurred; for example if animals were resting on a termitarium in zone 3, the sightings were recorded as occurring in zone 3). Termitaria were common in many parts of the intensive study area and were heavily used for feeding and resting at all times of the year. When disturbed lechwe often ran onto termitaria, probably to enable them to see further. It is also possible that lechwe bed on termitaria at night as a means of predator avoidance. There is a clear benefit to be gained from bedding on termitaria in the water, namely that the approach of any large mammalian predator will easily be heard. On many occasions groups of lechwe were seen to occupy a termitarium at sunset one evening and were found in the same place at sunrise the next morning. It is of course possible that these animals wandered during the night and returned to bed down in the same place (as in Walther, 1973) and the suggestion that lechwe spend the entire night on a termitarium in the water remains tentative.

Two sets of observation indicate that females used wetter and therefore more productive areas (Table 2.11) than males. Table 4.6 shows a highly significant preponderance of male groups in the drier peripheral floodplain habitat. Table 4.7 shows that the majority of animals observed feeding in water were females. A similar preponderance of females in wetter areas apparently occurs on the Kafue Flats (Sheppe & Osbourne, 1971; Rees, 1978c).

Intraspecific differences in habitat use have been noted, _inter alia_, in kudu (_Tragelaphus strepsiceros_) (Simpson & Cowie, 1967) and impala

TABLE 4.5: SEASONAL CHANGES IN THE PROPORTION OF SIGHTINGS IN SHALLOW WATER AND ON TERMITARIA

Season	% Sightings in shallow water	% Sightings on termitaria
Cool dry 1975	20,6	13,8
Hot dry 1975	5,1	11,8
Rains 1975/1976	3,6	15,8
Cool dry 1976	8,9	17,0
Hot dry 1976	5,7	19,3
Rains 1976/1977	6,4	8,4

TABLE 4.6: THE SIGNIFICANCE OF DIFFERENCES IN THE FREQUENCY OF SIGHTINGS OF ALL MALE GROUPS AND OF GROUPS WITH FEMALES IN PERIPHERAL FLOODPLAIN HABITAT IN THE INTENSIVE STUDY AREA

Season	No. groups with females	No. groups males only	Chi-squared *	P
Cool dry	12	56	27,191	< 0,001
Hot dry	30	151	79,558	< 0,001
Rains	31	109	42,350	< 0,001

* with Yates correction factor

TABLE 4.7: SEASONAL DIFFERENCES IN THE NUMBER OF TIMES THAT FEMALES AND MALES WERE OBSERVED FEEDING IN WATER (all animals older than one year)

Season	No. sightings females	No. sightings males	Chi-squared*	P
Cool dry	56	40	2,344	0,20 > p > 0,10
Hot dry	50	18	14,132	< 0,001
Rains	41	18	8,203	< 0,001

* with Yates correction factor

(Aepyceros melampus) (Anderson, 1972) and there are several factors which may contribute to the differences seen in lechwe habitat use. Territories are situated in zone 3 along the water's edge and it is likely that bachelor males avoid this zone because of harassment by territorial males. In respect of maternal-infant behaviour, lechwe are basically of the "Ablieger" (Walther, 1964b, 1965, 1968, 1969) or "hider" (Lent, 1974) type. Neonates "lie-out" mainly on termitaria and islands among the emergent vegetation of zones 1 and 2 and it may have been for this reason that females did not move great distances from the water's edge. Further, lechwe frequently used zones 1 and 2 as escape cover and this may be another reason why the more wary females (Chapter 8) stayed close to the water.

Two types of evidence indicate that juveniles feed less in the water than do older animals. Firstly, during observations on habitat use, animals older than one year were seen feeding in the water on 223 occasions, whereas animals less than one year old were seen feeding in the water on only three occasions.

Secondly, continuous behavioural observations showed that juveniles spent relatively little time in the water. For example, the proportions of time spent in the water by the different sex and age classes during the cool, dry season were as follows:

(i) females over one year old: 42,3%
(ii) adult males: 28,0%
(iii) subadult males: 2,0%
(iv) juveniles (less than one year old): 2,9%.

Subadult males spent a good deal of time in drier peripheral floodplain areas but juveniles were usually in proximity to water. These results thus tend to confirm that juveniles spend significantly less time in the water than do older age classes.

Apart from this quantitative evidence many ad hoc observations were made of juveniles showing fear in water. For example, when solitary juveniles had to go through water, they usually did so as quickly as possible, running and jumping even through very shallow water. In similar circumstances adults would walk slowly through the water, often stopping to feed.

A possible explanation for the relative reluctance of juveniles to enter water is that it takes time for them to become habituated to water (this is the case also with otters, personal observation).

4.3.2

Feeding Style

Hofman & Stewart's (1972) classification of food habits implies differences in both the amount and the type of food eaten by the three broad groups of ungulates (bulk and roughage feeders, concentrate selectors and intermediate feeders).

The amount of food eaten by lechwe is indicated in Table 4.8. A method of comparing these data with the amount of food eaten by other ungulates is suggested by Anderson (1978). He derived general regression equations for bulk and roughage feeders and for concentrate selectors which show an extremely high and significant correlation between ingesta mass and body mass. Anderson's (1978) equations were:

bulk and roughage feeders:

$$y = 0{,}199x - 0{,}649 \quad (r = 0{,}998; \; p < 0{,}001)$$

where y = ingesta mass; x = body mass

concentrate selectors:

$$y = 0{,}075x - 0{,}204 \quad (r = 0{,}998; \; p < 0{,}001)$$

From the data collected during this study similar regressions were calculated for lechwe.

The equation for lechwe females was:

$$y = 0{,}159x + 0{,}245 \quad (r = 0{,}709; \; p < 0{,}001; \; n = 142)$$

The equation for lechwe males was:

$$y = 0{,}128x + 0{,}805 \quad (r = 0{,}890; \; p < 0{,}001; \; n = 88)$$

The regression co-efficients for lechwe are in a range of values that would seem to be more appropriate to intermediate rather than to bulk and roughage feeders.

TABLE 4.8: MEAN FRESH MASS OF INGESTA AND INGESTA MASS AS A PERCENTAGE OF BODY MASS IN FEMALE AND MALE LECHWE OVER THREE YEARS OLD

	FEMALES			MALES		
Season	n	Fresh mass ingesta (kg)	Ingesta mass as % body mass	n	Fresh mass ingesta (kg)	Ingesta mass as % body mass
Cool dry 1975	25	11,2	14,9	10	17,0	15,2
Hot dry 1975	20	10,7	16,4	6	15,9	13,9
Rains 1975/1976	25	12,6	17,6	15	15,4	13,5
Cool dry 1976	20	11,5	16,7	11	15,4	15,4
Hot dry 1976	16	10,3	15,8	9	13,8	11,9
Rains 1976/1977	18	11,5	16,3	12	12,1	12,3

Although lechwe show affinities with intermediate feeders in terms of the amount of food they eat, the type of food they select is typical of bulk and roughage feeders. Direct feeding observations and examination of rumen contents indicate that the lechwe in the study area were predominantly grazers. Out of many thousands of direct feeding observations only 25 were of browsing. Most browsing incidents lasted less than one minute and only five browsing sessions in excess of one minute were observed. The longest browsing session observed lasted seven minutes.

Dicotyledonous material was found in 15% of rumena. The quantities found were invariably small, in all cases estimated at less than 1% of the material present in the rumen. Kafue lechwe (Handlos et al., 1976; Rees, 1978c) apparently make greater use of dicotyledonous material than was observed in lechwe on the Kwando.

An aspect of lechwe feeding behaviour which may explain why the quantity of their intake appears to be less than might be expected of a bulk and roughage feeder is the probability that they feed selectively. Lechwe are in theory likely to be selective because of their relatively small mouths (Field, 1970 and 1975) and in practise when observed from a hide while feeding at close quarters, they appeared to be selecting for new growth in the sward. Their general feeding behaviour had much in common with Field's (1970) description of kob food habits; in particular lechwe also had a "habit of feeding from above a short sward."

This selectivity was particularly apparent in females which fed more in the wetter areas (Table 4.7). Greater selectivity of female feeding has also been noted in Kafue lechwe (Rees, 1978c).

The fact that females feed more in wet areas than do males probably explains two facts which are apparently contradictory i.e. that males have a greater mass of ingesta in their rumena (Table 4.8) but females spend more time feeding (Chapter 8). The resolution of the apparent conflict is related to the fact that herbage in wet areas is kept at an early growth stage and is therefore of a higher quality (Table 2.11) and moister than mature grasses (Stanley Price, 1977) in drier areas. It is known that better quality forage is more easily digestible (McDonald et al., 1969) and has a shorter retention time in the rumen (Stanley Price, 1977) than poorer quality forage. This could well mean that, although females have less material in their rumena at a given time, their daily intake is as great as or greater than that of males because they process their food more rapidly.

The selectivity of lechwe feeding behaviour has important implications for management, as it means that when lechwe movements are restricted and stocking rates are high, either in sanctuaries of under ranching conditions, problems of localized overutilization of the range and loss of condition are likely (Mentis, 1977). This likelihood raises questions about the adequacy, from a management point of view, of Hofman & Stewart's (1972) classification of ungulate food habits. Mentis (1977) appears to have made it quite clear that it is as important to distinguish between the degrees of selectivity of bulk and roughage feeders (grazers) as it is to distinguish between bulk and roughage feeders and concentrate selectors (browsers). The distinction between more and less selective grazers may be implicit in Hofman & Stewart's (1972) classification but I believe that, in the context of management, it is sufficiently important to warrant explicit recognition and consideration.

In his discussion of ungulate feeding styles Jarman (1974) places lechwe in his Class C. The results of this study indicate that this is wrong and I suggest that lechwe would be more appropriately placed in his Class D i.e. "that in which species feed on grasses, being rather unselective for species ... but more selective for plant part or growth stage ... (their) diets are perhaps the least diverse of all." Lechwe perhaps exhibit a greater degree of selectivity than Jarman attributes to Class D but they use a small range of food and habitat types and, in my opinion, this distinguished them from Jarman's Class C.

4.3.3

Food Supply

Direct observation of feeding animals in the intensive study area gave a qualitative impression of the food values of the different vegetation zones (Chapter 2) and indicated that most feeding was done in zone 3. During the day males ranged also into zone 4 but in the evening they returned to zone 3 to spend the night. Females regularly fed in zone 2 but never in the large numbers that consistently fed in zone 3. Very few direct observations were made of animals feeding in zones 1 and 5.

Direct observations from the hides did not yield much information on grass species selection because species diversity around the hides was low. Observation from the hides did yield data on the use of plants other than grasses. These observations, *ad hoc* feeding observations in the general study area and examination of plants in areas where lechwe were observed feeding gave an idea of the type of plants other than grasses that are eaten by lechwe.

A list of plants other than grasses that were taken by lechwe is as follows:
Scirpus uninodus, *S. rogersii*, *Cyperus articulatus*, *C. denudatus*, *C. longus*, *Pycreus lanceus*, *P. polystachus*, *Fuirina pubescens*, *F. umbellata*, *Mariscus squarrosus*, *Fimbristylis ferruginea*, *Fimbristylis* sp., *Rhyncospora holoschoenoides*, *Nymphaea caerulea*, *Gomphocarpus rostratus*, *Potamogeton thunbergii*, *Nesaea crassicaulis*, *N. radicans*, *Orthanthera jasminiflora*, *Burnatia enneandra*, *Achyranthes aspera*, *Commicarpus africanus*, *Phoenix* sp., *Combretum imberbe* (shrub stage).

The fact that direct observation of feeding behaviour indicated that lechwe select for new growth was mentioned earlier but further communt on this selectivity is appropriate at this point because if the function of selection could be determined a fuller understanding of the nature of the lechwe's food supply would be forthcoming.

Similar selection was found in Kafue lechwe (Rees, 1978c) and by Afolayan & Fafunsho (1978). A number of potential advantages to such selection can be envisaged and have been suggested. Kreulen (1975) has shown that enhanced nutrient (calcium) intake may be one of the functions of selective grazing. Von Richter & Osterberg (1977) assert that lechwe on the Chobe River select for crude protein and in this study chemical analysis showed that relatively high crude protein values (Table 2.11) prevailed in zone 3 where most feeding occurred. Rees (1978c) suggests that the percentage digestible dry matter may influence selection and that selective grazing of new grass growth increases phosphorus intake. If all or most of these potential advantages do actually accrue, selective grazing must considerably enhance the nutritive value of the food harvested by lechwe. Thus plant growth stage is probably an important parameter to be considered in describing food supply.

Data from the transects along which utilization was assessed by Walker's (1976) method are presented in Tables 4.9 – 4.11. The grazing percentages in these tables are estimates of the proportion of plant material removed. The figure for all species is calculated from all plants examined, not only from those plants actually grazed.

TABLE 4.9: DEGREE OF UTILIZATION OF GRASS SPECIES IN ZONE 3

SPECIES	FREQUENCY OF OCCURRENCE %	% GRAZING
Panicum repens	89,7	10,4
Sporobolus spicatus	8,7	4,3
Eragrostis inamoena	1,3	40,2
Cynodon dactylon	0,2	0,0
All species	100,0	14,0

TABLE 4.10: DEGREE OF UTILIZATION OF GRASS SPECIES IN ZONE 4

SPECIES	FREQUENCY OF OCCURRENCE %	% GRAZING
Eragrostis lappula	37,9	12,0
Eragrostis trichophora	18,4	0,1
Setaria anceps	14,2	14,5
Cynodon dactylon	8,2	8,3
Panicum repens	5,2	2,9
Panicum dregeanum	5,0	0,0
Eragrostis inamoena	3,2	14,1
Aristida pilgeri	2,4	1,8
Brachiaria dura	1,9	0,0
Sorghastrum friesii	1,2	2,5
Aristida congesta	1,0	0,0
Paspalum orbiculare	0,9	26,9
Trachypogon spicatus	0,2	2,5
Cymbopogon excavatus	0,2	2,5
All species	100,0	7,6

TABLE 4.11: THE DEGREE OF UTILIZATION OF GRASS SPECIES IN ZONE 5

SPECIES	FREQUENCY OF OCCURRENCE %	% GRAZING
Cymbopogon excavatus	22,0	0,9
Imperator cylindrica	15,3	0,1
Eragrostis lappula	12,8	3,7
Trachypogon spicatus	6,5	0,2
Brachiaria dura	6,0	0,0
Eragrostis trichophora	4,6	0,0
Brachiaria humidicola	3,9	0,0
Sorghastrum friesii	3,6	2,3
Paspalum orbiculare	3,5	0,0
Aristida congesta	2,9	0,0
Hyperthelia dissoluta	2,7	0,0
Schizachyrium jeffreysii	2,6	0,0
Eragrostis pallens	2,1	0,0
Setaria anceps	2,0	0,0
Aristida pilgeri	2,0	0,0
Cynodon dactylon	1,6	0,3
Eragrostis echinochloidea	1,5	2,7
Elionurus argenteus	1,1	2,5
Setaria sphacelata	0,9	3,3
Panicum dregeanum	0,8	0,0
Sporobolus ioclados	0,5	0,0
Rhynchelytrum repens	0,4	0,0
Trichoneura grandiglumis	0,3	0,0
Aristida meridionalis	0,2	0,0
Hyperthelia dissoluta	0,2	5,0
All species	100,0	0,8

These results, as did the results of direct observations of feeding behaviour, indicate that most feeding is done in zone 3. They show further that zone 4 is used with moderate intensity and that zone 5 is scarcely used at all for feeding.

It was assumed that all of the grazing in zones 3-5 was by lechwe. This assumption could be made with some confidence. In three months of intensive behavioural work preceding the utilization survey, few sightings of other species were made in these zones and careful searches in the vicinity of transects revealed no tracks or signs of other species. There were hippo paths through the area but there were no signs of hippo having grazed along the transects.

It was not possible to make the same assumptions in zone 1 and 2 because sitatunga were regularly seen to be feeding in these areas.

The examination of grazed plants along transects in zone 2 indicated that grass species that were utilized included: Panicum repens, Paspalidium platyrrhachis, Sacciolepis typhura, Oryza longistaminata, Leersia hexandra and Brachiaria humidicola.

The degree of utilization of grass plants in zone 2 was 11,9%, but the biomass of grass in this zone is so low (Figure 2.10) that it is unlikely to be a major food supply for lechwe.

The degree of utilization of grasses in zone 1 was not assessed quantitatively but was clearly low. The grass Vossia cuspidata was obviously grazed and fragments of Phragmites sp. and Miscanthidium sp., both common in zone 1, were occasionally found in rumens, showing that these species were sometimes taken.

In the light of data from direct observations, the utilization transects and the subjective assessments of plant use in zone 1, the vegetation of zone 3 appeared to be the most important food supply for lechwe in the study area. There are several possible reasons for this. Continued heavy use of this zone tends to keep the grass at an early growth stage. The perennially moist soil means that there is in effect no dry season. The effect of the gradient of decreasing moisture from zone 3 to zone 5 is an increasing proportion of senescent or dead grass plants: 10% in zone 3, 16% in zone 4, 30% in zone 5. Between zones 3 and 5 there is also a change in growth form. Grasses in zones 4 and 5 are taller

(Table 2.5) and larger than in zone 3 (in zone 3 only 7% of grass tufts have a basal diameter larger than 5 centimetres, in zone 4 the proportion is 60%, in zone 5 79%). In comparison to those of zone 2, the grasses in zone 3 contribute a far greater proportion to the plant biomass (Figure 2.10), also there are indications that aquatic grasses are high in silica, which reduces their digestibility (Rees, 1978c; Moen, 1973).

The various data collected indicate that besides zone 3, the vegetation of zone 4 is also an important food supply and that the vegetation of zone 2 is clearly an added food resource although probably of limited importance. Zones 1 and 5 are utilized but to a very limited extent.

Thus the overall conclusion from data collected in the study area was that the major food supply was the vegetation (mainly grasses, Figure 2.10) of zone 3 and 4, supplemented by that of zone 2 and, to a very limited extent, that of zones 1 and 5. This establishes that it is the ecotone between the perennial swamp and the terrestrial communities that is the most important area with respect to the feeding ecology of lechwe.

The results of examinations of known feeding sites in many other parts of the general study area indicated that feeding patterns throughout the area were generally similar to those in the intensive study area. There was little variation in the seasonal patterns of habitat use, indicating that there is unlikely to be much seasonal variation in the different vegetation zones in terms of their importance as a food supply.

During the study three cases involving the ingestion of non-herbaceous material were recorded. On two occasions large fragments of bone were found in the rumen of a shot animal. One clear case of a juvenile lechwe nibbling at guano on a termitarium in the water was observed. These examples of "pica" or depraved appetite (McDonald et al., 1969) are consistent with a nutrient deficiency, perhaps of phosphorus. Osteophagia has been reported in other wild ruminants, for example nyala (Anderson, 1974).

4.3.4

Drinking Behaviour

To the best of my knowledge the drinking behaviour of lechwe has not previously been documented.

In view of their close association with water it seemed in theory likely that drinking would be a far less significant activity for lechwe than it is, for example, in impala, which may spend up to an hour a day gaining access to water during the dry season (Jarman & Jarman, 1973). In practice it was found that drinking episodes were usually brief, most lasting one or two minutes. There were seasonal differences in the frequency of drinking and sexual differences in the pattern of drinking.

During the cool, dry season the animals rarely drank. During the hot, dry season lechwe drank on average three times a day. During the rains they drank on average once a day.

There were no discernable spatial or temporal patterns in drinking behaviour. Animals, with the exception of bachelor males, seemed to drink at any convenient place at any time of the day. When bachelor males had been feeding on the drier peripheral floodplain areas they would often drink as soon as they returned to the water's edge in the evening. No nervousness or special caution was observed prior to drinking.

4.3.5

Distribution

The results of aerial surveys indicated that the distribution of lechwe on the Kwando remained rather constant. Figures 4.1 and 4.2 show the results of the two flights in the course of which lechwe distribution was fairly accurately plotted. The total number of animals counted in May 1977 was about 25% higher than that during June 1976, but there are otherwise general similarities in the pattern of distribution. Flood levels during May 1977 were higher than during June 1976 and this probably explains the presence of greater numbers of animals on the wetland margins in May 1977.

Observations on the ground in the intensive study area and during extensive travelling about the general study area confirmed the impression of a rather constant distribution. Lechwe were present in the intensive study area throughout the entire study and there were many places along the wetland edge where lechwe could invariably be found at any time of the year. Such movements as did occur appeared to be in response to water levels. When water levels were high the numbers of animals in the intensive study area and along the wetland edge increased, when levels were low they declined.

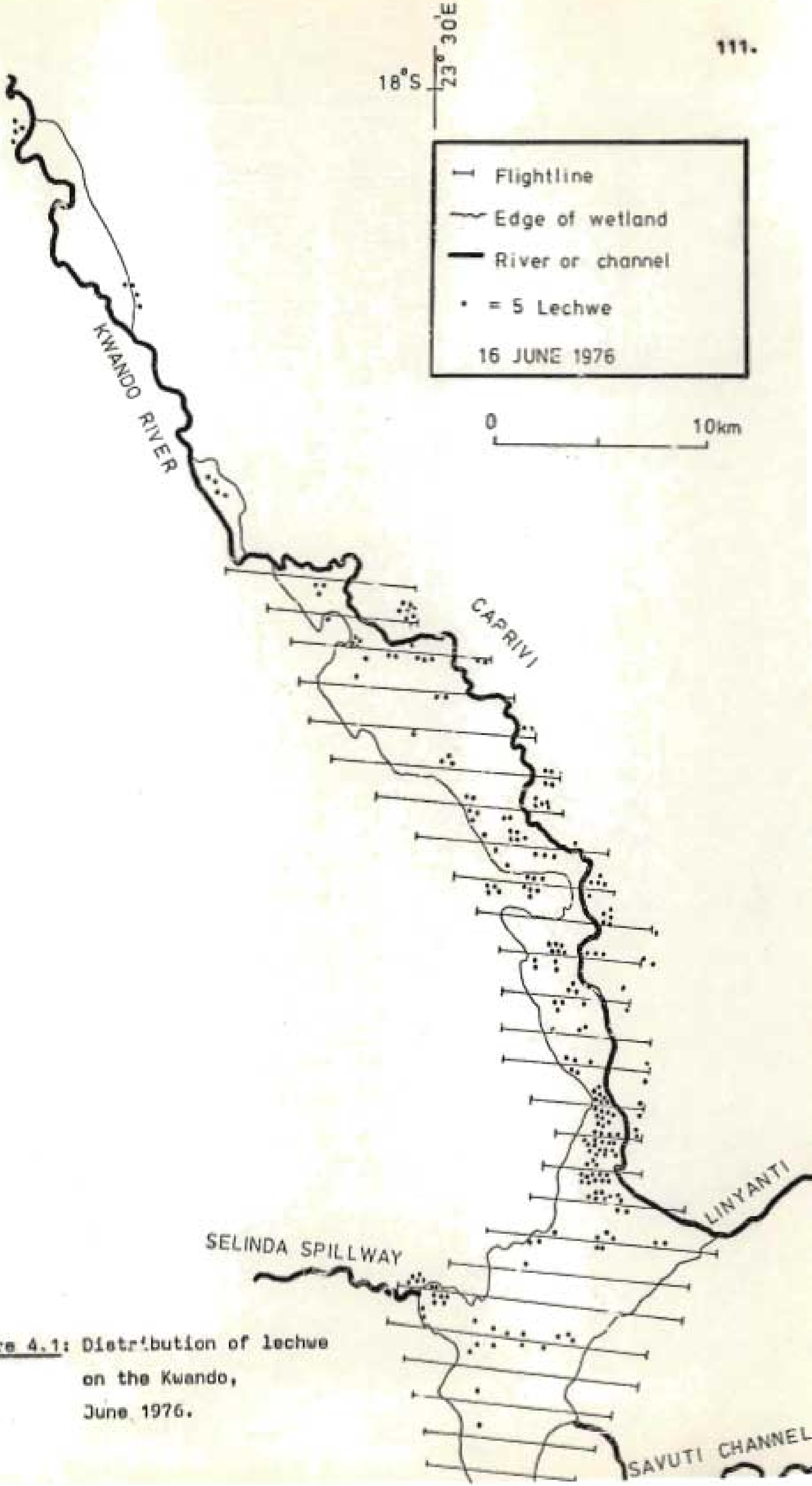

Figure 4.1: Distribution of lechwe on the Kwando, June 1976.

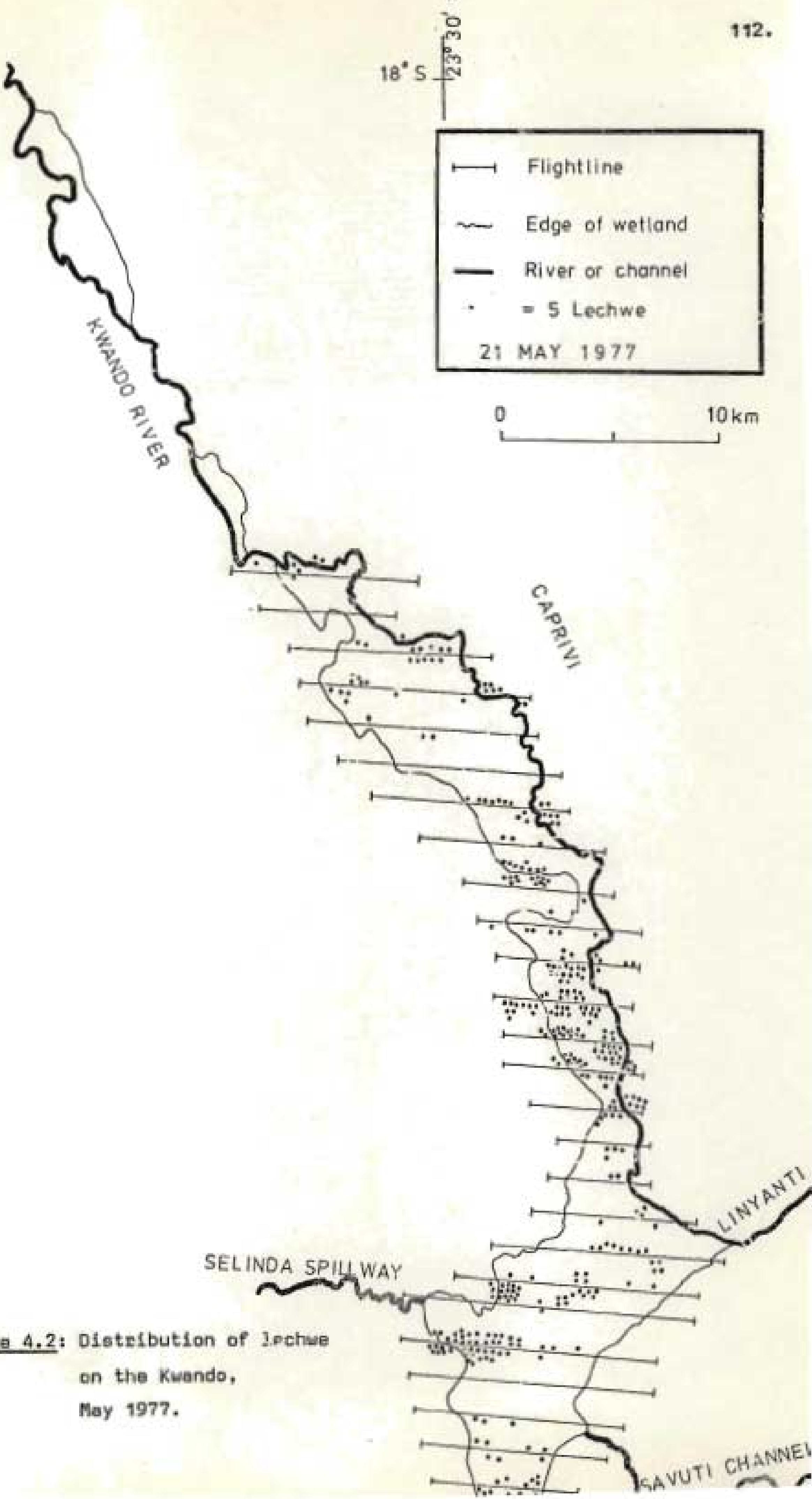

Figure 4.2: Distribution of lechwe on the Kwando, May 1977.

A likely explanation for lechwe movement in response to variation in water levels is that they do not feed in water much more than 50–60 centimetres deep (at least they were not observed to do so on the Kwando). Thus if the water level in a particular area rose or fell much above or or below this level, lechwe would either be forced to move out of the area or be able to move in and make use of it. On the Kwando, fluctuations in water level are relatively slight and lechwe movements correspondingly small. In the Chobe (Child & Von Richter, 1969), Kafue (Sayer & Van Lavieren, 1975) and Bangweulu (Grimsdell & Bell, 1975) systems, fluctuations in water level are much greater than on the Kwando and lechwe movements correspondingly greater, over 50 kilometres in places (Grimsdell & Bell, op. cit.).

The relatively constant pattern of lechwe distribution on the Kwando indicates that no marked changes in habitat use occur. This finding is consistent with the limited seasonal variation in habitat use that was observed in the intensive study area.

4.4

SUMMARY

The purpose of studying habitat use was to identify the habitat types in the study area that were of most importance to lechwe.

The main objects of this study with respect to food selection were:

(a) to determine to what extent lechwe in the study area conformed to previous classifications of their feeding style or behaviour;
(b) to identify the most important food supply of lechwe in the study area.

Data on habitat use were collected by direct observation, from pellet group counts and by examining vegetation for signs of lechwe use. Data on food habits were collected by direct observation, by examining the rumens of shot animals and by examining the vegetation in areas used by lechwe. In the latter exercise, objective (Walker, 1976) and subjective assessments of the degree of utilization were made.

With respect to habitat use it was found that zones 3 and 4 were most used in the intensive study area and it was concluded that the same probably held true for the general study area. Zone 3 forms a generally narrow band along the swamp margins in which soil is moist all year round, plant growth is continuous and grasses contribute most to the plant biomass. Zone 4 is flooded seasonally (for 3-8 months of the year) and, as in zone 3, grasses make up the bulk of the plant biomass in this zone.

Intraspecific differences in habitat use were observed: females used wetter areas than males, while juveniles tended to spend less time in the water than other age classes. A highly significant correlation was found between frequency of sighting and percentage crude protein of grass in zones 3, 4 and 5, and from this it was concluded that the quality of the food supply has an important effect on habitat use. Availability of escape cover was also thought to be an important factor in lechwe habitat use.

With respect to feeding style it was found that lechwe are predominantly grazers that select for new growth and it was suggested that their selectivity has important implications for management. From the results of this study it was concluded that Jarman's (1974) classification of lechwe in his Class C is incorrect and that lechwe more properly belong in his Class D.

With respect to food supply it was found that the vegetation, mainly grasses, of the ecotone between the perennial swamp and the terrestrial plant communities was the most important source of food for lechwe in the study area.

Distribution of lechwe on the Kwando remained rather constant, indicating that changes in the pattern of habitat use were limited.

CHAPTER 5

CONDITION

5.1

INTRODUCTION

5.1.1

Definition of Condition

The term "condition" is widely used but is seldom defined or circumscribed. Clarification of the term is important for the purposes of analysis and discussion and I have therefore attempted to formulate a tentative working definition of "condition".

My definition is a slightly expanded version of a statement by Lamond (1970) and is simply that:

> "An animal's condition is equivalent to the level of its body reserves of energy and nutrients."

The existence and variability of body reserves are clearly demonstrated, for example, by the work of Jones & Ward (1976) with red-billed queleas (*Quelea quelea*). They found that at the end of the day birds had accumulated a lipid reserve of about 0,7 gram (their total lipid content was 1,0 gram). They also found that before the inception of yolk formation females had a protein reserve of about 0,36 gram. Both lipid and protein reserves were subject to marked declines.

The relevance of the levels of the various types of body reserve is that they effect an animal's chances of both survival and reproduction. Jones & Ward (*op. cit.*) found the queleas which ended the day with low lipid reserves were unable to survive the night. Franzmann & Arneson (1976) found that marrow fat values for adult moose (*Alces alces*) killed by wolves (*Canis lupis*) or accidentally (road kill, shot or drug) were not significantly different from each other but were significantly higher than those of suspected starved moose. de Calesta *et al.*, (1977) found that in two groups of deer (*Odocoileus virginianus*) which were starved simultaneously mortality occurred in the group which had previously been under-fed but not in the group which had previously fed ad libitum.

In relation to reproduction, Jones & Ward (1976) suggest that queles can only breed successfully when protein is available in large enough amounts for females to accumulate sufficient reserves of protein for egg laying. Because the low protein value of food during the dry season precludes accumulation of a large protein reserve no breeding can occur at this time. In adult cows (Lamond, 1970; Buck *et al.*, 1976) and in red deer (*Cervus elaphus*) hinds (Lowe, 1971) it has been shown that there is a relationship between fecundity and body reserves, as reflected by body mass.

From the above it is suggested that by measuring the level of an animal's body reserves of energy and nutrients an indication is obtained of its chances of both survival and reproduction. The suggested definition of condition would therefore appear to be more than adequate in terms of Hanks's (1979) criterion that "if a measure of physiological changes is to be of practical value, it must be linked to the animal's chances of living or dying". As it is defined here the term "condition" appears to be synonymous with the term "nutritional status" as used, but not defined, by Warren & Kirkpatrick (1978).

Reference is often made to animals in "poor" or "good" condition but the meaning of these phrases is seldom obvious. In terms of the present definition "poor" condition would be equivalent to a state in which body reserves are depleted; "good" condition would be equivalent to body reserves standing at sufficiently high levels to meet all the demands of survival and reproduction.

5.1.2

Factors Affecting Condition

The levels of body reserves reflect the balances between demands for energy and various nutrients and their supply. At any particular time there are many interacting endogenous and exogenous variables which influence this type of balance. In broad terms, demand varies with growth stage, sex, reproductive status, social status and season while supply varies in terms of both quantity and quality (for example, energy content, protein content, mineral content, fat content, vitamin content and digestibility). A start has been made with explaining some of the interactions between these variables in domestic livestock

(Crampton & Harris, 1969; McDonald *et al*., 1969; Maynard & Loosli, 1969; Moen, 1973) but understanding of this type of interaction in wild ruminants is extremely limited. For this reason the ensuing discussion of condition is in largely descriptive terms.

5.1.3

The Relevance of Condition in the Study of Animal Populations

Condition has been shown (section 5.1.1) to affect both mortality (see also: Hirst, 1969; Ferrar & Kerr, 1971; Child, 1972; Keep, 1973) and reproduction (see also: Verme, 1967, 1969 and 1977; Abler *et al*., 1976; Thorne *et al*., 1976) and it also affects growth (Verme, 1963; Ulrey *et al* 1967; Young & Scrimshaw, 1971). It is thus clearly relevant to the study of animal populations and its importance has been recognized by, *inter alia*, Moen (1973), Grimsdell (1978) and Hanks (1979). Hanks, in particula has shown the importance of considering condition when assessing the status of a population.

5.1.4

Assessment of Condition

The purpose of this section is to discuss some aspects of condition assessment that are not dealt with in Hank's (1979) detailed review of the subject.

5.1.4.1

The use of body mass as an index of condition

Studies such as Klein's (1968) on the crash of the St Matthew Island reindeer (*Rangifer tarandus*) population clearly show the value of body mass as an index of condition. Nevertheless for at least three reasons it is an index that must be used with caution.

In the first place, body mass is subject to variation that is not related to condition. For example, Payne & Hutchison (1963) showed that live mas of zebu steers may increase by as much as 7% after a single drinking. If a shot sample is available this type of variation can be eliminated by using carcass mass, here defined as body mass minus mass of feet (from carpal/tarsal joints), head, skin and the entire contents of the body cavity (see section 6.2).

A second problem is that body mass needs to be corrected for skeletal size. Grimsdell & Bell (1975) divided body mass by several combinations of linear body measurements but found that "the most convenient single measurement of skeletal size was simple body length". They found that the index live mass divided by body length had a clear pattern of variation compatible with seasonal changes in the food supply and events in the reproductive cycle.

A third problem is that it is difficult to identify a specific cause for a decline in body mass because it involves simultaneous loss of different body components such as water, protein (nitrogen), minerals and lipids (Young & Scrimshaw, 1971). In view of this, variation in body mass is not a refined index but because of the incontrovertible relationship between nutrient restriction and decline in body mass (Young & Scrimshaw 1971; de Calesta et al., 1975; Warren & Kirkpatrick, 1978) it is undoubtedly a valid indication of a general decline in body reserves.

5.1.4.2
Liver mass as an index of protein status

Maynard & Loosli (1969) state that stored protein is important because it is the source from which plasma proteins, including hemoglobin, are synthesized and that liver cells contain both protein which is indispensable to their structure and stored protein which is disponsable and can be released to form plasma. McDonald et al., (1969) state that protein reserves in the liver are the first to be mobilized in times of nutritional stress. They also state that the carbohydrate reserves of the body, such as glycogen, are small and relatively constant.

On the basis of these statements it seems reasonable to infer that liver mass may be an index of protein status.

5.1.4.3
Relating condition to reproduction

Condition affects reproduction in two different ways. Firstly, it has been found in cattle (Joubert, 1963; Maynard & Loosli, 1969; McDonald et al., 1969; Lamond, 1970) and in deer (Moen, 1973) that before attaining puberty females must reach a critical mass. Thus a reduction in mass at age, which can be equated with poor condition (Hanks, 1979), will lead to delayed puberty and impaired reproductive performance.

Secondly, it has been found (Lamond, 1970; Buck et al., 1976) that there is also a critical mass above which adult cows are more fertile and below which they are less fertile. Thus condition also affects the reproductive performance of adult females.

5.1.5

Previous Studies on Condition in Lechwe

Child & Von Richter (1969) used Riney's (1960) method to assess condition of lechwe along the Chobe River and found that the animals were generally in "poor condition" (sic). Sayer and Van Lavieren (1975) used the Kidney Fat Index (Riney, 1955) and dressing out percentage on a shot sample of lechwe on the Kafue Flats. They found seasonal variation in the condition of males and females and related this to reproductive status and the flood cycle. Grimsdell & Bell (1975) used the method of Russel et al., (1969) and live weight/body length to assess the condition of a large sample of lechwe, mainly adult females, captured at Lake Bangweulu. They also found seasonal variation in condition and related this to flood cycle, reproductive status and range conditions. Rees (1978c) used the Kidney Fat Index (Riney, 1955) to show seasonal variatio in condition which she related to the reproductive cycle.

5.1.6

The Purposes of this Study with Respect to Condition

Condition was studied with the following objects in mind:

(a) to establish how much variation occurred in the condition of lechwe in the Kwando population;

(b) to consider possible causes for this variation;

(c) to consider the possible effects of condition on reproduction.

5.2

MATERIALS AND METHODS

Hanks (1979) identifies four broad types of condition index: deposited fat reserves, adreno-cortical hypertrophy, blood chemistry and hematology and body growth. All four types of index were used in this study but limited access to refrigeration and field laboratory facilities meant that, for the most part, only techniques which could be applied as part of routine autopsy procedures were used.

5.2.1

Deposited Fat Reserves

Two indices of deposited fat reserves were used. Riney's (1955) Kidney Fat Index (KFI) was calculated in the same way as was done by Attwell (1977) using the formula quoted by Hanks (1979). Variation in KFI was examined in relation to age, reproductive status and season.

Cheatum's (1949a) approach, involving assessment of the fat content of femur bone marrow and referred to as the femur fat index, was also used. With the criteria developed by Sinclair & Duncan (1972) bone marrow was subjectively graded according to colour, opacity and texture and placed into one of three classes denoting good, fair or poor condition (1 - good, 2 = fair, 3 = poor). The percentage frequency of each condition class was examined for each season to see whether seasonal changes occurred in the frequency of any class.

The KFI and femur fat index were obtained from each of the 231 animals shot between January 1975 and May 1977.

5.2.2

Adrenal Mass

Adrenal collections were undertaken only during the latter part of the study. Adrenal mass was obtained from 108 lechwe. After removal, the glands were trimmed of surrounding connective tissue and weighed to the nearest 10^{-1} gram on a triple beam balance. Attempts were made to relate adrenal mass to age, reproductive status and season.

5.2.3

Serum Cholesterol and Packed Cell Volume

In the course of assisting Dr N.Dräger (Dräger & Mehlitz, 1978) in a study of trypanosomiasis in lechwe, blood and serum were obtained from 26 animals: 10 in June 1976, eight in October 1976, eight in January 1977. Packed cell volume (PCV) determinations for all 26 animals were done in the field (within 1-6 hours of collection) with a portable centrifuge on separate blood samples collected by Dr Dräger. Serum from each animal was stored on ice for up to one week in the field and thereafter deep frozen until it was processed during July 1978. Serum cholesterol determinations were done colorimetrically, with the Biodynamics Unitest System in the Natal Parks Board laboratory. Attempts were made to relate serum cholesterol levels and PCV to age, sex and season and to other condition indices.

5.2.4

Body Mass

In addition to body mass two indices of condition based on body mass were used. The first was carcass mass (as defined in sections 5.1.4.1 and 6.2). The second was a carcass mass index (CMI) obtained by dividing carcass mass by body length. Both carcass mass and CMI were obtained from all 231 animals collected between January 1975 and May 1977 and from a further 20 animals shot during 1979. Attempts were made to relate variation in carcass mass and CMI to age, reproductive status and season. The relationship between body mass, carcass mass, CMI and reproductive performance was also considered.

5.2.5

Liver Mass

Data on liver mass were collected only during the latter part of the study. Livers from 112 lechwe were weighed to the nearest gram on a triple beam balance. The data from animals over 3,5 years old were used to determine whether or not seasonal variation in liver mass occurred. To allow for variation in body size the liver mass index (liver mass divided by body length) was also calculated for each adult animal and these data were also examined for evidence of seasonal variation.

5.2.6

Condition and Reproduction

Two approaches were used to investigate the relationship between condition and the attainment of puberty:

(a) the body mass and fecundity of yearling lechwe females in the Kwando and in other populations were compared;

(b) the carcass mass of pregnant and non-pregnant females in the youngest breeding age class in the Kwando population were compared.

To investigate the relationship between condition and fecundity in adult females, a comparison of carcass mass in reproductively active and non-reproductive females was made. Also, in the light of Lamond's (1970) suggestion that "it is possible that the fertility of lactating adult beef cows is a good index of the nutritional status of the herd", a comparison was made of the proportion of pregnant and lactating females in the Kwando lechwe population and in a Uganda kob (*Kobus kob*) population from which similar data were available.

5.2.7

Statistical Procedures

"t-tests" (Scheffler, 1969) were used to determine the significance of differences between sample means. Simple correlation coefficients (Scheffler, 1969) were calculated to test the relationship between variables that were thought to be influenced by a common factor or to be directly related to each other.

5.3

RESULTS AND DISCUSSION

5.3.1

The Relationship between Condition and Age

Because of the relatively small sample sizes in young and old age classes (Table 5.1) only three broad age classes were used for examining the variability of condition with age.

In respect of both reproductive status (Table 6.5) and season of collection (Table 5.1) the samples of females 3,5 - 6 and more than six years old were similar to each other but clearly different to that of females less than 3,5 years old. These differences complicate the interpretation of data. Differences in the season of collection (Table 5.1) of the male samples are apparent but less marked.

Table 5.2 shows age-related differences in the CMI and KFI of females. The CMI of animals less than 3,5 years old was significantly lower than that of either animals 3,5 - 6 ($p<0,001$) or more than six ($p<0,001$) years old. These differences may partly reflect differences in reproductive status and season of collection but are probably mainly a reflection of the demands of growth in younger animals which are passing through a phase of accelerating growth (Moen, 1973).

The CMI of animals over six was significantly lower ($p<0,001$) than that of animals 3,5 - 6 years old. This may indicate that females over six years old enter a phase of negative growth in mass (Moen, op. cit.).

The KFI of females 3,5 - 6 years old was significantly higher than that of both females less than 3,5 and more than six years old ($p<0,01$ in both cases). The most likely explanation for the lower KFI in younger animals is that it reflects the high energy demands of growth (Young & Scrimshaw, 1971; Hanks et al., 1976; Attwell, 1977). The lower KFI of females over six years old indicates that the condition of females declines with increasing age. Table 3.4 shows that there are also clear differences with age in the perinephric fat of females and again suggests that age has a significant influence on the condition of female lechwe.

TABLE 5.1: SEASONAL VARIATION IN THE AGE STRUCTURE OF THE SHOT SAMPLE (numbers shown indicate numbers of animals shot)

AGE	COOL DRY 1975		HOT DRY 1975		RAINS 1975/1976		COOL DRY 1976		HOT DRY 1976		RAINS 1976/1977	
(years)	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
0,25												3
0,5		1						2				
0,75	1	2	1	1			1	1				
1,0						1						1
1,25	1											2
1,5	1		1		1		2	1	1			1
2,0										1		
2,5	1	1	1		1	1	2		1		1	
2,75	1	1					1			1		
3,0	1				1		1	2	3	2		1
4,0	8	3	4		5	3	6	3	4	1	5	4
5,0	6	4	7	4	4	7	4	6	2	4	9	2
6,0	2		4	1	5	4	4	1	1	2	1	1
7,0	3	2	3	1	7	2	3		1		4	2
8,0	3		1		2	1	1	1	1	2		
9,0	1				1		1					1
10+	1	1							3			1
TOTAL	30	15	22	7	27	19	26	17	17	13	20	19

TABLE 5.2: CHANGES WITH AGE IN CARCASS MASS INDEX AND KIDNEY FAT INDEX (FEMALES) (C.L. = confidence limits)

AGE (years) (n)	CMI		KFI	
	Mean	95% C.L.	Mean	95% C.L.
0 - 3 (n = 24)	203,3	193,2 - 213,4	22,9	18,7 - 27,1
3,5 - 6 (n = 81)	265,9	258,5 - 273,4	38,1	30,5 - 45,7
over 6 (n = 37)	247,4	236,4 - 258,4	24,1	18,7 - 34,5

TABLE 5.3: CHANGES WITH AGE IN CARCASS MASS INDEX AND KIDNEY FAT INDEX (MALES) (C.L. = confidence limits)

AGE (years) (n)	CMI		KFI	
	Mean	95% C.L.	Mean	95% C.L.
0 - 3 (n = 26)	216,7	190,9 - 242, 5	17,0	13,4 - 20,6
3,5 - 6 (n = 49)	378,2	366,6 - 389,8	27,2	20,6 - 33,8
over 6 (n = 13)	392,5	373,1 - 431,9	22,0	15,8 - 28,2

TABLE 5.4: CHANGES WITH AGE IN PERINEPHRIC FAT MASS (FEMALES)

Age (years)	n	Mean	95% C.L.
0 - 3	24	22,9	20,8 - 25,0
3,5 - 6	81	54,1	43,1 - 65,1
Over 6	37	35,5	27,5 - 43,5

TABLE 5.5: CHANGES WITH AGE IN PERINEPHRIC FAT MASS (MALES)

Age (years)	n	Mean	95% C.L.
0 - 3	26	18,3	13,3 - 23,3
3,5 - 6	49	46,0	36,0 - 56,0
Over 6	13	42,9	27,9 - 57,9

Tables 5.3 and 5.5 show age related changes in the CMI, KFI and perinephric fat mass in males. CMI of animals less than 3.5 years old was significantly less than in either of the other age groups ($p < 0,001$ in both cases). The only significant difference in KFI was between 3,5 - 6 years old and animals less than three years old ($p < 0,05$). Perinephric fat mass was significantly lower in animals less than 3,5 years old than it was in either of the other two age groups ($p < 0,001$ in both cases). It is assumed that the lower indices in young males again reflect the demands of growth. It appears, however, that older males do not lose condition to the same extent as do older females. This probably reflects the different demands of reproduction in males and females.

Table 5.6 shows changes with age in the adrenal mass of lechwe females and males. In females there was a significant ($p < 0,01$) but not particularly high correlation ($r = 0,476$) between age and adrenal mass. In males the correlation between these parameters was highly significant ($p < 0,001$) and substantial ($r = 0,739$), age accounting for 54,6% of the variation in adrenal mass. From these data it is concluded that there is a tendency, more pronounced in males, for adrenal mass to increase with age.

From the data presented above the condition indices of animals less than 3,5 years old appear to be consistently low in both males and females. For this reason animals less than 3,5 years old were not considered in the sections relating condition to reproductive status and season.

5.3.2

The Relationship between Condition and Reproductive Status

The influence of reproductive status on condition was investigated in females only because no evidence of seasonal changes in male reproductive physiology was found (Chapter 7). Variation in male activity levels in di erent seasons was relatively minor (less than 10% of adult males shot were territorial).

Ideally the relationship between condition and reproductive status would have been assessed by examining females of the same age collected at the same time of the year. In general limited size sample precluded this although some comparisons of animals of a similar age could be made because the condition of animals between 3,5 and 5,5 years old varied little. Separation on the basis of season was more difficult because, for example, very few lactating females were collected in the cool, dry season. However, allowance was made for season of collection

TABLE 5.6: CHANGES IN ADRENAL MASS WITH AGE

(C.L. = confidence limits)

Age (years)	FEMALES			MALES		
	n	Mean	95% C.L.	n	Mean	95% C.L.
0 - 1	1	2,4		6	2,3	1,8 - 2,8
1 - 2	3	3,5	1,5 - 5,5	5	4,0	0,0 - 8,0
2 - 3	9	4,0	3,3 - 4,7	7	3,6	2,1 - 5,1
3 - 4	15	5,3	4,5 - 6,1	5	4,9	2,1 - 7,7
4 - 5	14	6,2	5,1 - 7,3	12	5,7	4,2 - 7,2
5 - 6	6	6,1	5,1 - 7,1	4	5,5	3,0 - 8,0
Over 6	14	6,8	5,8 - 7,8	7	7,5	6,4 - 8,6
Group mean	62	5,6	5,1 - 6,1	46	4,9	4,3 - 5,5

when interpreting differences in the condition of females in different reproductive states.

Tables 5.7 – 5.9 show variation in CMI, KFI and perinephric fat mass in different reproductive status (sample size in Table 5.1). Both CMI and KFI (Tables 5.7 and 5.8) of pregnant females were significantly higher than those of either lactating or non-reproductive females ($p < 0{,}001$ in all cases). The perinephric fat mass (Table 5.9) of pregnant females was significantly higher than that of lactating females ($p < 0{,}001$) and of both pregnant and lactating and non-reproductive females ($p < 0{,}05$). Other differences in Tables 5.7 – 5.9 were not significant.

An examination of the fraction of animals over six years old in each sample suggests that the differences noted above were probably not a function of age. On the other hand Table 5.10 shows marked seasonal changes in reproductive status and because of these the contributions of season and reproductive status to the differences in Tables 5.7 – 5.9 cannot be distinguished.

Because of this difficulty an attempt was made (despite inadequate sample size) to examine differences in the condition of females of more or less the same age, collected in the same season but in a different reproductive state. Tables 5.11 – 5.13 show variation in condition with season and reproductive status in animals 3,5 – 5,5 years old.

A number of differences in Tables 5.11 – 5.13 were statistically significant. During the cool, dry season the CMI of pregnant females (Table 5.11) was significantly higher than that of non-reproductive females ($p < 0{,}01$). During the rains the CMI of pregnant females was significantly higher than that of lactating females ($p < 0{,}05$).

The KFI of pregnant females (Table 5.12) was significantly higher than that of lactating females both during the hot, dry season ($p < 0{,}05$) and during the rains ($p < 0{,}01$).

During the rains the perinephric fat mass of pregnant females (Table 5.13) was significantly greater than that of lactating females ($p < 0{,}05$).

These differences establish clearly that reproductive status has a significant influence on the condition of lechwe females.

TABLE 5.7: THE RELATIONSHIP BETWEEN CMI AND REPRODUCTIVE STATUS OF FEMALES OVER 3,5 YEARS OLD

Reproductive status	Sample size	% of sample over 6 years	Mean	95% confidence limits
Pregnant	65	31	272,3	263,7 - 280,9
Lactating	25	24	245,1	237,1 - 253,1
Pregnant and Lactating	7	57	263,1	230,8 - 295,6
Neither pregnant nor lactating	20	35	237,9	223,2 - 252,6

TABLE 5.8: THE RELATIONSHIP BETWEEN KFI AND REPRODUCTIVE STATUS OF FEMALES OVER 3,5 YEARS OLD

Reproductive status	Sample size	% of sample over 6 years	Mean	95% confidence limits
Pregnant	65	31	43,7	35,7 - 51,7
Lactating	25	24	14,0	13,4 - 15,6
Pregnant and Lactating	7	57	23,4	9,6 - 37,2
Neither pregnant nor lactating	20	35	21,6	14,5 - 28,7

TABLE 5.9: THE RELATIONSHIP BETWEEN PERINEPHRIC FAT MASS AND REPRODUCTIVE STATUS OF FEMALES OVER 3,5 YEARS OLD

Reproductive status	Sample size	Sample over six years old	Mean perinephric fat mass	95% confidence limits
Pregnant	65	31	65,2	52,2 - 68,2
Lactating	25	24	23,5	19,5 - 27,5
Pregnant and lactating	7	57	33,0	15,0 - 51,0
Neither pregnant nor lactating	20	35	34,6	22,6 - 46,6

TABLE 5.10: SEASONAL CHANGES IN THE REPRODUCTIVE STATUS OF FEMALES OVER 3.5 YEARS OLD (all numbers in percentages)

	COOL DRY				HOT DRY				RAINS			
YEAR	P	L	P & L	NP	P	L	P & L	NP	P	L	P & L	NP
1975/1976	85	5	0	10	29	38	10	23	39	30	17	13
1976/1977	90	0	0	10	46	18	0	36	35	40	5	20

P : Pregnant
L : Lactating
P&L : Pregnant and lactating
NP : Neither pregnant nor lactating

TABLE 5.11: VARIATION WITH SEASON AND REPRODUCTIVE STATUS IN THE CARCASS MASS INDEX FOR FEMALES 3,5 – 5,5 YEARS OLD
(C.L. = confidence limits)

Reproductive status	COOL DRY			HOT DRY			RAINS		
	n	Mean	95% C.L.	n	Mean	95% C.L.	n	Mean	95% C.L.
Pregnant	21	285	271–299	5	274	227–321	10	284	257–311
Lactating	1	257		6	237	217–257	7	251	239–263
Neither pregnant nor lactating	2	257	154–268	4	250	199–301	6	262	245–279

TABLE 5.12: VARIATION WITH SEASON AND REPRODUCTIVE STATUS IN KIDNEY FAT INDEX OF FEMALES 3,5 – 5,5 YEARS OLD
(C.L. = confidence limits)

Reproductive status	COOL DRY			HOT DRY			RAINS		
	n	Mean	95% C.L.	n	Mean	95% C.L.	n	Mean	95% C.L.
Pregnant	21	67,3	49,3-85,3	5	19,6	13,6-25,6	10	62,9	33,9-91,
Lactating	1	36,0		6	13,3	10,3-16,3	7	16,7	11,7-21,
Neither pregnant nor lactating	2	15,0	2,0-28,0	4	17,0	4,0-30,0	6	33,2	9,2-57,

TABLE 5.13: VARIATION WITH SEASON AND REPRODUCTIVE STATUS OF PERINEPHRIC FAT MASS IN FEMALES 3,5 – 5,5 YEARS OLD (C.L. = confidence limits)

Reproductive status	COOL DRY			HOT DRY			RAINS		
	n	Mean	95% C.L.	n	Mean	95% C.L.	n	Mean	95% C.L.
Pregnant	21	94,8	68,8–120,8	5	24,8	14,8–34,8	10	87,1	39,1–135,1
Lactating	1	42,0		6	18,0	14,0–22,0	7	23,6	18,6–28,6
Neither pregnant nor lactating	2	17,5	0,0–44,5	4	21,2	17,2–25,2	6	49,8	24,8–74,8

TABLE 5.14: SERUM CHOLESTEROL AND PCV VALUES FROM KWANDO LECHWE (C.L. = confidence limits)

Season (n)	Statistic	Serum Cholesterol (mg %)	Packed cell volume %
Cool dry 1976 (n = 10)	Mean	66	38
	95% C.L.	60,4 – 71,7	33,7 – 42,3
	Range	55 – 85	32 – 50
Hot dry 1976 (n = 8)	Mean	62	36
	95% C.L.	46,2 – 77,8	30,3 – 41,8
	Range	50 – 85	22 – 43
Rains 1976/1977 (n = 8)	Mean	42	33
	95% C.L.	34,5 – 49,5	26,3 – 39,7
	Range	30 – 52	26 – 42

For the sake of completeness adrenal mass was compared in females in different reproductive states but no significant differences were found.

5.3.3

Seasonal Variation in Condition

To understand seasonal variation in condition it is necessary to consider not only variation in the demands for energy and nutrients but also changes in their supply. Some information on variation in pasture quality was collected during this study (Table 2.11) but not sufficient to produce a satisfactory understanding of important changes in the food supply. I have therefore relied mainly on the literature to develop a simple model of what were likely to have been the most important seasonal changes in the food supply of the study area.

One important type of change is a decline in the dry matter digestibility of herbage during the cool, dry season (Animal Production Research Unit, 1977). Other important types of change are illustrated in Figure 5.1, which shows monthly variation in crude protein content and nitrogen free extract i.e. carbohydrate (McDonald _et al_., 1969) in Rhodesia (Van Niekerk, 1974).

It appears likely that the decline in crude protein during the cool, dry season is a function of temperature and/or day length rather than of soil moisture (Animal Production Research Unit, 1978). The rapid rise in crude protein at the beginning of the rains (November; Topps, 1968) illustrates the close relationship between rainfall i.e. soil moisture and pasture quality once temperature and/or day length cease to be limiting.

The conclusion that has generally been drawn from the type of pattern illustrated in Figure 5.1 is that it is protein rather than energy which is the limiting factor for grazing ruminants under these conditions (Van Niekerk, 1974; Field, 1976; Pratt & Gwynne, 1977).

On the basis of the trends illustrated above and data on pasture quality and flood regime collected in this study (Chapter 2) the following broad pattern of annual variation in the food supply for lechwe on the Kwando is postulated:
during the rains quality is generally high and quantity is not limiting;
during the cool, dry season quality declines, particularly in drier areas (zone 5 and parts of zone 4) and quantity is reduced in zones 2, 3 and

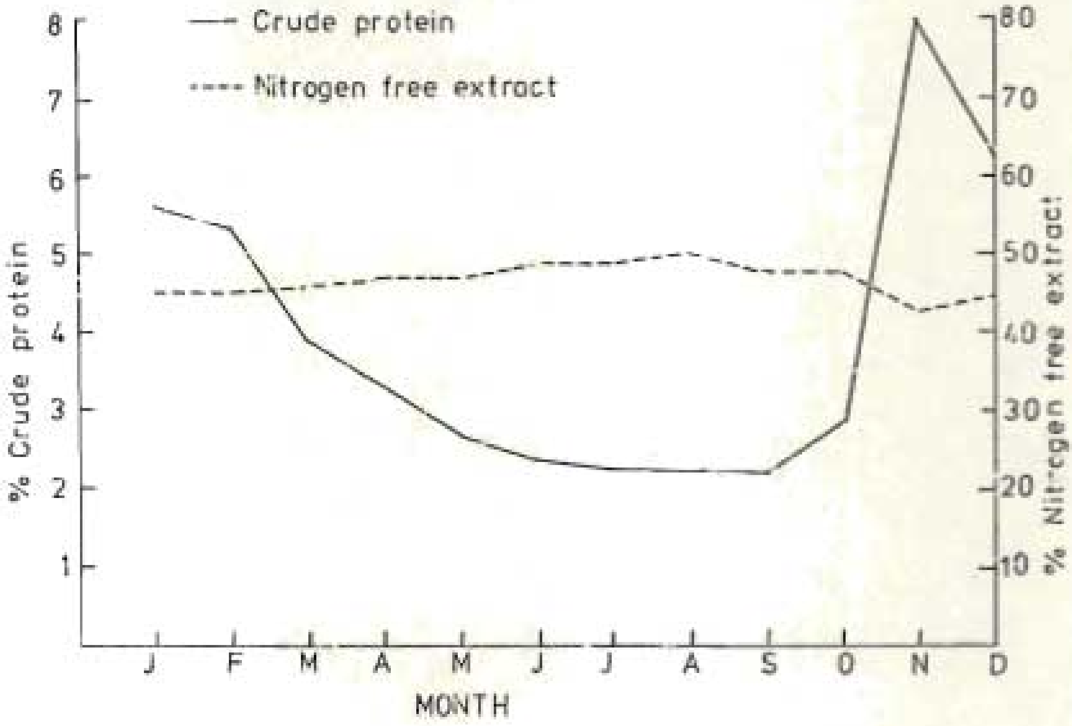

Figure 5.1: Monthly variation in crude protein and nitrogen free extract of grasses in Rhodesia 1961-1968. (after Van Niekerk, 1974)

parts of 4 because of flooding;
during the hot, dry season quality improves where soil moisture is adequate (zones 2, 3 and parts of 4) and the quantity of food available in zones 2 and 3 may increase as flood waters recede.

5.3.3.1

Deposited Fat Reserves

Figure 5.2 shows the KFI of females over 3,5 years old in different seasons. The following seasonal differences in KFI were statistically significant:
the KFI in the 1975 cool, dry season was highes than in all other seasons ($p< 0,001$ in all cases);
the KFI in the 1975 hot, dry season was lower than in all other seasons (significance ranged from $p< 0,05$ to $p< 0,01$) except the 1976 hot, dry season;
the KFI in the 1976 hot, dry season was lower than in the 1976 cool, dry season ($p< 0,01$).

The KFI can be distorted by seasonal variation in kidney mass (Dauphine, 1975) and it is therefore necessary to check kidney mass for seasonal variation (Hanks, 1979). Figure 5.3 shows seasonal variation in the kidney mass of females over 3,5 years old. The only statistically significant seasonal difference in kidney mass was between the rains of 1975/1976 and the cool, dry season of 1976 ($p< 0,001$).

To check the effect of variation in kidney mass on KFI, seasonal variation in perinephric fat mass (trimmed) was examined (Figure 5.4). The following seasonal differences were statistically significant:
perinephric fat mass in the cool, dry season 1975 was greater than all other seasons ($p< 0,001$ in all cases);
perinephric fat mass was greater during the 1975/1976 rains and the 1976 cool, dry season than in either hot, dry season ($p< 0,001$ in each case).

These differences and a comparison of Figures 5.2 and 5.4 indicate that variation in kidney mass did not greatly distort the pattern of change in fat reserves that was indicated by changes in perinephric fat mass.

Figures 5.5 – 5.7 show variation in KFI, kidney mass and perinephric fat mass in males. Although there were no statistically significant seasonal changes in KFI or perinephric fat mass in males, it is apparent that the trends of seasonal change in these indices are the same in males and females.

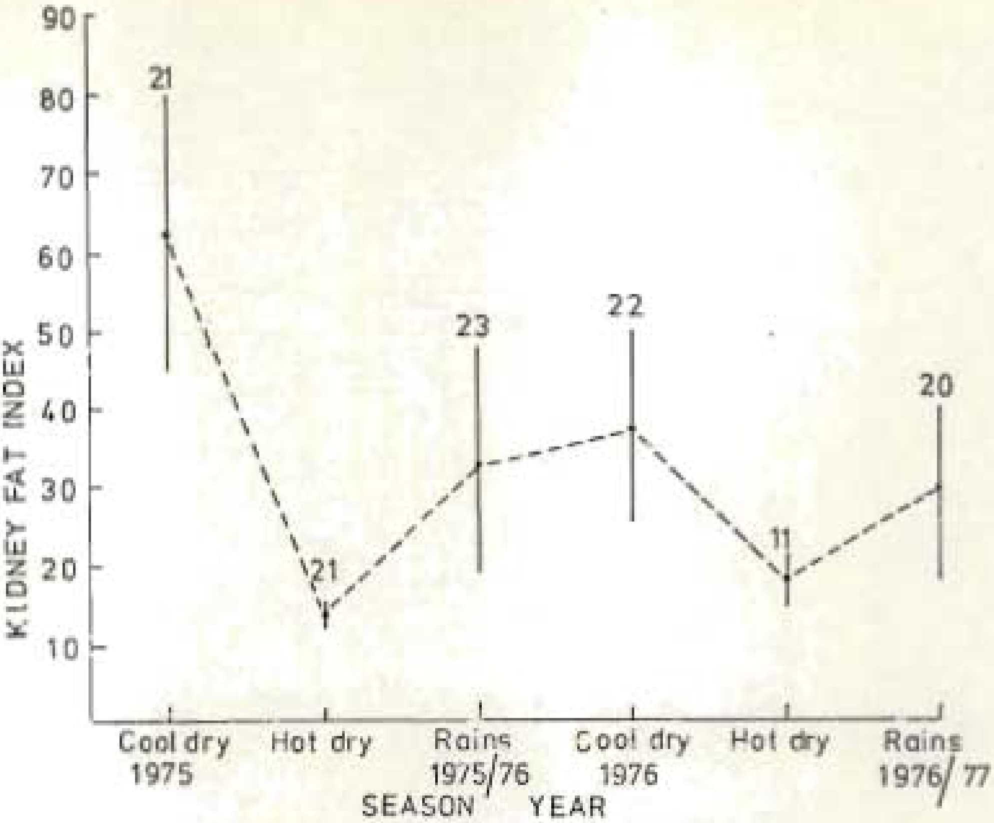

Figure 5.2: Seasonal changes in kidney fat index; females over 3,5 years old. Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

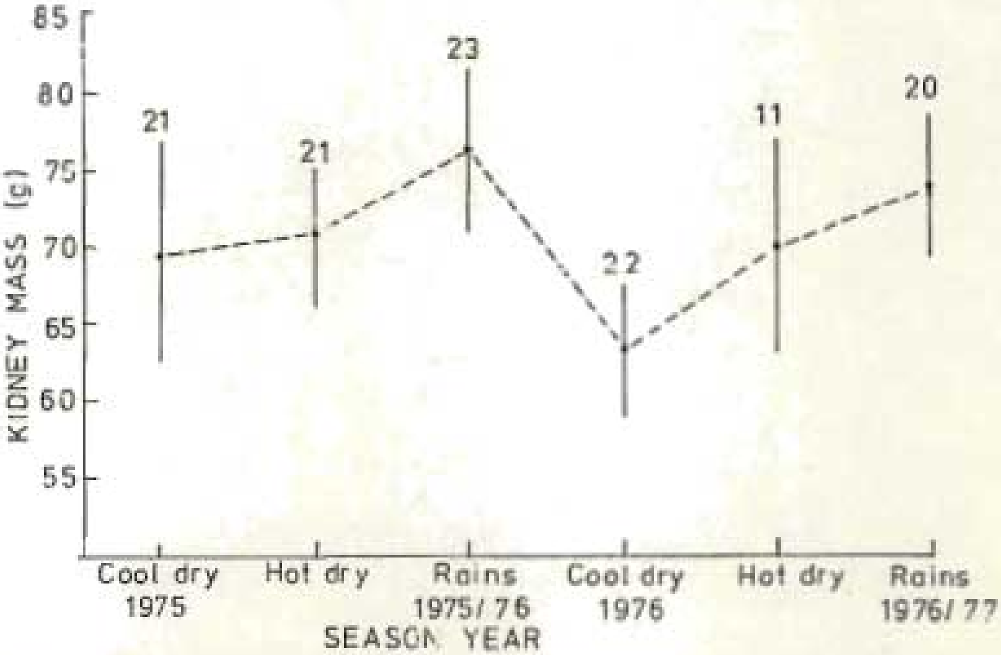

Figure 5.3: Seasonal changes in kidney mass; females over 3,5 years old. Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

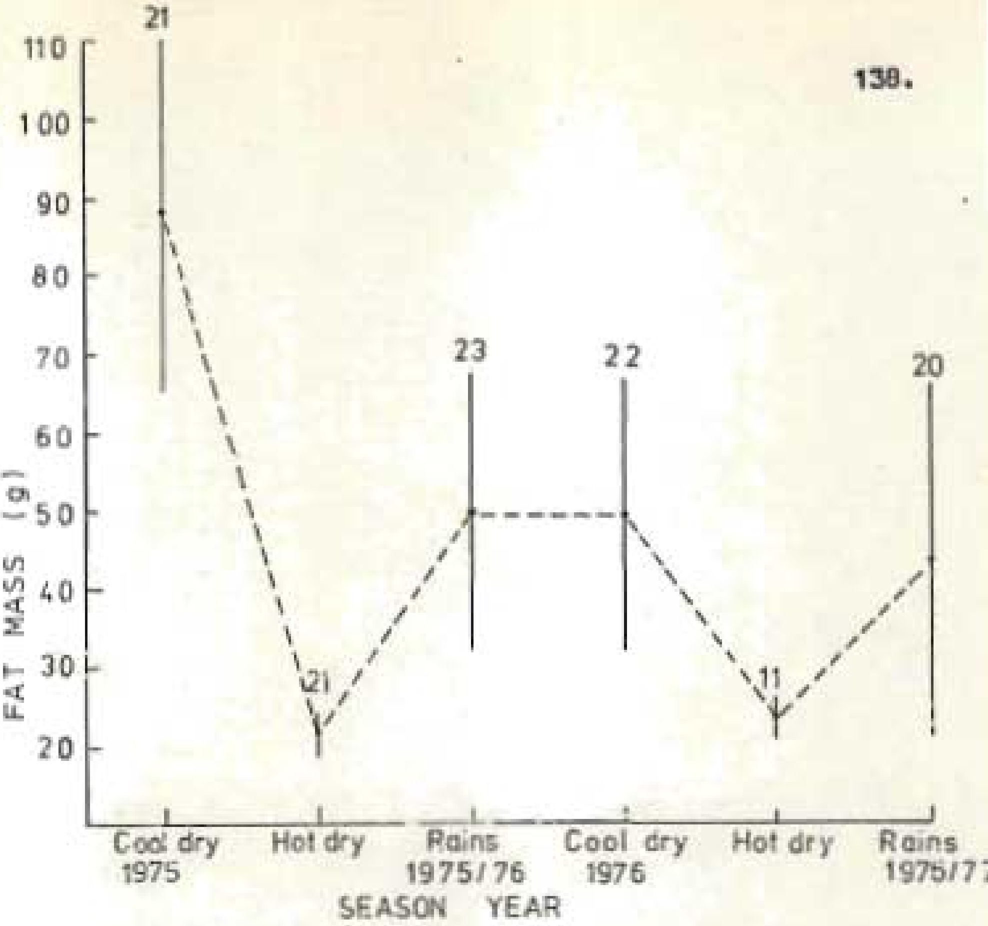

Figure 5.4: Seasonal changes in perinephric fat mass; females over 3.5 years old. Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

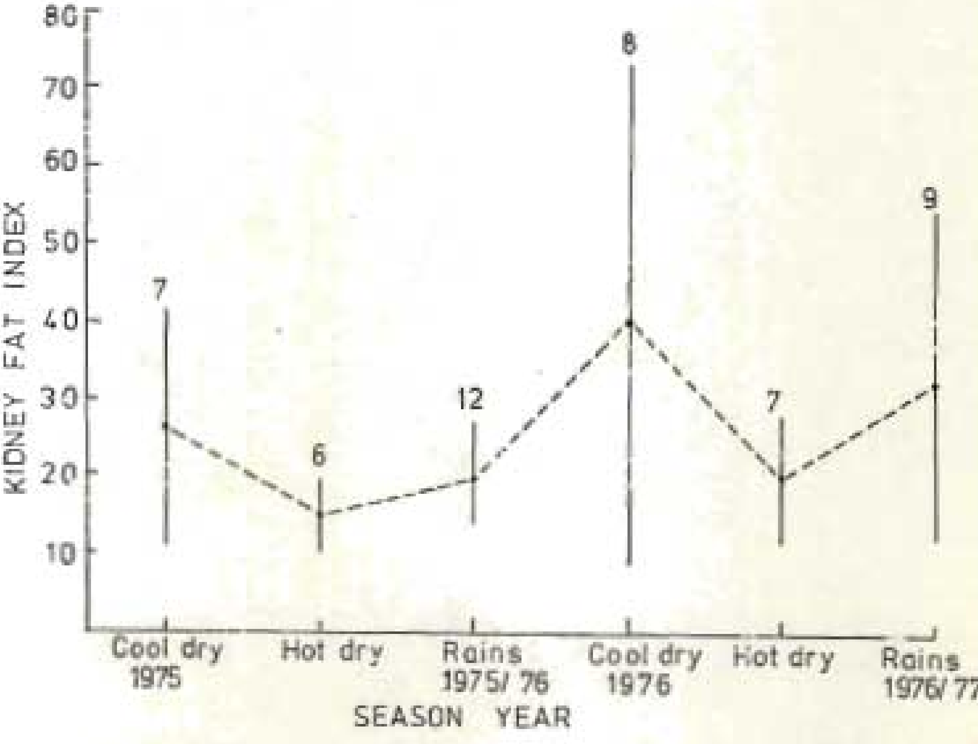

Figure 5.5: Seasonal changes in kidney fat index; adult males. Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

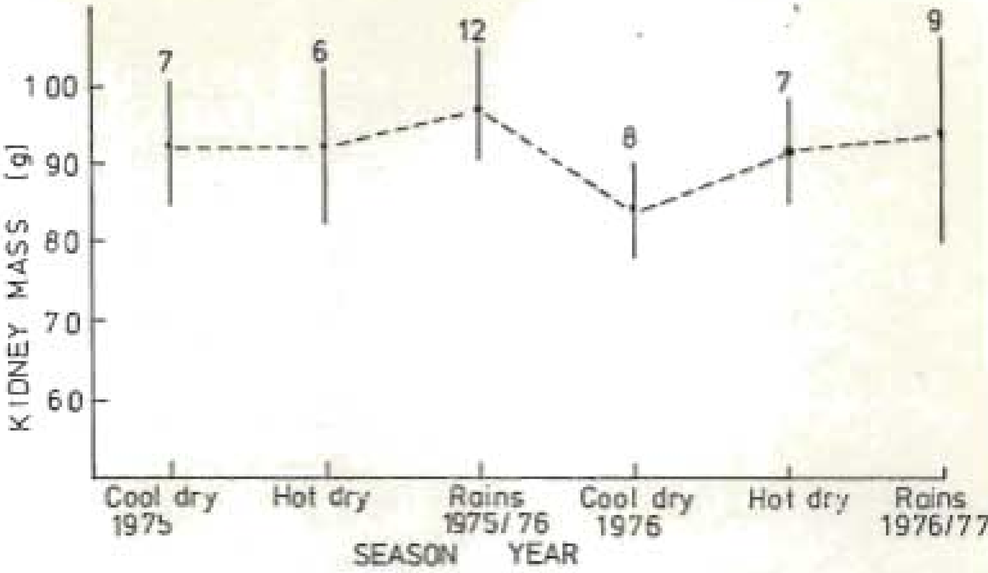

Figure 5.6: Seasonal changes in kidney mass (adult males). Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

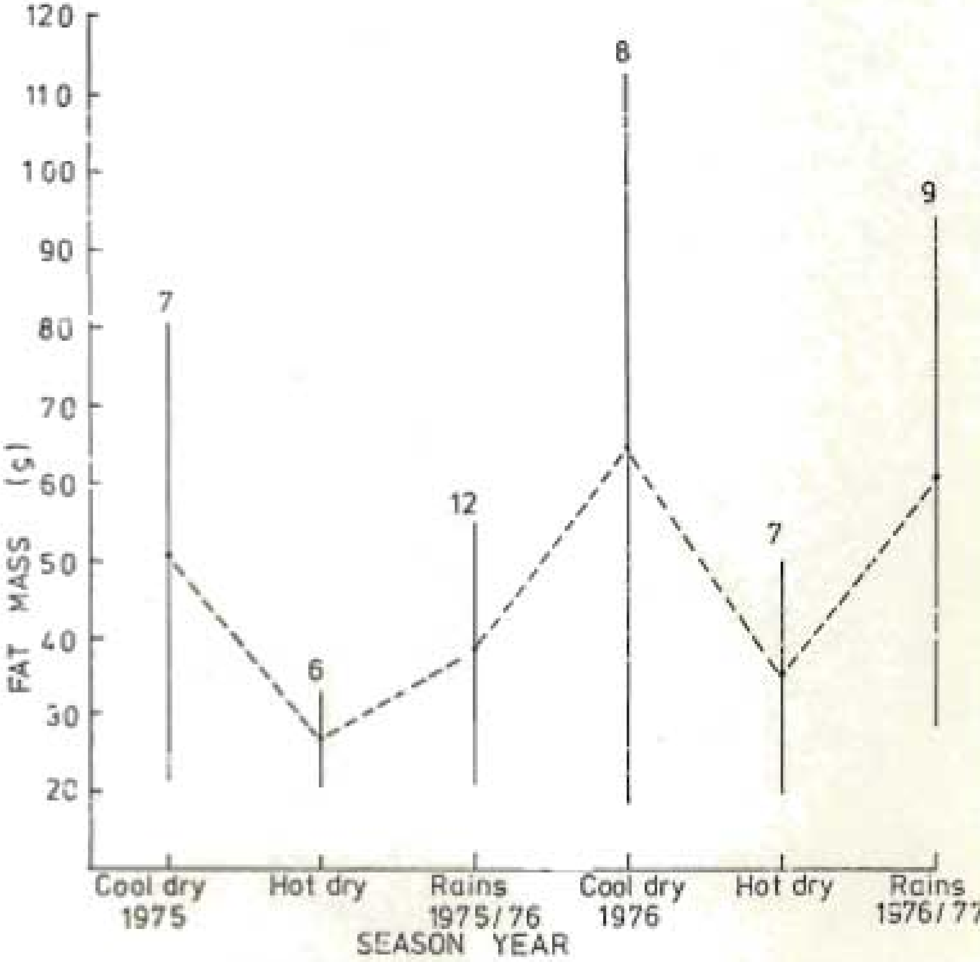

Figure 5.7: Seasonal changes in perinephric fat mass (males). Dashed line joins means, vertical lines indicate 95% confidence limits. Numbers indicate sample size.

Tables 5.15 and 5.16 show changes with season in the femur fat indices of females and males. In females variation in femur fat index followed the same seasonal pattern as KFI and perinephric fat mass. In males the femur fat index showed no consistent pattern of variation. This may have been a reflection of small sample size.

As fat serves purely as an energy store (McDonald _et al._, 1969) changes in fat reserves presumably reflect changes in either the demand for or the supply of energy. In female lechwe the decline of fat reserves during the hot, dry season probably reflects both the poor quality of pastures and the high energy demands of late pregnancy and lactation (Moen, 1973; Robbins & Moen, 1975). In lechwe males the slight decline in fat reserves during the hot, dry season is probably largely a reflection of poor pasture quality in the drier areas in which they tend to feed (Chapter 4).

There is some conflict in the literature about the validity of using either KFI (Smith, 1970; Monson _et al._, 1974) or visual estimation of femur fat content (Bear, 1971; Sinclair & Duncan, 1972) as an index of fat reserves. For this reason the findings in relation to fat reserves are not regarded as being definitive.

5.3.3.2

Serum cholesterol and packed cell volume (PCV)

Neither mean serum cholesterol nor mean PCV values differed significantly between sexes or between age classes. For this reason and because of small sample sizes, sex and age classes were grouped for the purposes of comparison between the seasons of collection.

Table 5.14* shows seasonal changes in serum cholesterol and PCV values. The mean serum cholesterol value, 60 mg/100 ml, was in the lower range of values reported by Coblentz (1975) and Franzmann & LeResche (1978) but higher than values reported by Warren & Kirkpatrick (1978). The difference between the mean serum cholesterol values in the cool, dry season 1976 and in the rains 1976/1977 was highly significant ($p < 0.001$). This difference is compatible with the suggestion that cholesterol levels may relate to the quality of recent forage intake (Franzmann & LeResche, 1978) because all the animals in the sample for the 1976/1977 rains were collected during the middle of a month long summer drought. However the relationship between serum cholesterol values and food quality is by no means well established (Hanks, 1979) and there was no

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TABLE 5.15: CHANGES WITH SEASON IN THE FEMUR FAT INDEX FOR FEMALES OVER 3,5 YEARS OLD

	Cool dry			Hot dry			Rains		
Year	%1	%2	%3	%1	%2	%3	%1	%2	%3
1975/1976	100	0	0	48	38	14	65	30	5
1976/1977	100	0	0	55	36	9	55	40	5

TABLE 5.16: CHANGES WITH SEASON IN THE FEMUR FAT INDEX FOR MALES OVER FOUR YEARS OLD

	Cool dry			Hot dry			Rains		
Year	%1	%2	%3	%1	%2	%3	%1	%2	%3
1975/1976	81	19	0	86	0	14	64	36	0
1976/1977	93	7	0	31	69	0	53	29	18

correlation between serum cholesterol values and either KFI or CMI.

PCV values did not differ significantly between seasons and were not significantly correlated with either KFI or CMI. They were, however, correlated with serum cholesterol levels ($r = 0,466$; $p < 0,05$). At present levels of understanding (see Hanks, 1979) the implications of this correlation are obscure and no conclusions can be offered on the value of serum cholesterol and PCV as condition indices.

5.3.3.3

Adrenal mass

There were no significant seasonal differences in adrenal mass in females over 3,5 years old. In adult males mean adrenal mass during the rains was significantly higher than during the cool, dry season ($p < 0,05$) but the age structure of the sample of males during the rains (50% were over six years old) made it impossible to distinguish between the effects of age and season. The results of attempting to relate adrenal mass to season were therefore inconclusive. Moreover in neither sex was there a significant relationship between adrenal mass and either CMI or KFI. The results of this study thus provide no evidence of a relationship between adrenal mass and condition and further study is clearly necessary if this relationship is to be understood (Hanks, 1979).

5.3.3.4

Body mass and CMI

Figures 5.8 and 5.9 show seasonal changes in carcass mass and CMI of females over 3,5 years old. The pattern of change in carcass mass and CMI is similar to that in KFI and perinephric fat mass - a distinct trough during the hot, dry season. The decline in carcass mass and CMI no doubt also reflects the heavy demands of late pregnancy and of lactation.

Figure 5.9 shows that the amplitude of seasonal change is considerably reduced by relating carcass mass to skeletal size. Use of total length may be an over-correction in the sense that it includes head length although head mass is not included in carcass mass. Atlas length (from the base of the tail to the atlas) could be used, but this measurement was not taken. As an experiment, mean skull length (after Biggs, 1979) was subtracted from total length in adult males and CMI calculated using the remaining length. The difference between the highest and lowest

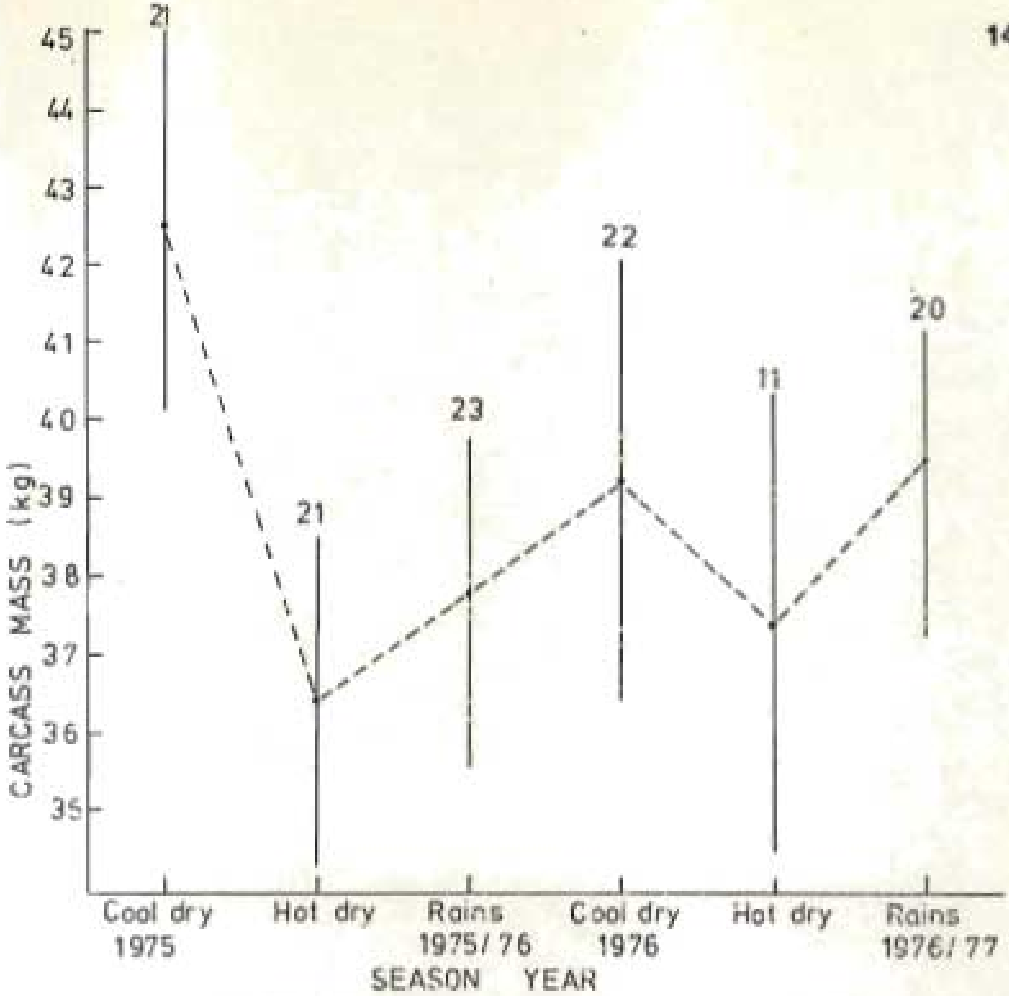


Figure 5.8: Seasonal changes in carcass mass (females over 3,5 years old). Dashed line joins means. Vertical lines indicate 95% confidence limits. Numbers indicate sample size.

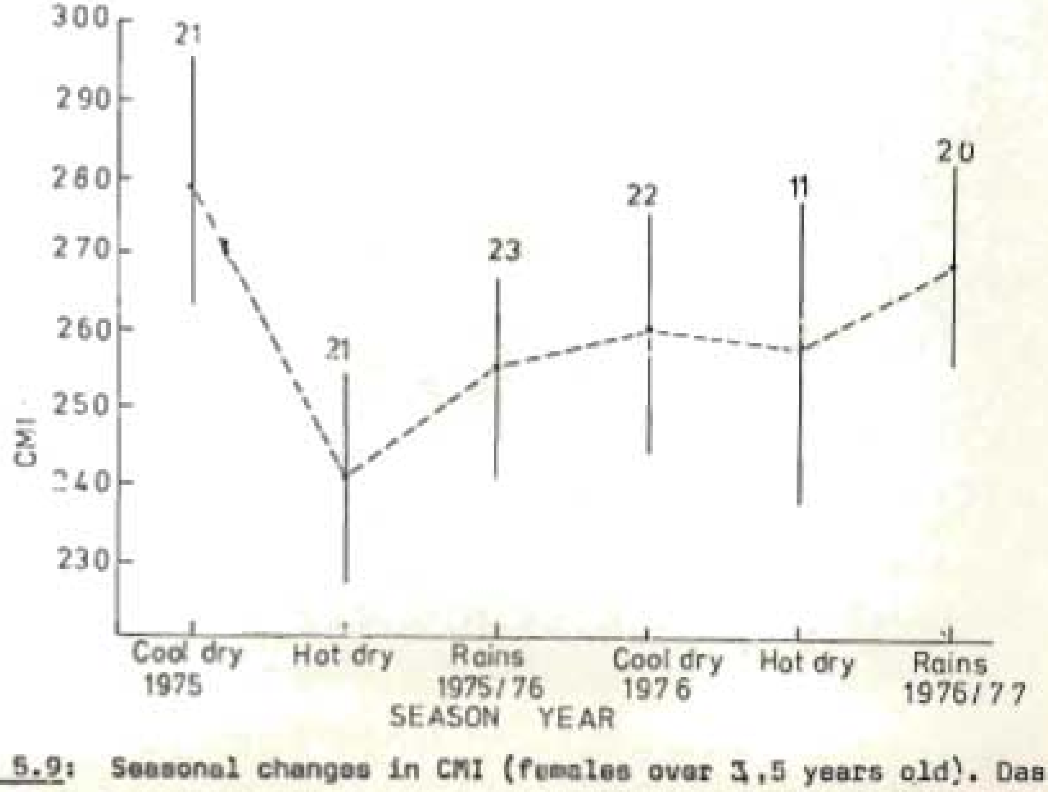


Figure 5.9: Seasonal changes in CMI (females over 3,5 years old). Dashed line joins means. Vertical lines indicate 95% confidence limits. Numbers indicate sample size.

yearly values increased by 9% in the first year and 33% in the second year. This suggests that the use of atlas length would facilitate seasonal comparisons.

There was no consistent pattern of change in carcass mass or CMI of adult males (over four years old). However in each yearly cycle carcass mass and CMI were highest during the rains, the period when pasture quality is generally high.

Table 5.17 shows that the carcass mass of both females and males declined significantly in the second year of study. This decline is attributed to a general rise in flood levels at the beginning of the study which forced animals to move into higher floodplain areas with poorer pasture quality. Males, which fed in drier areas (Chapter 4) were more severely affected than were females.

Some support for this suggested explanation was obtained by comparing the CMI of females in three different hot, dry seasons (Figure 5.10). In 1979 flood levels had declined to a marked extent after a very poor 1978/1979 rainy season. The CMI of females was significantly higher in 1979 than in either 1975 ($p < 0,001$) or 1976 ($p < 0,01$). The difference between the CMI of females in 1975 and 1976 is explained by the occurrence of regular but light showers and generally less severe conditions than during the 1976 hot, dry season.

Direct evidence of the effect of pasture quality on CMI was obtained from a small experiment conducted in September/October 1979. Of a sample of 11 females, six were collected from burnt areas with fresh green grass and five were collected from unburnt areas in which much of the herbage was moribund. All animals were 3,5 - 6 years old and were in the latter stages of pregnancy. The CMI of females from burnt areas was 307 while that of females from unburnt areas was 266. This difference was highly significant ($p < 0,01$).

5.3.3.5

Liver mass

Liver mass was not routinely determined and data from 3 - 4 year old males have been included in this analysis to supplement those from adult males. This was considered reasonable because by this age liver mass was well within the adult range. To allow for differences in

TABLE 5.17: VARIATION IN CARCASS MASS (kg) BETWEEN THE FIRST AND SECOND YEARS OF THE STUDY

Class	Year	n	Mean	Standard error	t	p
Adult female	1975/1976	64	39,31	0,76	12,326	< 0,001
	1976/1977	60	37,72	0,65		
Adult male	1975/1976	21	66,55	1,51	13,476	< 0,001
	1976/1977	26	61,20	1,21		

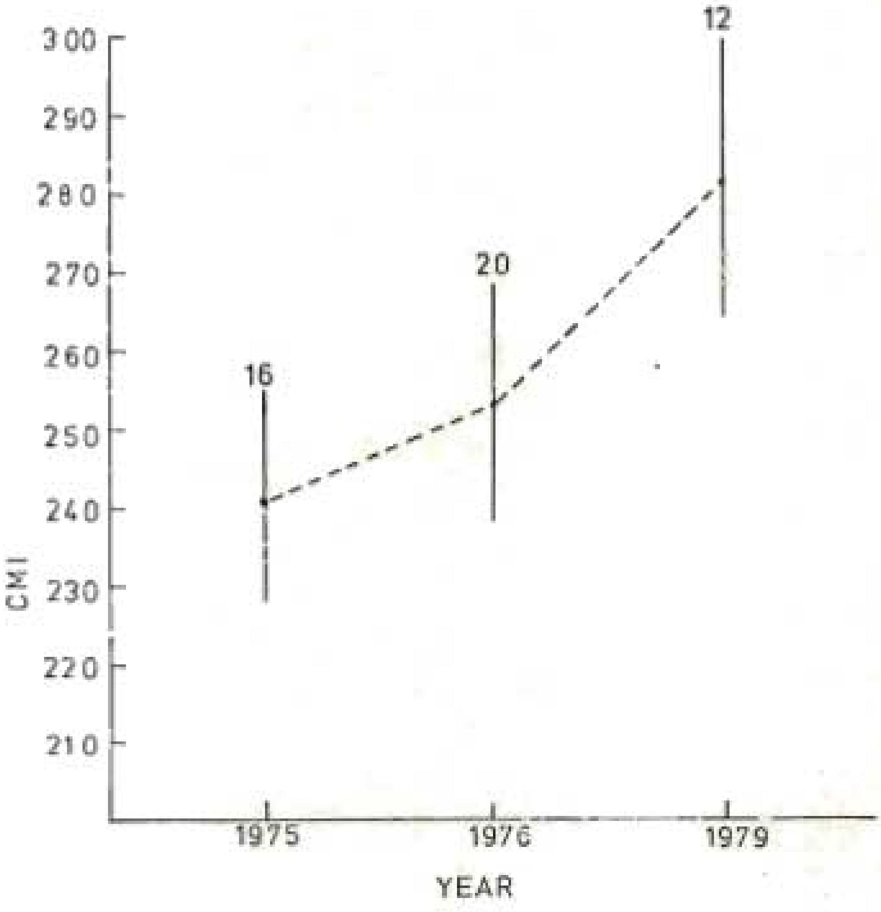


Figure 5.10: Variation in the CMI of females over 3,5 years old in the hot, dry seasons of different years. Dashed line joins means. Vertical lines indicate 95% confidence limits. Numbers indicate sample size.

body size a liver index (liver mass (g) over total length (m)) was used and seasonal variation in this index, as well as in liver mass itself, was considered.

Seasonal variation in liver mass and liver index for females and males is shown in Tables 5.18 and 5.19. Seasonal variation in female liver index is illustrated in Figure 5.11.

In females, both liver mass and liver index were significantly higher during the rains than in either the cool, dry season or the hot, dry season ($p < 0{,}001$ in all cases). Liver mass was significantly higher during the hot, dry season than during the cool, dry season ($p < 0{,}02$). Liver index was also higher in the hot, dry than in the cool, dry season ($p < 0{,}001$).

In males both liver mass ($p < 0{,}01$) and liver index ($p < 0{,}001$) were significantly higher during the rains than during the cool, dry season. Both values were also higher during the rains than in the hot, dry season ($p < 0{,}001$ in both cases).

A comparison of Figure 5.11 with Figure 5.1 indicates that changes in liver index may be a reflection of variability in protein supply. Both are lowest in the cool, dry season; higher in the hot, dry season and highest during the rains.

If protein supply does influence liver mass in this way it should have other similar effects. To test the possibility that carcass mass and kidney mass were affected in the same way as liver mass, regressions were done of carcass mass on liver mass and kidney mass on liver mass.

The equations for carcass mass / liver mass (y = carcass mass) were:

Females: $y = 0{,}013x + 26{,}170$ ($n = 41$; $r = 0{,}47$; $p < 0{,}001$)

Males: $y = 0{,}024x + 30{,}715$ ($n = 24$; $r = 0{,}656$; $p < 0{,}001$)

The equations for kidney mass / liver mass (y = kidney mass) were:

Females: $y = 0{,}063x + 82{,}555$ ($n = 41$; $r = 0{,}537$; $p < 0{,}001$)

Males: $y = 0{,}128x + 34{,}987$ ($n = 24$; $r = 0{,}613$; $p < 0{,}001$)

TABLE 5.18: SEASONAL VARIATION IN LIVER MASS AND LIVER INDEX OF FEMALES OVER THREE YEARS OLD (C.L. = confidence limits)

SEASON	SAMPLE SIZE	STATISTIC	LIVER MASS (g)	LIVER INDEX
Cool, dry 1976	9	Mean	834	543
		95% C.L.	708 - 961	469 - 617
Hot, dry 1976	14	Mean	891	617
		95% C.L.	799 - 983	560 - 674
Rains 1976/1977	18	Mean	996	688
		95% C.L.	914 - 1078	642 - 734

TABLE 5.19: SEASONAL VARIATION IN LIVER MASS AND LIVER INDEX OF MALES OVER THREE YEARS OLD (C.L. = confidence limits)

SEASON	SAMPLE SIZE	STATISTIC	LIVER MASS (g)	LIVER INDEX
Cool, dry 1976	2	Mean	998	606
		95% C.L.	796 - 1200	111 - 1101
Hot, dry 1976	11	Mean	1010	663
		95% C.L.	873 - 1147	584 - 742
Rains 1976/1977	14	Mean	1190	773
		95% C.L.	1054 - 1326	696 - 850

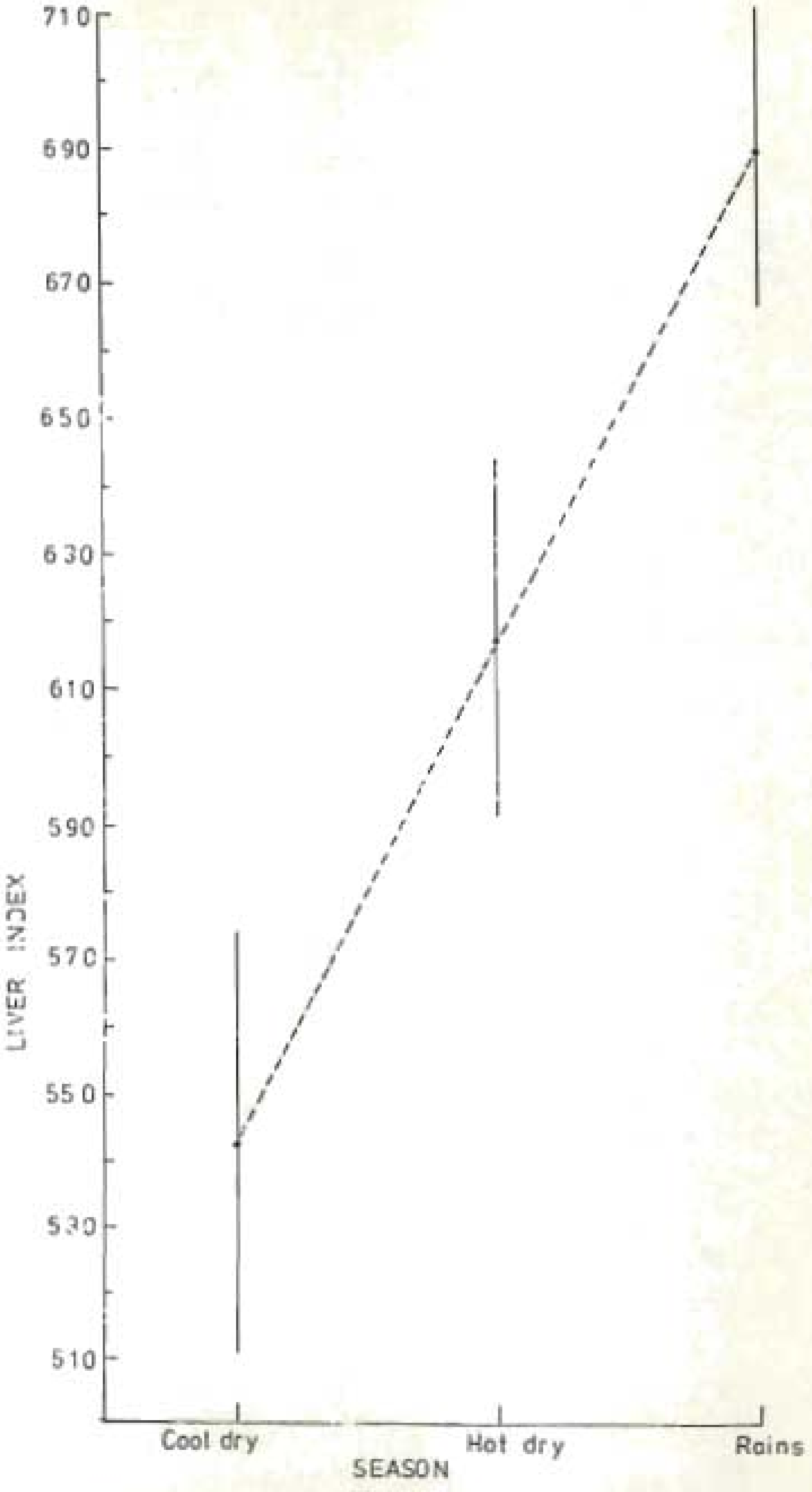


Figure 5.11: Seasonal variation in the liver index of females over 3.5 years old. Dashed line joins means. Vertical lines exten ± one standard error around the mean.

These results are consistent with a common influence of protein supply on liver mass, carcass mass and kidney mass. It is interesting to note that Dauphine (1975) has suggested that cervids generally experience a rise in kidney mass during summer - the time of optimum feeding conditions. The lower correlation in females may reflect the demands of the female reproductive cycle, which affect individual animals at different times of the year.

On the basis of seasonal variation in liver mass and liver index and the possible relationship between this variation and protein supply, I suggest that a more detailed investigation of changes in liver mass would be worthwhile. This simple measurement may provide a useful index of protein status. Such an index is desirable because of the likely importance of protein as a limiting factor (Van Niekerk, 1974; Field, 1976) and because, although it is widely used as an index of nutritive status (Klein, 1970) body mass is not a precise index of nutritional status for the reasons given above.

5.3.4

The Relationship between Condition and Reproduction

In a shot sample from the Kafue lechwe population Robinette & Child, (1964) found two yearlings that were pregnant. The individual mass of these animals (less gravid uterus) was 66,5 and 70 kilograms. The individual mass of three Kafue yearlings which had not conceived was 49, 54 and 60 kilograms. The individual mass of seven Kwando yearlings, none of which had conceived, was 42, 42, 44, 45, 47, 48 and 53 kilograms. The mean mass of pregnant Kafue yearlings (68,3 kilograms) was 49% higher than that of the Kwando yearlings (45,9 kilograms). This difference was highly significant ($p < 0,001$).

There was also a highly significant difference ($p < 0,001$) between the mean mass of the Kwando yearlings and that (52,6 kilograms) of 30 Bangweulu yearling females, of which 66,7% were pregnant (Grimsdell & Bell, 1975). These results clearly show a reduction in both mass at age and fecundity in Kwando yearling females. The likely cause of this situation is nutritional stress (Sadleir, 1969 a and b; Caughley, 1977) due to prevailing high flood levels during the study period. High flood levels are discussed in more detail below.

Comparison of carcass mass and CMI of pregnant and non-pregnant females in the youngest breeding class (2 - 3 year olds) also suggested a relationship between condition and reproduction. Thirteen animals in the sample of females were between two and three years old. Of these seven were pregnant and the remainder had not conceived. The mean carcass mass of pregnant females (33,3 kilograms) was significantly higher ($p < 0,001$) than that (27,7 kilograms) of females which had not conceived. The CMI of pregnant females (230) was also significantly ($p < 0,001$) higher than that (207) of females which had not conceived.

An unknown fraction of the difference in carcass mass is attributable to pregnancy anabolism (McDonald, et al., 1969) but this does not exclude the possibility of there being a relationship between condition and reproduction in the form of a critical body mass for successful conception. An association between mass and puberty has been shown, for example, in red deer (Cervus elaphus). Lowe (1971) found that as body mass of red deer on the Island of Rhum declined, the proportion of two-year old hinds attaining puberty declined from 64,1 ± 15,4% to 31,4 ± 10%. In Norway, Wegge (1975) found that in a relatively fertile area 40% of 2,5 year-old hinds attained puberty, whereas in a less fertile area no 2,5 year-old hinds attained puberty. The animals from the more fertile area were significantly heavier than those from the less fertile area.

In adult females (more than 3,5 years old) there were highly significant differences in the carcass mass and CMI of reproductive and non-reproductive females. The carcass mass of reproductive females ($n=105$) was 39,7 kilograms while that of non-reproductive females ($n=11$) was 31,1 kilograms ($t = 49,93$; $p < 0,001$). The mean CMI of reproductive females was 255, while that of non-reproductive females was 217 ($t = 41,666$; $p < 0,001$). These data clearly confirm the possibility that in adult lechwe females there is a relationship between mass and fertility, or, in other words, condition and reproduction.

A possible sign of nutritional stress in the Kwando lechwe population was that of 41 lactating females only eight (20%) were also pregnant. By comparison over 50% of lactating Uganda kob females collected by Morrison (1971) were also pregnant.

The carcass mass, CMI, KFI and perinephric fat mass of females over 3,5 years old were significantly higher during the cool, dry season of 1975 than in all other seasons up to and including the rains of 1976/1977 ($p < 0,001$ in every case). This suggests the possibility that the observed influence of condition on the reproductive performance of female lechwe on the Kwando was a reflection of the elevated flood levels which prevailed through much of this study and forced lechwe into higher areas. A decline in pasture quality along the gradient of increasing dryness (i.e. from lower areas to higher areas) has been demonstrated (Table 2.11) and the evidence for the occurrence of high flood levels during this study was substantial. It included the following:

an aerial photograph taken in December 1974 (a month before this study began) showed that the intensive study area was then completely dry - large parts of it flooded in March 1975 and remained flooded until October 1979;

there were many termitaria in areas that were flooded to over one metre in depth for the four years that I knew the area - these could only have been built when the areas in question were dry;

in several places trees (Acacia sp.) over five metres tall were killed by flooding - these could only have reached their observed size during a fairly protracted dry period.

Similar effects of pasture quality on reproduction have been noted in the Kenai moose population (Oldemeyer et al., 1977). The magnitude of these effects is illustrated by Table 5.20, which shows to what extent the fecundity of young females on the Kwando was depressed during this study. The influence of the fecundity of young females on the population's growth rate is examined in Chapter 10 (Population Status).

5.3.5

Conclusions

Two main conclusions were drawn from the results presented in this chapter. Firstly, that variation in condition cannot be understood without considering carefully at least the age, reproductive status and season of collection of the animals in question. Many studies have considered one or other of these aspects in part or in full but I am not aware of any published study in which all have been fully investigated.

TABLE 5.20: THE PERCENTAGE OF FECUND FEMALES IN THREE DISCRETE LECHWE POPULATIONS

	KAFUE 1961/1962[1]		KAFUE 1971/1972[2]		BANGWEULU 1973[3]		KWANDO 1975/1977[4]	
Age class (years)	No. in age class	% fertile	No. in age class	% fertile	No. in age class	% fertile	No. in age class	% fertile
1 - 2	5	40	14	36	24	67	7	0
2 - 3	14	93	37	95	25	100	8	50
3 +	82	96	94	83	87	99	126	90
age classes over 1 year combined	101	93	145	81	136	93	141	83

1 : Robinette & Child, 1964

2 : Sayer & Van Lavieren, 1975

3 : Grimsdell & Bell, 1975

4 : this study

Secondly, that, because of the relationship between condition and reproduction, the long term monitoring of condition should form part of any effort to understand population dynamics.

5.4

SUMMARY

The purposes of studying condition were the following:

(a) to establich how much variation occurred in the condition of lechwe in the Kwando population;

(b) to consider possible causes for this variation;

(c) to consider the possible effects of condition on reproduction.

Methods used involved consideration of deposited fat reserves, adrenocortical hypertrophy, blood chemistry and hematology and body growth.

Important findings included the following:

(i) condition in both males and females was significantly influenced by age;

(ii) reproductive status had a significant influence on the condition of lechwe females;

(iii) females showed significant seasonal variation in condition;

(iv) adrenal mass, serum cholesterol and PCV were of uncertain value as condition indices;

(v) liver mass showed promise as an index of protein status;

(vi) condition appeared to influence the reproductive performance of females of all ages.

From the results obtained two conclusions were drawn. Firstly, that variation in condition cannot be understood without considering carefully at least the age, reproductive status and season of collection of the animals involved. Secondly, that, because of the relationship between condition and reproduction, long term monitoring of condition should form part of any effort to understand population dynamics.

CHAPTER 6

GROWTH AND REPRODUCTION IN THE FEMALE

6.1

INTRODUCTION

6.1.1

The Relevance of Growth and Reproduction to Conservation and Management

A variety of reasons have been advanced for studying the growth of wild animals (Hanks, 1972a; Howells & Hanks, 1975; Bertram, 1975; Smuts, 1975; Hanks *et al*., 1976; Attwell, 1977; Jeffery, 1978). The following are amongst the more important in the context of conservation and management:

(1) to estimate population biomass and possible rates of exploitation;
(2) to compare the performance of different populations of the same species in different environments;
(3) to compare the performance of the same population at different times;
(4) to facilitate age classification in the field;
(5) to allow objective estimation of mass from the relationship between body dimensions and mass;
(6) for investigation of the population dynamics of a species;
(7) for establishing dosage rates of immobilizing or tranquilizing drugs;
(8) to optimize commercial exploitation;
(9) to facilitate taxonomic studies.

The study of reproduction is vital to both conservation and management because reproduction is one of the basic determinants of a population's growth rate. Attwell (1977) makes the important point that "Whether the aim of management is to maximize productivity or to maintain a population in harmony with the ecosystem, an understanding of the factors controlling reproduction and population growth is essential."

6.1.2

Previous Work on Growth in Lechwe

To my knowledge only two studies of lechwe have included work on growth and in neither study was growth a major preoccupation. Robinette & Child (1964) published subjectively fitted curves for growth with age in testis mass, body mass (male and female) and horn length and spread in Kafue lechwe. Grimsdell & Bell (1975) published subjectively fitted curves for growth with age in body mass (male and female) and horn length in black lechwe. There are no published data on growth in the red lechwe in either Zambia or Botswana.

6.1.3

Previous Work on Reproduction in Lechwe

Three studies of lechwe in Zambia have produced data on reproduction. Robinette & Child (1964) obtained information from 101 shot females and a number of shot males in the Kafue population. They published data on age-specific fecundity of females and reproductive seasonality in females and males. Sayer & Van Lavieren (1975) obtained data from a shot sample of 30 animals (10 male, 10 female and 10 immature) per month over a period of one year. They also published data on age-specific fecundity of females and on reproductive seasonality in females and males. They found that the fecundity of female lechwe in the Kafue population had declined in the period between their study and that of Robinette & Child (1964) and attributed this decline to nutritional stress caused by a general decline in range conditions.

Grimsdell & Bell (1975) collected data on pregnancy (using an ultrasonic foeta pulse detector) and lactation in a captured sample of 136 lechwe in the Bangweulu Sqamp. They produced a table of age-specific fecundity in females and made general observations about reproductive seasonality. They compared their results with those from the Kafue Flats and found a significantly higher reproductive rate in the Bangweulu population. This they attributed to the fact that the Bangweulu population was apparently well below the carrying capacity of the range whereas the Kafue population was right at the upper limit of the carrying capacity.

Little work has been done on lechwe reproduction in Botswana. Child & Von Richter (1969) made general observations on reproductive seasonality in the Chobe lechwe population and Lent (1969) did likewise in respect of the Okavango lechwe population. Biggs (1979) collected reproductive data from 22 females shot in the Okavango Delta and made some comments on reproductive seasonality.

6.1.4

The Objects of this study with respect to Growth and Reproduction

The objects of collecting growth data from the Kwando lechwe population were the following:

(1) to facilitate estimation of lechwe biomass;

(2) to optimize economic returns from the exploitation of lechwe;

(3) to assist investigation of population dynamics by enabling comparisons to be made of growth rates in different populations and at different times;

(4) to facilitate age classification in the field;

(5) to allow objective estimation of mass by developing predictive equations from the relationship between mass and body dimensions.

The purposes of investigating reproduction in the Kwando lechwe population were to:

(1) describe reproductive phenomena in the female lechwe;
(2) determine the prevailing reproductive rates;
(3) identify the most important factors influencing these rates;
(4) to document reproductive seasonality.

6.2

MATERIALS AND METHODS

Body mass, measurements and reproductive data were recorded from a sample of 142 females which were shot for research purposes during this study.

6.2.1

Growth

Ages of animals were determined by the procedures described earlier (Chapte Three). The method of Huggett & Widdas (1951) was used to estimate foetal ages. This will be discussed further in section 6.2.2.3.

Body mass was determined with a 150 kilogram Salter spring scale to the nearest 0,5 kilogram. The measurement taken was "dead mass" which I define as "the mass of a shot animal without correction for blood loss". Carcass mass was determined by the method of Ledger (1963), except that kidneys and kidney fat were removed. Thus carcass mass is equivalent to dead mass minu the mass of the entire contents of the body cavity and the mass of the feet (below the carpal/tarsal joint), skin and head. Carcass mass is synonymous with "dressed mass". Carcass composition was determined by the method of Ledger & Smith (1964) (see Table 6.3).

Body measurements were taken with a flexible steel tape (Ansell, 1965), measurements were taken "over the curve". The advantage of this method is that it records changes in muscular development or condition which may be important when attempts are made to relate body mass to body measurements (Smuts, 1975).

The following measurements were routinely made.

(a) Body length: along the mid-dorsal line from the lowest point of the upper lip to the point of flexure of the tail (hereafter referred to as "length").
(b) Chest girth: the circumference of the chest immediately posterior to the forelegs (hereafter referred to as "girth").

(c) Shoulder height: the distance from the tip of the hoof to the top of the scapula, with the foreleg lightly stretched.

(d) Neck girth: the circumference of the neck at the midpoint between the head and shoulders.

Mass and measurement data were analysed by computer (University of Natal IBM 1130), using the programme developed by Hanks (1972a) for the von Bertalanffy growth equation. The same programme was used by Smuts (1975), Attwell (1977) and Anderson (1978). The programme uses iteration to produce values of the von Bertalanffy coefficients that minimise the sums of squares of the deviations about the fit, taking into account the standard error of the mean of specific measurements. Curves are fitted to the growth data objectively by a curve fitting a subroutine.

6.2.2

Reproduction

Attwell (1977) identifies the following ways in which female reproduction is subject to variation:

(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 ratio of successful to unsuccessful pregnancies;

(g) the duration of lactation;

(h) the age of reproductive senescence.

Data on most of these aspects were collected and an attempt was made to identify regulatory factors. In this context Owen's (1976) distinction between proximate and ultimate factors was adopted. Proximate factors "are the environmental events that serve as a trigger to an animal's physiology" (Owen, 1976). Examples of proximate factors are changing day length and variations in temperature and seasonal rainfall. Ultimate factors are "events that determine why an animal breeds, migrates, moults, aestivates and so on at a particular time" (Owen, (1976). Examples of ultimate factors are availability of food and availability of breeding sites.

6.2.2.1

Field Methods

When the alimentary tract had been removed, the reproductive tract was cut below the cervix, removed and weighed intact. The ovaries were dissected away from the reproductive tract and weighed to the nearest 10^{-1} gram, on a triple beam balance, data from left and right ovaries being recorded separately. After weighing, ovaries were fixed and stored in 10% formalin for subsequent examination. The length of the uterus, from the cervix to the top of the right horn, was measured in various stages of pregnancy. All uteri were opened and carefully examined for signs of pregnancy. If a foetus was present it was weighed, body length and crown rump measurements were taken and, if possible, it was sexed.

A number of mammary glands in various stages of lactation were dissected out and weighed.

6.2.2.2

Ovarian examination

Ovarian structures were examined macroscopically by the method of Cheatum (1949b)and Golley (1957), as applied by, for example, Robinette & Child (1964). A scalpel was used to section the ovaries at approximately one millimetre intervals at right angles to the long axis. Sections were left joined to each other at the point of attachment to the mesovarium. Follicles were grouped into four size classes and counted. Corpora lutea were measured with a Vernier caliper in the section with the greatest diameter. Corpora nigra were counted.

Fourteen corpora lutea were removed completely from their ovaries and weighe to 10^{-3} on an electrical balance. Their mass was plotted against mean diameter, following Laws (1969) and Attwell (1977).

6.2.2.3

Calculation of foetal age

Seventy macroscopically visible foetuses were collected between January 1975 and March 1977. Foetal age since conception was calculated using the method of Huggett & Widdas (1951), which is based on a linear relationship between foetal mass and age since conception. This relationship has the form:

$$M^{\frac{1}{3}} = a\,(t - t_0)$$

where M = mass of foetus

a = slope of the line

t = age since conception

t_o= x-axis (age) intercept

In order to calibrate this function for a particular species it is necessary to know "t" and "M" for one foetus (for animals with a gestation period of 100-400 days, $t_o \doteq 0,2 \times$ gestation period). Gestation period and birth mass are commonly used for calibration of the function.

In this study, gestation was taken as 225 days (Robinette & Child, 1964; Mentis, 1972; Grimsdell & Bell, 1975). Birth mass was taken as 6,5 kilograms. This was the mean mass of six foetuses assumed to be at the point of birth because of the presence of colostrum in the udder. The same mass was calculated as the mean of 12 newborn fawns in a captive herd of Kafue lechwe in Zambia (Grimsdell & Bell, 1975).

Once the function has been calibrated, age since conception is given by:

$$t = \frac{M^{\frac{1}{3}} + at_o}{a}$$

This relationship can be expressed graphically (Huggett & Widdas, 1951; Smuts, 1975), a procedure which simplifies calculation, as age since conception can be read off the graph.

Calculated foetal ages were extrapolated backwards to estimate conception dates and forwards to estimate birth dates, the objective being to provide information on reproductive seasonality.

6.3

RESULTS AND DISCUSSION

6.3.1

Growth

6.3.1.1

Theoretical growth curves

The growth equations used in this study were based on the work of von Bertalanffy (1938) as developed by Beverton & Holt (1957). The equations and their solutions by computer are explained by Hanks (1972a).

The function for mass takes the form:

$$m_t = M_\infty (1 - e^{-k\ (t - t_o)})^3$$

where m_t = mass at age t

M_∞ = 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

t = age of the animal

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

Growth in length (or circumference) is described by:

$$l_t = L_\infty (1 - e^{-k\ (t - t_o)})$$

It will be seen that mass has a cubic function whereas length has a first order function.

In the use of these growth equations, Attwell (1977) found that the standard errors of specific mean parameters often extended above the theoretical asymptote before the asymptote met the fitted curve when projected from the y-axis. The same was found in this study and there were also several instances where the age-specific mean of a parameter was above the theoretical asymptote well before the projection from the y-axis met the fitted curve. To make some allowance for this situation, the projection from the y-axis was made from a point an arbitrary 2,5% below the theoretical asymptote. The age at which the asymptote was reached was read off from the point where this projection met the fitted curve.

The von Bertalanffy growth equations are listed, and where relevant, discussed below.

(a) <u>Growth in mass</u>

Two equations were derived for growth in the mass of females. The first was based on data from all females. The mass of the reproductive tract was subtracted from the mass of pregnant females and the remaining mass was used for the derivation of the equation. The second equation was derived from the dead mass of pregnant females.

The general equation for growth in the mass of females is:

$$m_t = 74,12 \ (1 - e^{-0,7023 \ (t + 0,6405)})^3 \text{ kg}$$

Figure 6.1 illustrates the curve for this equation. The theoretical asymptote is reached at about six years of age.

The equation for growth in mass of pregnant females is:

$$m_t = 77,34 \ (1 - e^{-0,9124 \ (t + 0,4704)})^3 \text{ kg}$$

Figure 6.2 illustrates the curve for this equation. The theoretical asymptote is reached at approximately four and a half years of age.

(b) <u>Growth in body length</u>

The equation for growth in body length of females is:

$$l_t = 152,49 \ (1 - e^{-0,5356 \ (t + 2,1577)}) \text{ cm}$$

Figure 6.3 illustrates the curve for this equation. The theoretical asymptote is reached at approximately five years of age.

(c) <u>Growth in Chest Girth</u>

The equation for growth in chest girth of females is:

$$g_t = 97,57 \ (1 - e^{-0,6512 \ (t + 0,6353)}) \text{ cm}$$

Figure 6.4 illustrates the curve for this equation. The theoretical asymptote is reached at about five and a half years of age.

(d) <u>Growth in shoulder height</u>

The equation for growth in the shoulder height of females is:

$$sh_t = 91,99 \ (1 - e^{-0,9775 \ (t + 0,7157)}) \text{ cm}$$

Figure 6.5 illustrates the curve for this equation. The theoretical asymptote is reached at about three years of age. The value of shoulder height as a feature diagnostic of age in the field is

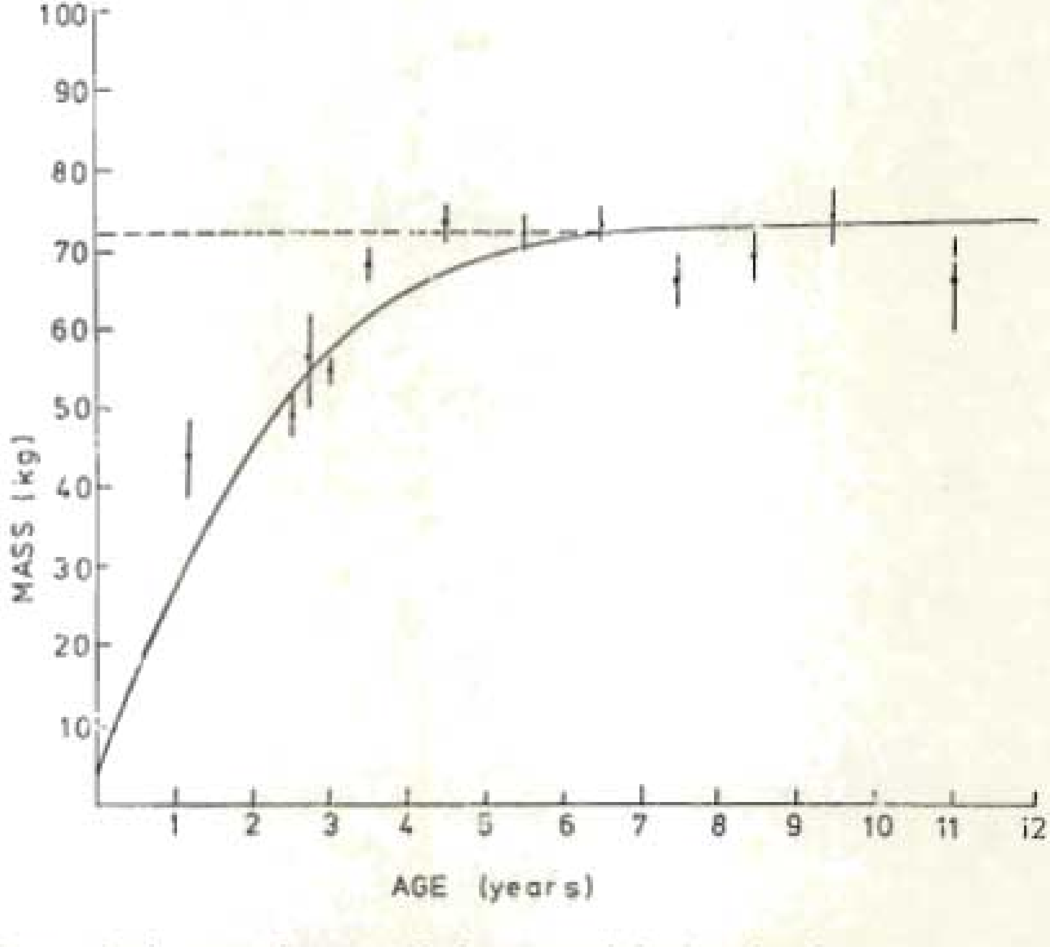


Figure 6.1: Theoretical curve for growth in mass of lechwe females. Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean (this statistic is shown because it is the datum used in the computer programme). Dashed line lies within 2,5% of the asymptote.

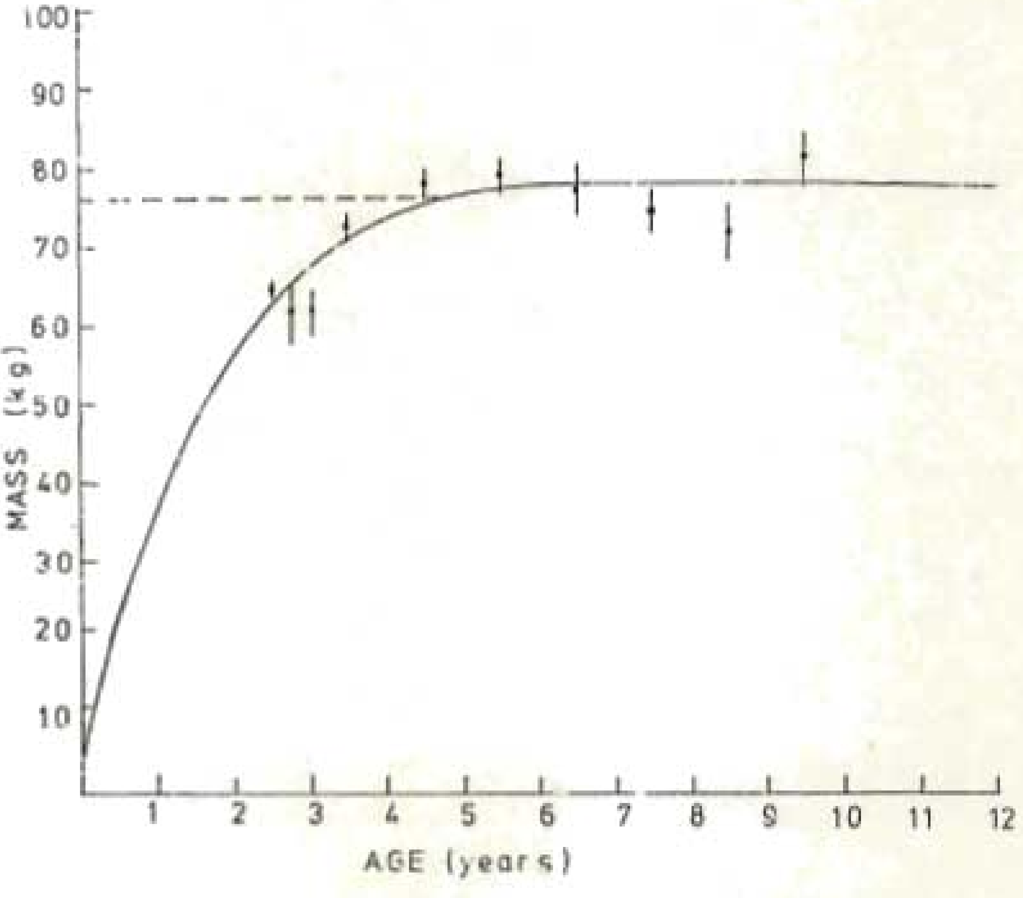
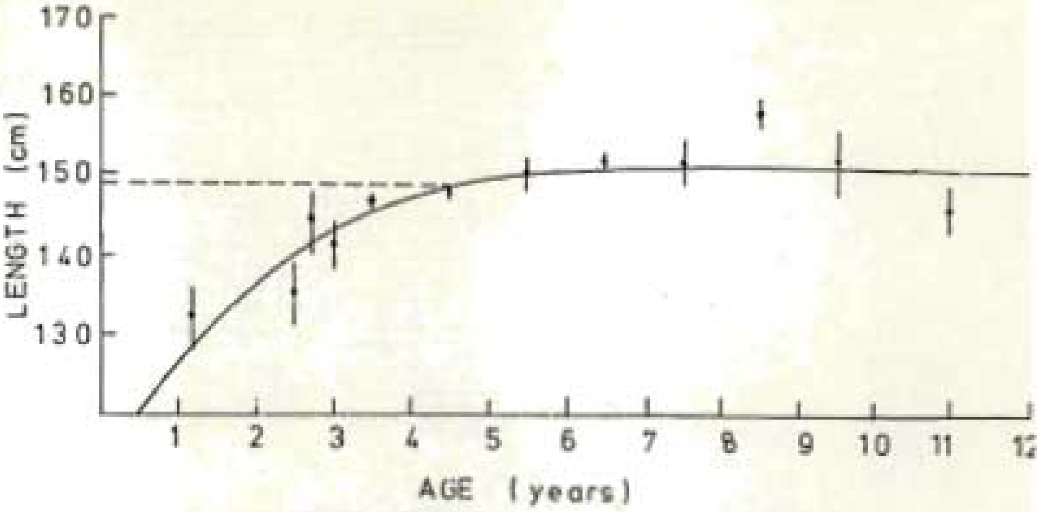
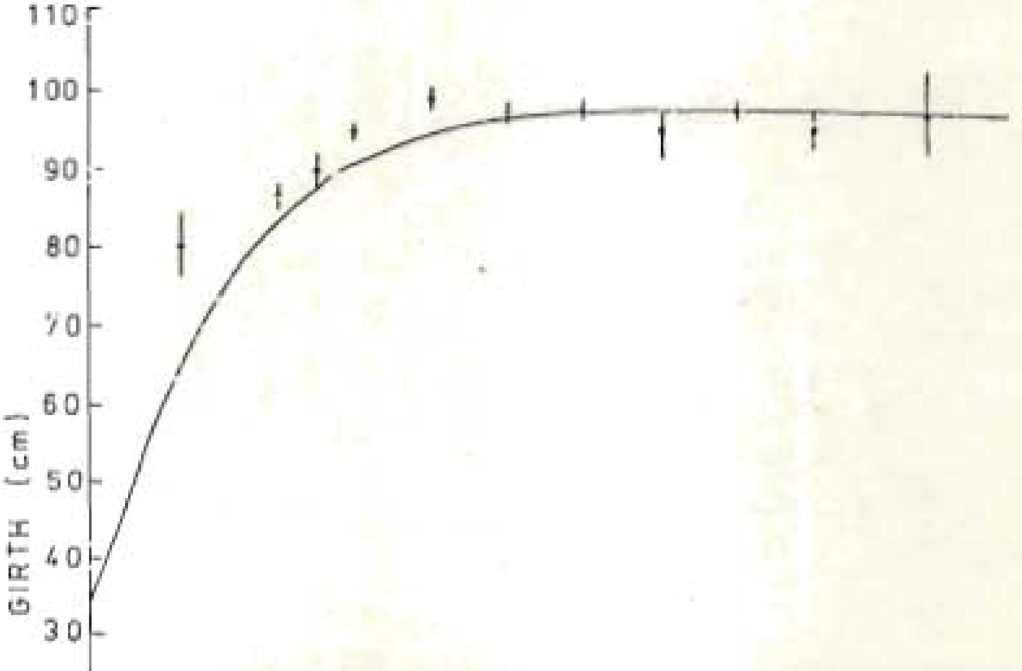


Figure 6.2: The theoretical curve for growth in mass of pregnant females. Points indicate age-specific mean values. Vertical lines extend ± one standard deviation around the mean. Dashed line lies within 2,5% of the asymptote.



<u>Figure 6.3</u>: Theoretical curve for growth in female body length. Points indicate age-specific mean values. Vertical lines extend ± one standard deviation around the mean. Dashed line lies within 2,5% of the asymptote.



<u>Figure 6.4</u>: Theoretical curve for growth in female chest girth. Points indicate age-specific mean values. Vertical lines extend ± one standard deviation around the mean. Dashed line lies within 2,5% of the asymptote.

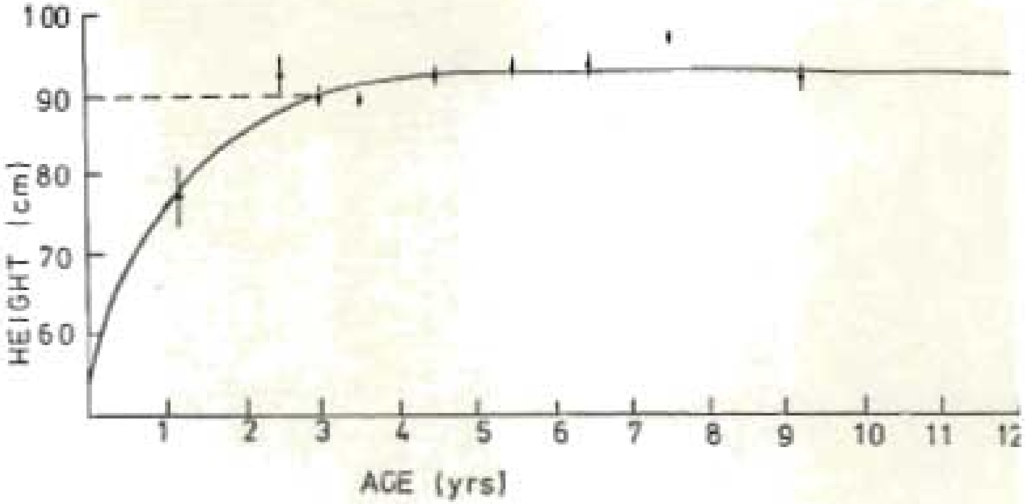


Figure 6.5: Theoretical curve for growth in female shoulder height. Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.

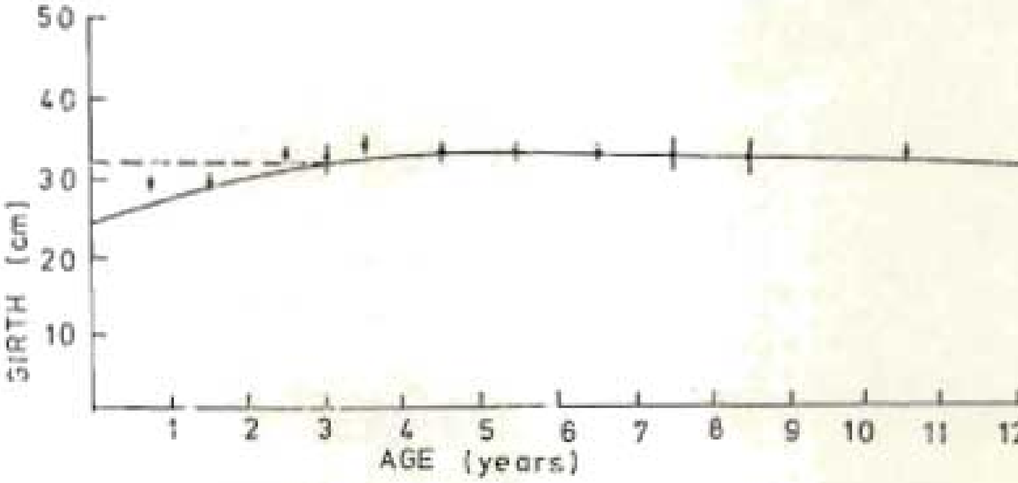


Figure 6.6: Theoretical curve for growth in female neck girth. Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.

diminished by the rapidity with which the asymptote is approached (Figure 6.5) and the fact that it is difficult to measure accurately on dead animals (Jeffery, 1979).

(e) Growth in neck girth

The equation for growth in the neck girth of females is:

$$n_t = 32{,}93 \ (1 - e^{-0{,}9935 \ (t + 1{,}0705)}) \ \text{cm}$$

Figure 6.6 illustrates the curve for this equation. The theoretical asymptote is reached at about two and a half years of age.

As far as can be established from the literature the curves illustrated above are the first theoretical von Bertalanffy curves generated for lechwe. These curves have a number of uses, which are discussed below, but they cannot be interpreted uncritically. They are in effect a reflection of the apparent growth rates which can be inferred from the values which particular parameters had attained by the ages at which the animals comprising the sample were collected. They are idealized representations of growth and take no cognizance, for example, of seasonal variation in growth rates (Jeffery, 1978). In addition the generation of these curves was dependent on techniques of age determination which are notoriously fallible under tropical conditions.

On the basis of these curves comparisons can be made between the growth rates of different population or of the same population at different times. From Grimsdell & Bell's data (1975) I generated theoretical curves for growth in mass, shoulder height and length of Bangweulu lechwe females, using the same computer programme that was used to analyze the data collected in this study. I then compared the ages at which asymptotic values for these parameters were attained by females in the two different populations (Table 6.1). It will be seen from Table 6.1 that there is a striking difference in the apparent growth rates of females in the two populations. It is very likely that the different growth rates reflect the fact that the Kwando population was under nutritional stress (Chapter 5) whereas the Bangweulu population was well below the carrying capacity of its range (Grimsdell & Bell, 1975).

Growth curves have further uses in the context of commercial utilization. For commercial purposes it is useful to know both the period of

TABLE 6.1: THE AGES AT WHICH ASYMPTOTIC VALUES FOR MASS, SHOULDER HEIGHT AND LENGTH ARE REACHED BY FEMALES IN THE KWANDO AND BANGWEULU LECHWE POPULATIONS (calculated from computer-generate von Bertalanffy growth curves)

Parameter	Kwando (years)	Bangweulu (years)	Difference in years	Bangweulu as % Kwando
Mass	6	2,5	3,5	42
Shoulder height	3	2	1	67
Length	5	3	2	60

TABLE 6.2: MASS GAINS (IN KG) IN LECHWE FEMALES CALCULATED FROM THEORETICAL CURVES AND AGE-SPECIFIC SAMPLE MEANS

Age (years) Interval	Theoretical Curves		Sample Means	
	Gain/Interval	Gain/Day	Gain/Interval	Gain/Day
0 - 1,2	21,8	0,051	37,5	0,088
1,2 - 2,5	23,9	0,052	5,5	0,012
2,5 - 3,5	10,5	0,028	18,8	0,051
3,5 - 4,5	5,5	0,015	4,7	0,013

maximum mass gain and the age at which asymptotic mass is approached.

Table 6.2 shows mass gains calculated from the theoretical growth curves and from age-specific sample means. The theoretical growth curves indicate that the growth rate is essentially constant up to two and a half years and drops off thereafter. The sample means show maximum growth during the first year and erratic growth thereafter. These results differ from those of most other species (see, for example, Smuts, 1975; Attwell, 1977) and may be an artefact of the small sample size in the lowest age classes. It would be advisable to treat these results with caution but it is possible that they simply reflect low growth rates among females in the Kwando population.

Attwell (1977) implies that in terms of meat production the optimal age at which animals should be harvested is immediately after the period of highest productivity. This may be a useful guideline under conditions of intensive management but it is certainly not applicable under the conditions prevailing in Botswana. In Botswana management is non-existent, production costs are zero and harvesting costs are high. Under these circumstances it is clearly economically advantageous to harvest the largest animals possible. A simple example will illustrate this point.

Table 6.3 shows carcass yield from lechwe females of different ages. Assuming that the cost of harvesting does not vary with age, it can be seen that by harvesting animals more than four years old rather than animals in their first year the yield in dressed mass per unit cropping effort is increased by:

$$\frac{(71,5 \times 0,546)}{34,7 \times 0,533} \times 100 = 211\%$$

This situation illustrates the point made by Mentis (1977) that "economic optima do not necessarily coincide with maximal biological production".

6.3.1.2

Predictive equations

The importance of body mass for estimating population biomass and for comparative studies (Howells & Hanks, 1975) makes an objective method of mass estimation desirable. A number of workers have derived equations for predicting mass (McCulloch & Talbot, 1965; Smuts, 1975; Howells &

BLE 6.3: BODY MASS (less gravid uterus plus contents) AND COMPOSITION OF LECHWE FEMALES ON THE KWANDO

AGE		DEAD MASS[1] (kg)		CARCASS YIELD[2] %		EXTERNAL OFFAL[3] %		INTERNAL OFFAL[4] %	
ears)	n	Mean ± S.E.	Range	Mean ± S.E.	Range	Mean ± S.E.	Range	Mean ± S.E.	Range
1	3	34,7 ± 0,6	33,5 - 35,5	53,3 ± 0,8	52,2 - 54,9	13,0 ± 0,7	11,9 - 14,3	33,7 ± 1,1	32,4 - 35,8
2	7	45,6 ± 1,5	41,5 - 53,0	55,4 ± 0,8	52,4 - 59,4	12,8 ± 0,6	10,5 - 15,5	31,7 ± 1,1	28,3 - 34,7
3	14	56,8 ± 1,9	46,5 - 67,0	54,1 ± 0,7	49,6 - 58,1	11,1 ± 0,2	9,0 - 12,8	34,8 ± 0,7	31,2 - 39,8
4	35	67,3 ± 1,3	53,5 - 84,5	56,9 ± 0,5	50,0 - 62,1	10,3 ± 0,2	8,6 - 12,1	32,8 ± 0,5	27,1 - 37,6
+	87	71,5 ± 0,9	52,0 - 89,0	54,6 ± 0,5	45,5 - 63,0	10,3 ± 0,1	8,5 - 12,0	35,1 ± 0,4	24,4 - 44,8

: mass of a shot animal without correction for blood loss

: $\frac{\text{dead mass - external offal - internal offal}}{\text{dead mass}} \times 100$ = carcass yield as a percentage of dead mass

: External offal is the mass of the feet (below carpal/tarsal joint), head and skin as a percentage of dead mass

: Internal offal is the mass of the contents of the body cavity (excluding gravid uterus) as a percentage of dead mass

Hanks, 1975; Hanks *et al.*, 1976; Attwell, 1977).

Of the various combinations tested in this study, the best results were obtained by relating mass to (a) length and girth and (b) girth. The equation for the relationship between mass, length and girth in lechwe females is:

$$y = 40{,}04x + 14{,}75 \quad (n = 140; \; r = 0{,}998; \; p < 0{,}001)$$

where y = mass
$x = L(G)^2 \; 10^{-6}$ (L = length; G = girth)

The relationship between mass and girth is given by:

$$y = 1{,}26g - 52{,}11 \quad (n = 140; \; r = 0{,}877; \; p < 0{,}001)$$

where y = mass; g = girth

In the context of utilization it is useful to be able to predict carcass mass as well as dead mass. Equations relating carcass mass to dead mass and to girth were therefore derived.

The relationship between carcass mass and dead mass in lechwe females is given by:

$$y = 0{,}58x - 1{,}53 \quad (n = 140; \; r = 0{,}923; \; p < 0{,}001)$$

where y = carcass mass; x = dead mass

The relationship between carcass mass and girth is given by:

$$y = 0{,}78x - 36{,}30 \quad (n = 140; \; r = 0{,}855; \; p < 0{,}001)$$

where y = carcass mass; x = girth

These equations are considered further in Chapter 7 during the discussion of similar equations derived for lechwe males.

Other uses to which growth data collected in this study were put included the development of field age determination criteria (Chapter 3) and calculation of lechwe biomass in the Kwando/Linyanti/Chobe system (Chapter 11).

6.3.2

Reproduction

Reproductive phenomona in lechwe females on the Kwando are described because it was by examining the ovaries, uterus and mammary glands of autopsied females that their reproductive status was assessed and age-specific reproductive rates were calculated.

6.3.2.1

The ovary

A small sample of foetal ovaries was examined for signs of hypertrophy. Foetal hypertrophy of the ovary has been documented in the elephant (Hanks, 1973) and the horse (Nalbandov, 1976) and according to Nalbandov (op. cit.) is typical of foetuses exposed to high levels of serum gonadotrophins. No signs of foetal hypertrophy of the ovary were found in lechwe.

The range of ovary mass occurring in non-pregnant adult females is attained by about two years of age (the presence of a corpus luteum significantly increases ovary mass and the ovary mass of pregnant adults is thus not comparable to that of immature animals).

There was wide variation in the number of macroscopic follicles recorded. The minimum number found in one animal was 16, in an 18 month old immature animal. The maximum number found was 253, in a 3.5 year old pregnant animal. Younger and older animals tended to have fewer follicles, but there was no clear relationship between the number of macroscopic follicles and age ($r = 0,070$; $p > 0,1$). All age classes had mean numbers of follicles per animal ranging from 30 to 60.

Although there is unilateral implantation in lechwe (section 6.3.2.4), the indications from this study are that ova are released at random from left and right ovaries. Figure 6.7 shows the relationship between the mass of left and right ovaries of sexually immature females. This figure gives no clear indication of a bias towards first ovulation in either ovary, assuming that the heavier ovary would be the first to ovulate. Table 6.4 details the number of corpora lutea, corpora nigra and largest follicles (where no corpus luteum was present) encountered in left and right ovaries. There is an apparent bias towards the right ovary but this is not statistically significant Buechner (1961a) reported approximately equal distribution of corpora lutea between left and right ovaries in Uganda kob but Robinette &

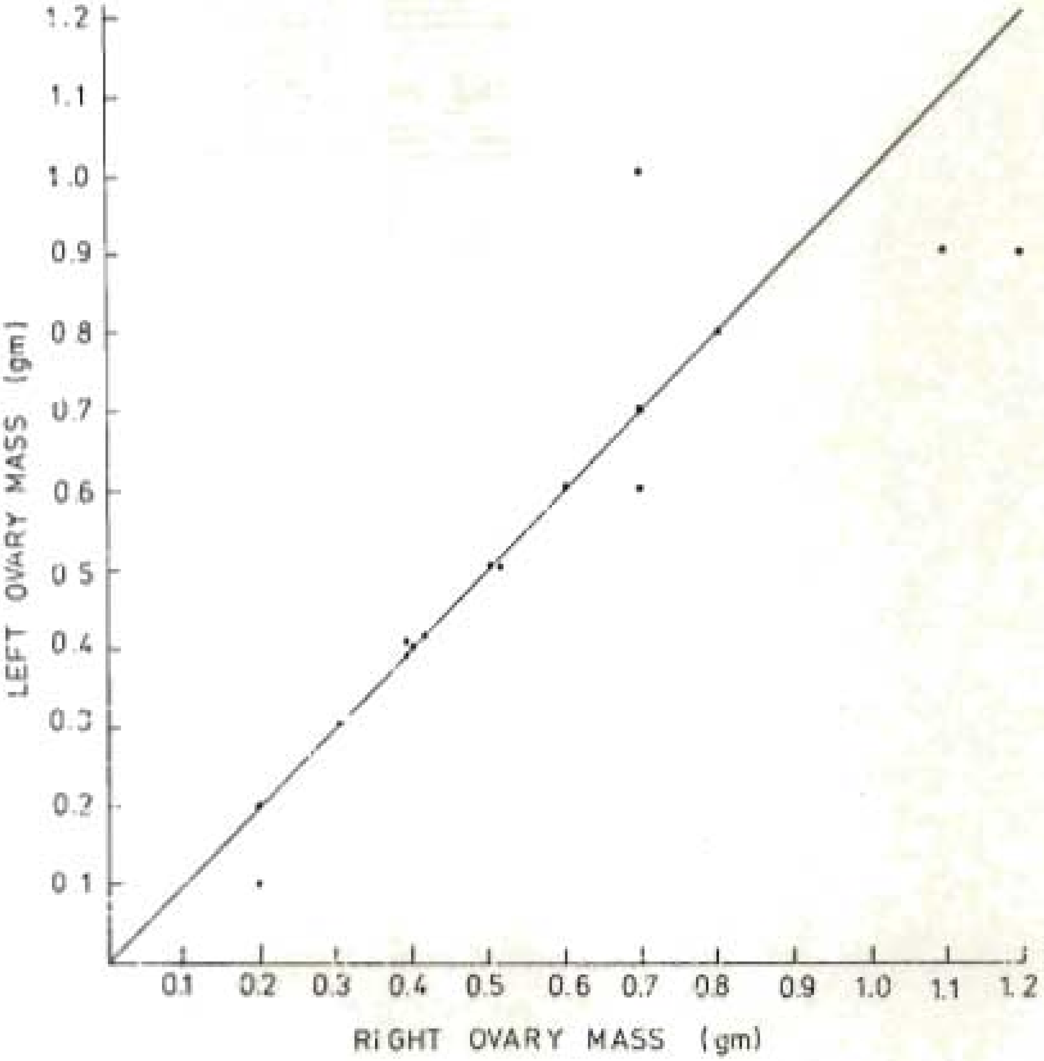


Figure 6.7: The relationship between the mass of left and right ovaries of sexually immature lechwe females. The 45° bisector indicates equality of mass.

TABLE 6.4: THE NUMBER OF CORPORA LUTEA, CORPORA NIGRA AND THE LARGEST FOLLICLES OCCURRING IN THE LEFT AND RIGHT OVARIES

Structure	Ovary	
	Left	Right
Corpora lutea[1]	31	51
Corpora nigra[2]	146	150
Largest follicle	15	17
Totals	192	219

1 : Refers only to current corpora lutea

2 : Includes all regressing pigmented corpora lutea

Child (1964) found significantly more current corpora lutea in the left than in the right ovary (57:33). Data from the present study show a bias towards the right ovary when a comparison is made using only current corpora lutea. The ratio between right and left ovary was 51:31 and this was statistically significant (chi-squared with Yatec correction factor = 4,402; $p < 0{,}05$).

Nalbandov (1976) states that most mammals can be divided into left and right ovulaters in the sense that they normally ovulate more eggs from one ovary than from the other and that as a rule the favoured ovary is slightly heavier. In the light of these statements differences in the mass of left and right ovaries were tested in two ways.

A one-tailed "t-test" (assuming the right ovary to be the heavier) for "matched-pair" data (Scheffler, 1969) was used. This test showed that the right ovary was significantly heavier than the left ovary ($n = 112$; $t = 2{,}445$; $p < 0{,}01$).

A chi-squared test, with Yates correction factor (Scheffler, 1969) was used to test whether the right ovary was heavier than the left ovary significantly more often than would be expected on the basis of random variation. The right ovary was heavier than the left in 62 animals, the left was heavier than the right in 41 animals (in nine animals ovary masses were the same). This difference in frequency was significant (chi-squared = 3,884; $p < 0{,}05$).

On the basis of the various data presented it would seem reasonable to infer that Kwando lechwe females ovulate more often from the right ovary than from the left.

6.3.2.2

Attainment of sexual maturity

Different workers tend to define puberty and sexual maturity in accordance with their own preoccupations (Sadlair, 1969a). For the pragmatic purposes of conservation and management the important factor is the age at which animals begin breeding. In males this is often complicated by social factors but in females it may be more or less contumporaneous with the age at which the physiological capability of reproducing is attained.

In this study the definition of Hanks (1972b) was adopted and females were considered sexually mature if their ovaries contained one or more corpora nigra. In the case of lechwe the use of this definition is complicated by the likelihood of infertile oestrous cycles (section 6.3.2.3). Because of these cycles it is likely that at least one animal that had not bred was classified as sexually mature. Errors of this kind are difficult to avoid because of the similarity of corpora nigra resulting from corpora lutea of cycle and of pregnancy (Buechner et al., 1966). It can be argued that these errors are in any event not serious because the fact that an animal is cycling is in itself an indication that it is approaching reproductive capability.

Of seven animals between one and two years old (yearlings) not one was sexually mature. Of eight between two and three years old four were pregnant, one was not pregnant but had a corpus nigricans in each ovary and three were not pregnant and did not have corpora nigra in their ovaries. In other words, of the eight animals between two and three years old, five (63%) were sexually mature and the remainder were not. Thus the age at which 50% of females attain sexual maturity is over two years. This is later than in other populations (Chapter 5).

6.3.2.3

Oestrus and ovulation

No data were forthcoming from this study of the length of the oestrous cycle in lechwe. Intense oestrous behaviour, for example the mounting of one female by another, was regularly observed, but it was never possible to keep a female under surveillance for the full oestrous cycle.

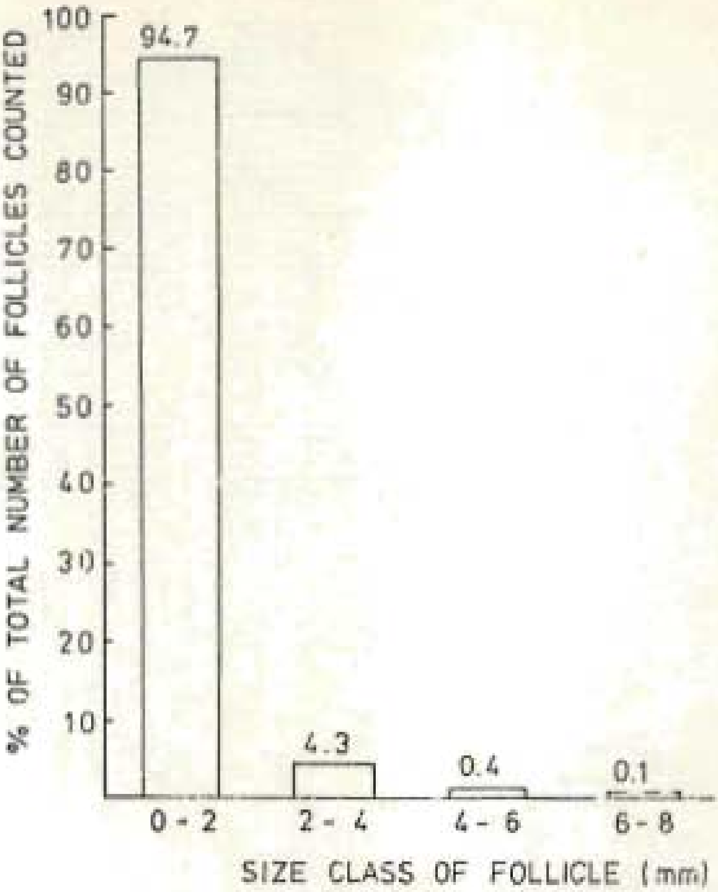
The duration of oestrus itself may be in the region of 24 hours. On two occasions an interaction between a territorial male and an oestrous female was monitored (daylight hours only) over a period of three days. On both occasions the pattern was the same. The female was detained by the male on the first day but, while not leaving his territory, was not receptive. On the second day the female permitted multiple copulations. On the third day the female had disappeared. This pattern of events is interpreted as meaning that the female was actually in oestrus only on the second day. Of course these facts are open to other interpretations but evidence from other species, for example, Uganda kob (Buechner et al., 1966), tends to support the interpretation adopted here.

It is helpful to have some idea of the size of the follicle at ovulation. As in other species, the majority of macroscopic follicles are small (Figure 6.8). The largest follicle measured had an average diameter of 7,1 millimetres. Four follicles of this size were found. One of them was about one millimetre from the surface of the ovary, suggesting that at ovulation the follicle may sometimes be slightly larger than 7 millimetres. One follicle in the process of luteinizing had a diameter of 7,2 millimetres.

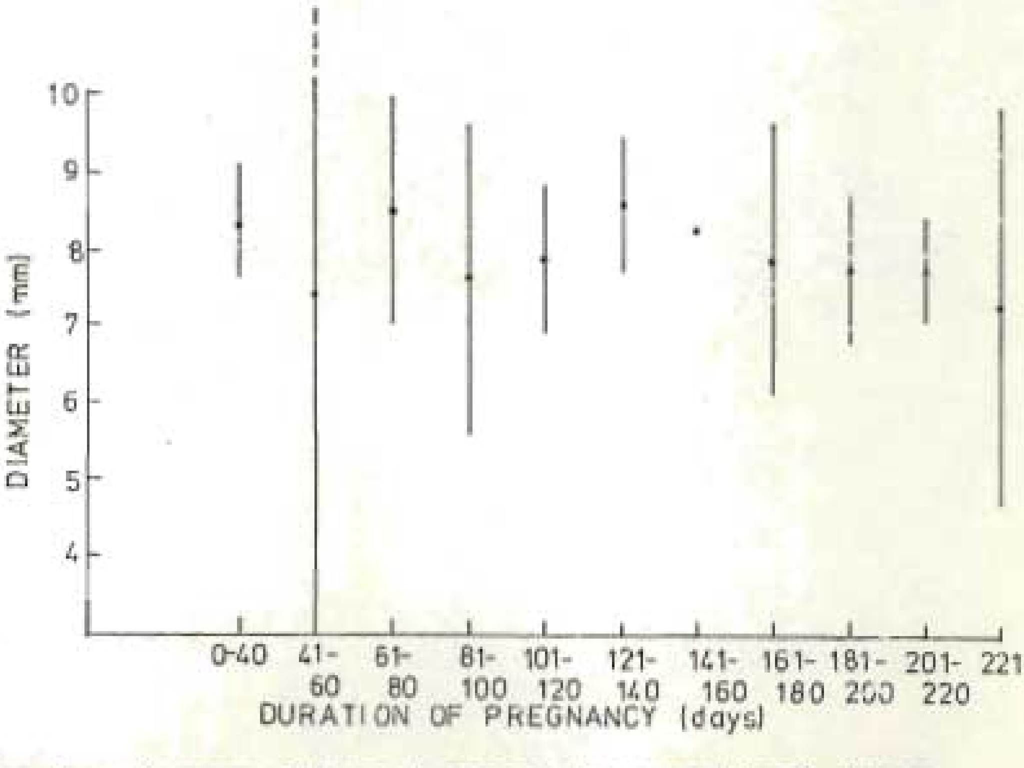
There were indications that ovulation in lechwe females follows much the same pattern as it does in the congeneric Uganda kob. The reproductive biology of the kob has been extensively documented by H.K.Buechner and his students. A number of papers describe reproductive anatomy and physiology in detail (Buechner, 1961a;Buechner et al., 1966; Buechner & Mossman, 1969; Morrison, 1971; Morrison & Buechner, 1971). The salient feature of ovulation in kob is the frequent occurrence of infertile cycles before conception, in both adolescent and mature animals. The existence of these cycles has been inferred by Buechner et al., (1966) from both examination of ovaries and observations on the behaviour of known individuals which were subsequently collected.

Buechner et al., (1966) examined the ovaries of animals of known breeding history after known post-partum or post-coital intervals. In this way stages in the development and regression of corpora lutea were determined. By comparing the average diameter of corpora lutea of pregnancy at known periods of gestation to that of corpora lutea of cycle, it was established that after conception the corpus luteum of pregnancy grows to a significantly larger size than does the corpus luteum of cycle. In Uganda kob stages in the development and regression of corpora lutea are: incomplete corpus luteum - complete (white) corpus luteum - regressing yellow corpus luteum - regressing orange corpus luteum - large orange-brown corpus nigricans - small (less than tw millimetres) brown corpus nigricans. Multiple cycles were inferred by Buechner et al., (1966) from the presence of supernumerary corpora lutea in the ovaries of females of known breeding history.

In Uganda kob (Buechner et al., 1966) behavioural evidence of repeated cycling took the form of repeated visits (up to six) by marked females to the territorial breeding grounds. Usually oestrus behaviour was evinced at these visits but on some occasions no overt sexual behaviour was manifested. Visits at which no sexual behaviour was manifested



<u>Figure 6.8</u>: Frequency distribution by size class of 7691 follicles counted in entire ovary collection.



<u>Figure 6.9</u>: Diameter of corpus luteum at progressive gestational stages. Points represent means. Vertical lines indicate 95% confidence limits.

were taken as evidence of "silent" ovulations (Buechner, et al., 1966).

The suggestion that a situation similar to that in Uganda kob obtains in lechwe is based entirely on examination of ovaries. Not enough females were individually observed for long enough periods to allow the collection of the relevant behavioural information.

Structures similar to the various corpora lutea and nigra described in Uganda kob were found in lechwe ovaries. The type of evidence from which it is assumed that ovulation in lechwe follows the Uganda kob pattern is most conveniently illustrated by reference to a few facts and case histories.

(a) Six ovaries (2%) contained more than one large (greater than four millimetres) follicle. This suggests that repeated cycles could occur after short intervals.

(b) Both ovaries of a 30-month old virgin female contained large (5,1 and 7,2 millimetres) pigmented regressing corpora lutea. The presence of these corpora lutea in a nulliparous female strongly suggests that infertile cycles had occurred.

(c) The right ovary of a primiparous 30-month old female contained both the current corpus luteum of pregnancy and a pigmented regressing corpus luteum, presumably of cycle. This female was judged to be primiparous because her udder and teats were of the same size and general appearance of those of a virgin female. The fact that two corpora lutea, one of which was regressing, were present in the same ovary is consistent with the occurrence of two cycles, the first of which was infertile.

(d) The left ovary of an eight year old adult female contained a regressing yellow corpus luteum 5,7 millimetres in diameter and a corpus nigricans less than two millimetres in diameter. This female's right ovary contained a luteinizing follicle, 7,2 millimetres in diameter (perhaps a developing corpus luteum of pregnancy), a regressing orange corpus luteum four millimetres in diameter and a small corpus nigricans. In this case the occurrence of infertile cycles is at least a plausible explanation for the presence of four or five (if the luteinizing follicle is assumed to be the corpus luteum of pregnancy) corpora lutea. In older animals, such as this one was, the occurrence of infertile cycles would not be surprising.

(e) The left ovary of an adult female in the very early stages of pregnancy contained a regressing corpus luteum 5,2 millimetres in diameter and a small orange corpus luteum. The right ovary contained the corpus luteum of pregnancy and a large follicle. Both ovaries contained small corpora nigra. Again, the structures in this female's ovaries are compatible with the occurrence of infertile cycles.

(f) Of the 70 females whose uteri contained a macroscopically visible foetus, 26 (37%) had one or more pigmented, regressing corpora lutea as well as a current corpus luteum. In view of the relatively long post-partum interval in Kwando lechwe females (section 6.3.2.7) infertile oestrous cycles probably account for at least some of the cases in which pregnant females had regressing corpora lutea in their ovaries.

Individually none of the cases or facts cited above are conclusive but their cumulative effect is a strong suggestion that infertile cycles occur in lechwe. Obviously this inference depends on correct identification of ovarian structures. The examination of microscope slides prepared from six ovaries confirmed that luteal tissue had been correctly identified.

In addition to Uganda kob infertile oestrous cycles have been documented in moose (Simkin, 1965), wildebeest (Watson, 1969), hippo (Sayer & Rakha, 1974) and nyala (Anderson, 1978). According to Nalbandov (1976) they also occur in sheep, cows, horses and pigs and he concludes that "it is probable that quiet heats are much commoner than is thought." Clearly the occurrence of infertile oestrous cycles in lechwe is neither improbable nor unique.

6.3.2.4

Implantation and pregnancy

In virgin females the right horn of the bicornuate uterus is larger than the left horn. Foetuses were invariably in the right horn. The right horn of non-pregnant mature females was invariably distended.

Clearly, the red lechwe exhibits the same unilateral implantation that was found in Kafue lechwe by Robinette & Child (1964). Other animals in which unilateral implantation has been documented include Uganda kob (Buechner, 1961a), impala, Aepyceros melampus (Mossman & Mossman, 1962) and Thompson's gazelle, Gazella thomsoni (Hvidberg-Hansen, 1970).

The fact that corpora lutea of pregnancy were found in both left and right ovaries establishes that transuterine migration of ova or zygotes takes place. Transperitoneal migration of ova is possible but unlikely (Buechner, 1961a).

In Figure 6.9* the mean diameter of the corpus luteum is related to gestational stage. As in Uganda kob (Morrison, 1971) there appears to be little change in corpus luteum size during pregnancy.

The validity of using mean diameter as an index of corpus luteum mass was investigated by a regression of mean diameter on mass, using the mass of 14 corpora lutea that were excised from their ovaries and weighed to the nearest 10^{-1} gram. The equation for the relationship between the mean diameter and mass is:

$$y = 5{,}01x + 6{,}45 \quad (r = 0{,}790;\ p < 0{,}001)$$

where y = diameter; x = mass

On the basis of this relationship mean diameter was accepted as an adequate index of the mass of the corpus luteum.

From the examination of the ovaries of two lactating females whose fawns were approximately six months old, it was apparent that corpora lutea of pregnancy have completely regressed by six months post-partum. Because the number of fully regressed corpora nigra is disproportionately low in comparison to the number of regressing corpora lutea, particularly when age is also taken into account, it seems that the regressed corpora nigra are not persistent. Three examples will be used to illustrate this point.

(a) Each ovary of a lactating six-year old female contained a regressing orange corpus luteum but there were no obvious fully regressed corpora nigra.

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(b) The left ovary of a pregnant seven-year old female contained the corpus luteum of pregnancy, a regressing yellow corpus luteum and a regressing orange corpus luteum. The right ovary contained a large follicle (6,3 millimetres). Each ovary contained only one fully regressed corpus nigricans.

(c) Each ovary of a pregnant five-year old contained a regressing orange corpus luteum. The right ovary also contained the corpus luteum of pregnancy and one fully regressed corpus nigricans. There were no obvious corpora nigra in the left ovary.

The ovaries of several of the older females did contain two or more corpora nigra, but these had invariably converged so that it was very difficult to establish the actual number present. This, and uncertainties due to lack of persistence and infertile oestrous cycles, mean that corpus nigricans counts need to be treated with caution.

A decline in maximum follicle size with advancing pregnancy has been documented in Uganda kob (Morrison & Buechner, 1971) and wildebeest (Attwell, 1977). The possibility of a similar trend in lechwe was investigated by means of a regression. Because of the way in which follicles were measured it was necessary to use follicle size class (rather than actual follicle diameter) for this regression. Each follicle was placed in one of four size classes (0-2, 2-4, 4-6, 6-8 millimetres) but the exact diameter of each follicle was not measured. To calculate the regression the midpoint (1, 3, 5, 7) of the size class of the largest follicle in each pregnant female was plotted against the duration of the pregnancy in days.

Figure 6.10 shows the relationship between duration of pregnancy and size class of the largest follicle. The equation for the regression is:

$$y = -0{,}026x + 7{,}11 \quad (n = 66;\ r = 0{,}743;\ p < 0{,}001)$$

where y = midpoint of size class; x = duration of pregnancy (days)

The number of macroscopic follicles did not change significantly with advancing pregnancy and was apparently unrelated to gestational stage ($r = 0{,}034$; $p > 0{,}1$).

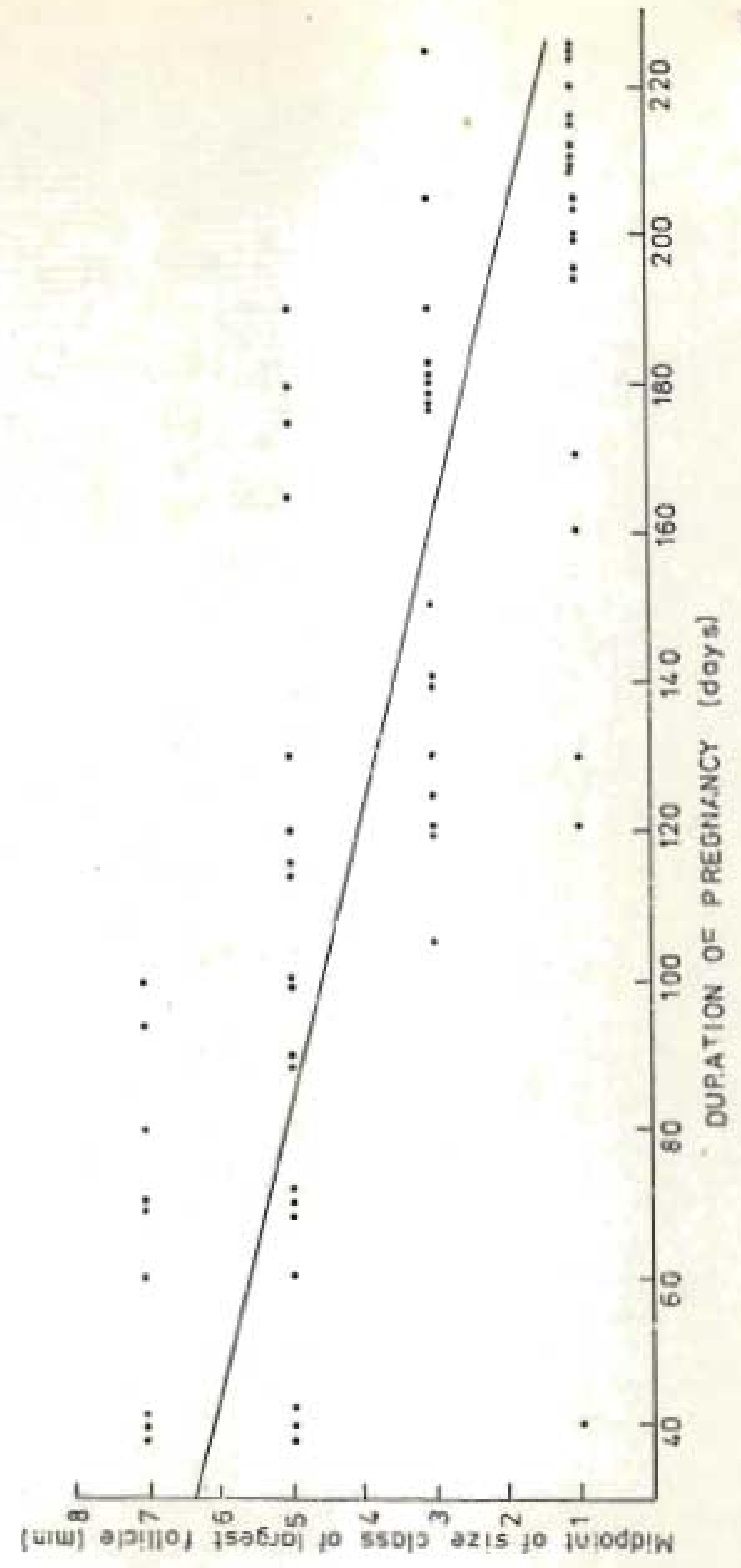


Figure 6.10: The relationship between duration of pregnancy and size of the largest follicle. Dots indicate midpoints of largest follicle size class. Regression equation in text

6.3.2.5

Fecundity

The term fecundity refers to the number of live births a female produces over a period of time, generally one year (Caughley, 1977). The number of pregnant and lactating animals in a sample of females gives an estimate of the proportion of fecund females in the population. This estimate cannot accurately reflect the proportion of unsuccessful pregnancies and thus represents the upper limit of fecundity under given conditions.

Table 6.5 presents data on apparent age-specific fecundity in the sample of females collected during this study. Some correction is needed for unsuccessful pregnancies, although the factor is probably small because no clear instances of resorption or abortion were recorded in this study. A further consideration is that 11 animals were classified as fecund on the basis of ovarian examination and the condition of the uterus and udder. Six were assumed to be in the early stages of pregnancy, while five were assumed to have produced young although their lactation had virtually ceased. If all 11 cases were incorrectly evaluated, overall fecundity would be reduced to a figure of 76%.

In Table 5.20 a comparison was made of the fecundity of three discrete lechwe populations. From this table it will be seen that the fecundity of Kwando females over three years old compares favourably with that of females in the same age class in the two other populations. It is believed that the lower fecundity of young Kwando females was largely a function of nutritiona stress (Chapter Five).

The possibility of reproductive senescence cannot be ruled out. The oldest female shot (12 years) was neither pregnant nor lactating. However, the animal was in very poor physical condition and its liver was grossly damaged by flukes (<u>Fasciola gigantica</u>). Her failure to reproduce may simply reflect the principle that stressful conditions affect the youngest and oldest animals first.

6.3.2.6

Lactation and weaning

Because lactation, especially in its early stages, is perhaps the most stressful period of the female reproductive cycle (Sadleir, 1969b; Moen, 1973) its duration and timing are important.

TABLE 6.5: OVERALL AND AGE-SPECIFIC FECUNDITY OF FEMALE LECHWE ON THE KWANDO

(years) Age Interval	Number pregnant	Number lactating	Neither pregnant nor lactating	% fecundity
0 - 1	0	0	3	0
1 - 2	0	0	7	0
2 - 3	4	0	4	50
3 - 4	22	7	9	76
4 - 5	21	9	2	94
5 - 6	9	8	0	100
6 - 7	14	7	0	100
7 - 8	6	3	0	100
8 - 9	3	0	0	100
9 - 10	2	0	0	100
10 - 11	1	0	0	100
11 - 12	0	0	1	0
Total 1 year	82	34	26	82

The duration of lactation in lechwe may be at least seven months. This can be stated with some confidence as two seven-month old males (the age of which could be determined fairly precisely on the basis of horn emergence) were each seen to suckle on several occasions. Several large female fawns were also observed suckling but their age could not be accurately assessed because they lack horns.

The mechanism by which fawns are weaned appears to be a simple refusal by the dam to allow suckling. One case was observed in which a nursing female, over a period of days, consistently refused to allow her large female fawn to suckle. The fawn eventually ceased its efforts. Termination of nursing by the dam is consistent with the observation of Talbot & Talbot (1962) that wildebeest of up to 16 months of age had milk in the abomasum, indicating a continued readiness to suckle on the part of the young animal.

Further data on suckling are presented in the context of the female-fawn relationship in Chapter 9 (Social Organization and Behaviour). The seasonal aspect of lactation is considered in section 6.3.2.8.

Data on udder mass in various reproductive states are presented in Table 6.6. The variability of mass in the last third of pregnancy is attributable to the pronounced increase in udder mass in the last few days of pregnancy. The variability of mass during lactation may be partly explained by the stage of lactation (McDonald et al., 1969), by differences before and after nursing and by the possibility that some of the lighter mammary glands were regressing when the animals in question were collected. Data on udder mass may be helpful in deciding whether or not a female has reproduced.

6.3.2.7

Parturition interval

The fact that 20% of the lactating females collected during this study were also pregnant establishes that strict lactational anoestrus does not apply to red lechwe. Other species without lactational anoestrus include Uganda kob (Morrison, 1971), wildebeest (Attwell, 1977) and nyala (Tragelaphus angasi) (Anderson, 1978).

TABLE 6.6: UDDER MASS (grams) IN LECHWE FEMALES

Class	Sample size	Mean	Range	95% confidence limits
Virgin	5	47	28 - 62	30 - 64
Non-pregnant adult	5	75	53 - 90	55 - 95
First third of pregnancy	5	73	50 - 85	64 - 82
Mid third of pregnancy	7	98	80 - 149	75 - 121
Last third of pregnancy	6	366	195 - 528	283 - 449
Lactating	23	420	168 - 953	343 - 497

From a very small sample of three animals in which the interval since parturition could be estimated, it appears that post-partum regression of corpora lutea and development of follicles in lechwe follow much the same pattern as in Uganda kob (Morrison, 1971; Morrison & Buechner, 1971). The three cases will be described individually.

(a) A three-year old female was collected, apparently within a few days of parturition. The uterus weighed 1,471 kilograms, the caruncles were fully developed and pedunculate and a large amount of placental material was present in the rumen. The regressing corpus luteum of pregnancy had a mean diameter of 8,5 millimetres. All macroscopic follicles were less than two millimetres in diameter.

(b) A five-year old female was collected, apparently also within a few days of parturition. The uterus weighed 0,884 kilograms, the caruncles were large and pedunculate, placental material was present in the rumen. The regressing corpus luteum of pregnancy had a mean diameter of 8,8 millimetres. All macroscopic follicles were less than two millimetres in diameter.

(c) A four-year old female was collected within 10-20 days of parturition, judging from data on Uganda kob (Morrison & Buechner, 1971). The uterus was still slightly enlarged and its mass was 0,114 kilograms. The regressing corpus luteum of pregnancy had a mean diameter of 5,6 millimetres. The right ovary contained one follicle greater than four millimetres in diameter. The left ovary contained one follicle greater than two millimetres in diameter. All other macroscopic follicles were less than two millimetres in diameter.

Few opportunities occurred to directly determine the interval between parturition and conception. Two females with 3-4 month old fawns were seen to copulate, each female permitting multiple copulations. It is possible that conceptions resulted from these matings. This indicates a postpartum interval of 3-4 months and a parturition interval of 10,5 to 11,5 months.

A further effort to estimate parturition interval was made using (after Anderson, 1978) the method of Short (1966) for calculating the length of the oestrous cycle in the elephant. The relationship used was:

$$\frac{\text{Interval between pregnancies (x)}}{\text{Gestation period}} = \frac{\text{number not pregnant}}{\text{number pregnant}}$$

Because no yearlings conceived, this age class was omitted from the calculations. Applying the formula to the remaining age classes:

$$x = \frac{50}{82} \times 225 = 137 \text{ days}$$

Parturition interval = Gestation period + 137 days
= 362 days

Caughley's (1977) method of calculating frequency of pregnancy was also used. He advocates separate calculations for each age class but this was not possible because the sample size in each age class was inadequate for this purpose. Using data from all females above two years of age, a frequency of 1,1 pregnancies per year was calculated. This indicates a parturition interval of about 11 months.

These calculations agree rather well with the two direct determinations of parturition interval. A fairly long postpartum anoestrus is also indicated by the fact that all lactating females that were also pregnant were in the very early stages of pregnancy. If some of them had conceived again soon after parturition the foetus would have developed to an advanced stage while the current fawn was being suckled.

On the basis of these estimates it is reasonable to assume that in the Kwando population females are producing approximately one young per year. It is necessary to recognize that this is an approximation. There is likely to be considerable individual variation in parturition interval and general changes in parturition interval related to range conditions are to be expected.

6.3.2.8

Seasonality

The results of the calculation of conception and birth dates (Huggett & Widdas, 1951) are presented in Figures 6.11 and 6.12. There is a very obvious preponderance of conceptions between December and March. Similarly, although births occur throughout the year the great majority occur between August and October.

As more or less equal numbers of females (4-6) were collected during each month of the study, these results can be used to determine seasonal variability without the type of correction factor employed by Anderson (1978). This involves a comparison of actual and possible

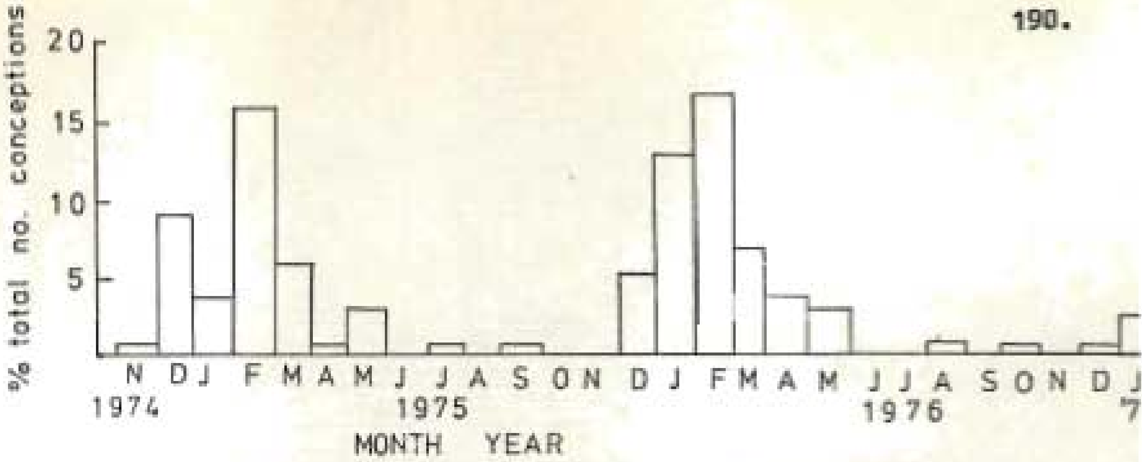


Figure 6.11: The percentage of the total number of calculated conception dates that occurred in specific months.

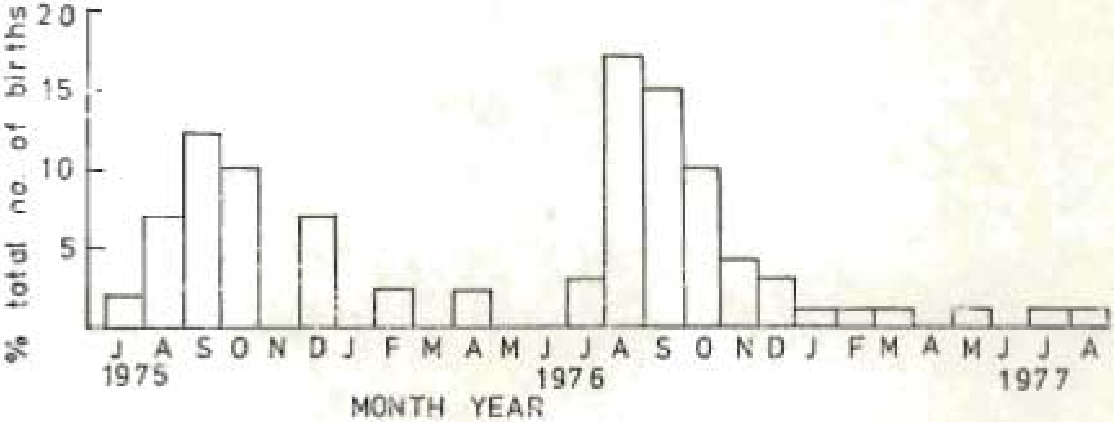


Figure 6.12: The percentage of the total number of calculated birth dates that occurred in specific months.

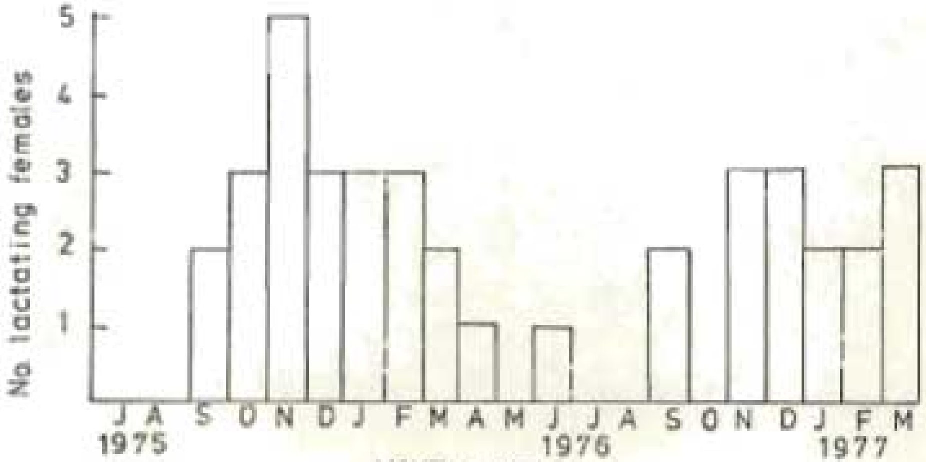


Figure 6.13: The number of lactating females shot in specific months.

numbers of conceptions occurring between the first day of the month of collection and the end of an interval of time equal to the gestation period after the last day of the month of collection.

In Figure 6.13 the distribution of lactating females is slightly anomalous, but in general agreement with calculated birth dates. The absence of lactating females in July and August is consistent with a cessation of births in December, but is not entirely consistent with the occurrence of births in these months. This may be explained by the fact that in the early part of the lambing period the proportion of females that has given birth is small in comparison to the overall size of the female segment of the population. This means that the probability of collecting a lactating female at this stage is much lower than it would be when all or most of the pregnant females had given birth.

Figures 6.14 and 6.15 were prepared as a means of assessing the validity of the Huggett and Widdas calculations. The logic underlying these figures is that as the size of the largest follicle is inversely related to the stage of pregnancy - it decreases as pregnancy advances - one would expect follicle size to decline at the time of year when females are in late pregnancy or giving birth (section 6.3.2.4). This being so, it is clear that Figures 6.14 and 6.15 are more or less consistent with the lambing period from July to December that is indicated by the calculated birth dates.

The peaks of breeding and parturition documented in this study are in very close agreement with the results of the two studies on Kafue lechwe (Robinette & Child, 1964; Sayer & Van Lavieren, 1975). The periods of breeding and parturition in Bangweulu are apparently shorter and later - breeding in March and April, parturition in September/October (Grimsdell & Bell, 1975). These results should probably be regarded with a measure of caution as the estimates are based entirely on field classifications of live animals. The position in the Okavango Delta is apparently similar to that in Bangweulu. Most conceptions occur between February and April, most births between September and November (Biggs, 1979). Biggs's estimates are based on a fairly small shot sample (22 animals) that was unequally distributed by month; 62% of the sample was collected between August and October, and no animals were collected in January, April or July.

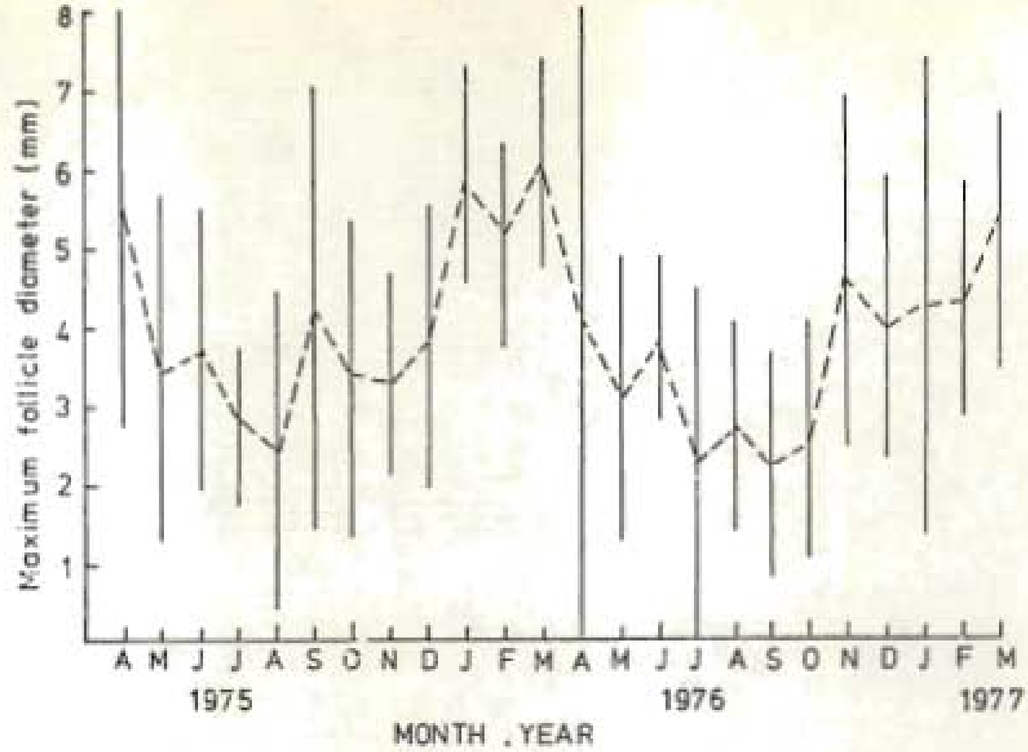


Figure 6.14: Monthly changes in the mean diameter of the largest follicle (calculated from midpoints of size classes). Points represent means. Vertical lines indicate 95% confidence limits.

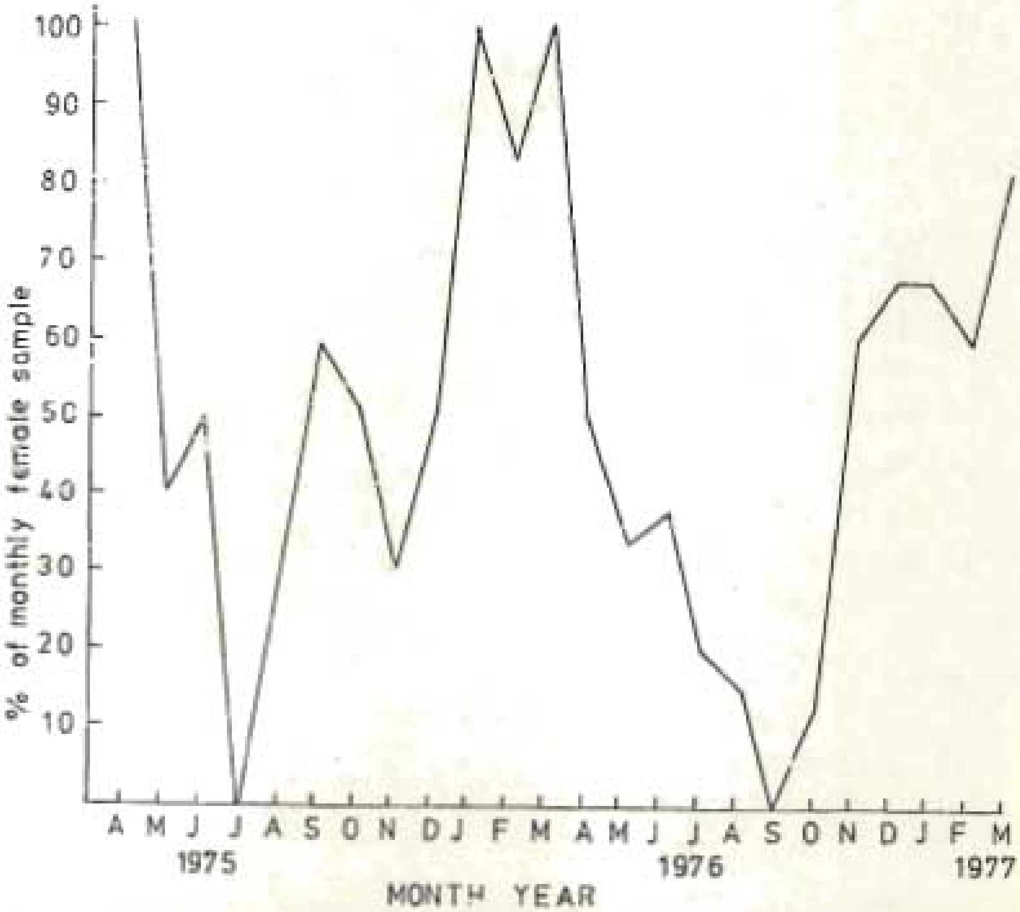


Figure 6.15: Proportion of females in each month with largest follicle greater than four millimetres in diameter.

The inferred peaks of breeding and parturition thus probably require corroboration.

The discussion of seasonality by Child & Von Richter (1969) is confusing. They were working on the Chobe segment of the same population that was the object of this study. They state: "Most calves were born between October and January in 1966 ... This is similar to the calving behaviour observed by Robinette & Child (1964) for Kafue Flats lechwe where a few calves were probably born in all months, although there is a decided peak in December and January". This in fact contradicts Robinette & Child who clearly state "While most lambs appear to be dropped from July to September, there is some evidence that a few are probably born every month". In view of this confusion conclusions about the reproductive seasonality of Chobe lechwe must necessarily be tentative.

In the context of management, reproductive seasonality of females is relevant at least in respect of the timing of harvesting. Female lechwe are either pregnant or lactating most of the time; sometimes they are both pregnant and lactating. If harvesting is carefully timed it may be possible to reduce losses among nursing fawns - foetuses are inevitably lost if females are harvested. Harvesting should be timed so that nursing fawns are as large as possible but any current pregnancy is not too far advanced. If the pregnancy is too advanced the female will have begun to lose condition because of the heavy demand for energy and nutrients in the later stages of pregnancy.

In the Kwando lechwe population the most favourable time (on this basis) to harvest females would be in March/April. At this time many females are in the early stages of pregnancy and fawns of the previous breeding season are mostly sufficiently large to allow a reasonable chance that they will survive without their dam. However, because there is still considerable activity on territorial breeding grounds during March (Chapter 9) it would probably be preferable to delay harvesting until April/May when breeding activity has declined. Delaying the harvest would have the further advantage that many fawns from the previous year would have been weaned.

In a discussion of the reproductive seasonality of female mammals, Clarke (1972) states that "complete understanding of mammalian (and other) population dynamics certainly will require full appreciation of what determines the onset and cessation of the sexual season." For this reason it is important to give some thought to the question of what determines reproductive seasonality.

Clarke (1972), in a similar way to Owen (1976), distinguishes between two types of factors which control breeding season: ecological or external factors and physiological or internal factors. The two groups come together at the level of the receptors by which environmental changes are perceived. Photoperiod, rainfall, nutrition and predation (Estes, 1976) are examples of ecological factors. Gestation period, the time at which sexual maturity is attained and digestive physiology, through its influence on the type of food supply that may be exploited, are examples of internal factors.

On the few data available from the present study only very tentative suggestions can be offered about the mechanisms controlling reproductive seasonality in lechwe females.

It is commonly asserted that reproduction is timed so that births occur at the most favourable time for the survival of the young (Sadleir, 1969b; Skinner et al., 1974; Attwell, 1977; Anderson, 1978). Skinner et al., (op. cit.), for example state that "many mammals have a definite breeding season which is initiated at such a time that environmental conditions will be optimum for the survival of the young after birth".

Many lechwe births occur at a time which may possibly not be optimal either for the lactating female or for the young which depend on the female for their survival. Not enough is known about range conditions to clarify this point but it can certainly be argued that a peak of births in November rather than September would be more conducive to survival of the young.

There is further cause for doubting that lechwe young are necessarily born at the most favourable time of the year, in the difficulty of identifying a mechanism which controls breeding behaviour to achieve a peak in births at the optimal time. The most commonly evoked and widely investigated mechanism for the control of breeding seasons is the photoperiod (Clarke, 1972). A photoperiodic stimulus has been suggested as the agency which induces the rut in wildebeest (Spinage, 1973a; Attwell, 1977). Anderson (1978) postulates a similar role for photoperiodicity in nyala and a number of other African ruminants, including lechwe. Anderson's suggestion that in lechwe breeding behaviour is bimodal and initiated by photoperiod is based on the work of Child & Von Richter (1969). Reservations about the comments on seasonality by these authors have already been expressed. Furthermore the apparent false rut reported by Wilhelm (1933) is quite possibly nothing more than a build-up of breeding activity, which begins in November and continues through to March. Data presented from this study indicate that conceptions may take place from November onwards and a build-up of breeding activity in November was actually observed in the field during this study and by Robinette & Child (1964) on the Kafue. All the data from the present study, including continuous behavioural observations, indicate a single period of sustained breeding behaviour. It is possible that intensified male breeding behaviour is triggered by a photoperiodic cue but a link between female reproduction and photoperiod seems unlikely in view of the fact that births can occur at any time of the year.

If the photoperiod is not the mechanism controlling reproductive seasonality in lechwe, what is? Because neonates are hidden, predation is unlikely to exert a selective pressure on the timing of births. The timing of the annual floods is not consistent and is therefore not a reliable cue for reproduction. On the other hand, rainfall is erratic in time and space, but most conceptions appear to occur during the rains. In these circumstances it seems reasonable to suggest that, at least with regard to females, lechwe reproductive seasonality is most probably determined more by nutrition than any other factor.

The lechwe is a grazer or bulk and roughage feeder (Hoffman, 1973). Leuthold & Leuthold (1975) suggest that reproductive seasonality in grazers is related to changes in the quality of the food supply. Grimsdell & Bell (1975) attribute to nutritional differences the non-synchronous breeding of a sub-population of lechwe in the Bangweulu Swamp. Data from the present study also suggest an important role for nutrition. Somewhat surprisingly, conceptions appear to be strongly correlated with rainfall. In the first breeding season of this study the rains began in November 1974 and continued to May 1975. The first calculated conception for that year fell in November and conceptions occurred consistently into May. In 1975, October and November were exceeding hot and dry. Heavy rains fell at the beginning of December and continued to fall regularly until the end of

March. The first conception for that season occurred in December and after March conceptions were sporadic.

On the basis of the above discussion a very tentative explanation of reproductive seasonality in lechwe females is offered along the following lines. Females come into oestrus and conceive when their body condition (or perhaps mass, see Chapter 5) reaches an undetermined threshold. This usually occurs in the rains because high quality herbage is then most abundant. The timing of individual conceptions is further influenced by a number of individual and internal factors. Animals may attain sexual maturity at different times of the year. The parturition to conception interval may vary with changes in condition and may also be influenced by genetic factors. The length of the gestation period makes it unlikely that a female will give birth at the same time each year. These individual factors may account for the manner in which conceptions are spread throughout the rainy season and occur sporadically throughout the year.

6.4

SUMMARY

6.4.1

Growth

The purposes of studying growth were the following:

(1) to facilitate estimation of lechwe biomass;

(2) to optimize economic returns from the exploitation of lechwe;

(3) to assist investigation of population dynamics by facilitating comparison of growth rates at different times and in different places;

(4) to facilitate age classification in the field;

(5) to allow objective estimation of mass.

Theoretical, computer-generated growth curves were produced for the growth of lechwe females in mass, body length, chest girth, shoulder height and neck girth. There were indications that growth in mass of lechwe females in the Kwando population is probably slower than that of females in the Bangweulu population.

Data on carcass composition were collected and on the basis of circumstances in Botswana, it is argued that large animals should be harvested rather than smaller animals just emerging from the period of maximum growth.

Predictive equations were derived which allow the prediction of mass from measurements of length and girth and the prediction of carcass mass from dead mass.

6.4.2

Reproduction

The purposes of investigating reproduction were:

(1) to describe reproductive phenomena in female lechwe on the Kwando;
(2) to determine prevailing reproductive rates;
(3) to identify the most important factors influencing these rates;
(4) to document reproductive seasonality.

Growth and functioning of the ovary are described and evidence is adduced which indicates that Kwando lechwe females ovulate more commonly from the right ovary than from the left. The attainment of sexual maturity by females in the Kwando population was delayed. There were indications that lechwe females experience infertile oestrous cycles or "quiet heats" (Nalbandov,1976). Implantation invariably occurred in the right horn of the uterus. There was little change in the size of the corpus luteum during pregnancy. Maximum follicle size appeared to decline with advancing pregnancy. Corpora nigra did not persist.

Apart from younger age classes, the fecundity of lechwe females on the Kwando was similar to that in other lechwe populations. The lower fecundity of younger Kwando females was believed to be largely a reflection of nutritional stress (Chapter 5).

Lactation may last up to seven months and is probably terminated by a refusal of the dam to allow further suckling. There was no strict lactational anoestrus. Kwando females were apparently producing about one young per year.

There were seasonal peaks in both conceptions and births. It was suggested that nutrition is the most important factor influencing reproductive seasonality.

CHAPTER 7

GROWTH AND REPRODUCTION IN THE MALE

7.1

INTRODUCTION

The relevance and methods of growth studies were considered in section 6.1. The principles discussed there in relation to female growth are equally applicable to that of males.

In males, the study of reproduction is mainly concerned with the attainment of puberty and sexual maturity and with reproductive seasonality. It has already been mentioned (section 6.3.2.2) that the concepts of puberty and sexual maturity in males are complicated by the influence of behavioural factors. A variety of mechanisms has been identified in in ungulate societies which prevent young males that are apparently sexually mature in physiological terms from obtaining access to oestrous females. In lechwe, ownership of a territory appears to be a prerequisite for successful mating and young males are probably unable to acquire territories until they are over four years old. A similar situation has been documented in several other species, for example, Uganda kob (Buechner, 1961a), wildebeest (Estes, 1969), pronghorn antelope, *Antilocapra americana* (Kitchen, 1974), bontebok, *Damaliscus dorcas dorcas* (David, 1973) and waterbuck (Spinage, 1974).

The sexual cycle of relatively few males has been adequately investigated (Chapman, 1972). Chapman (*op. cit.*) distinguishes between two categories of male reproduction on the basis that some species are capable of breeding throughout the year whereas others are fecund only at certain seasons and sexually quiescent at others. He makes the point that even animals which are fecund throughout the year may exhibit cyclic changes and warns against extrapolating from the female's breeding cycle to that of the male. Even if females conceive throughout the year it is possible that males have a cycle but that not all of them are at the same stage of the cycle at the same time.

The beginning of active spermatogenesis is usually accepted as the stage which marks the attainment of puberty in males (see, for example, Morris & Hanks, 1974). The attainment of full sexual maturity may be indicated by successful mating.

Techniques for investigating male reproductive seasonality range from simply monitoring changes in testis mass (Robinette & Child, 1964; Anderson, 1965) to sophisticated histological and histochemical studies of the testes and accessory glands. Chapman (1972) cites the work of Short & Mann (1966) on roebuck (*Capreolus capreolus*) as a model study of male seasonality. This study involved "investigation into the seasonal changes in the weights and histology of the testes, epididymides, seminal vesicles and ampullae together with the concentration of testosterone in the testes, fructose and citric acid in the seminal vesicles, and fructose in the ampullae" (Chapman, 1972). Other techniques include the monitoring of changes in seminiferous tubule diameter (Watson, 1969; Skinner & Huntley, 1971; Smuts,1976; Hanks *et al.*, 1976; Attwell, 1977; Anderson, 1978), observation of changes in epididymal sperm number (Skinner & Huntley, 1971) and measurement of sperm motility (Skinner, 1971).

7.2

MATERIALS AND METHODS

Body mass, measurements and reproductive data were taken from a sample of 89 males, which were shot during this study.

7.2.1

Growth

Growth data were collected from males in precisely the same way as from females except that horn measurements were taken in addition. Three horn measurements were routinely made:

(a) basal circumference of both horns;
(b) length along the front curve of the horn;
(c) distance between the tips of the horns.

7.2.2

Reproduction

Choice of methods in this study was limited by lack of refrigeration or field laboratory facilities. Histological examination of testis material was chosen as the means of assessing whether or not puberty had been attained. Changes in testis mass and seminiferous tubule diameter were chosen as indices of seasonality because of their simplicity; seminiferous tubule diameter is considered to be a good index of sexual function in ruminants (Chapman, 1970).

As soon as possible after collection the testes were removed and weighed to 10^{-1} grams on a triple beam balance. The pampiniform plexus was removed before weighing. The epididymides were not removed, being weighed with the testis. A portion of testis from each animal was fixed in ten percent formalin and stored for later processing.

After routine paraffin embedding, testis samples were sectioned at 7 μm and stained with haemotoxylin and eosin. Samples from five prepubertal and five postpubertal epididymides were also embedded, sectioned and stained.

Testis sections were microscopically examined for presence of spermatogenesis. Testes were regarded as prepubertal if no spermatids were found in the lumen of the seminiferous tubule and only a single layer of cells was apparent at the basement membrane of the tubule. Testes were classed as postpubertal if spermatids occurred in the lumen and several layers of cells were apparent along the basement membrane.

Seminiferous tubule diameter was calculated as the mean of 30 circular cross-sections of tubules, measured in micrometres with a micrometer eyepiece calibrated against an objective micrometer slide. Where distortion or autolysis had occurred, measurements were taken from the basal membrane and the degree of distortion was classed as gross, moderate or slight to none. An analysis of variance of adult tubule diameter in the different categories of distortion was done to establish whether distortion might have affected the results of tubule measurements

7.3

RESULTS AND DISCUSSION

7.3.1

Growth

7.3.1.1

Theoretical growth curves

The use of growth equations in this study was explained in section 6.3.1.

The various growth equations are listed below.

(a) Growth in mass

The equation for growth in mass of males is:

$$m_t = 118{,}11 \ (1 - e^{-0{,}5669 \ (t + 1{,}1559)})^3 \text{ kg}$$

Figure 7.1 illustrates the curve for this equation. The theoretical asymptote is reached at about seven years of age. By five and a half years the mean mass is within one standard deviation of the asymptotic value.

(b) Growth in body length

The equation for growth in body length of males is:

$$l_t = 164{,}05 \ (1 - e^{-0{,}5769 \ (t + 1{,}2334)}) \text{ cm}$$

Figure 7.2 illustrates the curve for this equation. The theoretical asymptote is reached at about five years of age.

(c) Growth in chest girth

The equation for growth in chest girth of males is:

$$g_t = 109{,}54 \ (1 - e^{-0{,}5874 \ (t + 1{,}1577)}) \text{ cm}$$

Figure 7.3 illustrates the curve for this equation. The theoretical asymptote is reached at about five years of age.

(d) Growth in neck girth

The equation for growth in neck girth of males is:

$$n_t = 91{,}55 \ (1 - e^{-0{,}1426 \ (t + 1{,}9152)}) \text{ cm}$$

Figure 7.4 illustrates the curve for this equation. The theoretical asymptote of 91,55 cm was never approached in reality and it appears that the function used to generate the theoretical curve is not readily applicable to describing growth in neck girth of lechwe males.

Comparison with Figure 6.6 indicates a radically different pattern of growth in neck girth in lechwe females and males; the female pattern fits the function used to generate the theoretical curve. Neck girth could possibly be described as a secondary sexual characteristic.

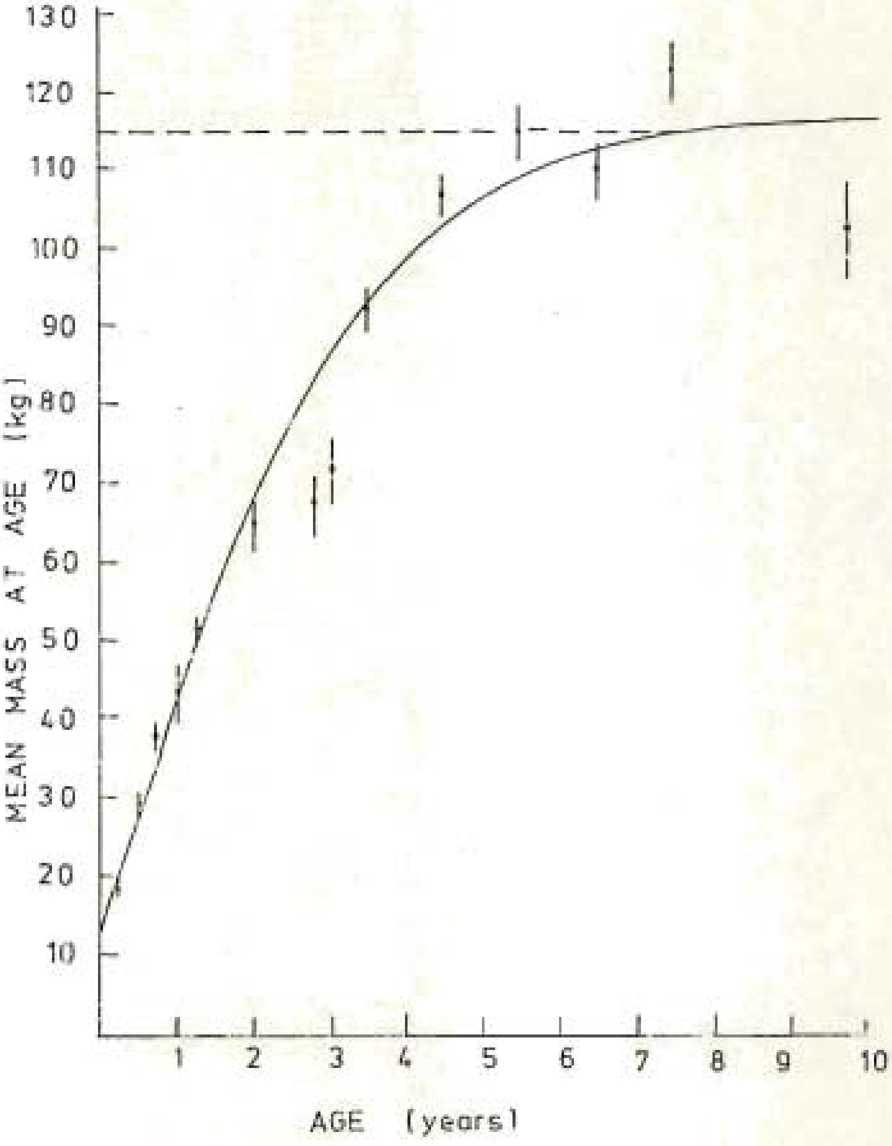


Figure 7.1: Theoretical curve for growth in mass of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

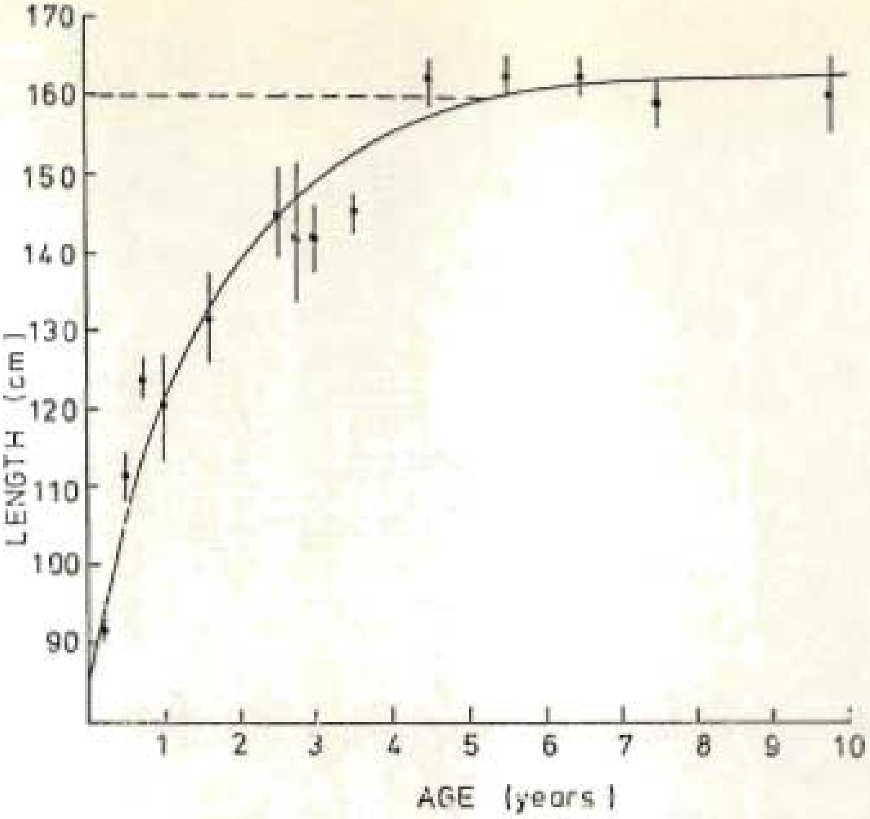


Figure 7.2: Theoretical curve for growth in body length of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

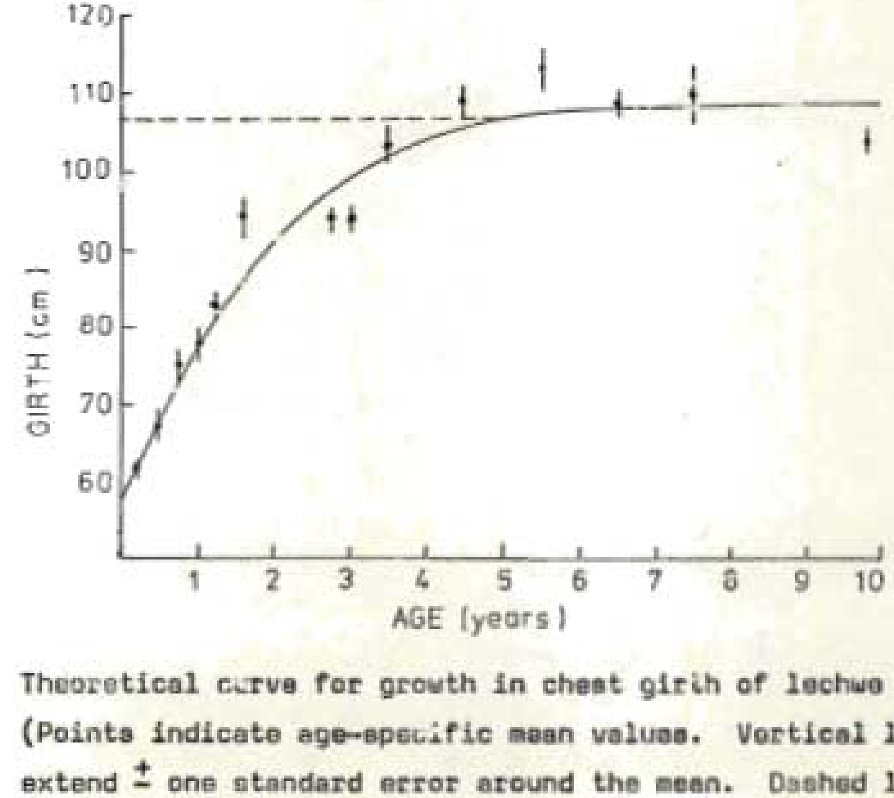


Figure 7.3: Theoretical curve for growth in chest girth of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

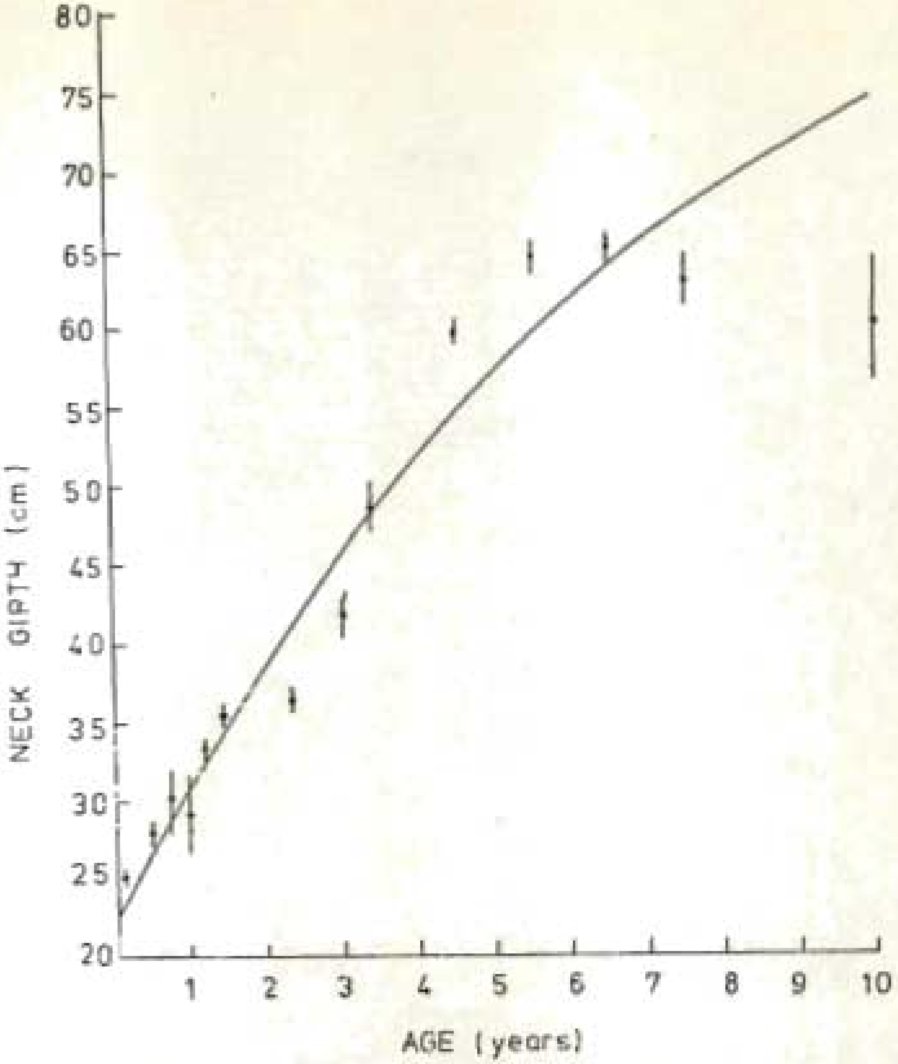


Figure 7.4: Theoretical curve for growth in neck girth of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean.)

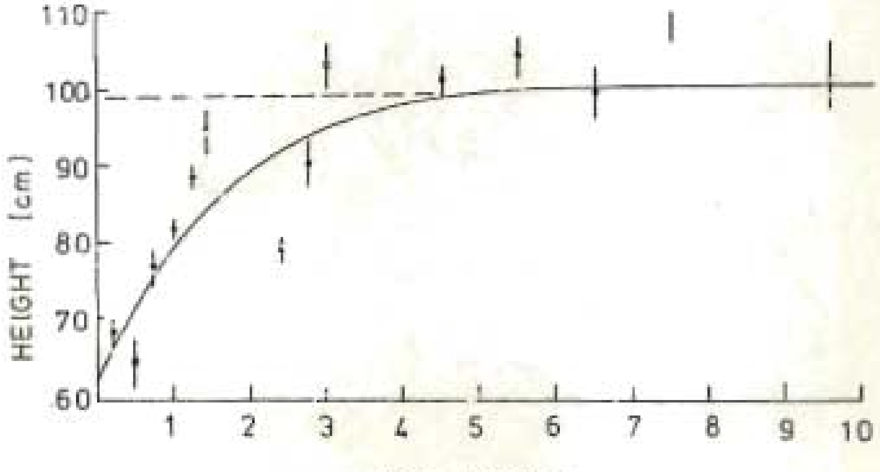


Figure 7.5: Theoretical curve for growth in shoulder height of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

(e) Growth in shoulder height

The equation for growth in shoulder height of males is:

$$sh_t = 101,41 \ (1 - e^{-0,6083 \ (t + 1,5239)}) \text{ cm}$$

Figure 7.5 illustrates the curve for this equation. The theoretical asymptote is reached by four and a half years. The difficulty of using this character as a criterion of age determination in the field is illustrated by the fact that the mean shoulder height of three year olds is above the asymptote. A further difficulty is that it is extremely difficult to measure shoulder height accurately on a dead animal(Jeffery, 197

(f) Growth in horn base circumference

The equation for growth in horn base circumference is:

$$hb_t = 18,36 \ (1 - e^{-0,6613 \ (t + 0,4289)}) \text{ cm}$$

Figure 7.6 illustrates the curve for this equation. The theoretical asymptote is reached by four and a half years. The raw data indicate that the adult range is attained by three and a half years.

(g) Growth in horn length

The equation for growth in horn length is:

$$hl_t = 54,59 \ (1 - e^{-0,9826 \ (t + 0,8345)}) \text{ cm}$$

Figure 7.7 illustrates the curve for this equation. The theoretical asymptote is reached at four and a half years. The raw data indicate that the adult range is attained by three and a half years. From figures 7.6 and 7.7 it is clear that after three and a half years of age, horn size is not a useful character for age determination in the field.

Changes with age in the distance between the tips of the horns are irregular and cannot be analysed with the von Bertalanffy equation. These data are summarised in Chapter Three (Age Determination).

A comparison of morphometric data from males and females is presented in Table 7.1. Substantial differences between the sexes, particularly in respect of mass and neck girth, are clear. A comparison of some mass

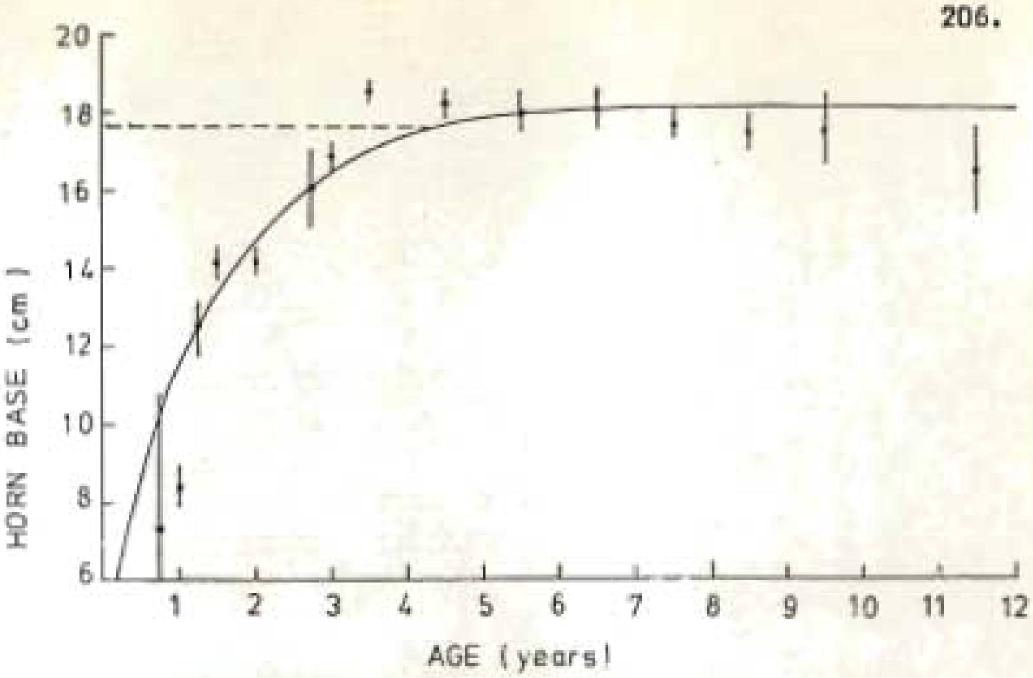


Figure 7.6: Theoretical curve for growth in horn base circumference of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

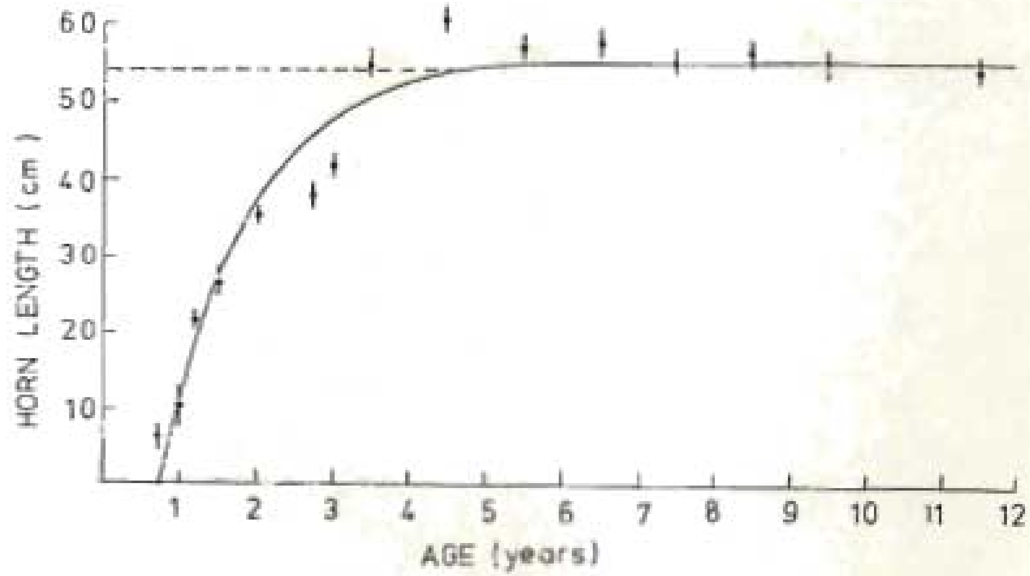


Figure 7.7: Theoretical curve for growth in horn length of lechwe males. (Points indicate age-specific mean values. Vertical lines extend ± one standard error around the mean. Dashed line lies within 2,5% of the asymptote.)

TABLE 7.1: DATA ILLUSTRATING SEX DIFFERENCES IN BODY MASS AND MEASUREMENTS IN KWANDO LECHWE. (Data are from animals of or above the age at which von Bertalanffy asymptotes are reached.)

Value	Mass (kg)		Length (cm)		Girth (cm)		Shoulder ht (cm)		Neck girth (cm)	
	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male
Maximum	89,0	135,0	162,0	175,0	112,0	128,0	101,0	112,0	41,0	73,0
Minimum	52,0	87,5	134,0	150,0	84,0	97,0	87,0	94,0	27,0	46,0
Mean	71,3	112,7	150,4	162,0	96,6	110,4	94,8	104,2	33,0	61,1
Asymptote	74,1	118,1	152,5	164,1	97,6	109,5	92,0	101,4	32,9	91,6
Sample size	54	22	86	49	86	49	60	30	49	41
Difference between means	41,4		11,6		13,8		9,4		28,1	
"t"	17,2		9,7		12,6		10,4		31,2	
"p"	< 0,001		< 0,001		< 0,001		< 0,001		< 0,001	

data from Zambia is made in Chapter 5. Unfortunately body measurement data from the Zambian populations were collected in slightly different ways from each other and from this study, which precludes their use in comparisons. The one clear subspecific difference is that in males the horns of Kafue lechwe are strikingly larger than those of either of the other two subspecies. The asymptotic value for horn length in Kafue males is approximately 70 centimetres, while for Bangweulu males it is approximately the same as in Kwando lechwe, about 55 centimetres. The maximum horn length encountered By Robinette & Child (1964) was 83 centimetres, while the longest set of horns measured in this study was 66 centimetres.

Table 7.2 presents data on the ages of attainment of asymptotic values in mass, shoulder height and body length in males on the Kwando, Kafue and Bangweulu populations. As with the females of the same populations, the data are not directly comparable but there is an indication of slower growth in the Kwando population. With males this indication is less clear than in females because Kwando males are appreciably heavier (23%) than Bangweulu males and this may account for some of the difference in the age at which the asympoiotic mass is attained.

Table 7.3 presents data on mass gains. The first year of life is the period of maximum mass gain. This conforms to the pattern found in most other wild herbivores that have been investigated (e.g. Smuts, 1975; Attwell, 1977) and it casts further doubt on the validity of the data from females in the Kwando population (section 6.3.1.1). Significantly, the sample of young males was larger than that of young females. This may well be related to the fact that by six to seven months males have visible horns, making the selection of a representative sample of each age class easier than it is in females.

Table 7.4 gives data on body mass and composition of lechwe males at different ages. In the case of males the yield per unit cropping effort would be increased by

$$\frac{(109,6 \times 0,582)}{(\ 31,8 \times 0,562)} \times 100 = 357\%$$

if animals over four years old rather than animals in their first year are harvested. It is thus clear that under conditions prevailing in Botswana, where production costs are non-existent and harvesting costs are high, there are economic advantages to harvesting older rather than younger animals.

TABLE 7.2: AGES AT WHICH ASYMPTOTIC VALUES FOR MASS, SHOULDER HEIGHT AND BODY LENGTH ARE ATTAINED BY LECHWE MALES IN THREE DISTINCT POPULATIONS

PARAMETER	KWANDO (This study)	KAFUE (Robinette and Child, 1964)	BANGWEULU (Grimsdell and Bell, 1975)
Mass	ca 7 years	ca 5,5 years	ca 4,5 years
Shoulder height	ca 4,5 years	No data	ca 4,5 years
Body length	ca 5 years	No data	ca 4,5 years

TABLE 7.3: MASS GAINS (KG) IN LECHWE MALES, CALCULATED FROM THEORETICAL GROWTH CURVES AND AGE-SPECIFIC SAMPLE MEANS

Age	Theoretical curves		Sample means	
interval (years)	Gain / yr	Gain / day	Gain / yr	Gain / day
0 - 1	35,0	0,096	36,0	0,098
1 - 2	26,8	0,073	22,1	0,061
2 - 3	19,3	0,053	6,5	0,018

TABLE 7.4: BODY MASS AND COMPOSITION OF LECHWE MALES ON THE KWANDO

AGE		DEAD MASS[1] (kg)		CARCASS YIELD [2] %		EXTERNAL OFFAL[3] %		INTERNAL OFFAL[4] %	
(years)	n	Mean ± S.E.	Range	Mean ± S.E.	Range	Mean ± S.E.	Range	Mean ± S.E.	Range
0 - 1	12	31,8 ± 2,8	17,5 - 47,5	55,2 ± 1,4	48,6 - 65,7	13,6 ± 0,7	10,6 - 18,8	30,2 ± 1,9	17,1 - 37,8
1 - 2	5	57,6 ± 4,0	45,0 - 71,5	56,2 ± 1,2	55,1 - 59,4	13,6 ± 0,8	12,4 - 15,4	30,3 ± 1,3	25,2 - 32,7
2 - 3	9	70,4 ± 2,9	57,5 - 78,5	57,3 ± 1,1	52,2 - 62,6	12,1 ± 0,6	8,4 - 14,0	30,6 ± 1,0	24,3 - 33,8
3 - 4	13	92,1 ± 3,0	70,5 - 111,5	58,9 ± 0,6	56,4 - 63,2	13.3 ± 0,4	10,9 - 15,4	27,8 ± 0,6	23,5 - 30,7
4 +	50	109,6 ± 1,5	87,5 - 135,0	58,2 ± 0,4	54,4 - 65,9	13,8 ± 0,1	12,4 - 16,8	28,0 ± 0,3	23,6 - 32,1

1 : mass of a shot animal without correction for blood loss

2 : $\frac{\text{Dead mass} - \text{external offal} - \text{internal offal}}{\text{Dead mass}} \times 100 = \text{carcass yield } \%$

3 : External offal = mass of feet (from carpal/tarsal joints), head and skin as a percentage of dead mass

4 : Internal offal = mass of the contents of the body cavity as a percentage of dead mass.

7.3.1.2

Predictive equations

The value of predictive equations was discussed in section 6.3.1.3.

The relationship between mass and body length x $(\text{girth})^2 \times 10^{-6}$ in lechwe males is (y = mass):

$$y = 52{,}54x + 4{,}29 \quad (r = 0{,}971;\ p < 0{,}001;\ n = 88)$$

The relationship between mass and chest girth in lechwe males is:

$$y = 1{,}88x - 101{,}74 \quad (r = 0{,}956;\ p < 0{,}001;\ n = 88)$$

In males there is a fairly good correlation between mass and neck girth. This relationship, plotted on a logarithmic scale is given by ($y = \log_e$ mass, $x = \log_e$ neck girth):

$$y = 1{,}44x - 1{,}24 \quad (r = 0{,}929;\ p < 0{,}001;\ n = 65)$$

In males the relationship between carcass mass and dead mass (y = carcass mass) is:

$$y = 0{,}59x - 1{,}29 \quad (r = 0{,}992;\ p < 0{,}001;\ n = 88)$$

The relationship between carcass mass and girth in lechwe males (y = carcass mass) is:

$$y = 1{,}12x - 61{,}86 \quad (r = 0{,}950;\ p < 0{,}001;\ n = 88)$$

When the correlation coefficients of the predictive equations for males and females (section 6.3.1.3) are compared, it is obvious that the correlation in males is consistently better than it is for females. Thi may be related to the fact that females experience greater fluctuations i condition than do males (Chapter Five) Fluctuations in the condition o females are no doubt aggravated by the stress of reproduction.

The relatively poor correlation obtained in the predictive equations for females may also be a result of not using the most appropriate measuremen for prediction. Smuts (1975) suggests that in zebra a predictive equati should probably incorporate some measurement over the hindquarters becau of the large contribution to total mass made by the hindquarters.

Lechwe also have powerful hindquarters, the conformation of which changes appreciably with condition. It may be that a predictive equation based on a measure of hindquarter curvature would give better results than the equations based on chest girth.

7.3.2
Reproduction

7.3.2.1
Puberty and sexual maturity

All animals 1,5 years old and older showed active spermatogenesis. In six animals, 1,5 to three years old, there were indications that spermatotogenesis was not fully in progress. Spermatids were not present in all seminiferous tubules and there were few spermatozoa in the epididymides of those animals (two) from which epididymal slides were made. The mean dead mass of these animals was 61,0 kilograms (95% confidence limits: ± 6,6 kg). Their mean testis mass was 20,7 grams (95% confidence limits: ± 3,8 grams), and mean seminiferous tubule diameter was 133,8 micrometres (95% confidence limits: ± 15 micrometres).

These animals were apparently at a developmental stage very similar to that found by Buechner et al., (1966) in pubertal Uganda kob. In both cases body mass was about half adult mass, slightly more in lechwe, and testis mass was about a quarter of adult testis mass (in lechwe mean testis mass of males older than four years was 78 grams, 95% confidence limits ± 4,7 grams). In kob this point was reached by about one year old which is earlier than in lechwe. This may be related to the fact that lechwe are larger than kob.

The relationship between body mass and testis mass was investigated by means of regressions. Figure 7.8 illustrates this relationship. Regressions for pre- and postpubertal testes were calculated separately. The equation for prepubertal testes (y = testis mass) is:

$$y = 0{,}23x - 3{,}16 \quad (r = 0{,}847; \; p < 0{,}001)$$

The equation for postpubertal testes is:

$$y = 1{,}05x - 38{,}55 \quad (r = 0{,}842; \; p < 0{,}001)$$

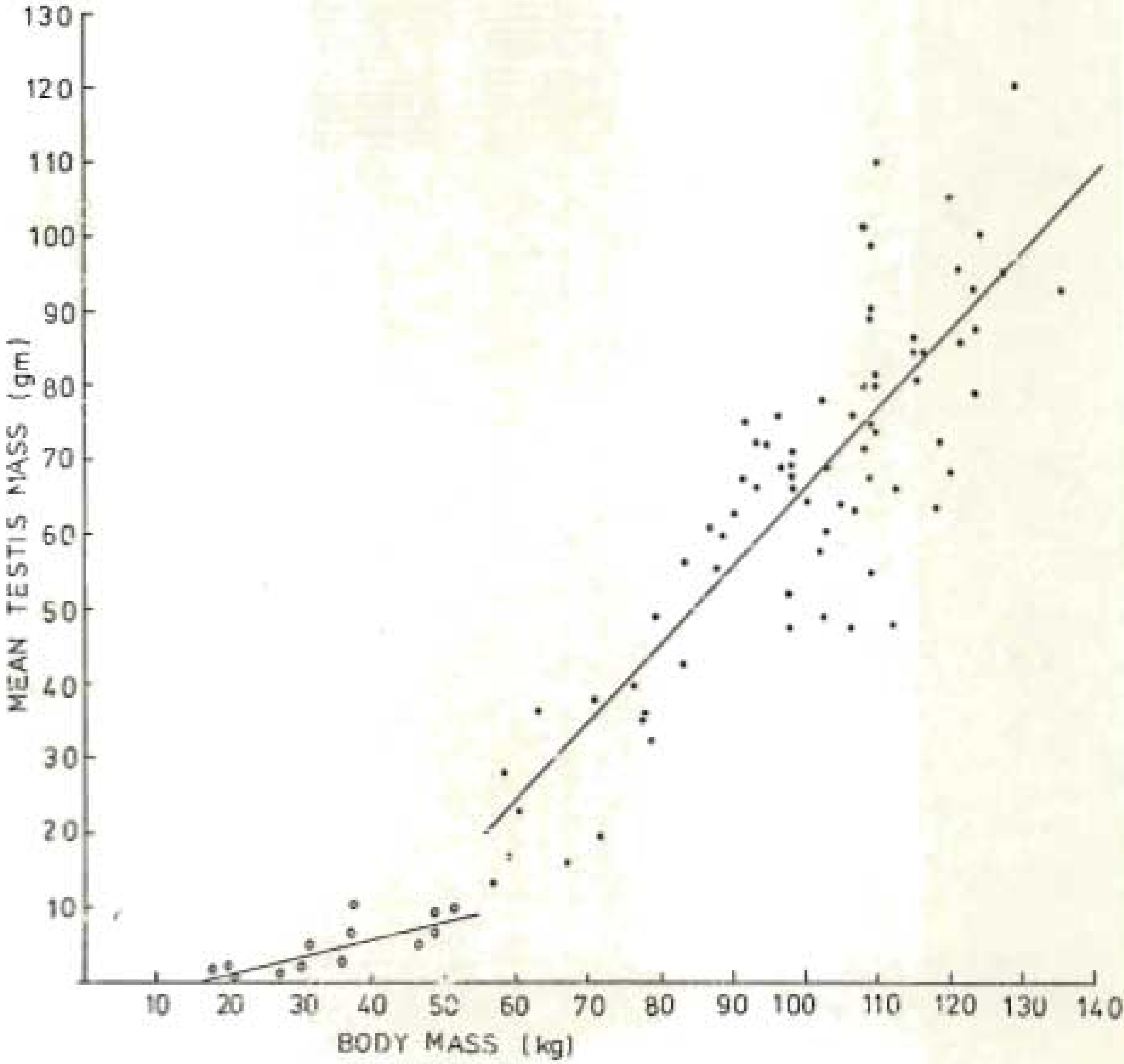


Figure 7.8: The relationship between body mass and mean testis mass. Open circles indicate prepubertal animals. Dots indicate postpubertal animals. Regressions in the text.

The correlation between testis mass and body mass in postpubertal animals is considerably better than that found, for example, in either impala Hanks <u>et al</u>., 1976) or wildebeest (Attwell, 1977). This may be related to the fact that seasonal changes in testis mass are less pronounced in lechwe than they are in impala or wildebeest. This suggestion receives a measure of confirmation from Anderson's (1978) data on nyala, which also show relatively little seasonal change in testis mass. The correlation between testis mass and body mass in nyala is extraordinarily high ($r = 0{,}98$; Anderson, <u>op</u>. <u>cit</u>.).

Figure 7.8 shows that spermatogenesis begins at a body mass of between 55 and 60 kilograms. There is active spermatogenesis in all animals above 55 kilograms and no spermatogenesis in animals below this figure. Presumably this situation accords with the idea of a critical body mass for the onset of puberty (Frisch, 1974, quoted by Attwell, 1977).

Regressions were also used to investigate the relationship between seminiferous tubule diameter and body mass. The equation for prepubertal testes (y = seminiferous tubule diameter) is:

$$y = 1{,}97x - 4{,}07 \quad (r = 0{,}871; \ p < 0{,}001)$$

The equation for postpubertal testes is:

$$y = 0{,}83x + 106{,}89 \quad (r = 0{,}594; \ p < 0{,}001)$$

The correlation in prepubertal animals is good. After the onset of puberty the relationship between body mass and seminiferous tubule diameter appears to become less pronounced although the correlation remains highly significant.

Figure 7.9 illustrates the relationship between testis mass and seminiferous tubule diameter. The regression equation for prepubertal animals (y = seminiferous tubule diameter) is:

$$y = 5{,}71x + 40{,}30 \quad (r = 0{,}799; \ p < 0{,}01)$$

The regression equation for postpubertal animals is:

$$y = 0{,}76x + 139{,}46 \quad (r = 0{,}678; \ p < 0{,}001)$$

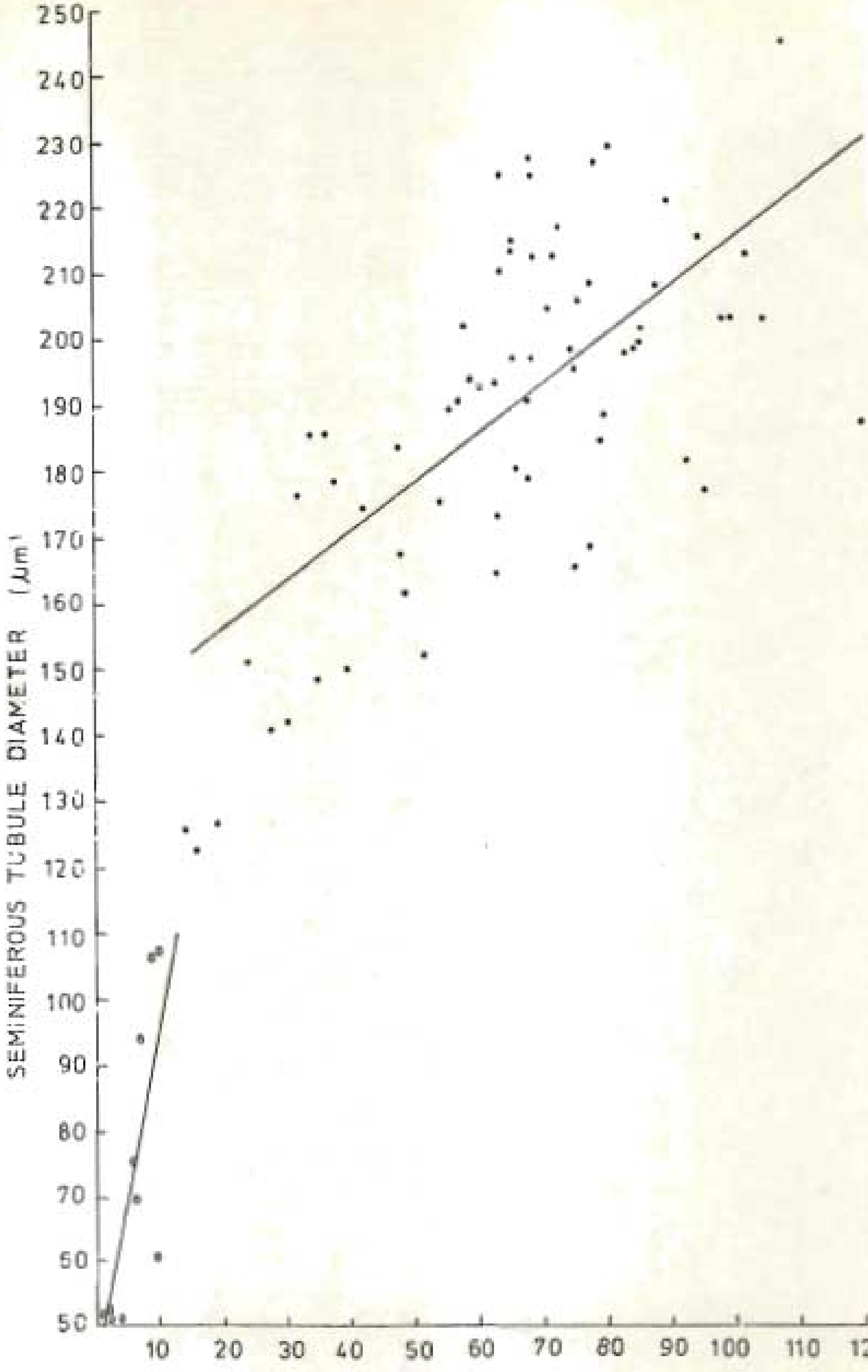


Figure 7.9: The relationship between testis mass and seminiferous tubule diameter. Open circles indicate prepubertal animals. Dots indicate postpubertal animals. Regressions in the text.

Although the correlation between tubule diameter and testis mass in postpubertal animals is highly significant, Figure 7.9 shows that testis mass may decline appreciably without greatly affecting tubule diameter. For example, tubule diameters in excess of 200 micrometres occurred in testes ranging from 59 -108 grams in mass. A similar situation has been documented in impala (Hanks et al., 1976) and wildebeest (Attwell, 1977).

Figure 7,9 shows that spermatogenesis begins at a tubule diameter of about 120 micrometres and a mean testis mass of around 15 grams.

Data presented thus far establish that spermatogenesis is occurring by 1,5 years of age. Further requirements for the attainment of sexual maturity, in terms of achieving successful mating, are erection of the penis and gaining access to oestrous females.

No conclusive data were obtained during this study on the age at which erection of the penis occurs. Several yearlings were seen to attempt to mount females but on no occasion did erection of the penis accompany these attempts. This does not conclusively show that yearlings are incapable of an erection because it was common to see territorial males mount females without erection of the penis. Robinette & Child (1964) report that a male lechwe judged to be 15 months old was observed to cover a female twice. This indicates that by 18 months lechwe have the capability to mate successfully.

Data from the present study indicate that it is only territorial males that have access to oestrous females. Numerous sexual interactions between non-territorial adult and subadult males and females were observed, but none of these appeared to approach the point of successful copulation. All observed copulations were by territorial males. Two known territorial males were collected. Their ages were estimated at 5,5 and 6,5 years. Judging by neck girth (Chapter Three), no known territorial male was less than 4.5 years old.

Despite their frequent involvement in abortive sexual encounters with females, there were indications that subadult males are subject to the "psychological castration" referred to by Altmann (1960). For example, subadult males were invariably submissive in the presence of territorial males. The case of one very large young male was particularly striking in this respect. This animal was appreciably larger than several territory holders and yet was persistently submissive when approached by even the smallest territorial male and never made an overt challenge to the dominance of the territorial males.

If 4,5 years is the earliest age at which males acquire territories, this means that there is an hiatus of three years between the onset of spermatogenesis and the achievement of successful mating. A similar situation has been documented in wildebeest (Watson, 1969; Attwell, 1977), buffalo (Syncerus caffer) (Grimsdell, 1969), Uganda kob (Buechner et al., 1966), impala (Kerr, 1965) and nyala (Anderson, 1978).

The delay between the onset of spermatogenesis and successful mating in males is probably related to the different strategies by which males and females within a polygamous mating system strive to maximize reproductive success (Williams, 1975). Females are primarily concerned with mate selection whereas males compete with each other in trying to inseminate as many females as possible. In this competition, which may take the form of territoriality, older males are more experienced and successful and younger males have less chance of gaining access to females so that selection for early reproduction is opposed (Emlen, 1973). Because there is lessened selection for efficient 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. This delayed maturity may be express in behavioural rather than anatomical or physiological terms, for example, through the "psychological castration" that has been postulated by Altmann (1960).

7.3.2.2

Reproductive seasonality in males

Because of small sample sizes it was necessary to group data by seasons. Only data from males more than four years old were considered in the investigation of seasonality. This was because testis mass in 3-4 year olds was appreciably lower than in 4-5 year olds and because of the indications that only males over four years old were fully mature sexually.

The analysis of variance did not reveal any significant differences between tubule diameter in the different classes of distortion. On this basis it was assumed that distortion had not affected the validity of measurements.

Every mature testis examined showed active spermatogenesis. Figure 7.10 illustrates seasonal changes in seminiferous tubule diameter. None of these seasonal differences were statistically significant. The difference between the highest and lowest seasonal value is 8,4% of the maximum value. In impala Hanks <u>et al</u>., (1976) found a maximum seasonal difference of 36,5%. The higher seminiferous tubule diameter during 1976 may be due to the occurrence of a less severe dry season in 1976 than in 1975.

Figure 7.11 illustrates seasonal changes in testis mass. None of the seasonal differences were statistically significant. The difference between the highest and lowest seasonal values was 9,9%. This compares with a difference of 41,7% in impala (Hanks <u>et al</u>., 1976) and 48,6% in wildebeest (Attwell, 1977). Interestingly, Robinette & Child (1964) found a much larger seasonal difference, 37%, in Kafue lechwe. This is perhaps a reflection of a different nutritional plane related to the very high population density on the Kafue Flats.

Figure 7.12 shows the results of a further effort to investigate seasonal changes in testis mass. In order to take into account the possible effect of body mass, testis mass was expressed as a percentage of body mass and the mean percentage for each season was calculated. The difference between the highest and lowest seasonal values was 13,1%, but there were no statistically significant differences between the seasons. The rise in testis mass during 1976 may be due to the fact that in 1976 the hot, dry season was less severe than in 1975.

These data and the fact that conceptions take place in all months strongly suggest the absence of a sexual cycle in adult male lechwe. Nevertheless, because relatively simple techniques were used to investigate seasonality and because there is seasonal variability in the intensity of breeding behaviour (Chapter Nine) it is probably necessary to regard as provisional the conclusion that lechwe males have no sexual cycle.

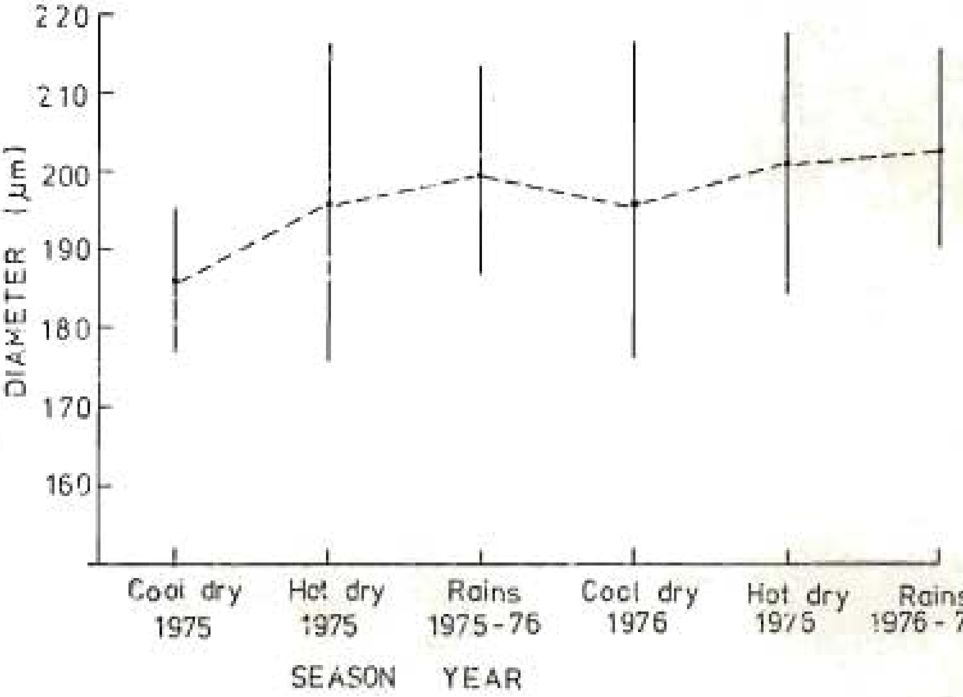


Figure 7.10: Seasonal changes in seminiferous tubule diameter. Vertical lines indicate 95% confidence limits. Dashed line joins means.

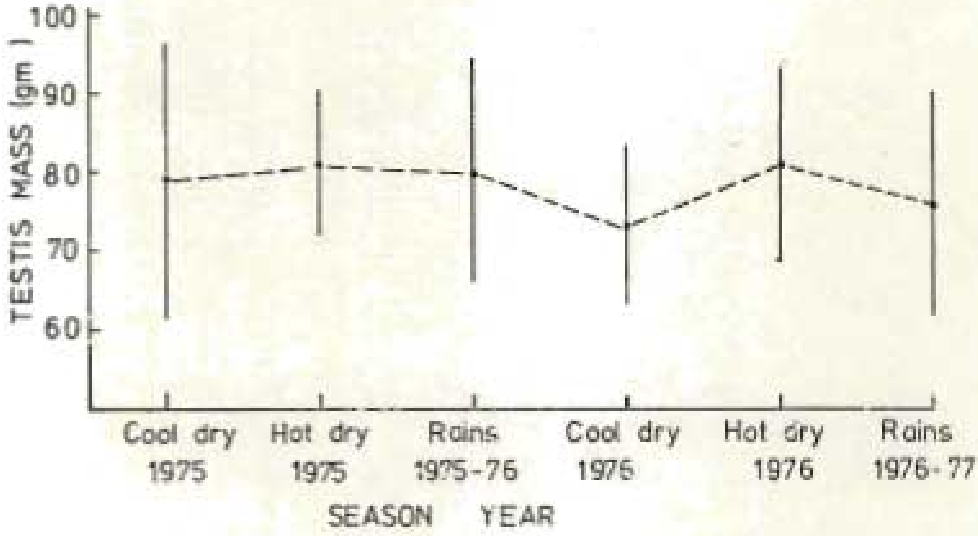


Figure 7.11: Seasonal changes in testis mass. Vertical lines indicate 95% confidence limits. Dashed line joins means.

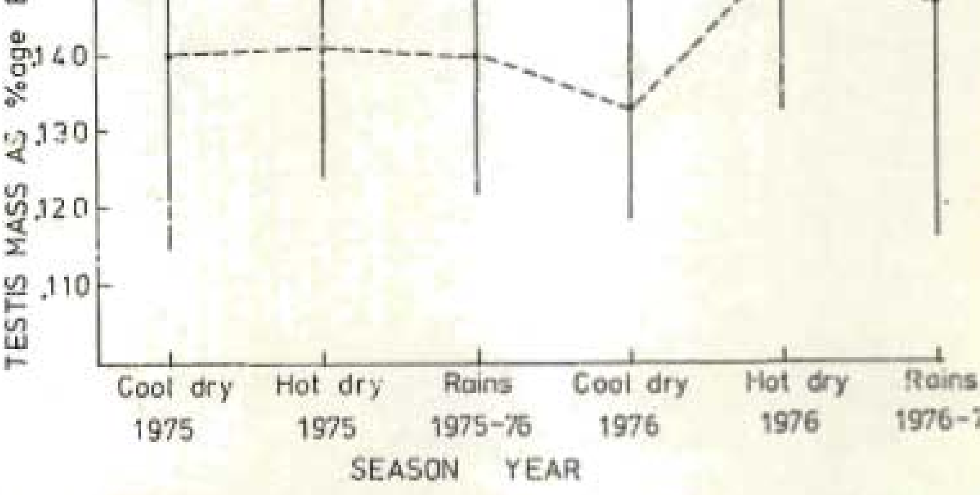


Figure 7.12: Seasonal changes in testis mass expressed as a percentage of body mass. Vertical lines indicate 95% confidence limits. Dashed line joins means.

7.4

SUMMARY

7.4.1

Growth

Computer-generated theoretical curves for growth with age in mass, body length, chest girth, shoulder height, neck girth, horn base circumference and horn length are presented. Differences between the sexes in respect of body mass and measurements are documented and marked sexual dimorphism is apparent. As with females, it is possible that growth in males on the Kwando is slower than in other populations.

Equations for the prediction of body mass and carcass mass from body measurements are presented and compared with similar equations derived for females. Correlation coefficients for the regressions for males are higher than those for females. This may be because of greater variability in female condition because of the stress of reproduction.

7.4.2

Reproduction

Spermatogenesis occurs by 18 months of age. For it to occur it is apparent that body mass must exceed 55 kilograms, testis mass must exceed 15 grams and seminiferous tubule diameter must exceed 120 micrometres. There is a delay of perhaps three years between the onset of spermatogenesis and successful mating.

No clear evidence was found to indicate that there is a seasonal sexual cycle in adult male lechwe.

CHAPTER 8

ACTIVITIES, PHYSICAL MAINTENANCE BEHAVIOUR AND RELATIONS WITH OTHER SPECIES

8.1

INTRODUCTION

8.1.1

The Relevance of Behaviour to Conservation and Management

The significance of behavioural aspects in the context of management has been discussed by a number of writers (e.g. Geist, 1971; Buechner, 1974; Cowan, 1974; Leuthold, 1977) and as management becomes more intensive and sophisticated recognition of the importance of a knowledge of social organization and behaviour is growing. Management activities in which there is a need to consider social and behavioural aspects include: capture and re-introduction, census, domestication, harvesting and the selection of areas for the protection of particular species.

8.1.2

Previous Work on Lechwe Behaviour

De Vos & Dowsett (1966) made some general, qualitative observations on lechwe behaviour on the Kafue Flats, but did not provide a comprehensive picture of social organization and behaviour. Lent (1969) provided an outline of lechwe social organization in the Okavango Delta on the basis of a few months field work. Child & Von Richter (1969) provided some information on the social grouping of lechwe along the Chobe River but did not elucidate their social organization in any detail. Child & Robbel (1975) reported the occurrence of territoriality in lechwe along the Khwai River in the Okavango Delta. Schuster (1976, 1977) studied the social organization and behaviour of Kafue lechwe over several years and established that there were marked similarities between the lekking behaviour of Kafue lechwe and that of Uganda kob (Buechner, 1961b; Buechner, 1963; Buechner & Schloeth, 1965; Leuthold, 1966; Buechner & Roth, 1974).

8.1.3

The Objects of this Study with respect to Behaviour and Social Organization

The primary objective of behavioural work in this study was to provide an outline of social organization and behaviour that would facilitate recognition of social and behavioural attributes of actual or potential importance in the conservation and management of lechwe. It was also an objective to record lechwe behaviour in as much detail as possible because the lechwe is a rare animal and opportunities for observing it under "natural" conditions are steadily diminishing. For example, both the major Zambian populations now live in the virtual absence of predators other than man (Sayer & Van Lavieren, 1975; Grimsdell & Bell, 1975).

Management considerations will be discussed in detail in Chapter 11 (Conservation and Management).

8.2

MATERIALS AND METHODS

Behaviour was studied by direct observation from two hides and from a vehicle (Toyota Land Cruiser) using binoculars (Zeiss 8x56) and a stop watch for timing. If an individual was being observed a continuous record of all activities and interactions was kept. If a group was under observation, only the occurrence and duration of interactions were recorded. A total of about 1 000 hours of observation of individuals and groups was completed on 208 days during the study period.

Diurnal activity budgets were calculated for territorial males, adult males, adult females, subadult males and juveniles, using a method of individual sampling similar to that of Struhsaker (1967). The activities of individuals were monitored for sample periods of 30 minutes. In each 30-minute interval the time devoted to each activity was summed. The activity budget for each season was calculated by summing the amount of time spent on each activity in all sampling intervals, dividing by the total sampling time and expressing the result as a percentage. An annual activity budget was calculated in the same way, pooling the data for all seasons. At least 40 sampling periods were accumulated for each sex/age class in each season over a period of a year. Observations on territorial males extended into the second year because too few territorial males were known in the first year to provide a complete picture of year-round activity.

Types of activity recorded were similar to those identified by Jarman & Jarman (1973) and Walther (1973).

To investigate activity rhythms, the day was divided into four periods of three hours, beginning at 06h00 and ending at 18h00. Three-hour periods were used so that each period would include observation on five to ten different animals, rather than two or three, as would have been the case if one-hour intervals had been used, because it was felt that a sample of two to three animals was too small to have much meaning. Within each three-hour period the amount of time spent active (as opposed to resting) was totalled. A comparison was then made of levels of activity in the early morning (06h00 - 09h00), late morning (09h00 - 12h00), early afternoon (12h00 - 15h00) and late afternoon (15h00 - 18h00).

Some idea of daily fluctuations in activity was also obtained from the sightings collected in the course of studying habitat selection. For each hour of the day the percentage of active groups was calculated and this was taken as an index of the level of activity during that hour.

During the second year of study, behavioural work was concerned mainly with territoriality. On several occasions it was possible to observe known territorial males for fairly extended periods, of eight to twelve hours. Activity budgets were calculated also from these data.

8.3

RESULTS AND DISCUSSION

8.3.1

Activity Budgets

Diurnal activity budgets for all sex/age classes are presented in Table 8.1. Important differences in the activity budgets of different sex/age classes are summarized in Table 8.2. Table 8.3 shows the amount of time allocated to different activities by territorial males under continuous observation for fairly long periods.

Seasonal differences in the amount of time allocated to each activity were generally neither very marked nor consistent in the various sex/age classes. A few consistent and appreciable seasonal differences are illustrated in Table 8.4.

Before discussing differences in the activity budgets of various sex/age classes, two basic similarities in the activities of most classes

TABLE 8.1: DIURNAL ACTIVITY BUDGETS FOR DIFFERENT LECHWE SEX AND AGE CLASSES (percentages are of total observation time during the year)

CLASS / ACTIVITY	Territorial male	Adult male	Adult female	Subadult male	Juvenile
Feed/Drink	34,6%	39,3%	56,1%	34,8%	40,7%
Walking	1,8%	3,6%	2,1%	3,8%	3,2%
Running	-	0,1%	0,1%	0,1%	0,1%
Interacting with female	12,8%	3,2%	0,1%	0,5%	1,8%
Interacting with male	0,8%	0,8%	0,8%	1,1%	0,1%
Interacting with juvenile	-	-	0,9%	-	0,2%
Standing idle	4,9%	6,6%	5,1%	4,0%	4,8%
Ruminating while standing	1,1%	2,7%	2,7%	1,7%	2,1%
Ruminating while lying	18,7%	23,2%	15.9%	22,8%	11,8%
Lying idle	23,4%	18.4%	13,2%	28,6%	32,1%
Comfort behaviour	1,6%	1,7%	2,7%	2,2%	2,9%
Urinating/ defecating	0,2%	0,2%	0,2%	0,1%	0,2%
Number of individuals sampled (n)	19	68	83	92	81

TABLE 8.2: IMPORTANT DIFFERENCES IN THE ACTIVITY BUDGETS OF DIFFERENT SEX/AGE CLASSES

Activity	Classes compared	% Difference between classes[1]	Larger percentage as a multiple of smaller[2]
Courtship and mating[3]	Territorial male vs adult female	12,0	16,0
Courtship and mating	Territorial male vs adult male	9,6	4,0
Courtship and mating	Territorial male vs subadult male	12,3	25,6
Feeding	Adult female vs territorial male	21,5	1,6
Feeding	Adult female vs adult male	16,8	1,4
Feeding	Adult female vs subadult male	21,3	1,6
Feeding	Adult female vs juvenile	15,4	1,4
Lying idle	Subadult male vs adult female	15,4	2,2
Lying idle	Juvenile vs adult female	18,9	2,4
Ruminating while lying	Adult male vs juvenile	11,4	2,0
Ruminating while lying	Subadult male vs juvenile	11,0	1,9

1 : $\% X_1 - \% X_2$ = % difference between classes X_1 and X_2.

2 : $\frac{\text{larger percentage}}{\text{smaller percentage}}$ = larger percentage as a multiple of small

3 : refers to interactions between adult or postpubertal animals of th opposite sex.

TABLE 8.3: ACTIVITIES OF TERRITORIAL MALES ON DIFFERENT DAYS

DATE	6.10 1976	3.12 1976	4.12 1976	14.2 1977	15.2 1977	22.2 1977	25.2 1977
Number hours observation	9	12	10	8	8	12	10
Number of interactions with female/day[1]	28	67	52	104	48	1	2
Mean duration (minutes) of interaction with female	16,7	1,5	2,9	2,0	2,5	2,8	2,6
% time interacting with female	65,5	13,8	21,2	25,8	16,7	0,4	0,9
% time interacting with male	-	0,1	2,5	-	0,7	1,0	-
% time feeding	28,2	52,3	48,0	43,8	37,9	51,6	57,9
% time walking/running	0,2	1,6	1,3	2,2	0,6	0,2	0,1
% time idle or ruminating	6,0	30,2	25,4	24,7	44,1	45,6	40,8
% time other	0,1	2,0	1,6	0,3	0,1	1.2	0,3

1 : One day equivalent to 12 hours observation; interaction rates converted to a common base for comparative purposes.

TABLE 8.4: SEASONAL DIFFERENCES IN THE PROPORTION OF TIME DEVOTED TO DIFFERENT ACTIVITIES

CLASS	ACTIVITY	% time engaged in activity		
		Cool dry	Hot dry	Rains
Adult female	feeding	57,5	66,8	44,1
Territorial male	feeding	29,1	41,6	17,0[1]
Adult male	feeding	35,0	43,8	39,1
Territorial male	interacting with female	3,3	16,9	7,7
Adult male	interacting with female	0,9	5,9	3,2

1 : The actual figure is probably higher; see discussion in text

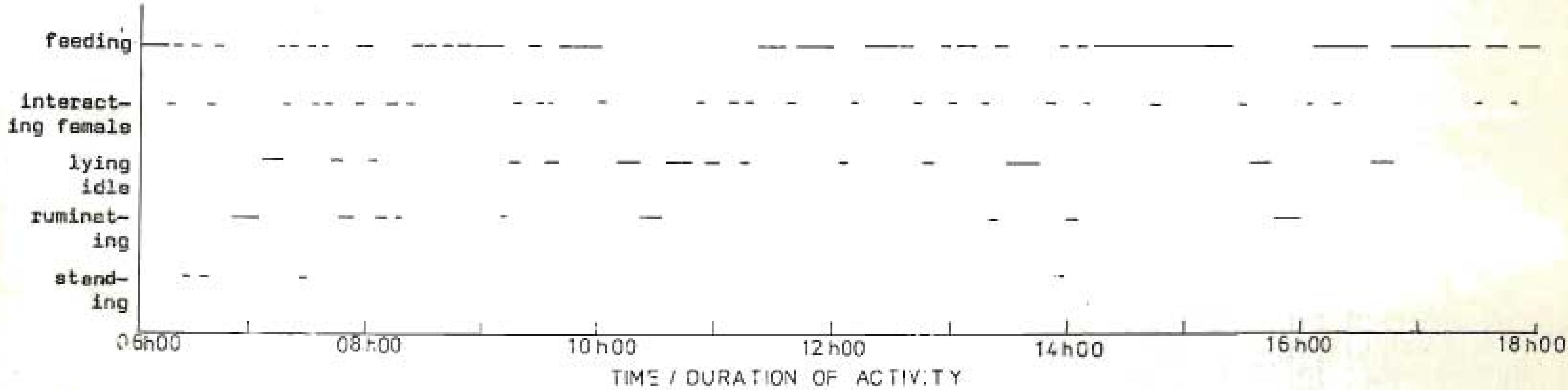
will be mentioned. These are the negligible amount of running in all classes and the low levels of social activity in classes other than territorial males. The minimal amount of social contact between adult females is particularly striking. In view of the cost of gestation and lactation, clear benefits for females in a reduction of social activity can be envisaged (Geist, 1974).

The differences in Table 8.2 relate to a variety of activities and sex/age classes. These differences are discussed below in the order in which they appear in Table 8.2.

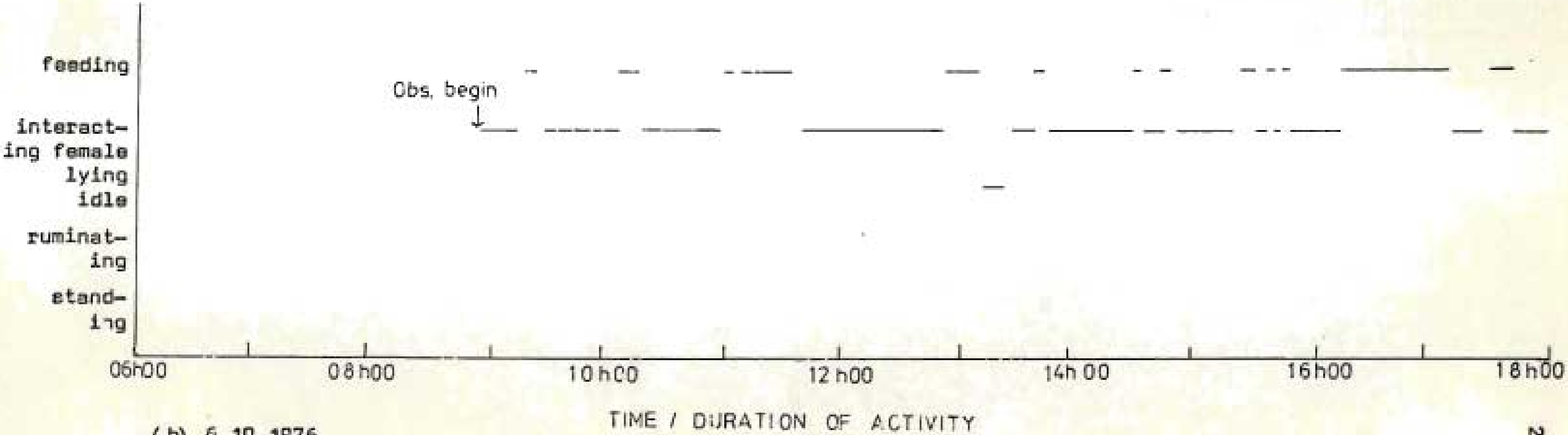
Two factors are responsible for the marked difference in the amount of time invested in courtship and mating by territorial males and adult females. Firstly, a few territorial males out of the whole adult male segment of the population are responsible for most of the courtship and mating. Secondly, males are sexually active all year round, whereas females are receptive for only about one day every year (females produce one fawn per year and therefore mate once a year). These factors combine to produce a situation in which territorial males may court many females each year and mate with a number of these, whereas females are engaged in only one protracted courtship and mating during the year.

Females exert a pronounced influence on the activities of territorial males. Table 8.3 illustrates situations ranging from a receptive female being present in a territory all day (6.10.76) to only one unreceptive female passing briefly through a territory during a whole day (22.2.77) (data in Table 8.3 were collected from two different males and each interacted with different females on each day). The effect of the presence and receptivity of females on the activity of territorial males is illustrated graphically in Figure 8.1. The figure shows the activities of one territorial male on two days, two different females being involved. In Figure 8.1 (a) (3.12.76) a female was present all day but was not receptive. In Figure 8.1 (b) (6.10.76) a receptive female was present for the entire observation period (multiple copulations occurred). The effect of the receptivity of the female on the activity of the male is clear. Jarman & Jarman (1973) noted that impala (<u>Aepyceros melampus</u>) females had a similar effect on the activities of territorial impala males.

Figure 8.1: Graphical representation of the activities of a territorial male on two different days



(a) 3.12.1976



(b) 6.10.1976

Differences in the amount of time devoted to mating activity by territorial and other classes of male probably reflect dominance ranking and access to females. Within a territory only the holder had access to females. Observations on habitat use (Chapter 4) showed a clear preference by females for the areas in which territories were situated and a preponderance of bachelor males in marginal habitats which were much less frequented by females. Apparently non-territorial males were being pushed into less favourable areas where the chances of gaining access to receptive females were reduced.

The substantial difference in the amount of time spent feeding by adult females and all other sex/age classes is almost certainly a reflection of the cost of gestation and lactation i.e. the cost of producing offspring. The difference in the amount of time spent feeding by territorial males and adult females may have been exaggerated by a sampling bias. Data on feeding by territorial males during the rains (Table 8.4) included observations on several individuals which regularly spent long periods feeding among bachelor males in marginal areas, subsequently returning to their territories to rest. Monitoring the activities of these individuals while they were on their territories probably led to an overestimate of the amount of time spent resting and an underestimate of feeding time. In other seasons these males were not included in the sample and it seems unlikely that this bias materially distorted the substantial difference in the amount of time devoted to feeding by adult females and territorial males.

It has been argued that in mammals the sexes invest unequally in the production of offspring and that because the costs of reproduction are different for males and females they employ different strategies to maximize reproductive success - males try to achieve fertilization to the maximum degree and females try to optimize it in a qualitative sense (Trivers, 1972; Williams, 1975). The substantial differences in the time, and hence energy, invested by territorial male and adult female lechwe in feeding and in courtship and mating appear to be consistent with the above arguments.

The differences in the amount of time spent lying idle by adult females and younger animals are probably related to differences in the amount of time spent feeding. Adult females feed appreciably more than younger animals and therefore have less time for idling.

The differences in the amount of time spent ruminating by juveniles and adult and subadult males can be explained in terms of diet. For the first six to seven months of its life milk is an important component of a juvenile's diet whereas older animals are entirely dependent of the vegetation for their food supply. In Table 8.1 this difference is masked by the fact that the sample of juveniles included many weaned individuals, also completely dependent on the vegetation for their food supply. It would have been more satisfactory to sample only unweaned animals.

Seasonal differences in the amount of time allocated to feeding (Table 8.4) have also been documented in other African ungulates (Spinage, 1968; Jarman & Jarman, 1973) and may be related to pasture quality. Possibly the reason for increased feeding time in the dry season, when pasture quality is poor, is that under these conditions feeding becomes more selective and that the amount of time required to ingest a given quantity of food increases. This suggestion is made in view of Stanley Price's (1977) finding that the amount of food ingested in the dry season is less than in other seasons because dry food takes longer to process.

Seasonal differences in the amount of time males spent interacting with females probably reflect seasonal variation in female receptivity. As it is known from the shot sample that very few conceptions occurred during the cool, dry season, it is reasonable to infer that few females are receptive at this time of the year.

Because the sampling of territorial males and juveniles was in some respects not entirely satisfactory and because total observation times (120 hours for territorial males, 60 hours for all other classes) were relatively short, my results are first approximations. Subject to this qualification it seems reasonable to conclude that there are real differences in the activity budgets of lechwe which are related to sex, social status, age and season and that a knowledge of these differences is helpful in understanding how the animals relate to each other and to their environment.

8.3.2

Activity Rhythms

Jarman & Jarman (1973) state that "the basic pattern of daily activity of impala is shown by all social categories and is probably least obscured by variations in females". It was difficult to discern a "basic pattern of daily activity" in lechwe except in the most general way. All activities occurred during all hours of the day and although there was synchronization within groups there were few indications of synchronization between groups. even when they were in fairly close proximity. At any one time there were usually some groups engaged in active and others in resting behaviour.

Figures 8.2 -8.13 illustrate diurnal peaks and declines in activity in different sex/age classes during the different seasons. The patterns of activity shown are different from those reported in impala by Jarman & Jarman (1973). The data on which these figures are based were collected from a small sample and some of the variability may be due to this.

The seasonal differences in adult activity are obvious. Younger animals tended to show the morning and evening peaks in activity that are found in, for example, impala (Jarman & Jarman, 1973) and Thomson's gazelle (<u>Gazella</u> <u>thomsoni</u>) (Walther, 1973). The activity pattern of adult females during the cool, dry season is particularly striking and it seemed logical to consider whether there were any seasonally variable factors which could account for this pattern. De Vos & Dowsett (1966) noted that at this time of year females spent much time feeding in the water and in this study it was found (Chapter 4) that females spent over 40% of the day in the water. It is quite possible that they reduce their heat load in this way and that they can therefore sustain levels of activity which would otherwise be untenable. Significantly, subadult males, which spent virtually no time in the water, showed reduced activity during the warmest parts of the day, as has been found in a number of other species (Leuthold, 1977). If this explanation is correct, it provides an interesting illustration of the interaction between behaviour and environmental factors.

In general Figures 8.2 - 8.13 indicate that the simple model of peaks of activity early and late in the day with reduced activity during

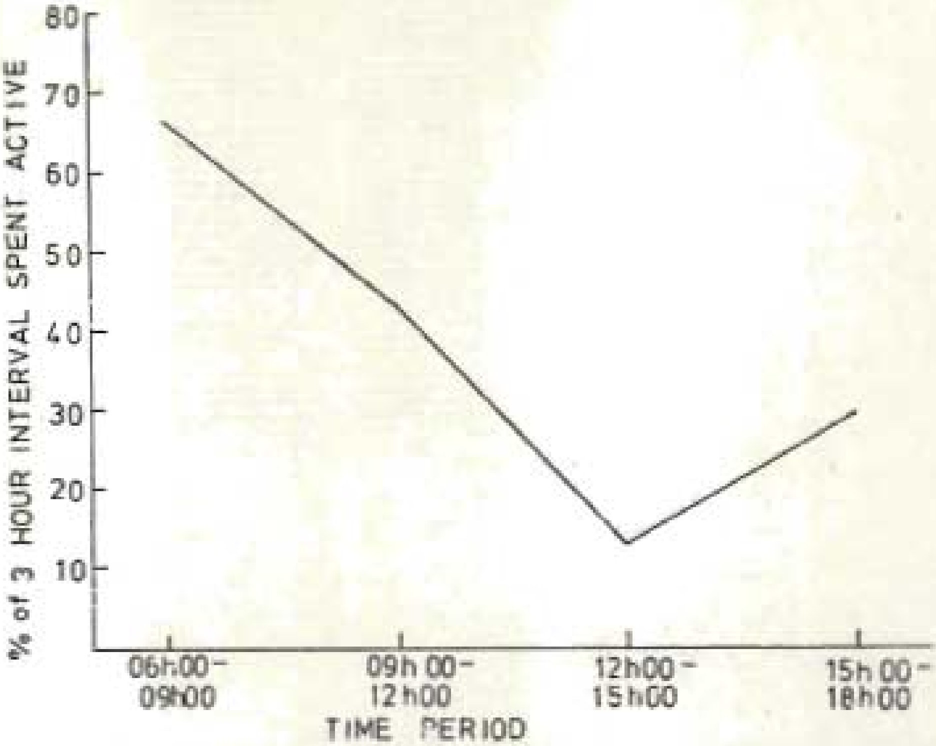


Figure 8.2: Adult males: the proportion of three-hour intervals spent activ in the cool dry season.

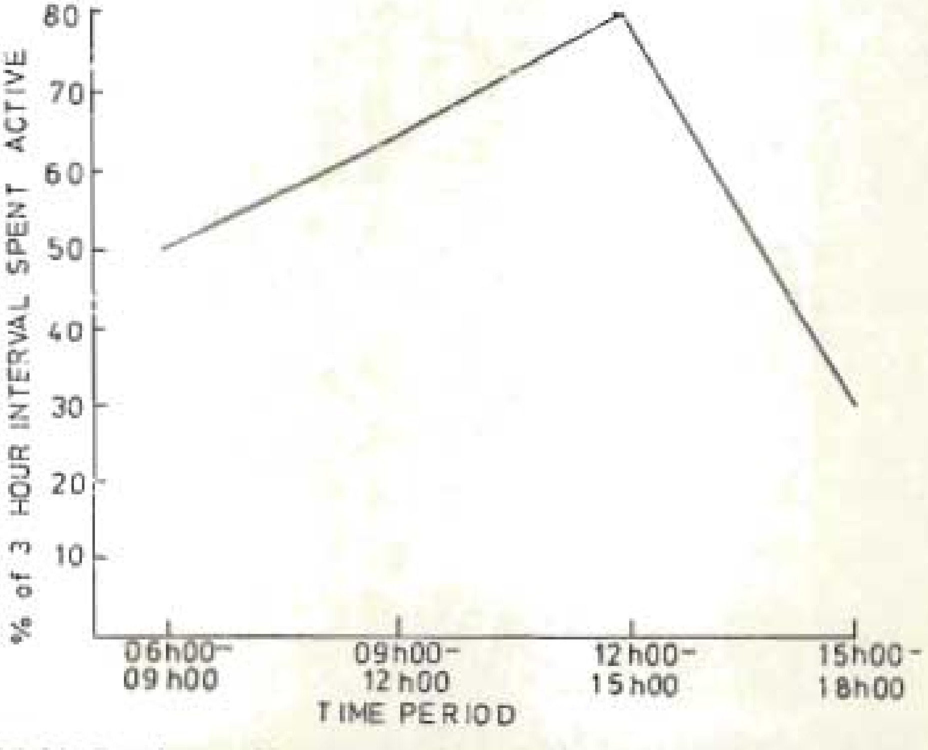


Figure 8.3: Adult females: the proportion of three-hour intervals spent active in the cool dry season.

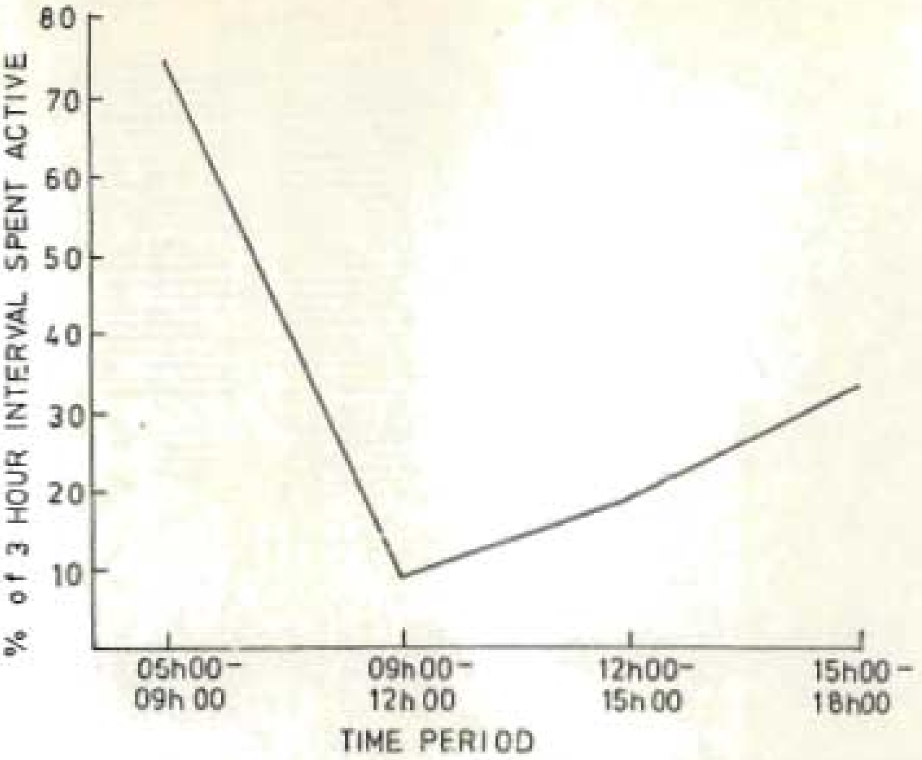


Figure 8.4: Subadult males: the proportion of three-hour intervals spen active in the cool dry season.

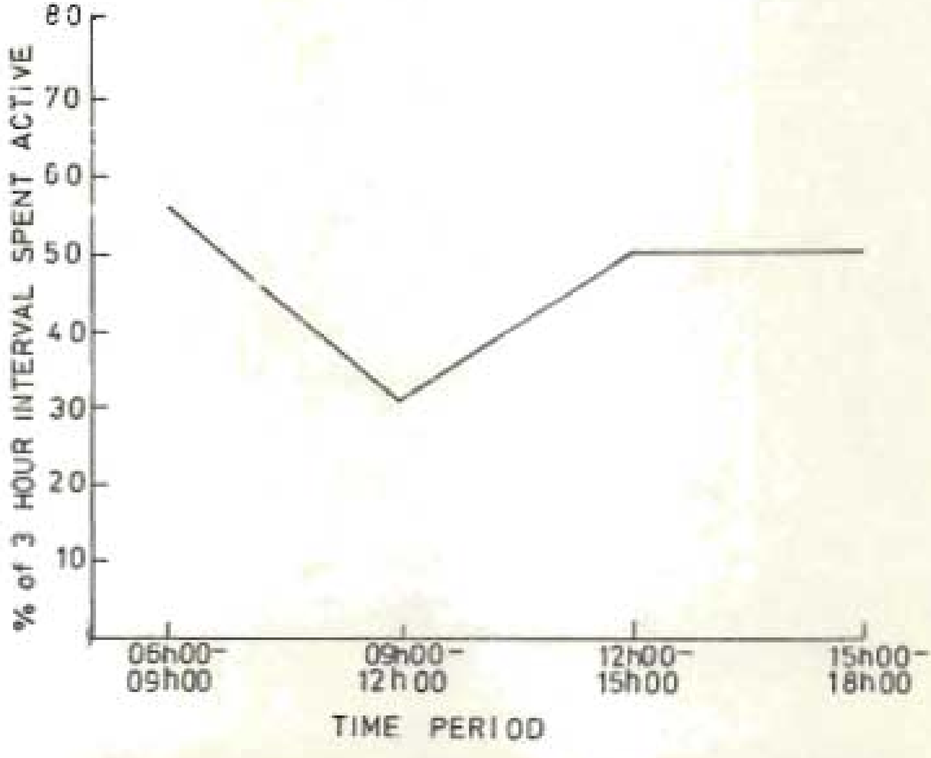


Figure 8.5: Juveniles: the proportion of three-hour intervals spent active in the cool dry season.

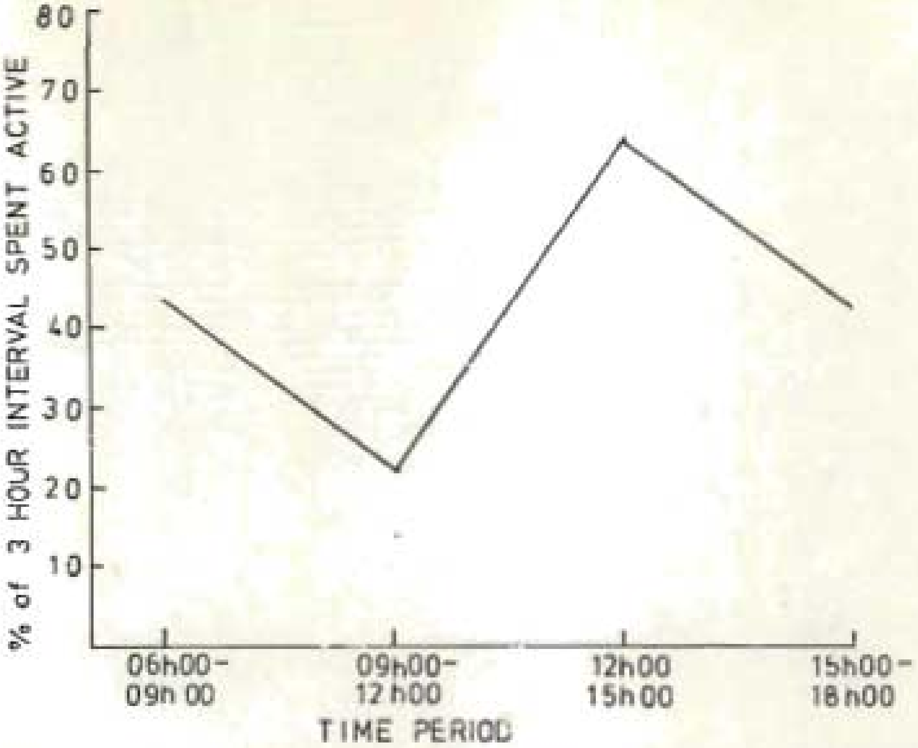


Figure 8.6: Adult males: the proportion of three-hour intervals spent active in the hot dry season.

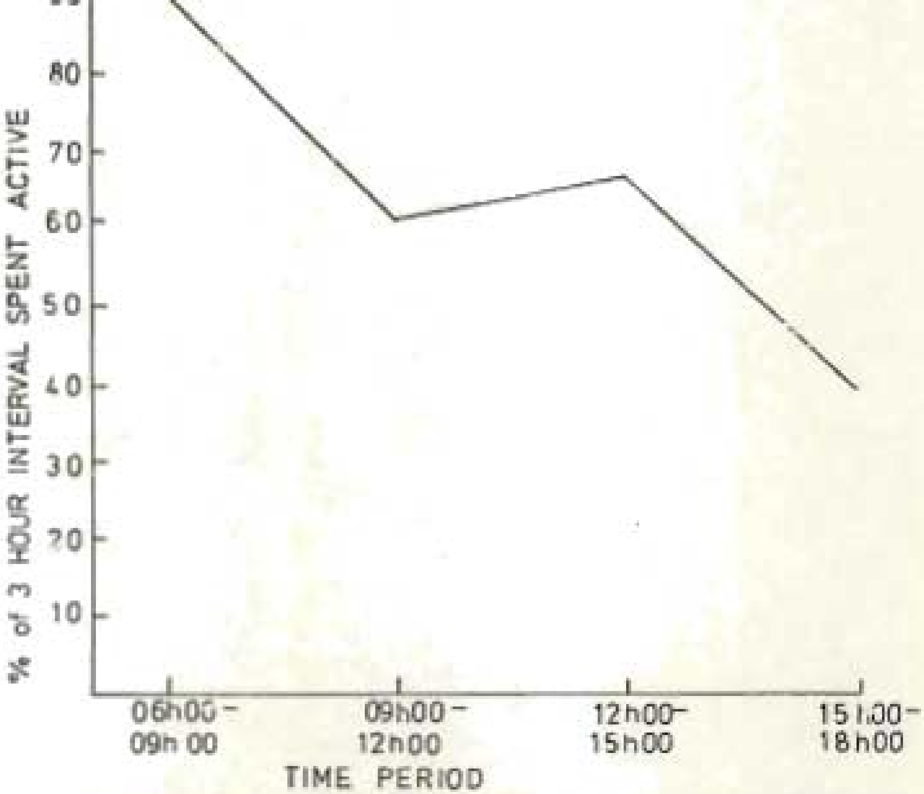


Figure 8.7: Adult females: the proportion of three-hour intervals spent active in the hot dry season.

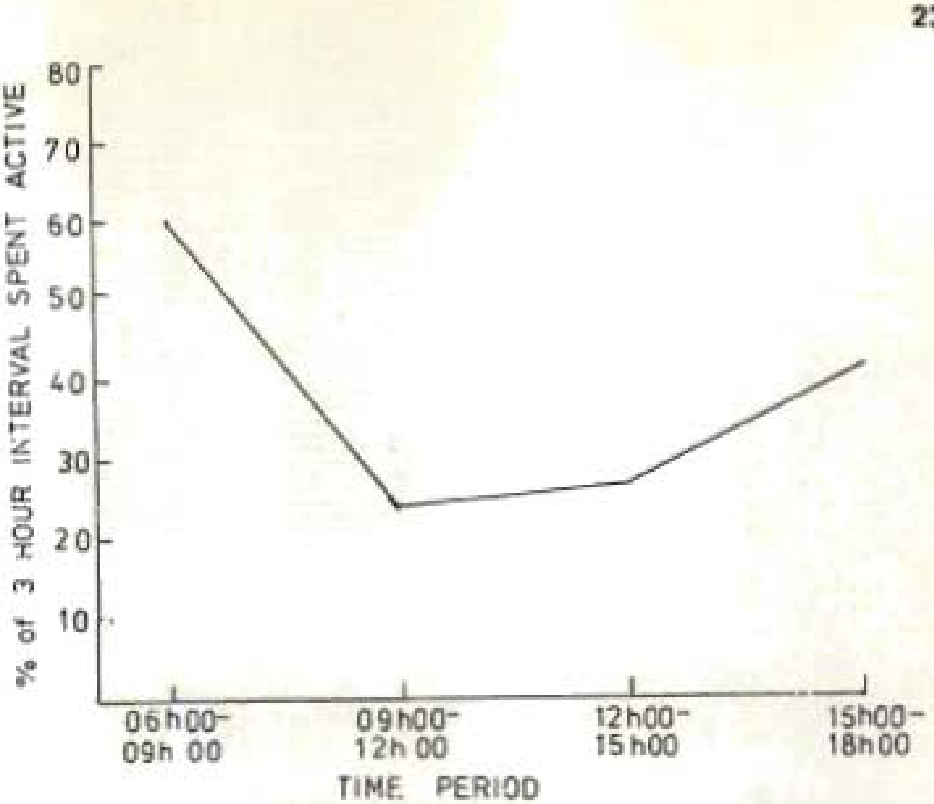


Figure 8.8: Subadult males: the proportion of three-hour intervals spen active in the hot dry season.

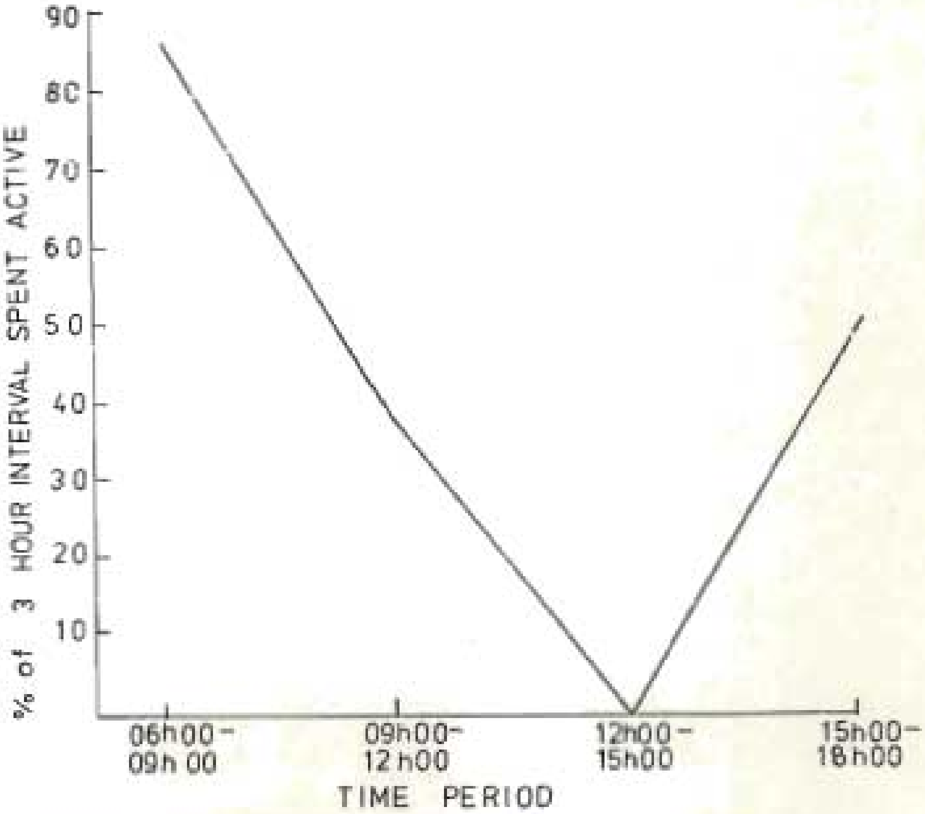


Figure 8.9: Juveniles: the proportion of three-hour intervals spent active in the hot dry season.

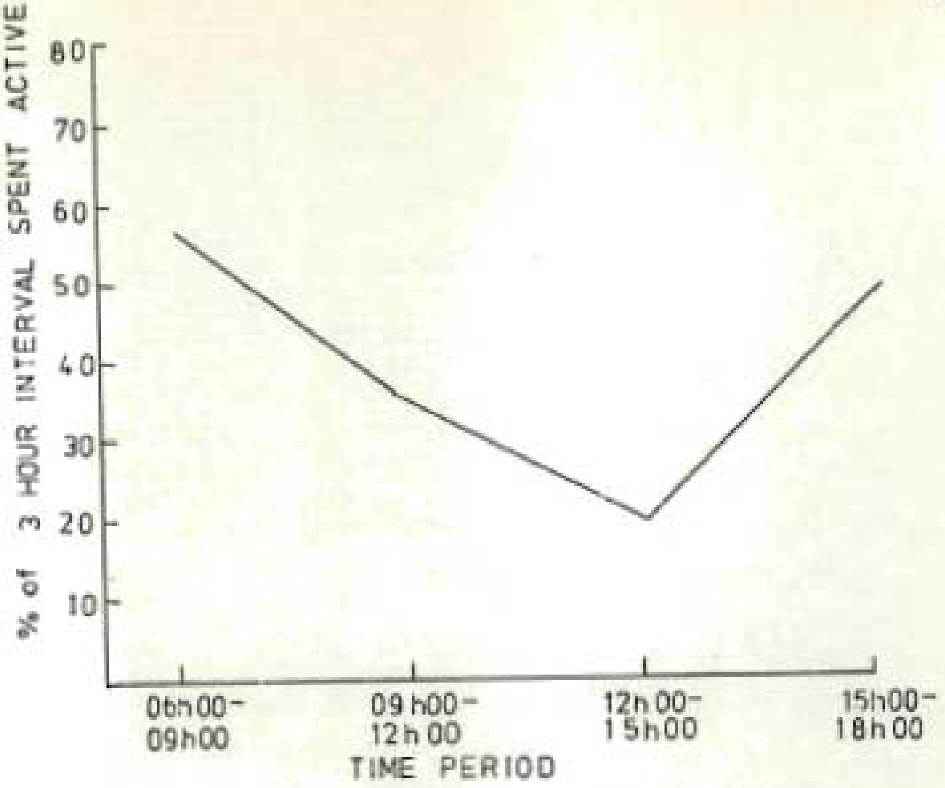


Figure 8.10: Adult males: the proportion of three-hour intervals spent active in the rains.

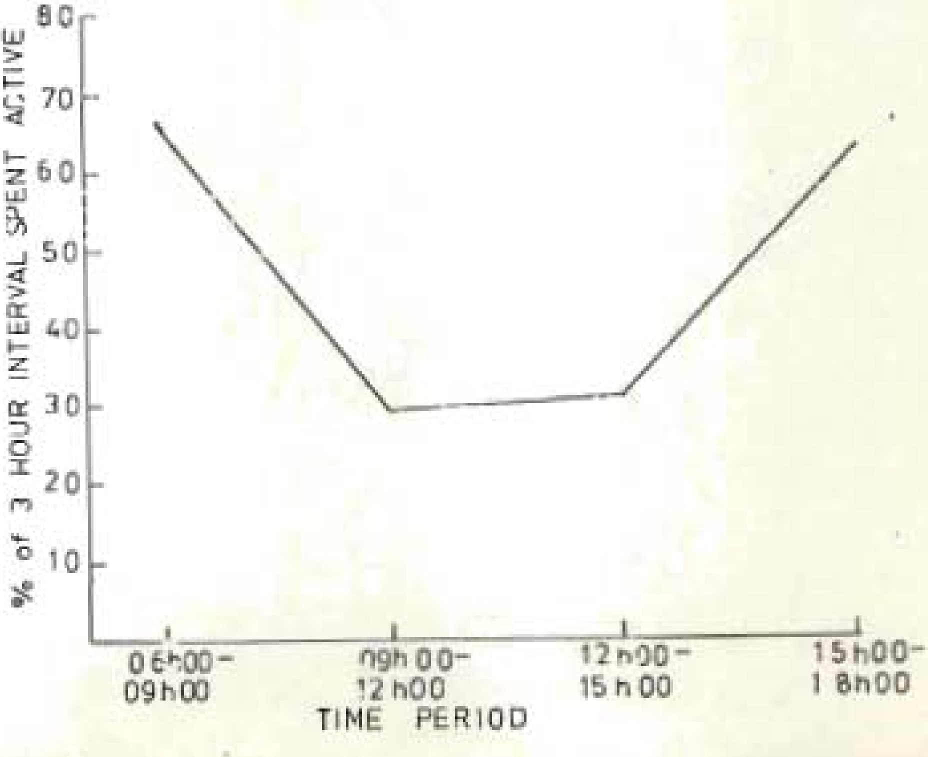


Figure 8.11: Adult females: the proportion of three-hour intervals spent active in the rains.

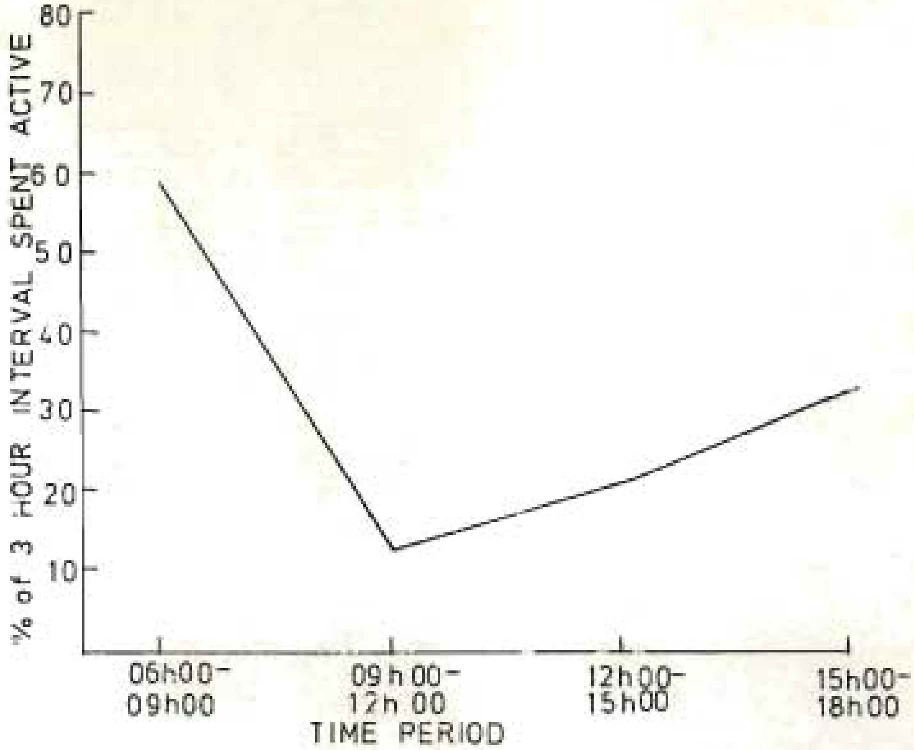


Figure 8.12: Subadult males: the proportion of three-hour intervals spen active in the rains.

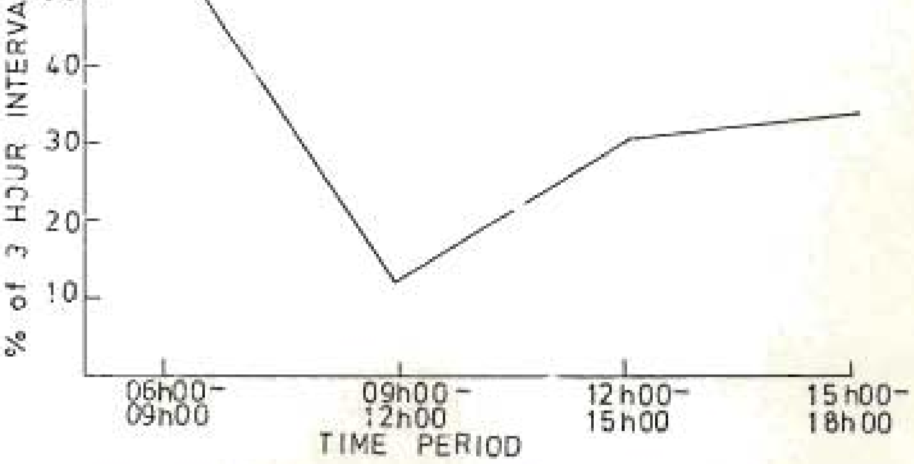


Figure 8.13: Juveniles: the proportion of three-hour intervals spent active in the rains.

the middle of the day cannot be uncritically applied to lechwe. It seems that the activity rhythms of lechwe may be modified by the influence of environmental factors peculiar to its specialized niche.

A further insight into the timing of activities came from grouping the sightings collected for documentation of habitat use on the basis of time. Owen (1970) used a similar procedure to assess the activity of sitatunga. The proportion of active groups in each hour of the day in each season is shown in Figures 8.14 - 8.16. This method is flawed by the bias that active animals are more readily seen than inactive ones, particularly if the latter are lying down. This bias probably accounts for the high proportions of active groups.

All groups were considered for this exercise and it appears that when there is no discrimination between sex and age classes a general pattern of reduced activity in the middle of the day emerges. In view of the patterns illustrated in Figures 8.2 - 8.13 it seems that this method oversimplifies the patterns

One feature that is clearly illustrated by Figures 8.14 - 8.16 is reduced activity in the early hours of the morning. At this time it was common to find most lechwe lying down near the water. Jarman & Jarman (1973) found a similar pattern of behaviour in impala and Walther (1973) also found this in Thomson's gazelle.

On the basis of Figures 8.2 - 8.13 it is suggested that the best time to census lechwe would be either between 08h00-10h00 or between 14h00-16h00. The reason for this suggestion is the general reduction in the activity of younger animals during the middle of the day. In practice most aerial counting during this study was done between 08h00-11h00 and good results (in terms of repeatability) were obtained (Chapter 10).

8.3.3

Daily Movements

Data on activities presented thus far convey no information on daily movements. No quantitative work on daily movements was attempted but regular observations of known animals and distinctive groups (e.g. a bachelor herd resident on the north side of the intensive

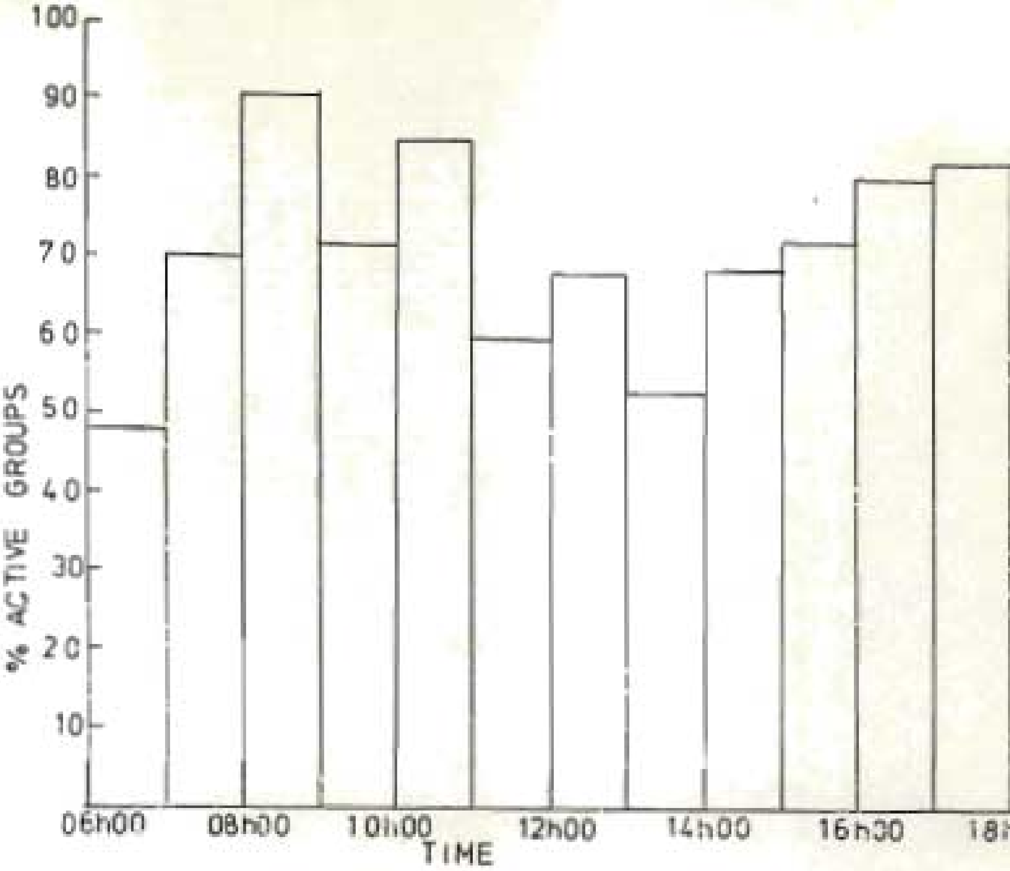


Figure 8.14: Cool dry season: proportion of groups that were active durin one-hour intervals from morning until evening.

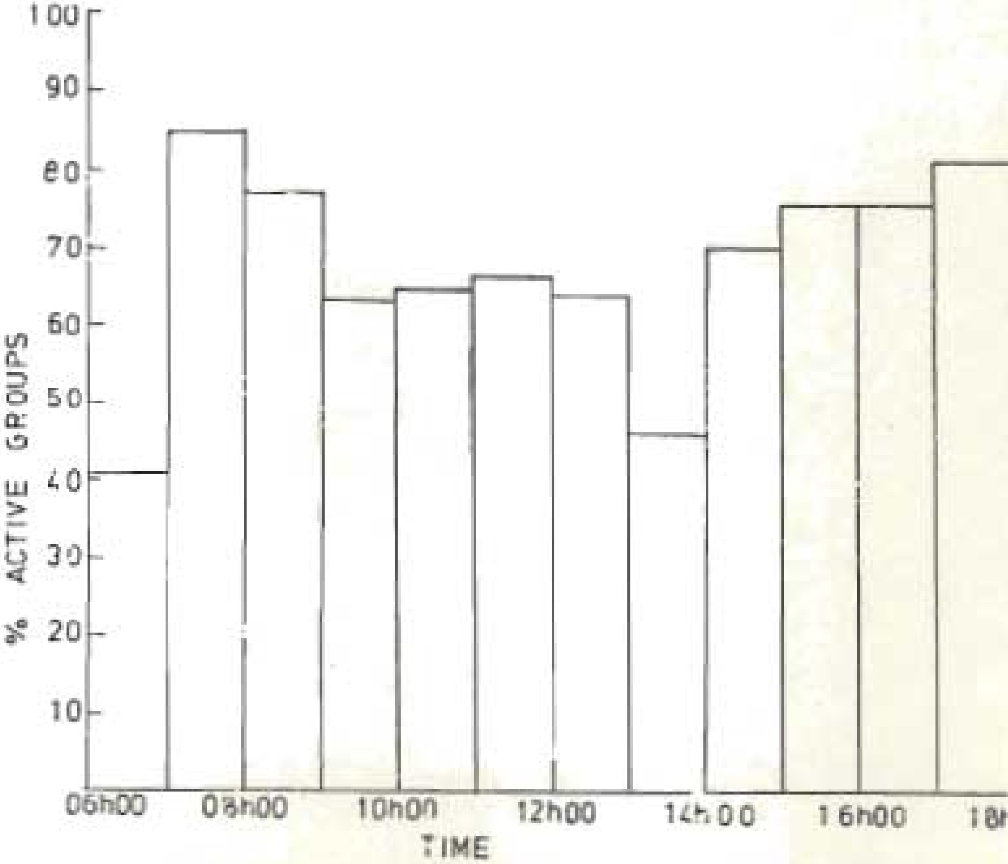


Figure 8.15: Hot dry season: proportion of groups that were active during one-hour intervals from morning until evening.

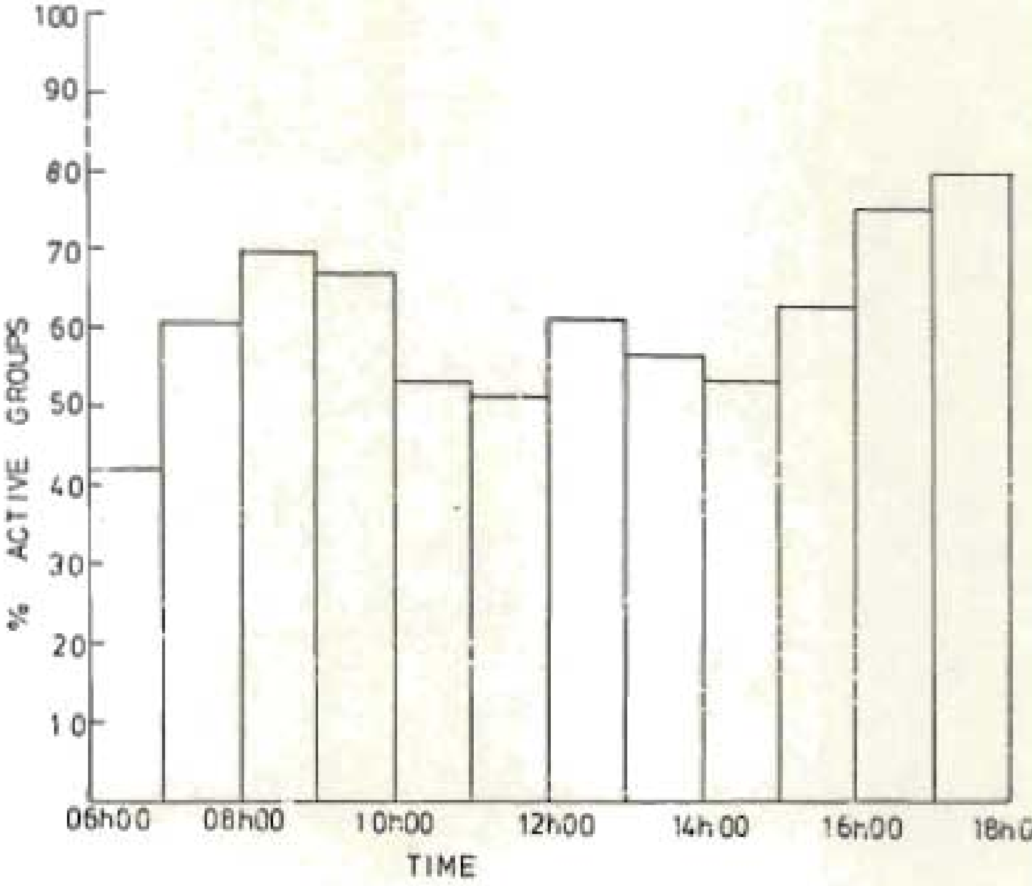


Figure 8.16: Rains: proportion of groups that were active during one-hour intervals from morning until evening.

study area) did provide some preliminary information on daily movements. These were variable but never seemed to be extensive. The bachelor herd referred to above seldom moved more than one to two kilometres from my northern hide. Territorial males regularly spent the entire day in their territories.

There were only two patterns of movement which were regularly repeated. One pattern consisted of movements between resting sites and feeding sites. This was particularly common in bachelor groups and female groups. Animals would spend time lying down at one site, after which they stood up and walked in an apparently deliberate way to another site, up to a kilometre away, where they started feeding. Resting sites were mainly in short grass, usually near water, while feeding sites were more diverse. Good visibility, to facilitate predator detection and hence avoidance, seemed to be one of the factors determining the choice of resting sites.

The other common pattern, particularly evident in the bachelor herd, was movement in the early morning away from resting sites near the water into peripheral floodplain areas and movement in the evening back to the resting sites near the water.

8.3.4

Weather and Activity

Weather conditions were seldom seen to have an obvious effect on activity.

Lechwe seemed remarkably tolerant of direct sun. Even during the hottest time of the year many animals could be found lying out in the full sun during the middle of the day. Animals did seek shade but this was surprisingly uncommon in the intensive study area, perhaps simply because there was relatively little shade in the area. It is possible that extremes of heat are moderated by the water in and around which lechwe spend their time. Also,breezes off the swamp are common and these may reduce heat stress.

High winds did seem to make the animals more nervous, but this was an entirely subjective impression. Occasionally the cool winds preceding a storm did induce bouts of running and playing.

Light rain had no discernable effect on behaviour. Ongoing activities usually ceased in heavy rain and animals would stand or lie down with their backs to the wind. Lying down probably assists conservation of body heat (Moen, 1973). A similar response to heavy rain has been documented in, for example, impala (Jarman & Jarman, 1973).

8.3.5

Comfort Behaviour

On average lechwe spent 15–20 minutes per day engaged in comfort behaviour (Table 8.1). Although occasional grooming bouts in excess of 10 minutes were observed, most grooming episodes lasted for less than one minute.

All the different types of auto-grooming listed by Jungius (1971) and Leuthold (1977) were observed in lechwe. Comfort behaviour involving external objects was not observed. Oxpeckers (Buphagus sp.) were never seen on lechwe, although giraffe (Giraffa camelopardalis) and buffalo (Syncerus caffer) visiting the floodplain were often accompanied by oxpeckers.

Lechwe apparently entered the water for thermoregulation. Although juveniles usually seemed to avoid the water, on several occasions groups of juveniles stood idly in shallow water for long periods during the hottest part of the day. This behaviour was also occasionally seen in adults. For example, on 22.2.79, a cloudless day, a territorial male near my hide stood up and walked from where he had been lying in short grass into water about 20 centimetres deep. He stood stationary in the water from 13h16 to 14h27 (71 minutes) before walking out of the water to begin feeding.

Allo-grooming was not seen except in the context of the mother-young relationship.

8.3.6

Voidance Behaviour

The diurnal frequencies of urination and defecation were noted during work on activity budgets. These data are presented in Table 8.5. In two 12 hour watches on territorial males during December and February the defecation rates were three and seven times per 12 hours.

TABLE 8.5: OBSERVED DAILY FREQUENCY OF DEFECATION AND URINATION IN DIFFERENT SEX AND AGE CLASSES AND IN DIFFERENT SEASONS (data from observations on individuals for compilation of activity budgets)

CLASS	COOL DRY SEASON		HOT DRY SEASON		RAINS	
	Defecation	Urination	Defecation	Urination	Defecation	Urination
Adult male	9	1	7	0	6	1
Adult female	7	3	8	1	5	2
Subadult male	4	1	11	0	5	2
Juvenile	4	2	7	2	7	0
Mean (to nearest whole number)	6	2	9	1	6	1

Defecation postures were similar in males and females. When stationary the animals stood with head held high, lower back slightly arched and tail raised. Both males and females regularly defecated while grazing, in which case the tail was raised but no other postural changes were apparent. Males also regularly defecated while walking, a raised tail again being the only postural change.

Males and females had different urination postures. Females stood with lower back slightly arched and tail raised. Males did not seem to have any particular posture for urination and often urinated while walking. In comparison to the males of species like Thomson's gazelle (Walther, 1964a) the voidance behaviour of lechwe males was remarkably unstructured.

The spatial distribution of defecation/urination appeared to be random or diffuse. No behaviour specifically associated with voidance was observed in lechwe.

8.3.7

<u>Relations with Other Species</u>

8.3.7.1

<u>Herbivores</u>

Although lechwe responded to the alarm calls of impala and wildebeest they were seldom seen to associate with other ungulate species. When they did, for example with tsessebe (<u>Damaliscus</u> <u>lunatus</u>), impala or wildebeest, these were probably chance associations of species attracted to the same resource (Leuthold, 1977). There was no clear evidence that lechwe were involved in a grazing succession as envisaged by Vesey-Fitzgerald (1960) and Bell(1971). They did occasionally feed in areas where hippo had been feeding, but this was rare.

The reactions of lechwe to other herbivores seemed to be influenced by a number of the factors which Walther (1969) identified as flight-releasing factors in Thomson's gazelle. These factors appeared to operate in similar ways to those described by Walther (<u>op</u>. <u>cit</u>.). A few examples will illustrate these points.

The response of lechwe to the size of an animal was a function of their own age i.e. size and of familiarity. All lechwe gave way to tsessebe and juvenile lechwe gave way to adult impala, but adult lechwe ignored or displaced impala. A territorial male was quite unconcerned by a hippo bull which regularly walked through his territory but fled from an errant giraffe which wandered into his territory.

Suddenness of contact was another factor which had a marked effect on the response of lechwe to other herbivores. On several occasions a group of lechwe feeding along the edge of a stand of tall grass was put to flight by the sudden appearance of a warthog (Phacochoerus aethiopicus) as it trotted out of the long grass, although lechwe otherwise usually ignored warthog.

The question of ecological separation was not specifically studied but striking differences in the extent to which lechwe habitat was used by terrestrial ungulates were noticed and may be worth recording. During the rains the only other ungulate regularly observed on the floodplain in significant numbers was wildebeest. They used open areas near water for resting but were never observed feeding in the same areas as lechwe. Reedbuck (Redunca arundinum) were at all times of the year seen in tall grass areas but always in small numbers.

There were marked differences in the extent to which other ungulates used lechwe habitat in the two dry seasons for which I was continuously in the field. In 1975 there were seven months without any rain and October and November were extremely hot. Towards the end of the dry season tsessebe regularly fed in the same areas as lechwe and occasionally displaced feeding lechwe. Wildebeest and impala also fed at lechwe feeding sites and sable (Hippotragus niger) and buffalo regularly appeared on the floodplain but were never seen to feed at lechwe feeding sites.

In 1976 there were only three months completely without rain; from August onwards light showers fell occasionally. Neither tsessebe nor buffalo visited the floodplain and sable appeared less frequently than in 1975. Wildebeest and impala were seen on the floodplain but they never fed at lechwe feeding sites.

The indications that lechwe habitat is more intensively used by other herbivores during periods of nutritional stress when conditions are dry were reinforced by observations made in 1979. The 1978/79 rains were poor (Kasane received 30% of its mean annual rainfall) and drought conditions prevailed in the woodland and savanna communities adjoining the Kwando floodplain. Until heavy rains fell in early March, wildebeest, zebra and tsessebe were regularly seen feeding in the drier floodplain areas used by bachelor lechwe males. Also during my second follow-up visit during the dry season of 1979 (September/October) the same three species were regularly seen on the floodplain.

The fact that other ungulates made limited use of lechwe habitat. although it contained an attractive food supply in the form of perennial new growth, may have been due to soil conditions. In the short grass areas along the water's edge the soil was usually soft and wet or moist, and movement may have been impeded in species that do not possess the rather elongated hooves of lechwe. Soil conditions have been postulated as a factor influencing habitat selection in the Serengeti (Anderson & Talbot, 1965).

There is undoubtedly a certain niche overlap between lechwe and sitatunga. They were occasionally seen feeding in the same areas and their ranges overlap to a considerable extent. There is probably also a certain amount of niche overlap between lechwe and hippo.

8.3.7.2

Primates

Two medium-sized primates occurred in the study area, baboons (*Papio ursinus*) and vervet monkeys (*Cercopithecus aethiops*). Lechwe ignored vervets but there were distinct differences in the reactions of the various sex and age classes to baboons. Adult males completely ignored baboons and allowed them to approach within a few metres. Females and young fled from baboons, although flight distance for baboons was less than for major predators, 50-100metres as opposed to 300-400 metres. Presumably this behaviour means that baboons may prey on lechwe neonates or very small fawns.

8.3.7.3

Predators

As in Thomson's gazelle (Walther,1969) the most common method of predator avoidance in lechwe was the simple precaution of looking around at regular intervals. All animals did this at least once every 10-15 minutes but adult males seemed to do it less often than females. Males often fed for 10-15 minutes, sometimes as long as 20 minutes, before looking around; females seldom fed for more than four to five minutes before looking up. The fact that lechwe usually occurred in groups (mean group size 10-15) meant that at any particular time there was probably at least one animal looking around (Walther, op. cit.).

In addition to sight, sound appeared to provide important cues for predator avoidance. From my hides I noted alert/alarm responses to a wide variety of sounds including: vocalizations by lion, leopard and hyena; the alarm calls of impala and wildebeest; the alarm call of the blacksmith plover (Holopterus armatus); the sound of other lechwe running through the water; distant gunshots and the sound of an approaching motor vehicle.

The sense of smell appears to be less acute in lechwe than in other ungulates. On windy days lechwe would approach to within 100-200 metres of my hide from the downwind side, whereas other species (impala, wildebeest, giraffe and eland) fled at 300-400 metres. Presumably scent is therefore correspondingly less important to lechwe as a means of predator detection than it is to other ungulates.

If lechwe detected something unusual they adopted an alert posture with head held high, ears forward and body tense. If they could not immediately identify the object they commonly approached it showing great attentiveness and alertness. In this respect their behaviour resembles that described in other species (Walther, 1969; Jungius, 1971; Leuthold, 1977).

When lechwe were disturbed by an animal or object they made an alarm vocalization by forcing air through half-closed nostrils. Through binoculars movements of both chest and flanks (inhalation/exhalation) and movements of the nostrils could be seen. The vocalization usually sounded like a snort but the pitch could be raised with increasing anxiety. For example, when I approached a badly wounded female that had taken cover in dense reeds, she made a whistling sound very similar to that of a reedbuck.

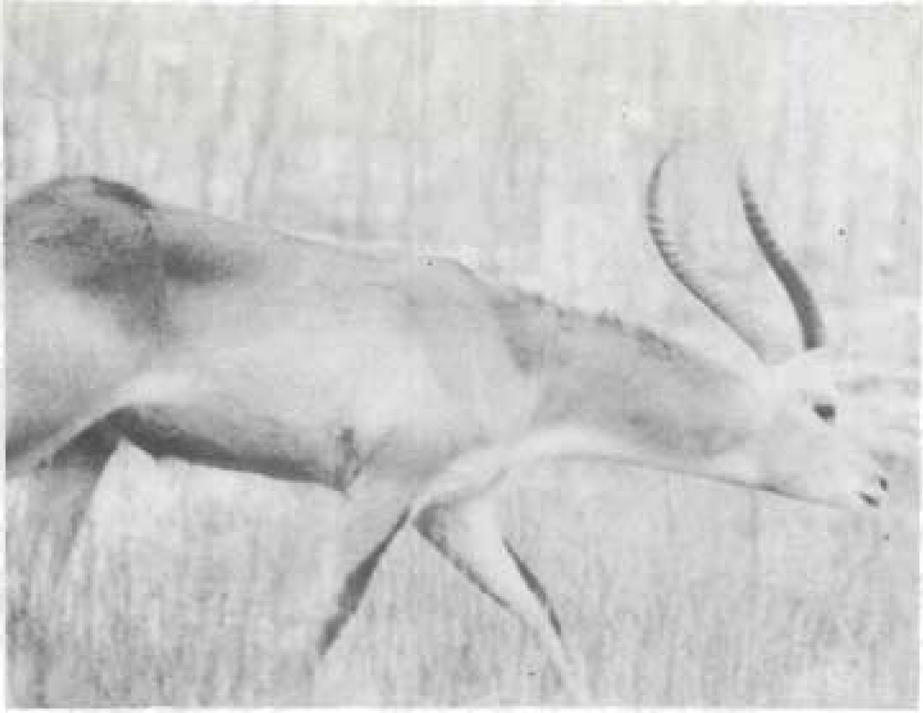
Other lechwe responded initially to both the alert posture and the alarm snort by becoming alert themselves. The subsequent response of alerted animals was variable, depending on such factors as the proximity of the cause of alarm, the suddenness of its appearance and the speed with which it was moving. If predators were involved, the number of animals and their direction of travel were influencing factors. Thus the flight-releasing factors noted in Thomson's gazelle (Walther, 1969) appear to operate with lechwe in this context also.

Another alarm response, not previously noted in lechwe, was stotting in a manner very similar to that described in Thomson's gazelle (Walther, op. cit., see Fig. 9). It was seen on only four occasions. An example of this behaviour occurred when an interaction between a territorial male and a female was interrupted as four hyenas emerged from cover and trotted along the edge of the floodplain about 200-300 metres from the lechwe pair. The male turned towards the hyenas and made a series of short stiff-legged jumps in the direction of the predators. All four legs came off the ground simultaneously and the animal's back was arched during the jump. This behaviour was accompanied by alarm snorts .

At the beginning and end of flight lechwe often trotted with heads lowered and necks extended (Plates 8.1 and 8.2). Lent (1969) suggests that this gait may have signalling and predator avoidance functions but I suggest that it is simply a submissive i.e. fearful response that usually occurs in an intraspecific context but is also carried over into interspecific situations. Walther (1969) saw similarities in the response of Thomson's gazelles to predators and very dominant conspecifics and in lechwe the similarity in these responses can be seen by comparing Plates 8.1 and 8.2 with Plate 9.2.

In flight lechwe often, particularly in water, bounded in a manner very similar to the arched jump described by Walther (op. cit., see Fig. 8). This gait also commonly appeared in play. When fleeing on land lechwe would gallop, but seldom for more than a few hundred metres before turning or bounding in a different direction.

Only 28 lechwe-predator interactions were seen. Reactions to predators varied from indifference to immediate flight. The extreme of indifference was shown by a territorial male that fed to within about 50 metres of where a pack of 17 wild dogs were lying in the shade at the edge



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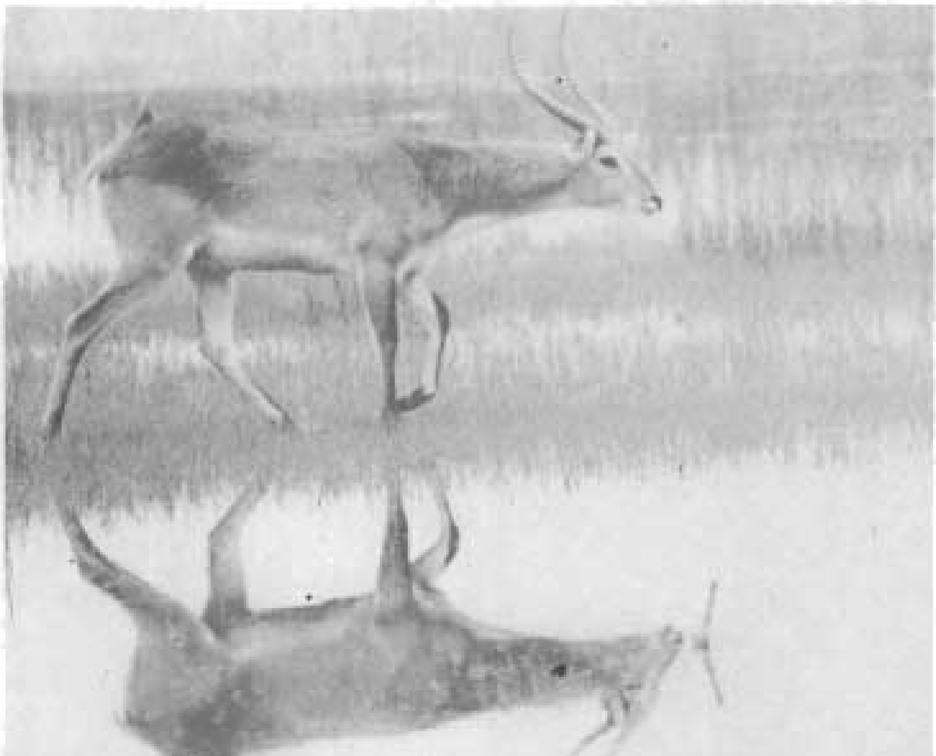


8.2

of the water. Another reaction was fascination behaviour (Walther,1969) shown, for example, by a group of females that stared intently and walked towards a lioness that was walking slowly along the edge of the floodplain. The lechwe approached to within about 200 metres of the lioness and kept her under close observation until she disappeared from view.

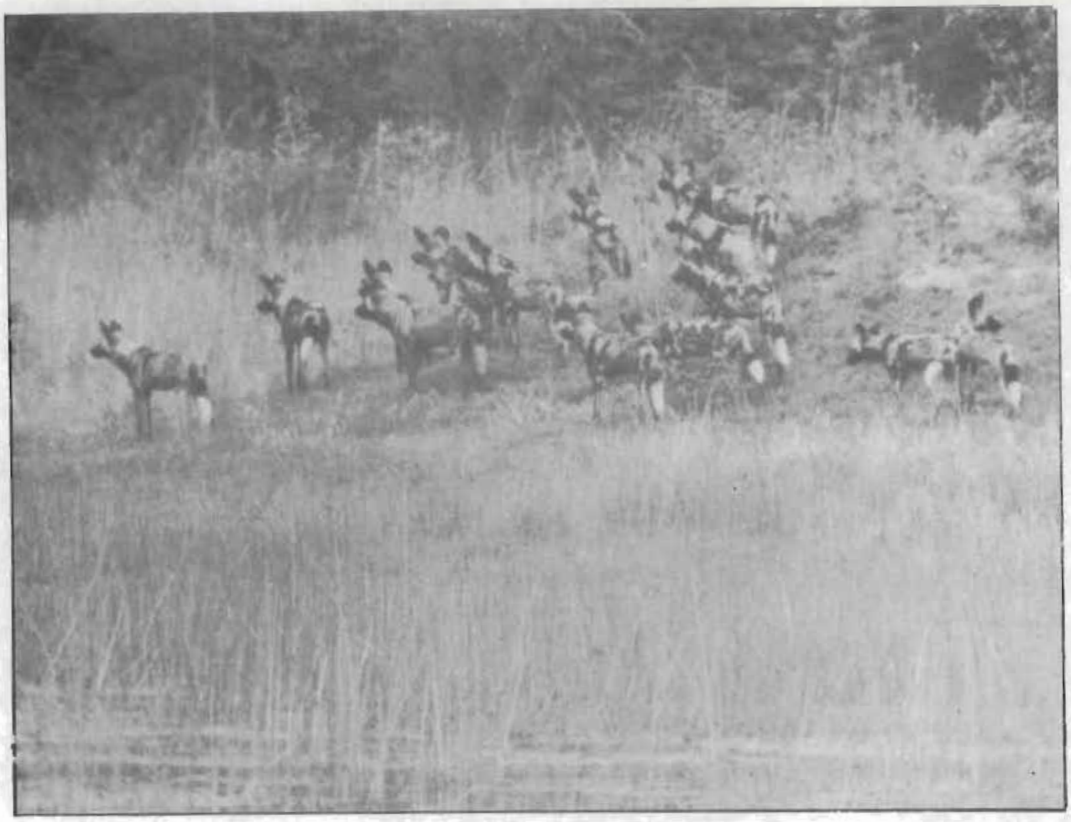
In 17 out of 18 cases which involved pursuit lechwe took to the water. On the one occasion that they did not enter the water, it was a low intensity flight and they ran towards the water away from a group of lions approaching from trees on the edge of the floodplain. The flight stopped when the lions stopped after a perfunctory approach.

Two incidents vividly illustrate the importance of water as escape cover for lechwe. In one case wild dogs killed two adult male lechwe that were feeding in a group of males about 800 - 1 000 metres from water (Plates 8.3,8.4 The lechwe fled towards the water when the dogs began their pursuit but two were caught 100 - 200 metres from the water's edge. On 11 other occasions lechwe successfully evaded wild dogs by running into water.

The other case involved an attempt by a cheetah to kill a yearling male. When first sighted the cheetah was loping after a mixed group of lechwe feeding along the edge of the water. The cheetah suddenly accelerated and appeared to single out a yearling male at the back of the group. As the cheetah got close, the lechwe made a right angle turn into the water, crossed about 100 metres of open shallow water and disappeared into a dense stand of emergent vegetation. The cheetah pursued it into the water but abandoned the chase at the edge of the reeds.

In all cases where lechwe fled there were clear differences in the flight distances of, on the one hand, females and younger animals, and, on the other hand, adult males, in particular territorial males. Females and younger animals had an estimated flight distance of 300 - 400 metres. Adult males had an estimated flight distance of 100 - 200 metres. Differences in male and female flight distances have been noted in other species (Walther, 1969; Rowe-Rowe, 1974).

An anti-predator response that was seen only in response to my own presence was lying down in thick cover. Juveniles did this often and only flushed when approached to within five to ten metres. On one occasion an adult male lay down in a dense stand of sedges and did not



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8.4

flee until approached to within about 20 metres.

Lechwe fawns are of the "lying type" (Walther, 1969; Lent, 1974) and were usually hidden on termitaria or small islands amongst dense emergent vegetation. I saw no sign of defence of young by females, although on one occasion a female did approach her few-days-old fawn which was giving loud distress bleats after I had captured it.

The dependence of lechwe on water as escape cover has an influence on their patterns of habitat use and they seldom moved more than one to two kilometres from water (Chapter 4). Lechwe are, however, obviously wary of deep water. This was probably due to fear of crocodile (Crocodylus niloticus), which are common in the Linyanti Swamp, because they have no reason to fear the water itself. Even the smallest fawns swim strongly and adult lechwe swam the main Kwando channel, which is both deep and strongly flowing, with ease and, when alarmed, without hesitation.

It was also my impression that the lechwe's reliance on visual detection of predators influenced habitat use. Large groups of lechwe occurred only in areas where there were extensive open floodplains, and places in which the tree line was close to the swamp were usually avoided by lechwe. Also, the fact that lechwe always rested in open areas with good visibility appears to be another sign of their dependence on visual detection of predators (section 8.3.3).

8.4

SUMMARY

The primary objective of behavioural work in this study was to facilitate recognition of social and behavioural attributes of actual or potential importance in the conservation and management of lechwe.

Behaviour was studied by direct observation from two hides and from a vehicle. Important findings in respect of activities, physical maintenance behaviour and relations with other species were the following:
(1) there were real differences in the activity budgets of different classes of lechwe which are related to sex, social status, age and season;
(2) activity rhythms appear to be less clearcut in lechwe than in other

African ungulates which have been studied;

(3) daily movements are apparently not extensive;

(4) heavy rain was the only type of weather which obviously affected lechwe activity;

(5) a feature of lechwe comfort behaviour is that they may enter water for thermoregulation;

(6) voidance behaviour in lechwe males is remarkably unstructured;

(7) in lechwe, flight-releasing factors appeared to operate in much the same way that has been described in Thomson's gazelle;

(8) on four occasions animals used a "stotting" gait that has not previously been recorded in lechwe;

(9) the normally clear ecological separation between lechwe and terrestrial ungulates appeared to break down during dry periods;

(10) lechwe females and juveniles reacted to baboons as predators while males ignored them;

(11) sight appeared to be the most important sense for predator detection in lechwe;

(12) lechwe use a distinctive snort when alarmed;

(13) water is very important to lechwe as escape cover;

(14) both the presence of water and good visibility appeared to be important factors in determining lechwe habitat use.

CHAPTER 9

SOCIAL BEHAVIOUR AND ORGANIZATION

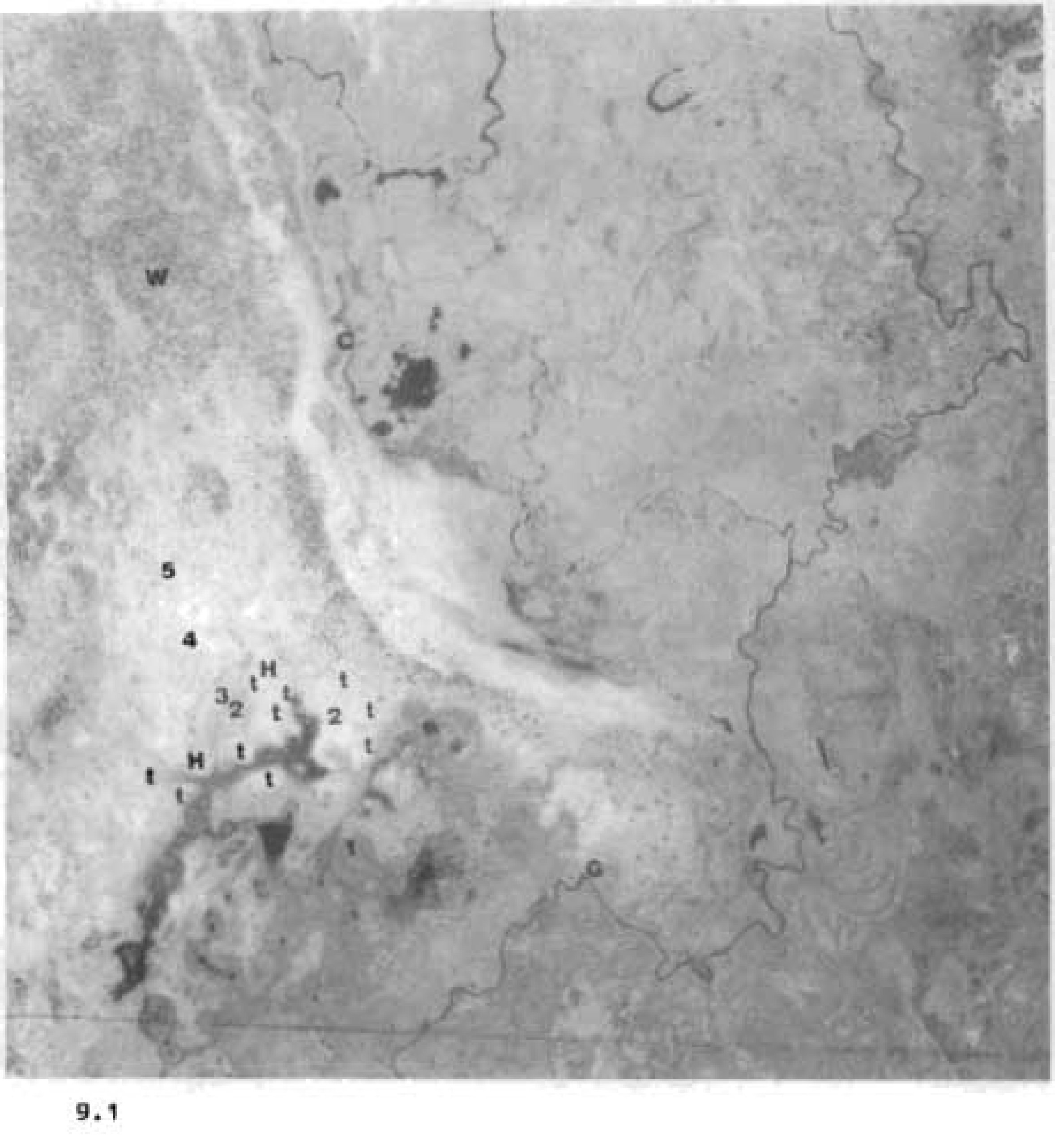
9.1

INTRODUCTION

Considerable attention was paid to social behaviour because an understanding of social organization is vital to conservation and management and a knowledge of social behaviour is a prerequisite for understanding social organization. When this study began relatively little was known about the social organization and behaviour of lechwe but recent publications by Schuster (1976 and 1977) have more fully documented these aspects in the Kafue lechwe population.

Most of the data on social behaviour and organization were gathered in the intensive study area (Plate 9.1). Theoretical considerations (Emlen & Oring, 1977; Clutton-Brock & Harvey, 1978) and empirical evidence from other species (e.g. Leuthold, 1966) suggest that the social organization of lechwe should be influenced by ecological factors. As the flood regime in the intensive study area was remarkably constant in contrast to those in other areas supporting lechwe populations (Child & Von Richter, 1969; Grimsdell & Bell, 1975; Schuster, 1976 and 1977), the picture of social organization that emerges from this study may in some respects be unusual for the species.

Earlier studies (De Vos & Dowsett, 1965; Child & Von Richter, 1969) established that lechwe are gregarious bovids exhibiting at least the three basic social divisions (female/nursery herds, bachelor herds, and single adult males) mentioned by Estes (1974). On the Kwando the single adult males were found to be territorial, as had been found in the Okavango Delta (Lent, 1969; Joubert, 1972; Child & Robbel, 1975) and on the Kafue Flats (Schuster, 1976 and 1977). Territoriality is the pivotal feature of lechwe social organization because " To a very large extent, antelope social systems have been built around the territorial male, whose role is by no means limited to inseminating females, as sometimes portrayed. Indeed the other two classes owe their separate identities very largely to territorial behaviour." (Estes, 1974).



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9.2

EXPRESSION AND COMMUNICATION

The purpose of this section is to document behaviour which appeared to have expressive and/or communicative functions.

9.2.1

Visual Signals and Displays

A variety of postures and actions appeared to operate as signals or displays. Visual signals and displays that were commonly used by lechwe are listed below.

Erected posture (Walther,1974; Table 4): Territorial males used this posture as a form of static-optical marking (Hediger,1949). Schuster (1977) notes that this is "the most frequent display by a male lechwe on his territory" and it was noted also by Joubert (1972) in the Okavango. On the Kwando this posture was not often used as a form of territorial marking, perhaps because territory size was much greater than in the situation observed by Schuster (op. cit.). Lechwe males on the Kwando frequently used the erected posture as a broadside dominance display (Plates 9.2, 9.4, 9.6) although the orientation varied and was occasionally frontal.

Extended-neck-horns-laid-back(Plates 9.3., 9.6): This signal was a gesture rather than a static posture. The laying back of the horns was usually accompanied by a rapid up and down tossing of the head. The gesture appeared to be a submissive display because on every occasion that it occurred the animal using it fled or withdrew from an animal in the erected (dominant) posture described above.

Of 137 male:male interactions involving the use of dominance/submissive signals 54% were between adult males, 42% between adult and subadult (mostly older) males and only 4% between subadult males. These data tend to support the dictum of Walther (1974) that "dominance displays mature relatively late in the ontogeny".

The reciprocal use of the dominance posture and of submissive gestures appeared to be a form of dominance ritual and I referred to interactions involving this ritual as "dominance encounters".

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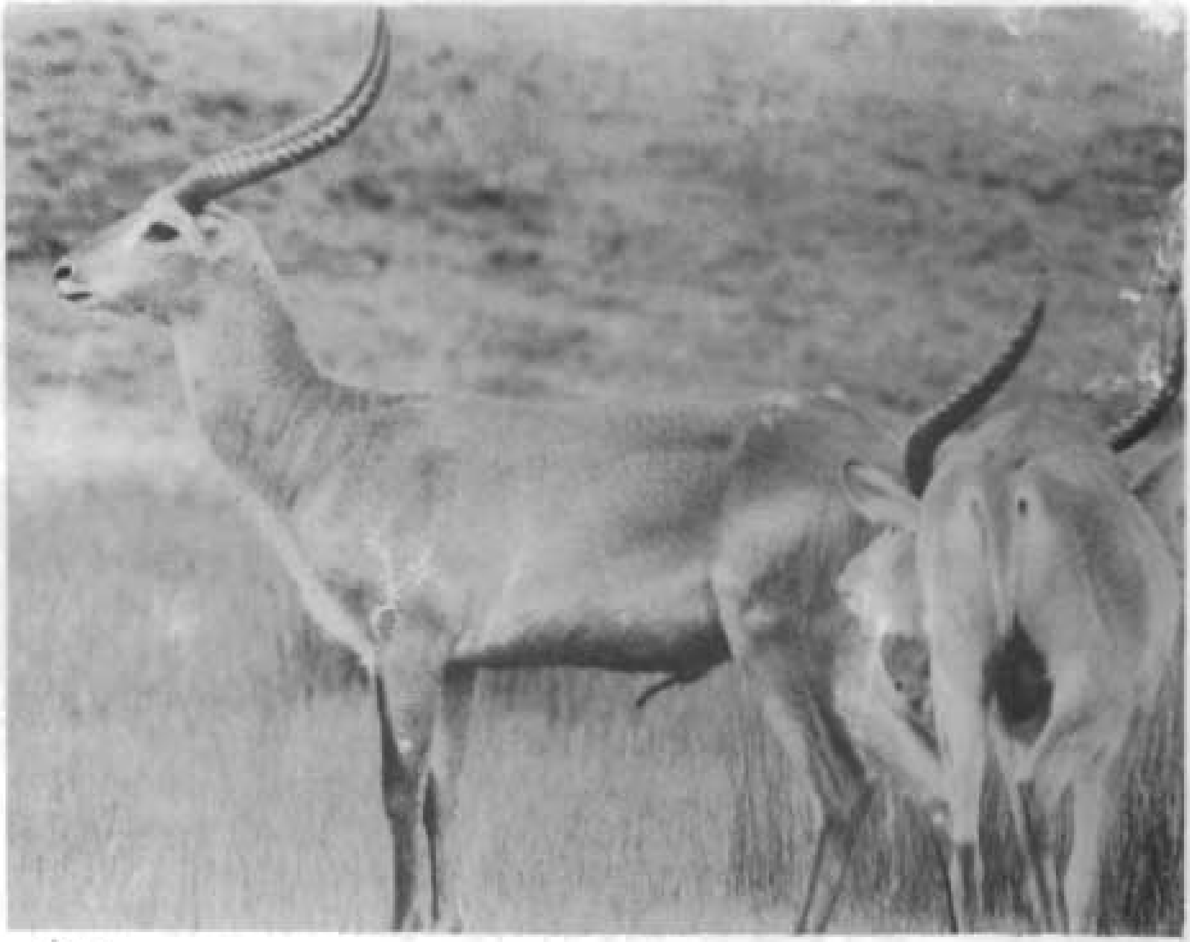

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Threats (Plate 9.5): Three of the threats listed by Walther (1974: Table 3) were seen in lechwe. These were: high presentation of horns, medial presentation of horns and the head-low posture. The medial presentation of horns was used much more frequently than the other two forms of threat. A low presentation of horns (Walther, *op. cit.*) was never seen.

Dominant males usually terminated dominance encounters with a fourth type of horn threat. This was an over-the-shoulder threat directed at the submissive male, standing to the side or rear of the dominant animal (Plat 9.5).

A further type of threat was used by dominant males to initiate dominance encounters. This was a *direct approach* similar to that described by Underwood (1975) in eland (*Taurotragus oryx*) and Grau & Walther (1976) in mountain gazelle (*Gazella gazella*). The speed at which this approach was made varied from a run to a normal walk or a slow walk with a head-low posture. The speed of approach seemed to be related to the age/size of the animal being approached - the smaller the animal the faster the approach

The head-low posture was also used by territorial males that were blocking females from leaving their territory. It was used mainly as a broadside display, the male standing in front of the female and physically obstructing her path.

Head-and-neck-stretched-forward posture (Walther, 1974: Table 5): This posture was commonly used by males during courtship. It was used mainly when approaching a female, occasionally while following her. On 37 occasions tongue flicking occurred during this type of approach, in much the same way as has been documented in impala (Schenkel, 1966). The origins of this posture may be aggressive (Walther, 1974).

Horning (Plate 9.7*): This action was often performed by males and was mainly directed at conspicuous tufts of grass or low shrubs. In the absence of some such object, horning of the earth occurred and during horning bouts it was not unusual for a male to lie down and vigorously sweep his horns along the ground. On several occasions an animal rose after sweeping his horns on the ground in this way and continued horning when upright.

* page 255.

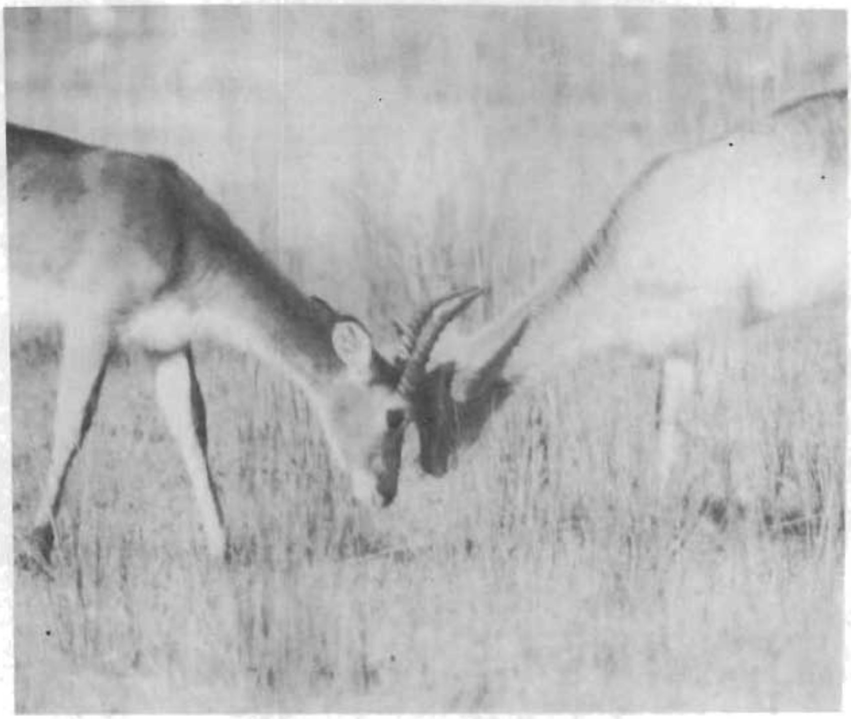
The function of this type of "object aggression" (Walther, 1978a) is not clear, although Walther (op. cit.) found some evidence that it may function as a threat in Thomson's gazelle. In lechwe 69% of 131 horning incidents occurred in a clearly agonistic context, 21% in an unknown context, 7% in a context that may have been either sexual or agonistic (e.g. a male courting a female breaks off the interaction to horn when another male passes by) and 4% in a context that was clearly sexual. On three occasions (2,3% of observations) either ejaculation or urination occurred. Weak thrusting of the pelvis (Child & Robbel,1975) was never seen. No case was observed in which the addressee of a horning display fled or withdrew.

Agonistic grazing: Occurred before, during or after clashes between territorial males (in 22 out of 99 clashes) and also in the less common clashes between territorial and non-territorial males (in six out of 18 clashes). Differing interpretations have been offered for this behaviour (Estes,1969; Walther,1974 and 1978a) and its meaning in lechwe was not obvious.

Grooming: In the form of scratching, nibbling etc., was common in agonistic encounters. As with agonistic grazing, the fact that it occurred often indicates that it may have some expressive function but again this was not obvious in lechwe.

Head-turn (Walther,1974: Table 4): Turning of the head while in an erected posture occurred in the context illustrated by Plates 9.8,9.9 and 9.11, 9.12. Most (95%) of the interactions involving head-turning were between territorial males and all involved horn contact. This gesture occurred only in an erected posture which indicates that it may be a modified expression of dominance as inferred by Walther's (op. cit) mentioning of "an abbreviation of a broadside display".

Erection of the penis: Occurred during dominance interactions (Plates 9.2-9.6), during horning (Plate 9.7), during fights (Plates 9.11,9.13) and, of course, in sexual interactions. Because it occurs in various contexts which clearly involve excitement it is reasonable to suggest that in lechwe erection of the penis is a generalized manifestation of a high level of excitement, i.e. an "excitation activity" (Walther,1974) or a form of "excitatory neural overspill" (Leuthold,1977).



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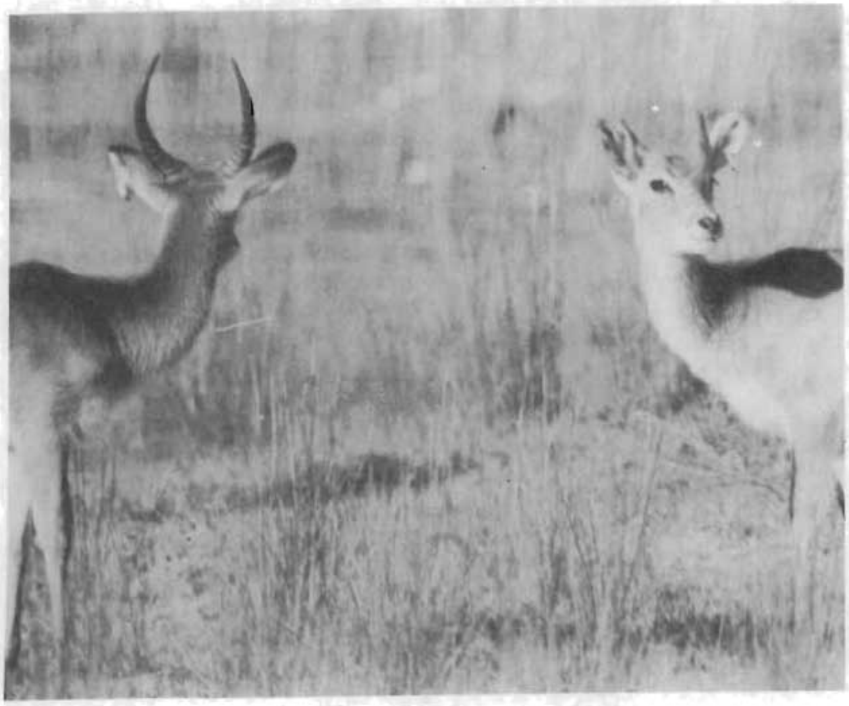

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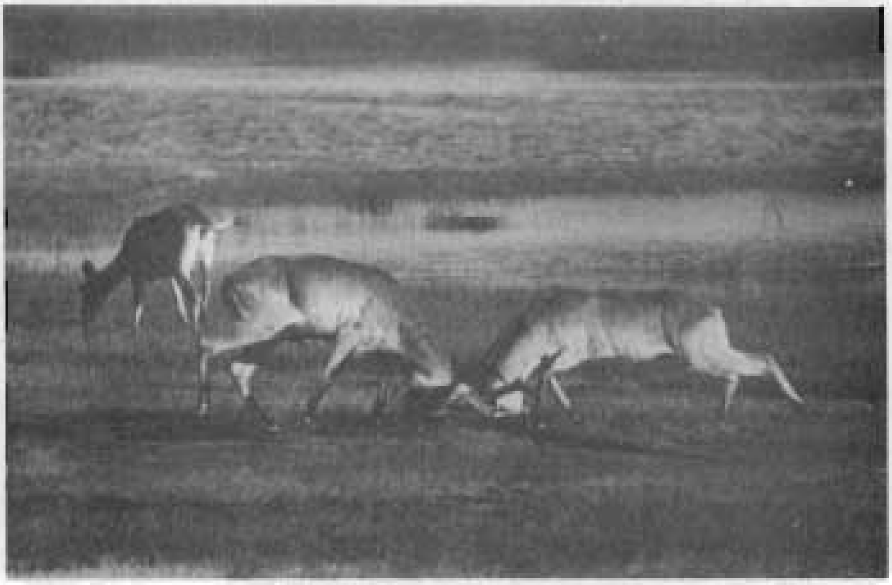

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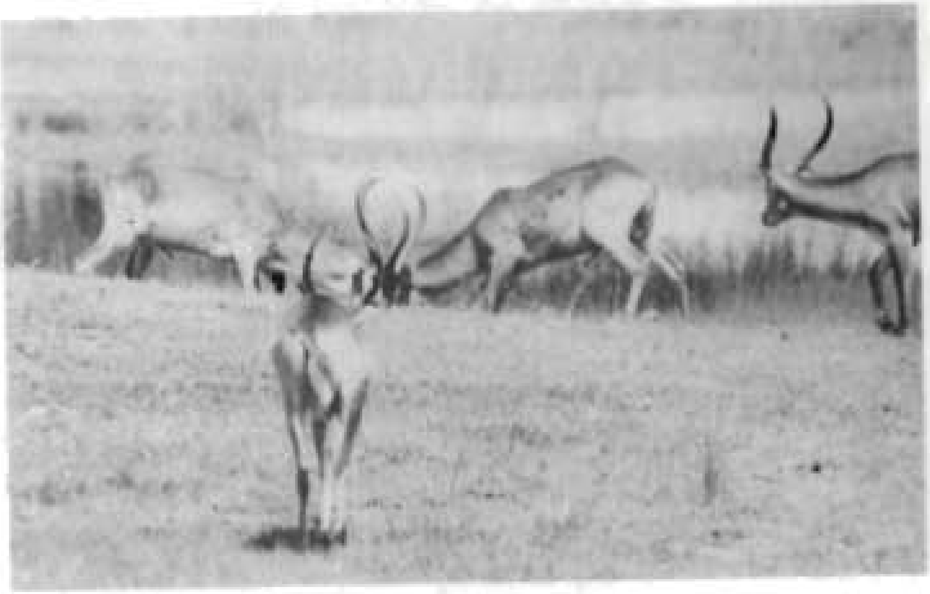

9.13

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9.2.2

Auditory Signals

The following types of vocalization were noted:

Mother-young calls: On approaching each other both females and fawns uttered repeated bleats of varying pitch and duration. Contact calls between mother and young have also been documented in Uganda kob (Leuthold, 1967).

Isolation call (Kiley,1972): A known female whose 3-4 month fawn was taken by a cheetah was seen on three occasions in the following two days apparently searching and uttering repeated loud bleats. On different occasions two other females behaved in a similar way.

Dominance vocalization: Males used repeated grunting bleats during or after agonistic encounters and occasionally after pursuing females. Territorial males used this vocalization most often, usually when an intruder entered their territory or when a nearby male vocalized, but also sometimes when they were alone on their territories. Initially this call was believed to be a territorial advertisement but a more general and therefore more satisfactory explanation is that it is an "expression of activated male dominance" (Schenkel,1966) like the roaring of impala (Schenkel, op. cit.; Leuthold,1970) and the snort-wheeze of the pronghorn (Antilocapra americana Ord) (Kitchen & Bromley, 1974). A fact supporting the latter conclusion is that this vocalization was regularly used in interactions between non-territorial males, both adult and subadult. That this vocalization is an expression of dominance does not, of course, exclude its use as a form of territorial advertisement.

Courtship sounds: When courtship occurred close to a hide a wide variety of muted sounds was heard. These included humming or moaning, soft grunting bleats, muted alarm snorts and puffing, and during one chase a breathless rasping sound was heard which may well have been involuntary.

Alarm snorts (described in Chapter 8) :Were uttered by all animals except the very young and evoked either alert postures or flight from animals in the vicinity of the individuals giving the alarm.

Distress: Three neonates caught by hand for ear-tagging uttered loud prolonged, braying bleats. The same call was heard from a year-old male that was apparently dying of a horn wound.

Kiley (1972) found a single continuum of sound in domestic species, but lechwe appear to vocalize in at least two, perhaps three, continua of sound. Two distinct sound types in lechwe are, on the one hand, various types of bleat, and, on the other hand, the alarm snort, which is produced by the expulsion of air through the nostrils. A possible third type of sound is moaning or humming, but this may be a low amplitude bleating with the mouth closed.

In two ways lechwe vocalization conforms to Kiley's (op. cit.) hypothesis relating to vocalization in domestic species. Firstly, it is quite clear that there are sounds which are not situation-specific. For instance, the grunting bleat is used by territorial males alone on their territories, it is used before, during and after fights, and after chasing females, and also in a muted version during courtship. Secondly, males frequently vocalize in response to vocalization from another male, as was found in domestic species.

9.2.3

Combined Visual-Auditory Signals

On a few occasions a territorial male stood on higher ground on the edge of his territory, more or less in an erected posture, intermittently uttering grunting bleats. This appeared to be an example of the use of combined visual and auditory territorial marking (Hediger,1949).

Territorial males performed what was ostensibly a post-copulatory display (Plate 9.21)*. Immediately after copulation the male stood with back arched,penis erect and palpitating, licking its lips and moaning or humming. This performance lasted for 0,5 - 1,0 minutes.

In all 21 copulations were seen. The post-copulatory behaviour described above was clear on 13 occasions (62% of copulations). On four occasions the animals moved out of sight immediately after copulation. On another four occasions the behaviour did not occur.

The function of the post-copulatory behaviour observed in lechwe is obscure. The vocalization is very muted,the visual aspects are unspectacular and the whole performance is brief. Further, this behaviour was never seen to elicit a response from other animals.

* page 268.

The same behaviour was observed three times in circumstances unrelated to copulation. On one occasion, a territorial male exhibited it while apparen watching a boundary skirmish between two nearby territorial neighbours. On another occasion a territorial male exhibited it while "watching" his neighbour mount a female. In the third instance a subadult male exhibited this behaviour after winning a sparring encounter and going through a dominance ritual with another subadult male. This behaviour is most probably another example of an "excitement activity" (Walther, 1974) or of "excitatory neural overspill" (Leuthold, 1977).

9.2.4

Olfactory Signals

The occurrence of naso-nasal contacts and other sniffing interactions between females and young and between juveniles indicated that breath and bod scent have signalling functions. This was particularly evident from severa sets of observations which involved a fawn approaching a female, sniffing her or inviting naso-nasal contact, being rejected and trying again with ot females before wandering off alone after being rejected in each case.

As in waterbuck (Kiley-Worthington, 1965), Uganda kob (Leuthold, 1966) and impala (Leuthold, 1970) no obvious form of olfactory marking was found in lechwe.

As in many other ungulates, lechwe males test the urine of females and exhibit different reactions to the results of these tests. Females would usually urinate "when closely followed and/or nudged by a male" (Estes, 197 and males would then test the stream of urine, in the process giving the "distinctive grimace known as flehmen" (Estes, op. cit.). After flehmen males often lost interest in the female, or occasionally began to court her assiduously. Estes (op. cit.) postulates that flehmen serves to block the external nares and facilitate the bringing of odorants to the vomeronasal organs as the animal breathes in. He accepts Fraser's (1968) suggestion th "it is a reasonable assumption that oestrus cycle phasing may be recognizab to the male by the odour-testing of urine."

9.2.5

Tactile Signals

On one occasion a courting male laid his chin on a female's rump and on two further occasions a male appeared to be doing this. On three occasions a juvenile laid its chin on its mother's rump. This form of contact is obvio ly far more rare in lechwe than it is in the congeneric waterbuck (Kiley-Worthington, 1965; Spinage, 1969).

During courtship males on 12 occasions (1,3% of observed male:female interactions) stood with their heads underneath the female's belly, perhaps nuzzling her inguinal region as in the courtship of waterbuck (Spinage, 1969).

Laufschlag (Walther, 1958 and 1974) was extremely common and was directed at more or less any part of the female's body, although usually at her hindquarters and occasionally between her hind legs. If the female was lying down when approached, the male commonly nudged her hindquarters and occasionally the inguinal region with his foreleg or nose.

Animals of all ages and both sexes used nudges with the head to displace or supplant conspecifics standing or lying near them.

9.2.6

Individual Recognition

There were indications of individual recognition in two contexts. Firstly, territorial males appeared to recognize the holders of territories near to their own. They tolerated non-territorial males passing through their territories but immediately pursued and harassed a territorial male that violated a boundary. Recognition was apparently by visual means. Secondly, females rejected fawns after the latter had approached and mutual sniffing had occurred (section 9.2.4). This suggests that females and fawns may recognize each other on the basis of breath and/or body scent. Vocal cues may also be important in the mother-fawn relationship. Females and fawns often vocalized when approaching each other and one incident was witnessed which suggested recognition of the female's voice by her fawn. A female approached a mixed group of about 20 fawns and females, bleating softly as she did so. As she drew near the group, a fawn of about three months old ran out, approached the female and almost immediately began to suckle.

9.3

SOCIAL BEHAVIOUR

The criteria for field age classification that are given in section 3.3.9 were developed by correlating laboratory age determinations with measurements of body and horn dimensions taken from autopsied specimens. During the field study I was not able to distinguish all the classes listed in section 3.3.9. Sex/age and social classes that could be recognized in the field are listed below with abbreviations:

TM= territorial male; i.e. an adult male regularly seen in the same small area and seen to defend it or assert dominance over other males entering it;

ABM= adult bachelor male; i.e. non-territorial adult male (Plate 9.16);

AF= adult female; i.e. a female over about one year of age;

SABM= subadult bachelor male; i.e. males about one to four years old (Plates 9.9*, 9.14 and 9.15);

* page 257.

Plate 9.15: Subadult male with dislocated carpal joint. This picture was taken in April 1976 when the animal was 2-3 years old. It was first seen during April 1975.

Plate 9.16: The same male now fully adult photographed in March 1979. This picture was taken within 20-30 metres of the spot where Plate 9.15 was taken. The animal looked extremely fit when last seen in March 1979 but was submissive to all adult males. It appeared very unlikely that he would ever breed.

9.15

9.16

J = juvenile ; i.e. animal less than one year old. Within the juvenile class it was also possible, on the basis of features listed in section 3.3.9, to recognize neonates, animals of 3-4 months (Plate 9.23*) and males of 6-9 months (Plate 9.9), the latter being at the age at which horns become visible.

9.3.1

Agonistic Interactions

The purpose of this section is to describe the patterns and sequences of behaviour that occurred in agonistic encounters. These varied from fleeting interactions involving no physical contact to protracted conflicts with a great deal of physical contact. The duration and intensity of agonistic interactions were apparently a function of their "situational motivation" (Walther, 1978a) and differences or similarities in the age, sex and status of the rivals.

9.3.1.1

Agonistic interactions without physical contact

In this context several behaviour patterns occurred which have not previously been described in this chapter. These are listed and described below:

<u>withdrawal</u>: a submissive animal moves away from a dominant animal at a walk;
<u>flight</u>: a submissive animal runs away from a dominant animal;
<u>chase</u>: a dominant animal pursues a submissive animal at a run;
<u>air cushion fight</u> (Walther, 1978a): both animals make a frontal horn thrust but no contact is made.

Table 9.1 illustrates the most common forms of agonistic interaction without physical contact. The sequences given in this table are typical but were by no means invariable. Table 9.1 shows that as the difference in age and status diminishes so the interactions become more complex and more ritualized. Interactions between a territorial male and a juvenile seldom lasted more than a few seconds. Interactions between neighbouring territorial males sometimes lasted for 5-10 minutes. About 57% of all observed agonistic interactions (405) involved no physical contact.

9.3.1.2

Agonistic interactions with brief physical contact

Agonistic interactions with physical contact involved three different types of contact. These were:

<u>horn contacts</u>: which included "push-fighting", "twist-fighting", "fight-circling", and "clash-fighting" (Walther, 1958; Grau & Walther, 1976);
<u>head butting</u>: butting of heads between hornless animals;
<u>body attack</u> (Walther, 1978a): butt or shove body with head or horns.

* page 272.

ABLE 9.1: COMMON FORMS OF AGONISTIC INTERACTION WITHOUT PHYSICAL CONTACT (the performer of each behavioural act is given in brackets after each act is listed)

ituational otivation	Addressor	Addressee	Behaviour Sequence
erritorial nvasion	TM	J male	Enter territory (J) - rapid direct approach (TM) - flight (J) - chase (TM)
ssertion of ominance	TM	SABM young	(a) Dominance vocalization (TM) - rapid direct approach (TM) - flight (SABM) - chase (TM)
		SABM older	(b) Walking direct approach (TM) - erected posture (TM) - submissive display (SABM) - withdrawal (SABM)
erritorial nvasion	TM	ABM	Enter territory (ABM) - slow direct approach (TM) - erected posture (TM) - submissive display (ABM) - horn threat (TM) - withdrawal (ABM)
erritorial atification	TM	TM	Approach mutual boundary (both TM) - medial horn threat (both TM) - air cushion fight (both TM) - head turn (both TM) - agonistic grazing (both TM) - feed away from boundary (both TM)

Table 9.2 illustrates common situations in which brief (not more than a few seconds) physical contact occurred. Again the sequences are typical but were subject to considerable variation. Interactions of this type between juveniles or between females were very brief, while those between territorial males often involved more than one contact and could last up to 15 minutes. About 34% of all observed agonistic interactions involved brief physical contact. Plates 9.10,9.11,9.12* and 9.13** illustrate clash fights between territorial neighbours.

9.3.1.3

Agonistic interactions with continuous physical contact

Two different types of interaction involving continuous physical contact occurred. These were: low intensity sparring and horn wrestling between young males and "all-out fights" (Grau & Walther,1976) between adult or nearly adult animals.

The most common types of horn contact between young males were "twist-fighting" and "push-fighting" (Grau & Walther, op. cit.). Interactions between young males were relatively mild but did not appear to be playful. They lasted from 0,1-12,0 minutes, the mean of 24 timed interactions being 3,9 minutes (SE 0,9). Within bachelor groups sparring was highly contagious with up to 40 interactions per hour occurring on occasion. This type of interaction accounted for 5% of all observed agonistic interactions.

Fifteen all-out fights lasting more than five minutes were observed. Thirteen of these were between adult males and probably involved territorial ownership - territories changing hands as a results of fights in at least three cases. The longest fight observed lasted slightly more than 20 minutes.

All fights involved head-on clashes, which belong to Geist's (1966) third stage in the evolution of fighting techniques. Fights consisted mainly of violent "push-" and "twist-fighting". Clashes could be extremely violent and some were heard across water at distances of up to one kilometre. During all-out fights interruptions were brief, as in mountain gazelle

*page 257

**page 257

TABLE 9.2: TYPICAL INTERACTIONS WITH BRIEF PHYSICAL CONTACT (performer's class in brackets after each act)

Situational motivation	Addressor	Addressee	Behaviour sequence
Dominance interaction	J1 male	J2 male	Approach J feeding (J1) - briefly butt heads (both J) - withdraw (loser)
Refusal of milk	AF	J	Approach AF feeding (J) - attempt to suckle (J) - body attack (nudge away with head) (AF) - withdraw (J)
Supplantation	AF1	AF2	Approach AF1 lying and ruminating (AF2) - nudge rump of AF1 with nose (AF2) - stand up and walk off (AF1) - lie down in vacated spot (AF2)
Supplantation	J1	J2	Approach group of J's lying down (J1) - nudge rump of J2 with nose (J1) - stand up and walk off (J2) - lie down in vacated spot (J1)
Territorial ratification	TM1	TM2	TM1 chase AF to boundary of TM2's area - TM2 run to boundary, horn threat to TM1 - TM1 horn threat - clash-fight - head turn (both TM) - parallel walk (both TM) - air-cushion fight (both TM) - clash-fight - horning (TM1) - agonistic grazing (TM2) - clash-fight - head turn (both TM) - agonistic grazing (both TM) - feed away from boundary (both TM)

(Grau & Walther,1976) and stereotyped behaviour tended to be reduced. Erection of the penis (Plates 9.11,9.13)*occurred during serious fights but it was not possible to determine whether or not it invariably occurred or persisted throughout fights. In protracted fights the participants usually ended up having their muzzles blackened with mud. Every all-out fight ended with vigorous pursuit by the victor for distances of up to 500 metres or more.

Two all-out fights between 3-4-year-old males were observed. In both cases the fight was interrupted by a territorial male and both contestants made submissive gestures to the territorial male.

All-out fights attracted the attention of other males, which commonly approached to "watch" fights from close quarters (Plate 9.13). Spinage (1974) noted the same behaviour in Defassa waterbuck.

9.3.1.4

Relative frequency of forms of aggression in different age and social classe

In gazelles there are differences in the frequency with which forms of aggression appear in interactions between animals of various sex, age and social classes (Grau & Walther,1976; Walther,1978a). Insufficient data were obtained from juveniles and females to make the same comparisons in lechwe but on the basis of limited data obtained from males it appears that similar differences in frequency occur. Table 9.3 illustrates this point, using selected patterns of agonistic behaviour and classes for which an appreciable number of interaction records were accumulated. The Table shows marked differences in the frequency of dominance rituals. These differences are related to status and age. Animals of equal status and young animals are seldom involved in dominance rituals.

Table 9.3 shows further that in relationships within which dominance rituals are rare, horn contacts are relatively frequent. It also shows that air-cushion fights are a prominent feature of encounters between territorial males, as was found in the mountain gazelle (Grau & Walther, 1976), but not in encounters with other classes. As the difference in dominance status increases the complexity and degree of ritualization of interactions appears to decline. Similarly, interactions between young animals are relatively simple and unritualized.

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* page 257.

TABLE 9.3: THE FREQUENCY WITH WHICH SELECTED PATTERNS OF AGONISTIC BEHAVIOU OCCURRED IN INTERACTIONS BETWEEN DIFFERENT AGE CLASSES OF MALES

(N = the number of interactions)

Behaviour patterns	CLASSES INTERACTING			
	TM:TM N=155	TM:ABM N=176	TM:SABM N=210	SABM:SABM N=114
Dominance/ submission	1,9%	40,3%	27.6%	4,4%
Supplanting	-	4,0%	4,8%	1,8%
Air-cushion fights	22,6%	1,1%	-	-
Head turn	12;3%	-	-	-
Parallel walk	5,8%	-	-	-
Agonistic grazing	14,2%	3,4%	-	-
Horn contact	40,0%	9,1%	-	42,1%
Chase	18,1%	25,0%	48,6%	1,8%

A slightly surprizing feature of Table 9.3 is the low frequency of chases in interactions between subadult males. This probably reflects the low intensity of most interactions between young males.

9.3.2
Sexual Behaviour

Sexual behaviour in lechwe was typical of Reduncinae (Kiley-Worthington, 1965; Spinage, 1969; Jungius, 1971; Leuthold, 1977). The common patterns of sexual behaviour observed in Kwando lechwe are described below, approximately in increasing intensity of courtship leading to copulation and post-copulatory behaviour.

9.3.2.1
Precopulatory behaviour

All observed copulations were by territorial males and a prerequisite for copulation was detention of the female within a territory. This sometimes involved a chase (Plate 9.17) and capture of the female and usually involved herding (Plate 9.18) to keep the female within the territory.

A territorial male tested most females entering his territory. The testing procedure, involving flehmen, was described in section 9.2.4. Flehmen is illustrated in Plate 9.19.

The prancing, short-stepping approach by the male to a female described in Uganda kob (Buechner & Schloeth, 1965) and in Kafue lechwe (Schuster, 1977) was rarely seen in Kwando lechwe.

If the courtship proceeded beyond testing, laufschlag (Plate 9.20) (Walther, 1958 and 1974) was the most common pattern used for beginning more intense courtship. If the female was lying down when approached laufschlag preceded testing. The male usually stood in reverse parallel orientation to the female lying down and nudged her hindquarters with his foreleg and/or nose until she stood up.

If the female was not immediately receptive, a mild form of driving often occurred, the male following the female and the latter continually turning away in the same direction so that a circling by both animals resulted.

__Plate 9.17__: Two territorial males (left) and a very large subadult male (right) pursue an oestrous female. The male on the left is NH. This chase ended with NH detaining the female in his territory and mating with her the next day.

__Plate 9.16__: A subadult male herding a female.

9.17

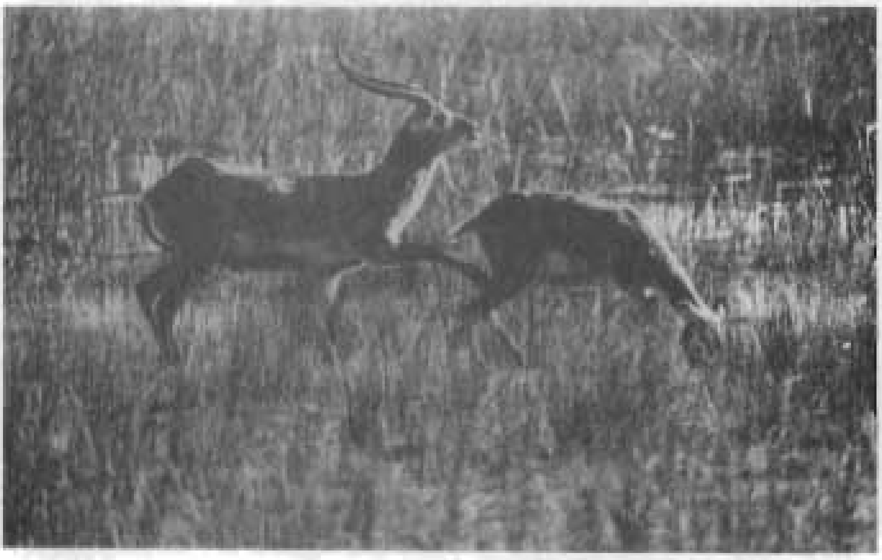
9.18

Plate 9.19: Flehmen.

Plate 9.20: Laufschlag. Note the female's right ear; she was one of the few known females.

Plate 9.21: Post-copulatory behaviour.

9.19



9.20

9.21

When a break in the courtship occurred the male generally began again by approaching the female in a low-stretch posture, sometimes licking his lips. On 12 occasions this approach ended with the male standing with his head under the female's belly(section 9.2.5).

If the female did not move or moved slowly after laufschlag, mounting without an erect penis followed. The final stage before copulation was a series of repeated but unsuccessful mounts with an erect penis.

In protracted courtships each pattern could be repeated many times and in varying sequences. In one courtship laufschlag occurred 124 times and there were 42 unsuccessful mounts before intromission occurred.

Female response to the attentions of a male ranged from immediate flight to complete recptiveness. An unreceptive female commonly continued with her ongoing activity, for example feeding (Plates 9.19,9.20). With increasing degrees of receptiveness the female moved progressively less, to the point where she stood still to allow intromission.

9.3.2.2

Copulation

Copulation (Plate 9.22) was extremely brief as in other bovids. Intromission was achieved with a single pelvic thrust by the male, which usually brought his feet off the ground.

In lechwe the male coital position appears to between the positions "q" and "r" illustrated in Walther's (1974) Table 5. The forelegs do clasp the female's side but the chest does not touch the female's back (Plate 9.22).

In Uganda kob females are promiscuous, copulating with as many as 10 males (Buechner & Schloeth, 1965). No conclusive data on this point were gathered in this study, but my impression was that lechwe males detained females in their territories for the duration of oestrus so that females mated with only one male each oestrus. It is possible that Kwando male lechwe are able to do this because their territories are relatively large in comparison to those of Uganda kob.

Plate 9.22: The achievement of intromission.

9.22

9.3.2.3

Post-copulatory behaviour

Male post-copulatory behaviour was described in section 9.3.2 and is illustrated in Plate 9.21.

Females stood quietly or lay down for 1-2 minutes after copulation and thereafter began some routine activity such as feeding or rumination. The male also continued with his routine activities after 1-2 minutes of either standing still or engaging in the post-copulatory behaviour previously described.

Lechwe post-copulatory behaviour was far less elaborate than that of the congeneric Uganda kob (Buechner & Schloeth. 1965). Also, sexual interactions culminating in copulation were far longer in lechwe than in Uganda kob. In kob the mean duration of an uninterrupted sequence of displays in 100 copulations was 5,6 minutes, with a range of 1-26 minutes (Buechner & Schloeth, op. cit.). In lechwe the mean duration of an uninterrupted sequence of displays in 15 copulations was 19,3 minutes, with a range of 1,5-73,4 minutes.

9.3.3

Maternal/Filial Behaviour

Only two opportunities arose for observation of more than fleeting interactions between females and neonates. On one occasion a female spent about 20 minutes grooming a neonate, particularly in the anal region, before leaving it resting on a termitarium situated in the water and surrounded by tall emergent vegetation. On the other occasion, the female waded out to a neonate lying on an eroded termitarium in fairly open water. The female approached cautiously and I only became aware of the neonate when it raised its head as the female approached. On the female's arrival the fawn almost immediately began to suckle and did so for 11,1 minutes. During this time the female groomed the fawn, again particularly in the anal region. The female allowed the fawn to nurse until it stopped of its own accord. Within a few minutes she left the termitarium and slowly made her way back to the mainland, constantly looking back at the fawn which had followed her from the termitarium.

On the mainland the fawn ran ahead of the female, which trotted after it for ca. 100 metres until the fawn stopped. The female again groomed the fawn's anal region for two minutes after which the fawn capered around the female and finally approached and made a mounting attempt against the female's hindquarters. Thereafter the female fed while the fawn rested, occasionally rising to feed briefly on grass. One hour after the first nursing bout the fawn tried three times to nurse, but the female rejected it each time. The female walked and fed for a further 20 minutes and then slowly led the fawn out to the termitarium in the water where she again groomed it for three minutes. After grooming, and 90 minutes after the first nursing bout, the fawn suckled again for six minutes, stopping of its own accord. After termination of nursing, the female again led the neonate back to the mainland. On reaching the mainland the fawn skipped and played in front of the female briefly, and then followed her as she slowly fed out of sight along the edge of the water. While following the neonate occasionally fed briefly on grass.

These limited observations indicate that, like the Defassa waterbuck (Spinage,1969), lechwe mothers may lead their young to hiding places and that hiding places may be changed. Observations on a number of solitary neonates, on small fawns and on one ear-tagged neonate, showed that fawns lie up alone for at least part of the day until they are about two months old.

The prone response (Lent,1974) was observed in three neonates. Two were lying together on a termitarium and fled when I approached to within a few feet of them. The third was alone on a termitarium and slid into the water as I approached and submerged its entire body except for the nostrils and a small part of the rump. While in this position it allowed me to approach within touching distance.

The prone response is an alarm response which wanes with the development of the flight response (Lent,1974). By this behaviour neonates can conceal themselves in fairly short grass or shallow depressions. The submerging behaviour observed in the lechwe neonate would enhance its ability to avoid predators. Neonates are usually hidden amongst dense emergent vegetation and if they submerged on hearing the approach of a predator this would diminish the predator's chances of locating them.

Two neonates caught for ear-tagging uttered loud distress bleats. Most lechwe in the vicinity appeared to pay little attention to these calls. In one case a solitary female, presumably the dam, approached shortly after the fawn called. She approached from the opposite side of a large termitarium and came to within about five metres of me before becoming aware of my presence. That this female responded to the fawn's calls while other lechwe ignored them is another fragment of evidence in support of the idea that there is acoustical individual recognition.

On only one occasion were a female and her fawn under observation for an entire day. On this occasion the fawn suckled twice with an interval of 10 hours between the two nursing bouts. This indicates a frequency of about twice a day for this animal's age class, which was 3-4 months. That a neonate suckled twice within 90 minutes, as described above, suggests that newborn fawns may nurse more frequently than twice a day.

One hundred and thirty four nursing bouts were observed. The time of suckling was noted and its duration timed with a stop watch. The mean duration of total nursing bout, including brief interruptions, was 9,7 minutes for fawns less than three months old and 10,8 minutes for fawns 3-7 months old. This difference was not statistically significant but nursing bouts in the Kwando population were appreciably longer than the five minutes noted by Lent (1969) in the Okavango population.

Nursing interactions were fairly evenly spread through the day. Twenty six percent occurred from 06h00-09h00, 29% from 09h00-12h00, 16% from 12h00-15h00 and 29% from 15h00-18h00. This finding differs from those of Leuthold (1967) and Lent (1969) who found early morning and evening peaks of nursing in Uganda kob and lechwe.

Fawns usually approached from the side and nursed in a reverse parallel orientation (Plate 9.23). Larger fawns commonly nursed on their carpal joints and bunting (Lent, 1974) was often observed.

Females usually allowed small fawns to nurse until they stopped of their own accord. As fawns grew larger there was in increasing tendency for the dam to terminate nursing. Females occasionally lay down to prevent further nursing but usually simply walked or trotted away from the fawn.

Fawns of less than three months were occasionally seen lying together during the day and groups made up exclusively of fawns, although not common, were regularly seen (Table 9.5). Small fawns tended to follow their dams rather closely but increasing independence was noted in fawns of six months or older.

Weaning probably occurs at 6-8 months (section 6.3.2.6) as in Defassa waterbuck (Spinage, 1969). In males, the bond with the female may be severed when the fawn is evicted from a female group by a territorial male. On 11 occasions subadult females were seen associating with a female and a small fawn (Plate 9.24). This indicates that the bond between a mother and her female offspring persists into the latter's second year of life.

9.3.4
Play

It was difficult to distinguish play fighting from other horn contacts and I therefore treated all interactions which involved only horn contacts i.e. which did not involve running plays, as agonistic encounters.

Running plays were observed on only 17 occasions in over two years. Play consisted mostly of running, high leaps, kicking up of hind legs and chasing. Chases ended in head butting on five occasions. The mean length of play bouts was 1,7 minutes, the range being 0,5-5,5 minutes.

Adults were seen to play on only two occasions. Both of these involved adult females joining in play initiated by juveniles. Adult males were never seen to play.

9.3.5
Territoriality

The purpose of this section is to describe the patterns of behaviour from which territoriality was inferred. Noble's (1939) description of a territory as"any defended area" has been widely accepted but a number of workers (e.g. Walther, 1972 a&b; Floody & Arnold,1975; Owen-Smith, 1977) have more recently characterized territoriality as a form of spatially localized dominance. My discussion of lechwe territoriality is based on this latter characterization because it affords a clearer insight into the operation of lechwe territoriality than the simple notion of a defended area.

Various criteria have been suggested for the recognition of territorial behaviour. Those criteria which were clearly met by lechwe on the Kwando are discussed below.

Plate 9.23: Fawn of about three months old nursing. This is the same known female (note her right ear) which appears in Plate 9.20.

Plate 9.24: Adult female with small fawn and subadult female. The group spent several hours near the hide before leaving the area of the hide, still together.

9.23

9.24

9.3.5.1

Limitation of movements (Owen-Smith, 1977)
As in impala (Leuthold, 1970) and Thomson's gazelle (Walther, 1972c) territorial males were individually recognizable on the basis of horn shape, distinctive pelage and various scars or markings. At various times 10 territorial males were individually recognized. These males at different times showed unmistakable attachment to circumscribed areas 2-3 hectares in extent. They were frequently seen alone in their respective areas and their movements around the intensive study area were far less extensive than those of the few known individuals in the bachelor groups. Two related case histories will be used to illustrate these points.

The longest studied male (KE) was first recognized in April 1975. Between April 1975 and December 1976, KE was found either on or near his territory nearly every time I visited the intensive study area. He disappeared a few times for periods of one or two days but soon reappeared on the territory.

During January 1977 another male (NH) took over the most important part of KE's territory. From January to April 1977 observations were made in the intensive study area virtually every day and NH was invarialby present on the territory taken over from KE. KE was present on the periphery of the territorial ground and was regularly, although not invariably, found in the same place.

9.3.5.2

Dominance/intolerance towards conspecifics of the same sex within territorial boundaries (Walther, 1972b; Owen-Smith, 1977)
Territorial males frequently exerted dominance (in dominance rituals) or exhibited intolerance (by chasing or threatening) towards males of all ages entering their territories. Challenges and pursuits were particularly common when intruding males paid attention to females within the territory.

There were clear changes in the behaviour and status of territorial males which were outside their territories. They were less aggressive towards other males and were submissive towards and fled from other territorial males through whose territories they were passing.

9.3.5.3

Elevated flight threshold within territorial boundaries (Walther, 1972b)
On many occasions I approached lechwe on foot or in a vehicle and from these encounters it was clear that territorial males had much the shortest flight distance of any class of lechwe. This was obvious also from observed encounters between lechwe and predators. For example, one morning an hyena walked through the territorial area. Females fled when the hyena was 200-300 metres away while a territorial male did not flee at all and allowed the hyena to pass within 100 metres of it.

9.3.5.4

Herding/blocking of females attempting to leave territories (Walther, 1972b; Owen-Smith, 1977)
Males frequently pursued, herded or blocked females attempting to leave their territories. This behaviour was most prevalent when courtship proceeded beyond a perfunctory investigation but sometimes occurred without any courtship taking place. For example, on one occasion a territorial male blocked the exit of two juveniles from his area for over 10 minutes although no investigation or interaction had occurred.

9.3.5.5

Sudden halting by occupier at territorial boundary (Walther, 1972b)
Territorial males engaged in chasing conspecifics usually stopped these chases abruptly at their territorial boundaries, particularly if the animal being pursued fled into a neighbouring territory whose occupant was waiting at the boundary. Chasing reversals in pursuits involving territorial neighbours were observed on a number of occasions. These incidents clearly illustrated mutual recognition of boundaries by territorial neighbours.

9.3.5.6

Self-advertisement (Owen-Smith, 1977)
Hediger(1949) distinguished between optical, acoustical, olfactory and combined methods of territorial marking. The presence of territorial males in their territories and the use of the erected posture served as forms of optical advertisement or marking. Territorial males often vocalized when intruders entered their territories, or when their neighbours vocalized. Combined optical-acoustical displays were also used for territorial advertisement. No clear evidence of olfactory marking was found.

9.3.5.7

Competition for specific areas (Leuthold, 1966)

Leuthold (op. cit.) considered that competition between males over a specific area of ground was confirmation of its nature as a "true territory". A total of seven territorial interchanges were observed. No territory was seen to change ownership as a result of ritualized dominance and submission interactions. Intense fights were involved on each occasion.

The length of time needed for the takeover varied from a few days to several months. A case history will be used to illustrate the process of changeover.

Between 1.12.1975 and 24.1.1976 KE was seen to be involved regularly in agonistic encounters at his boundaries with a non-territorial male, BN. On 24.1.1976 KE embarked on a vigorous and protracted chase of BN and no further interactions between these two animals were seen until October 1976.

On 8.10.1976 KE and BN were again engaged in an agonistic encounter on KE's boundary. Encounters of varying intensity occurred intermittently until I left the study area in the latter half of December 1976. On my return in mid-January, it seemed that a third male.NH, had become involved in the dispute as several ambiguous interactions involving all three males were seen. Finally, on 19.1.1977, BN chased KE out of the area and took over part of KE's territory while NH took over the larger and more important part.

BN interacted with KE over at least a five-month period (over a year including the period in which no interactions between the two were seen) before evicting KE. By contrast, a different male, N_3, evicted another territory holder, CM_1, after only two days of intermittent fighting.

9.3.6

Relations within and between sex, age and social classes

The purpose of this section is to provide a brief description of the nature and frequency of interactions within and between different sex, age and social classes.

Table 9.4 gives an indication of the frequency with which classes interacted

TABLE 9.4: THE FREQUENCY WITH WHICH DIFFERENT AGE CLASSES INTERACTED WITH THEIR OWN AND OTHER CLASSES (N = the number of interactions in which each class was involved; percentages sum horizontally.)

Class	TM	ABM	AF	SABM	J
TM N=618	6,0%	4,9%	81,1%	6,0%	2,1%
ABM N=124	0,8%	17,7%	61,3%	19,4%	0,8%
AF N=76	9,2%	34,2%	22,3%	7,9%	26,3%
SABM N=94	3,2%	9,6%	24,5%	51,1%	11,7%
J N=61	-	1,6%	32,8%	23,0%	42,6%

TABLE 9.5: THE FREQUENCY WITH WHICH DIFFERENT TYPES OF GROUP WERE SIGHTED

Group type	Number of sightings	% of all groups sighted
Mixed sex/age	870	26,9
Adult male	798	24,7
Adult female	564	17,5
Mixed male	449	13,9
Female/juvenile	411	12,7
Juvenile	138	4,3

with each other. In constructing this table data were taken from continuous observations of individuals in each class (about 100 hours for each class except territorial males, for which over 300 hours were accumulated). Observations were not pooled, so that if a territorial male interacted with a juvenile while the male was under observation this interaction was not included in the total for juveniles. The purpose of analysing the data in this way was to avoid the bias created by the disproportionate sampling of territorial males. The existence of a bias was established when pooled data were analysed and all classes were found to interact with territorial males with disporportionate frequency.

Table 9.4 includes all types of interaction. In this respect it differs from Grau & Walther's (1976) TableIII, which relates only to agonistic interactions. It is interesting that despite this difference immature animals show the tendency to interact most with members of their own class that was noted in mountain gazelle with respect to agonistic encounters. The disappearance of this tendency in older animals reflects increased reproductive activity in older animals.

9.3.6.1

Interactions between males

All interactions between territorial males were agonistic. The frequency with which various patterns of agonistic behaviour occurred in interactions between territorial males was given in Table 9.3 (section 9.3.1.3). Approximately 24% of these interactions occurred at the boundaries of neighbouring territories. The frequency with which boundary clashes occurred between two territorial neighbours varied from a maximum of about five per day to a minimum of one or two over a period of weeks.

Other interactions between territorial males resulted from incursions by one male into the other's territory, or in pursuit of a female.

Interactions between territorial males and bachelor males were also agonistic. Territorial males tended not to fight with subordinate males but had frequent dominance encounters with them (Table 9.3). Walther (1978b) found a similar interaction pattern between dominant and subordinate males in the Serengeti oryx (Oryx beisa) population.

Interactions between juvenile and adult (territorial and bachelor) males were rare. The following types of interaction occurred:

Juvenile male approaches and sniffs at adult male (seven times); adult male threatens juvenile male(twice); dominance encounter (four times); adult male chases juvenile male (29 times).

Most interactions between immature (subadult and juvenile) males were low intensity agonistic encounters. Both mounting (three times) and body attacks (five times) occurred occasionally in encounters between immature males. Neither of these patterns was seen in encounters between adult males.

9.3.6.2

Interactions between males and females

Interactions between adult males (territorial and bachelor males are pooled because initially no distinction was made between them) and adult females (n=954) were usually sexual. Testing by males, flehmen, laufschlag and mounting were extremely common in these interactions. The frequency of less common interaction patterns is given below:

overt aggression (horn thrusts) by male: 2,8%;
pursuit by male: 11,1%;
blocking of female by male: 2,6%;
blocking with head low: 0,4%;
lip licking/smacking by male: 3,9%;
male stands with head under female's belly: 1,3%;
chinning (Fraser,1968) by male: 0,3%;
headflick with head-low-extended-neck by female in flight: 0,3% .

Subadult males interacted less frequently with adult females (n=115) and most of these interactions were brief sexual encounters. In the course of these interactions, overt aggression by the male occurred twice; lip licking by the male occurred three times; pursuit by the male occurred eight times.

On one occasion a territorial male blocked two juvenile females that were trying to leave his territory. On another occasion a territorial male tested a juvenile female.

On six occasions (15,4% of interactions) subadult males made ano-genital olfactory investigations of juvenile females.

Seventeen sexual interactions between male and female juveniles occurred. Behaviour patterns observed included:

ano-genital sniffing (five times);
laufschlag (twice);
lip licking (once);
mounting (six times).

9.3.6.3

Interactions between females

Interactions between females were rare (n=46). Behaviour patterns observed included:

naso-nasal contact (twice);
supplanting of one female by another (eight times);
head butting (three times);
body attacks (four times);
laufschlag (twice);
mounting of one female by another (19 times).

Mounting among oestrous females was found to be common in Uganda kob (Buechner & Schloeth, 1965) and in my opinion the mounting observed among lechwe females was largely oestrous behaviour. Aggression may have been involved in these interactions but it was never clear.

The low interaction rate between adult females is consistent with Geist's (1974) principle that females will strive to reduce the high energy costs of excitement and physical work since these detract from the resources available for reproduction.

9.3.6.4

Interactions between females and juveniles

Many (60,4%) female:juvenile interactions were related to nursing. On 19 occasions (8,5% of interactions) fawns mounted their mothers. This usually occurred after the female had terminated a nursing bout and in these cases may have been aggressively motivated (Walther, 1964b). On a few occasions no interaction had occurred before the mounting and the motivation was unclear. On nine occasions (4,1% of interactions) juvenile males mounted females that were not their mothers and these interactions were clearly sexual. Laufschlag was observed in four of these sexual interactions and chinning was noted on three occasions.

The frequency with which other types of interaction between females and juveniles occurred is listed below:

naso-nasal contact: 2,7%;
juvenile sniffs female: 3,6%;
female sniffs juvenile: 0,9%;
female grooms juvenile: 5,4%;
female butts juvenile (body attack): 3,2%;
head-pushing/butting: 0,9%;
play: 0,9%;
female follows juvenile: 1,8%.

9.4

SOCIAL ORGANIZATION

9.4.1

Social Groups

In all situations other than fighting, mating and nursing, spacing was maintained between individuals. No quantitative observations of spacing were carried out but there were obvious differences in the individual distances maintained by the various sex/age classes. Distances were smallest between females and young and between juveniles and were largest between adult males. It was also my impression that individual distance varied with activity. It was small when animals were lying down or moving in a group but increased when animals were feeding. These findings are very similar to those of Walther (1977) with respect to distances between Thomson's gazelle and indicate that similar causal factors may be acting in the spacing behaviour of lechwe and Thomson's gazelle.

In discussing grouping behaviour it is necessary to define what is meant by "group" because this is not always easily recognizable in the field. Leuthold (1977) stated: "In the field, it is often impossible to distinguis between aggregations and social units, and between open and closed groupings, without prolonged observations and means of recognizing many different individual animals."

No distinction was made between aggregations and social units because very few animals were individually recognizable. Any aggregation of animals whose members were not more than about 100 metres apart and were moving or behaving in a co-ordinated way was treated as a group. Where it was difficult to decide whether or not animals were in the same group, the activity, sex and age of the doubtful animals were taken into account. Thus if, for example, a number of females and young were lying together and a number of adult males were feeding in their vicinity, so that some males were 50 metres while others were 250 metres from the females and young, two separate groups were recognized.

Most groups gave the impression of being open and unstable and lechwe groups have usually been characterized as open and extremely fluid (e.g. De Vos& Dowsett, 1966; Child & Von Richter, 1969; Biggs, 1979). The only indication of a stable grouping was the sighting, mentioned earlier, of family groups comprised of an adult female with a young fawn and a subadult female.

9.4.1.1

Group types

Six different types of group could be easily and regularly recognized in the field. These were:

groups composed of mixed sex and age classes;
adult male groups;
groups of apparently adult females;
male groups of mixed age classes;
groups of females with juveniles;
juvenile groups.

Data on group composition and size were collected manily during the course of work on habitat use in the intensive study area. In the course of this work the composition and size of groups were recorded whenever possible.

Table 9.5* shows the frequency of sighting of the different types of group. These frequencies give no indication of population structure, because the behaviour of different classes renders them more or less conspicuous. For example, territorial males are far more conspicuous than neonates. The purpose of Table 9.5 is to show that a reasonably large sample of groups was observed.

* page 277.

9.4.1.2

Group size

Single animals are included in the analysis of group size because their occurrence reflects a tendency to isolation that is relevant in understanding lechwe social organization.

The analysis of group size is based on the use of frequency distributions. These have two advantages over the use of measures such as mean or typical (Jarman, 1974) group size. Firstly, they are less affected by the occurrence of exceptional values. For example, in the cool,dry season 1975 about 240 groups were counted, of which all had less than 120 members except one which had about 250 members. If this one group was excluded from the calculation of typical group size this changed from 50,6 to 32,3 - a difference of 38,1%. By contrast,one group comprised 0,4% of the sample and this makes very little difference to the picture of group size that is presented by a frequency distribution.

The second advantage is that there is a simple test for differences between frequency distributions, the Kolmogorov-Smirnov two-sample test (Siegel, 1956), which "is sensitive to any kind of difference in the distributions from which the two samples were drawn - differences in location (central tendency), in dispersion, in skewness etc." (Siegel, op. cit.). By contrast both mean and typical group size are purely measures of central tendency and there is apparently no realistic way of testing differences in typical group size (Underwood, 1978).

Table 9.6 gives frequency distributions for the different types of group and for all groups combined. Two groups of about 250 (0,06% of the groups counted) were excluded from this analysis because they did not affect the statistical significance of differences between frequency distributions and they would have made the frequency distributions excessively unwieldy.

I looked for two types of difference in group size - differences in the sizes of the different types of group and seasonal differences.

Table 9.6 shows marked differences in the frequency distributions of different types of group and Table 9.7 shows the significance of these differences. There is an obvious tendency for groups of mixed composition to be larger than peer groups. As in Grant's gazelle (Walther, 1972a) mixed sex/age groups were largest, 29,8% of these having more than 30

TABLE 9.6: FREQUENCY DISTRIBUTIONS (% frequency) FOR DIFFERENT TYPES OF GROUP AND ALL GROUPS COMBINED

Type / Size	Mixed sex/age	Adult male	Adult female	Mixed male	Female/ juvenile	Juvenile	Combine
1-5	23,6	91,0	95,2	32,7	46,5	77,5	59,2
6-10	15,8	7,6	4,3	16,9	29,0	10,9	13,4
11-15	10,5	1,3	0,5	12,5	10,7	4,4	6,5
16-20	9,0	0,1		6,2	6,3	5,1	4,3
21-25	5,3			6,5	2,0	0,7	2,6
26-30	6,1			7,1	2,0	0,7	2,9
31-35	3,6			3,1	1,5	0,7	1,6
36-40	5,1			4,0	1,2		2,1
41-45	2,4			3,3	0.7		1,2
46-50	4,0			3,3	0.2		1,8
51-55	1,8			1,1			0,7
56-60	2,2			0,2			0,7
61-65	0,9			0,2			0,3
66-70	2,2			1,1			0,7
71-75	0,7						0,3
76-80	1,5						0,4
81-85	0,3						0,1
86-90	0,6						0,2
91-95	0,6						0,2
96-100	1,8			1,1			0,5
101-105	0,2						0,1
106-110	0,6						0,2
111-115	0,2						0,1
116-120	0,3						0,1

TABLE 9.7: THE SIGNIFICANCE OF DIFFERENCES IN THE FREQUENCY DISTRIBUTIONS OF DIFFERENT TYPES OF GROUP

Group	Mixed sex/age	Adult male	Adult female	Mixed male	Female/ juvenile	Juvenile
Mixed sex/age						
Adult male	xxx					
Adult female	xxx	NS				
Mixed male	NS	xxx	xxx			
Female/ juvenile	xxx	xxx	xxx	xxx		
Juvenile	xxx	x	xx	xxx	xxx	

NS : not significant

x $p < 0,05$

xx $p < 0,01$

xxx $p < 0.001$

members.

About 64% of adult male sightings were of solitary animals but only 5,6% of subadult male sightings were of solitary animals. Thus there was a clear change in male gregariousness with age, no doubt associated with territoriality. This situation is again similar to that found in Grant's gazelle (Walther, op. cit.).

Approximately 46% of female sightings were of solitary animals. Many of these sightings were of animals feeding in the water. Their solitude may well have been a result of the reluctance of fawns and immature animals, likely companions, to enter the water.

It is difficult to reconcile such obvious intraspecific differences in group size with Jarman's (1974) arguments relating to the determination of group size. If group size is determined largely by a species' feeding style and its behaviour towards predators, why are there such enormous intraspecific differences in group size ? A possible shortcoming of Jarman's (op.cit.) explanation of group size is that he does not distinguish clearly between the immediate causes and the evolutionary advantages of group formation. It is suggested that the immediate causes of group formation are the types of factor, no less than 16, to which Walther (1972a) attributes an influence on social grouping and the composition and size of groups in Grant's gazelle. These include, for example, the attraction which different classes of animal exert on other animals, the circumstances in which animals are attracted to conspecifics and the situations in which animals seek isolation. It seems likely that these factors would exert varying forces of attraction on animals in different sex/age and social classes and in differing circumstances, so that the determination of group size is probably much more complex than indicated by Jarman (1974). His arguments appear to relate mainly to the evolutionary advantages of group formation.

Seasonal differences in group size were investigated in three ways. Firstly, for each season mean and typical group size (for all groups combined) were calculated. Mean group size varied from 9,4 – 15,2 but showed no consistent seasonal trends. Typical group size varied from 33,7 – 56,4 but also showed no consistent seasonal trends.

Secondly, frequency distributions of group size (all groups combined) in each season were compared. The distribution for the cool, dry season of 1975 differed significantly from those of all other seasons ($p < 0,05$ in all cases) but there were no other significant differences. During the cool, dry season of 1975 there were fewer small groups (1-5 members) than in other seasons. Water levels in the entire study area rose in June 1975 and remained relatively high for the remainder of the study. It seems possible that the rise in water level caused a concentration of the population in the cool, dry season of 1975 which was followed, as has been observed in other areas (Grimsdell & Bell, 1975; Biggs, 1979), by fragmentation and dispersal into alternative areas.

Thirdly, within each type of group frequency distributions of group size in different seasons were compared. For this exercise it was necessary to pool data from two years because of the small sample sizes for some groups in some seasons. Seasonal differences were found only in adult male and mixed male groups. There were significantly fewer small adult male groups (1-5 members) during the cool, dry season than during the rains ($p < 0,05$). This is almost certainly a reflection of the abatement of territoriality during the cool, dry season. In both the cool and hot dry seasons there were significantly fewer small mixed male groups than during the rains ($p < 0,05$ in both cases). This was probably related to sustained high water levels during the dry season (Figure 2.2) which cause flooding in the peripheral floodplain areas used by bachelors. In other words it was probably a concentration effect.

9.4.2

The Functioning of Territoriality

9.4.2.1

Location, arrangement and size of territories

Plate 9.1 shows the location of the territories of known males in the intensive study area and illustrates the characteristic situation of territorial grounds on the Kwando. Territories were situated in the short-grass areas adjoining water (zone 3, Chapter 2). Statistical evidence from the intensive study area indicated that these areas were heavily favoured by females. The expected number of sightings of females in zone 3 was 637 while the observed number was 1529 (Chi-squared with Yates correction = 183,260).

Detailed study of territoriality was conducted only in the intensive study area but three similar localities were found in the general study area. Limited observations in these areas suggested that similar territorial grounds were functioning in these places. In addition to the territorial grounds there were a number of small areas along the edge of the swamp which appeared to be functioning as single territories.

In the intensive study area territories were strung out along the edge of the water in a narrow band of favourable habitat. This band of habitat had a total area of approximately 1,4 km^2. There were only two places in which small clusters (three and four respectively) of territories occurred.

The size of territories was estimated by noting where boundary conflicts occurred and thus building up a picture of the extent and shape of each territory. Not all boundaries could be discerned with equal clarity because interaction rates along boundaries varied and some boundaries were in the water.

Each territory was approximately classified in terms of geometrical shape; they were all more or less circular or rectangular;the necessary measurements, radius or length and breadth, were paced out on the ground and the areas were calculated with the appropriate formulae.

There was both spatial and temporal variation in territory size. Most territories were 2-4 hectares in extent but two on the eastern side of the intensive study area were each approximately 5-6 hectares. One territory near the northern hide (Plate 9.1) was about two hectares for most of the study, but for a period of two weeks in March 1977 it was subdivided into three smaller territories, one of about one hectare and two of about 0,5 hectare.

The territories near the northern hide were very close to it and could be monitored in some detail. It was thus possible to document changes in the areas of these territories. At the end of February 1977 heavy rains fell in the study area and the water levels in the entire area rose appreciably. There was an obvious movement by two territorial males (NH and N_3) from the area south of the hide to the areas surrounding and to the north of the hide. NH by moving increased the area of his territory from ca. two hectares to ca. six hectares. This movement occurred after the rise in water level and coincided with increased use of areas north of the hide by females. This shift of territories in response to changed water levels may well have been a small-scale version of the shifts in location of leks on the Kafue Flats (Schuster, 1977).

9.4.2.2

Behaviour of different sex/age and social classes in relation to territories

In certain species, for example the common reedbuck (Jungius, 1971), females confine themselves within individual territories. This was not the case with lechwe on the Kwando. Females ranged freely from one territory to another, inhibited only by courtship and herding by territorial males.

Bachelor males had a tendency to avoid territorial areas (Chapter 4) but they regularly passed through territories and usually spent all night along the edge of the water in a territory. They were generally submissive to territorial males, the exceptions being those cases in which a contest for a territory was in progress.

Territory holders passing through territories of other males were submissive when approached by the holder and usually fled as he approached. Few interactions between territorial males off their territories and bachelor males were observed, but in all cases territorial males retained and asserted dominance.

Territorial males evicted from their territories joined bachelor groups, as observed in Uganda kob (Leuthold, 1966), tsessebe (Joubert, 1972) and in topi (*Damaliscus korrigum*) "herdmaster bulls" that had lost their females (Jewell, 1972).

9.4.2.3

Seasonal variation in breeding activity

In Chapter 6 evidence was presented which showed that there were seasonal peaks in conceptions. These occurred during the rains. Table 9.8 shows seasonal variation in the frequency and duration of interactions between territorial males and adult females. In both 1975 (Chi-squared =5,33, $p<0,05$) and 1976 (Chi-squared =7,23, $p<0,05$) the frequency of interactions was significantly higher during the hot dry season than it was during the cool, dry season.

TABLE 9.8: SEASONAL VARIATION IN THE FREQUENCY AND DURATION OF INTERACTIONS BETWEEN TERRITORIAL MALES AND ADULT FEMALES

(C.L. = confidence limits)

Season	No. TM:AF interactions per day	Mean duration of male:female interactions (minutes)	95% C.L. (minutes)
Cool dry 1975	7	1,0	0.8 - 1,2
Hot dry 1975	20	2,5	1,9 - 3,1
Rains 1975/1976	16	2,6	2,1 - 3,1
Cool dry 1976	11	1,9	1,5 - 2,3
Hot dry 1976	29	3,6	3,0 - 4,2
Rains 1976/1977	23	2,5	1,6 - 3,4

Although the frequency of interactions was greatest during the hot, dry season, there were relatively few observed copulations in this season, one in November 1975 and three in October 1976. All other observed copulations occurred during the rains. Seasonal variation in the frequency of observed copulations was as follows: none in the cool,dry season; four in the hot,dry season and 17 (81% of the total observed) during the rains. These results are consistent with a peak of conceptions during the rains.

9.4.2.4

Quality of territories

Several kinds of evidence indicated that territories were not of equal quality in the intensive study area.

The amount of time spent away from territories varied from 0% to 80-90% of the day. Some males left their territories each day to feed in areas removed from the breeding ground. Other males spent most of their time on their territories. For example, KE and NH were males that occupied the same territory consecutively and both spent very little time away from the territory while controlling it.

Inspection on the ground of the various territories revealed very clear differences between territories in the proportion of bare ground and open water and in the quality of the grazing. There appeared to be a direct correlation between the amount of time spent off the territory and the amount of grazing available within the territory. Animals occupying territories with limited food resources spent most time away from their territories feeding elsewhere.

There were no territories in which females were present all the time, but females clearly favoured some territories more than others. During March 1977 the territories in the vicinity of the northern hide were monitored over a period of four days and the presence of females in each territory was checked at hourly intervals. Over this period females were present in the most favoured territories for 60-80% of the time but were present for less than 10% of the time in the least favoured territories. Females appeared to be favouring those territories with the best grazing and the most favourable resting sites.

At any one time there were 15-20 males occupying territories in the intensive study area, yet 15 copulations (71% of all those observed) occurred in the same territory. This was the territory occupied successively by the known males KE and NH. The territory changed shape when it changed ownership but the same central area was favoured in terms of food resources and presence of females.

There may have been some observational bias due to the fact that this territory was close to the northern hide but males occupying other territories closer to this hide were as closely watched and were never seen to copulate. Also, although 10-12 territories were regularly monitored, copulations were observed on only four territories in two years. There can thus be little doubt that reproductive success among territorial males is very uneven. In this respect Kwando lechwe resemble Kafue lechwe (Schuster, 1977) and Uganda kob (Leuthold, 1966).

Using data collected between 1.10.1976 and 30.4.1977 I calculated Owen-Smith's (1977) Potential Mating Enhancement Factor (PMEF) for territorial males and found that the PMEF for this one season may have been as high as 14. This compares with a range of 4-8 times suggested by Owen-Smith (op. cit.) and indicates that territoriality may have greater cost/benefit advantages over other systems than envisaged by Owen-Smith.

9.4.2.5

Duration of territorial occupation

Observed periods of occupation by known males ranged from 20 months (KE) to a few weeks. NH, the male that took over KE's territory, occupied the area for 75 days before being evicted and rejoining the bachelor herd. This was probably the mean duration of territorial occupation.

The territorial ground on which most observations were made was occupied and active from January 1975 to March 1979. During September/October 1979, when water levels were considerably lower than during the main study period, there were as many as 15 apparently territorial males in the area but no females were on the territorial ground. They had all moved further into the swamp.

During September/October 1979 territorial males were apparently in Walther's (1972b) final phase of territoriality. When a bachelor entered a territory the holder dominated it but did not chase it and bachelors seemed to remain in territories until they left of their own accord. The intensity of territorial behaviour was obviously declining and it seemed that males would have to move if they were to participate in breeding.

9.4.2.6

Differences in the expression of territoriality in the Kwando and Kafue lechwe populations

Table 9.9 summarizes the most obvious differences in the expression of territoriality in the Kafue and Kwando populations. Table 9.10 lists important ecological and demographic differences between the two populations Figure 9.1 illustrates a simple model, described below, of the way in which ecological and demographic factors may interact to determine the form of territoriality i.e. the mating system in each population.

Soil fertility determines the primary productivity of the floodplain. The lateral distance of flooding determines the extent of the floodplain. The timing of flooding influences the seasonal accessibility of higher quality pasture on the lower, wetter parts of the floodplain. On the Kafue Flats these factors interact to produce a broad expense of productive floodplain on which high quality grazing becomes available as flood waters recede during the dry season. On the Kwando edge of the Linyanti Swamp the interaction of these factors has produced a narrow, less productive floodplain, subject to two high floods per year, the second of which arrives from the Angolan Highlands in mid-winter and reduces the accessibility of higher quality pastures for much of the dry season. These differences in the extent and productivity of the floodplain and in the dry season food supply probably explain the marked differences in the size and density of the two populations and they may also explain the differences in the prevailing mating systems.

The difference in population density explains the difference in territory size - higher densities result in more competition and increased energy expenditure per unit area for territorial defence (Clutton-Brock & Harvey, 1978). This difference may also explain the fact that the Kafue lechwe exhibit lekking in the same way as the Uganda kob (Buechner, 1961b; Buechner & Roth, 1974) while Kwando lechwe exhibit a form of territoriality that is similar to the system of "single territories" (Leuthold, 1966) in Uganda kob.

An alternative explanation for the occurrence of lekking in one population but not the other is that the mating system is determined by the distributic of resources. Emlen & Oring (1977) argue that lekking occurs where individual males are unable economically to control or monopolize the resources essential for female acquisition. The differences in the breadth of the Kwando and Kafue floodplains and in the mating systems

TABLE 9.9: DIFFERENCES IN THE EXPRESSION OF TERRITORIALITY IN THE KAFUE AND KWANDO LECHWE POPULATIONS

FEATURE	KAFUE	KWANDO
Duration of lek/TG* occupation and use	1 - 2 months each year	Year round
Number territorial males per lek/TG	50 - 175	15 - 20
Territory size	0,03 - 0,2 ha	0,5 - 6,0 ha
Approx. number agonistic interactions per male per hour	1 - 3 (up to 30)	0,3 - 0,5
Amount of time spent feeding by territorial males	"minimal"	Up to 50% of daylight hours
Length of time territories held by males	"not long"	Up to 20 months

* Territorial ground

TABLE 9.10: ECOLOGICAL AND DEMOGRAPHIC DIFFERENCES BETWEEN THE KAFUE AND KWANDO LECHWE POPULATIONS

FEATURE	KAFUE	KWANDO
Soil fertility	Relatively high	Relatively low
Fluctuation in water level	5 - 7 metres	0,1 metre
Lateral spread of flood waters	10 - 25 km	Less than 1 km
Timing of high floods	April/May	February/March and June/July
Population movement pattern	Migratory	Sedentary
Population size	ca. 100 000	ca. 15 000
Overall population density	60 - 90 km^{-2}	7 - 12 km^{-2}
Lek/TG* density	500 km^{-2}	70 - 90 km^{-2}

* territorial ground

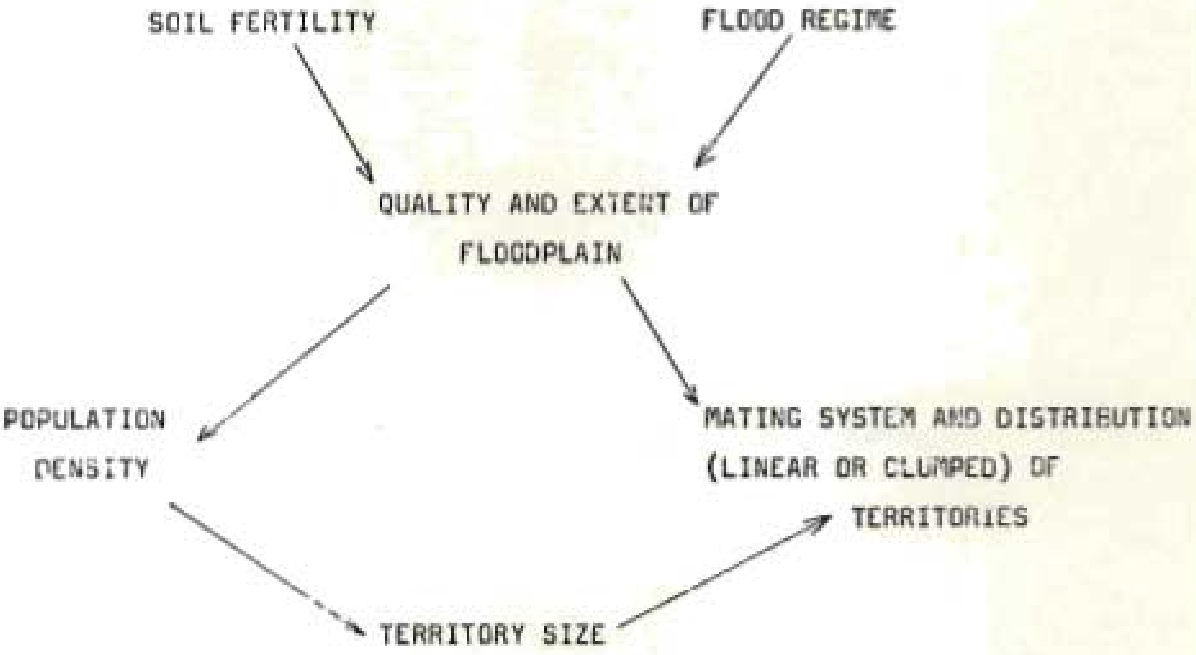


Figure 9.1: A simple model of the way in which ecological and demographic factors may interact to determine mating system and distribution of territories.

of the two populations are compatible with this argument. On the Kafue Flats resources are too widely and evenly dispersed to allow monopolization while on the Kwando the narrowness of the band of favourable habitat allows control of resources.

The manner in which the location of leks is determined on the Kafue is not clear from the literature but on the Kwando it is obvious that males set up territories in the narrow ecotone (zone 3, Chapter 2) that is preferentially used by females. The size of these territories and the narrowness of the ecotone in general prevent the clumping of territories. These are mainly strung out along the water's edge, but occasionally clusters of 3-4 territories occur where either the territories are smaller or the ecotone is broader.

9.4.2.7

The incidence of breeding by non-territorial males

Lent (1969) and Schuster (1976) reported that non-territorial males copulated successfully in the Okavango and Kafue populations. This was never seen in the Kwando population. A likely explanation for this difference is that during my study the Kwando population was essentially sedentary while the other two populations were more mobile. Lent's observations on sexual behaviour were made during May, when Okavango water levels are rising rapidly (United Nations Development Programme, 1977) and lechwe are forced to move out of low-lying areas. On the Kafue breeding occurs while the population is migrating before rising flood waters (Schuster, 1976 and 1977).

The significance of the extent to which a population is sedentary or migratory is that "Since it is largely the presence of territorial males that creates typical social organization .... there may appear to be little organization in populations while they are mobile or migratory." (Jarman, 1974).

9.5

SUMMARY

The data on social behaviour and organization collected during this study may in some respects be untypical for lechwe because flood levels on the Kwando were far less variable than those in other systems supporting lechwe populations.

Lechwe used a variety of signals and displays as means of expression and/or communication. Thirteen visual, six vocal, two visual-auditory and four tactile signals or displays are described and discussed.

Evidence of individual recognition of one lechwe by another was found in two contexts.

Three types of agonistic encounter are described - those without physical contact, those with brief physical contact and those with continuous physical contact. It was found that the forms of aggression appearing in agonistic encounters varied with the age and status of the rivals.

The sexual behaviour of lechwe was typical of Reduncinae. Precopulatory, copulation and postcopulatory behaviour in lechwe are described.

Some data on maternal/filial behaviour and on play are presented.

Lechwe were found to be territorial. The evidence from which territoriality was inferred is reviewed in some detail.

The nature and frequency of interactions between different sex/age and social classes are described qualitatively and quantitatively.

Spacing behaviour in lechwe is briefly described and found to be similar to that in Thomson's gazelle.

Six different types of social group were recognized and variation in group size was analysed by means of frequency distributions. There were marked differences in the sizes of the different types of social group. It was suggested that the determination of group size is probably more complex than indicated by Jarman (1974).

Some seasonal differences in the size of male groups were found. These differences were probably related to seasonal variation in territorial behaviour and in the flood regime.

The functioning of territoriality is outlined. Aspects which are considered in some detail include:

the location, arrangement and size of territories;
the behaviour of different sex/age and social classes in relation to territories;
seasonal variation in breeding activity;
differences in the quality of territories;
the duration of territorial occupation;
differences in the expression of territoriality in the Kafue and Kwando lechwe populations;
the incidence of breeding by non-territorial males.

CHAPTER 10

POPULATION STATUS

10.1

INTRODUCTION

There were two main purposes in trying to assess the status of the Kwando lechwe population. Firstly, in the context of conservation, it was important to establish the trend of the population because of reports that it was declining rapidly (Child & Von Richter, 1969; Child, 1975; Sheppe & Haas, 1976). Secondly, in the context of management, it was desirable to determine the level of sustainable take-off from the population.

In the light of arguments advanced by Hanks (1979) it seemed important to consider more than simply the number of animals in the population when trying to assess its trend. I therefore attempted to assess the "condition" of the population in the sense used by Hanks (op. cit.).

Previous studies of lechwe populations are exhaustively reviewed by Grimsdell & Bell (1975) and their review will not be repeated here. Where necessary or relevant, references to previous studies are made in the discussion.

10.2

MATERIALS AND METHODS

10.2.1

Population Condition

Hanks (1979) argues that several factors need to be included in a description of the condition of a population. These include demographic vigor, behavioural attributes and habitat condition and trend. Behaviour (Chapters 4, 8 and 9) and habitat (Chapters 2 and 4) were considered earlier and little will be said about them in this chapter. It need only be noted that neither behavioural anomalies nor adverse habitat trends were identified in this study.

Different opinions have been expressed on the assessment of demographic vigor (Caughley, 1977; Hanks, 1979). Caughley (op. cit.) suggests that the exponential rate of increase "r_s" is an adequate measure of demographic vigor. I disagree with this suggestion both for the reasons given by Hanks (1979) and because in most field studies of large mammals, it is virtually impossible to measure "r_s" accurately, since it can only be calculated from a life-table.

A life-table portrays, in various ways, the temporal age distribution (or survival history) of a cohort i.e. a large group of animals born simultaneously. In order to construct a life-table it is, strictly speaking, necessary to follow the fate of a cohort for the life-span of the species. This is usually impossible for long-living mammals so what wildlife biologists tend to do is to describe the standing age distribution of the population (i.e. the number of animals, relative to the number of newborn – the newest cohort – in each age class or cohort) from either a shot sample or a collection of found skulls and to treat this standing age distribution of the population as if it were the temporal age distribution of a cohort. Now the standing age distribution of a population and the temporal age distribution of a cohort can only be the same if (a) all cohorts have been the same size for some time and (b) age-specific mortality has been constant for some time, i.e. the rate of increase has been zero (Caughley, 1977). Therefore when a life-table is constructed from the standing age distribution of a population it must be assumed that the rate of increase has been zero for some time. Thus, although life-tables constructed in this way may provide "a valid approximation to the mortality pattern" (Caughley & Birch, 1971) an estimate of "r_s" based on this type of life-table "has no relationship whatsoever to the true value of r_s" (Caughley & Birch, 1971). Given this latter conclusion it is obvious that "r_s" must usually have very little value as a measure of the demographic vigor of a large mammal population.

In view of the arguments advanced above, "r_s" was not used as an index of demographic vigor in this study and my assessment of population condition largely followed the recommendations of Hanks (1979). This assessment included consideration of the following:

the observed rate of increase in the population;
foetal development;
juvenile mortality;
physiological condition;
population models.

10.2.1.1

The observed rate of increase

Aerial census data were used to make two independent estimates of '$\bar{r}$' the observed rate of increase. Caughley's (1977) formula was used for these calculations. It is:

$$\bar{r} = \frac{Nt - (\Sigma N) \quad (\Sigma t) \quad /n}{t^2 - (\Sigma t)^2 \quad /n}$$

N = population estimate
t = the time unit, scaled so that the first equals one
n = the number of estimates

One estimate was made with data from the Kwando side of the swamp, the other with data from the Linyanti side. On the Kwando side a total count was undertaken because the area was small and the distribution of animals clumped. On the Linyanti side a transect about 55 kilometres long and two kilometres wide was flown. The purpose of flying this transect was to see whether lechwe density on the Linyanti side was similar to that on the Kwando side of the swamp.

All surveys flown were at a speed of approximately 160 kilometres per hour and a height of about 91 metres. All flights were made in a Maule Rocket fixed wing aircraft belonging to the Department of Wildlife, Botswana.

For flying west of the Kwando channel, 1:40 000 scale aerial photographs were used for navigation. The location and size of lechwe groups sighted were noted directly onto the photographs with a chinagraph pencil. For all other flying a 1:250 000 scale map was used for navigation and data recorded on data sheets.

10.2.1.2

Foetal development

An assessment of the "normality" of foetal development in the Kwando population was made by comparing peri-natal mass in different populations.

10.2.1.3

Juvenile mortality

Juvenile mortality was estimated in three different ways. Firstly, the method of Spinage (1968) and Buechner (1974) was used to estimate fawn mortality from an examination of the reproductive tracts and udders of non-pregnant or lactating females. The assumptions on which this method is based are that females that have given birth can be distinguished from those that have not and that the udders of females whose fawns have died can be distinguished from those whose fawns are alive. These are reasonable assumptions. A careful examination of a female's reproductive tract and udder usually indicates whether or not the animal has given birth. When a fawn dies the udder regresses rapidly and can soon be distinguished from that of an actively nursing female (Spinage, 1968). This method gives an indication of fawn mortality during the period of lactation, which is six to seven months in lechwe.

Secondly, the method of Grimsdell & Bell (1975) was used to estimate juvenile mortality from fawn to female ratios observed in the field. Taking into account the female mortality and fecundity, the expected number of fawns produced in a birth season is calculated and this is compared with the number observed in the field at the time of counting to give an estimate of juvenile mortality.

Thirdly, Attwell's (1977) method, also based on female to fawn ratios observed in the field, was used. The female to fawn ratio at two different times is compared, again taking female mortality into consideration, to give an estimate of fawn mortality in the period between the two counts.

10.2.1.4

Physiological condition

The physiological condition of the population was assessed by comparing the kidney fat index (Chapter 5) of Kwando females with that of females in the Kafue lechwe population.

10.2.1.5

Population models

Although life-tables constructed from shot samples taken over a relatively short period of time cannot be used to calculate a population's true rate of increase they may provide "a valid approximation to the mortality pattern" (Caughley & Birch, 1971). Also model life-tables can be used to investigate the influence of various factors on the population's rate of increase (Hanks & McIntosh, 1973).

To obtain some idea of mortality in adult lechwe an attempt was made to construct realistic model life-tables for female and male lechwe in the Kwando population. The model female life-table was also used to investigate the influence of juvenile mortality and the fecundity of young females on the population's rate of increase.

Four life-table symbols are employed in this chapter. They are:

"x": age at intervals of one year;
"1_x": the probability at birth of surviving to the exact age "x";
"d_x": the frequency of mortality, calculated as the difference between two consecutive values of "1_x";
"q_x": the mortality rate, the proportion of animals alive at age "x" that die before age "x + 1"; calculated as "d_x / 1_x".

The female life-table is combined with fecundity schedules involving "m_x", which is the mean number of female offspring born per female per year of age centred at "x". "m_x" values were obtained from the female shot sample. The female and male shot samples were used to form the 1_x series for life-tables. Because in a few instances older age classes contained more members than younger age classes, age frequencies were "smoothed" by grouping the frequencies in threes and attributing the mean of each group to the second age class. Because of sampling bias against animals under three years of age, the first four values (0, 1, 2, 3) of each series were filled by extrapolating backwards from the frequency of animals in age class 4 and assuming 10% mortality from one year onwards and a 60% mortality in the first year of life.

To investigate the influence of juvenile mortality on the population's rate of increase, "r_s" values were calculated from the model female life-table using different rates of juvenile mortality. To investigate the influence of the fecundity of young females on the population's rate of increase, "r_s" values were calculated using different "m_x" values for young females.

The population's differing rates of increase were calculated using the equation of Andrewartha & Birch (1954). By this method:

$$r_s = \frac{\log_e R_o}{T_c}$$

where T_c is the mean length of a generation (mean time from birth of parents to birth of offspring), and R_o is the number of times a population increases itself per generation.

$$T_c = \frac{\sum l_x \ m_x \ x}{\sum l_x \ m_x}$$

and $R_o = \sum l_x m_x$

10.2.2

Calculation of Harvesting Rate

Sustainable off-take was calculated from population size (section 10.3.1.1) and structure. Population structure was determined from a total of six ground counts of the population between January 1976 and September 1979.

In the course of these counts the area from the northern limit of the study area to the Savuti Channel was traversed in a four-wheel drive vehicle and on foot. Binoculars (8 x 56) were used to classify all lechwe located into the following groups:

(i) juveniles (less than one year old);
(ii) subadult males (1 - 4 years old);
(iii) females over one year old;
(iv) adult males (more than four years old).

The sustainable off-take was taken to be 10% of the number of animals in each sex/age class. This figure is regarded as a safe off-take (Cowan, 1974) and is well below the 20% or more regarded as sustainable by Mentis & Collinson (1971).

Caughley's (1977) more sophisticated approach to determining sustained off-take could not be used because it was impossible to calculate the variables in his equation with any degree of accuracy. These calculations are likely to be impractical in Botswana for the foreseeable future.

The use of a rule of thumb method for determining off-takes necessitated constant monitoring of the population. This aspect is considered further in Chapter 11 (Conservation and Management).

10.3
RESULTS AND DISCUSSION

10.3.1
Population Condition

10.3.1.1
Observed rate of increase

Between May 1975 and September 1979 seven aerial counts on the Kwando side and five on the Linyanti side of the swamp were completed. The results of two of the Kwando counts were discarded because of impaired visibility at the time of flying. In July 1975 visibility during an early morning survey was severely affected by reflections off the water because of the low sun angle. In September 1979 smoke from numerous fires in the region severely limited visibility.

For comparative purposes the counts on the Kwando and Linyanti flights were treated as total counts of subpopulations. On the Kwando side a mean of 1651 animals (95% confidence limits = ± 22,7% of the mean) were counted in five flights. The mean on the Linyanti side was 876 animals (95% confidence limits = ± 27,6% of the mean). Densities on the two sides were similar, a mean of 7,1 per square kilometre on the Kwando and 8,1 per square kilometre on the Linyanti side of the swamp.

"$\bar{r}$" was calculated for the Kwando from flights during March-May in 1975, 1977 and 1979. Flights from more of less the same time of the year were used because, although the standard deviation from the mean birth date (39 days) exceeded the 30 days prescribed by Caughley (1977) as being indicative of a birth pulse model, the population was judged to be closer to a birth pulse than a birth flow model. A two-year interval was used because this spanned most of the time during which the population was under observation. For the Kwando $\bar{r}$ = + 0,09. On the Linyanti side $\bar{r}$ was calculated from flights in 1975, 1976 and 1977, because no flight was made on this side during 1979. On this side $\bar{r}$ = -0,10.

There are several possible explanations for the differing apparent rates of increase from the Kwando and Linyanti flights. In the first place, although aerial survey techniques have developed considerably in recent years (Jolly, 1969; Bell _et al_.,1973; Norton-Griffiths, 1978) as a census method aerial counting is by no means refined, even under optimum conditions (Caughley, 1976; Grimsdell, 1978). Various sources of error and bias have been identified (Graham & Bell, 1969; Pennycuick & Western, 1972; Grimsdell & Bell, 1975) and it is possible that the differences in $\bar{r}$ simply reflect sampling error.

Another difference between the two estimates is that on the Kwando side there was a fairly discrete survey area in which animal movement was not great (Chapter 4). On the Linyanti side the area surveyed was a small part of a much larger area of swamp and I collected little information about movements on this side. It is therefore possible that the counts on this side were affected by movements of which I was not aware.

It may be thought that part of the difference in the estimates of $\bar{r}$ can be accounted for by the two-year interval between counts on the Kwando side. This is not the case. When a one-year interval is used, $\bar{r}$ on the Kwando side is + 0,11.

Of the two estimates of $\bar{r}$, I have more confidence in that from the Kwando side because nearly all ground work was done on that side, leading to a much greater familiarity with animal numbers and distribution. My impression from four years of acquaintance with the Kwando subpopulation is that it is not declining. On this basis and in view of the relative precision of the aerial counts (95% confidence limits = ± 22,7%), my conclusion is that the estimate of $\bar{r}$ on the Kwando side, although of unknown accuracy, can be taken as a valid indication that no drastic decline of the lechwe population in the Linyanti Swamp is occurring.

10.3.1.2

Foetal development

The only comparative data that were available were from the Kafue population The mean mass of 12 newborn Kafue lechwe (Grimsdell & Bell, 1975) was 6,5 kilograms. The mean mass of six near term Kwando foetuses was also 6,5 kilograms. This strongly suggests that foetal development in the Kwando population was within normal range.

10.3.1.3

Juvenile mortality

The method of Spinage (1968) and Buechner (1974), produced an estimate of juvenile mortality of 45% during the first six or seven months of life. This is the most reliable way of estimating juvenile mortality that was used during this study. Errors in determining mortality no doubt occur when this method is used but the sources of error are fewer and of smaller magnitude than those inherent in the other methods that were used to estimate juvenile mortality in the present study.

Grimsdell & Bell (1975) assume that most juvenile mortality occurs within the first three months of life. The only detailed study of which I am aware supports this assumption. Cook _et al_. (1971) found that in white-tailed deer (_Odocoileus virginianus_) fawns, of all mortality in the first 60 days of life, 93% occurred within the first 30 days and 7% in the second 30 days.

On the assumption that by seven months of age juvenile mortality is dropping off sharply, a figure of 60% mortality in the first year of life was assumed. This figure was used as the basis for the yearling "l_x" value in the life-table.

Estimates of juvenile mortality by other methods are set out in Table 10.1 and 10.2. Using Grimsdell and Bell's (1975) method, estimated mortality varies from 2,4 - 8,5% per month. Using Attwell's (1977) method estimated mortality varies from 5,4 - 8,8% per month.

Both methods assume that all individuals in the population are equally observable. This is almost certainly not the case (Downing _et al_., 1977). Both methods depend on an estimate of adult mortality. In this study this came from a life-table which was probably realistic but certainly not accurate. Both methods assume a birth pulse model for the population. The Kwando lechwe population showed a considerable spread in the timimg of births, which may well be a further source of error. It thus seems obvious that the estimates of juvenile mortality based on female:fawn ratios are subject to a large margin of error. These estimates are nevertheless of interest because where a shot sample is not possible, female:fawn ratios are one of the few available indices of juvenile mortality.

TABLE 10.1: JUVENILE MORTALITY ESTIMATED BY THE METHOD OF GRIMSDELL AND BELL (1975)

Month	Number of females	Number of juveniles	Estimated number of births	% mortality	Period (months) since median birth date
1.1976	680	343	380	9,7	4
8.1976	455	79	281	71,8	11
12.1976	582	261	321	17,4	3
4.1977	436	164	258	36,5	8
2.1979	309	101	176	42,6	5
9.1979	392	73	246	70,3	12

TABLE 10.2: JUVENILE MORTALITY ESTIMATED BY THE METHOD OF ATTWELL (1977)

Interval between counts	Juvenile:Female first count	Juvenile:Female second count	% mortality
8 months 1.1976 - 8.1976	50:100	17:100	70,2
4 months 12.1976 - 4.1977	45:100	38:100	21,4
7 months 2.1979 - 9.1979	33:100	19:100	48,8

10.3.1.4

Physiological condition

Physiological condition is relevant to the population condition in that it indicates enhanced or reduced chances of survival (Hanks, 1979). A comparison between kidney fat index of Kwando and Kafue females (Sayer & Van Lavieren, 1975) showed that the mean kidney fat index of Kwando females was higher than that of Kafue females (Chapter 5). As the Kafue lechwe population had been studied over a period of a decade (Robinette & Child, 1964, Sayer & Van Lavieren, 1975) and was not known to be declining, it is reasonable to assume that the kidney fat index of Kwando females does not indicate substantially reduced chances of survival.

10.3.1.5

Population models

Model life-tables for female and male lechwe are set out in Tables 10.3 and 10.4. In seeking to understand the dynamics of a population it is the life-table for females that is of particular interest.

Table 10.3 shows a mean mortality rate of 31,7% for all female age groups, based on the relationship

$$\bar{q} = 1 / \Sigma l_x \qquad \text{(Caughley,1966)}$$

This compares with 11,4% in Bangweulu lechwe (Grimsdell & Bell, 1975) but assumed juvenile mortality in the Bangweulu population was 25% (as opposed to 60%) and this accounts for much of the difference. On the same basis a mortality of 18,6% for all animals older than one year is indicated. The latter is the figure used in estimating juvenile mortality from female:fawn ratios in the field. This compares with an apparent mortality rate of 9,7% in the Bangweulu Swamp (Grimsdell & Bell, 1975).

It was not possible to make direct measurements of mortality in the field but there were no indications of particularly high mortality due to any of the major mortality factors - predation, disease and parasitism, accidents and environmental stress.

Lechwe are vulnerable to a wide spectrum of predators on the Kwando but no direct evidence of heavy predation was found. There is a possibility that the high flood levels which prevailed throughout this study may have been conducive to increased juvenile mortality.

TABLE 10.3: MODEL LIFE-TABLE FOR LECHWE FEMALES OF THE KWANDO POPULATION, ASSUMING 60% JUVENILE MORTALITY

x (age)	l_x	d_x	q_x	m_x	$l_x m_x$	$x l_x m_x$
0	1,000	0,600	0,600	0	0	0
1	0,400	0,036	0,090	0	0	0
2	0,364	0,033	0.091	0	0	0
3	0,331	0,030	0,091	0.25	0,083	0,248
4	0,301	0,052	0,173	0,38	0,114	0,457
5	0,249	0,114	0,458	0,47	0,117	0,585
6	0,200	0,065	0,325	0,50	0,100	0,600
7	0,135	0,041	0,303	0,50	0,068	0,473
8	0,094	0,054	0,575	0,50	0,047	0,376
9	0,040	0,023	0,575	0,50	0,020	0,018
10	0,017	0,006	0,353	0,50	0,009	0,065
11	0,011	0,002	0,182	0,50	0,006	0,061
12	0,009	0,009	1,000	0	0	0

TABLE 10.4: MODEL LIFE-TABLE FOR LECHWE MALES OF THE KWANDO POPULATION, ASSUMING 60% JUVENILE MORTALITY

x (age)	l_x	d_x	q_x
0	1,000	0,600	0,600
1	0,400	0,036	0,090
2	0,364	0,033	0,091
3	0,331	0,030	0,091
4	0,301	0,057	0,189
5	0,244	0,034	0,139
6	0,210	0,112	0,533
7	0,098	0,039	0,398
8	0,059	0,030	0,509
9	0,029	0,019	0,655
10	0,010	0,000	0,000
11	0,010	0,003	0,300
12	0,007	0,007	1,000

Lechwe neonates are hidden, usually on termitaria or mounds of vegetation in or near the perennial swamp. When high flood levels force females to the edge of the wetland it may well be that neonates are more vulnerable to predation because they are left in more exposed positions. Evidence in support of this suggestion is that on three occasions fawns were seen lying up on termitaria that were conspicuous from the mainland. On two occasions the fawn was easily caught by wading through shallow water to the termitarium and simply picking it up as it lay flattened on the ground.

Disease levels on the Kwando seemed to be appreciably lower than those reported by Gallagher et al. (1972). Parasite burdens were generally found to be low. The only external parasites found were ticks (Rhipicephalus spp.) and there were only a few of these on each of four (1,7%) of the animals examined. Nineteen animals (8,3% of the total) mostly immatures, were found to have subcutaneous warble fly larvae (Strobiloestrus sp.) along their backs. Cestodes (Taenia spp.) and nematodes (Setaria spp., Haemonchus spp.) were occasionally found, but invariably in small numbers. Only one animal was found to have an infestation of schistosomes (Schistosoma spp.) in the liver, but it is likely that a fairly high proportion of the population is infected with this parasite (Pitchford, 1974 and 1976). About 15% of lechwe in areas of low tsetse fly (Glossina morsitans) density are sublethally infected with trypanosomes (Trypanasoma spp.) (Dräger & Mehlitz, 1978).

All but the youngest animals are subject to varying degrees of infestation by Paramphistomum spp. in the rumen and by flukes (Fasciola spp.) in the liver. An incidental but interesting finding in this respect is that significantly higher levels of infestation occur in females than in males.

The level of rumen infestation in each animal autopsied was rated on a scale 0 - 3 (0 = no infestation; 1 = $\pm 10^{1}$ parasites; 2 = $\pm 10^{2}$parasites; 3 = $\pm 10^{3+}$parasites). Each liver was assessed on a similar scale (0 = no infestation; 1 = slight; 2 = moderate; 3 = severe infestation). The results of these assessments are presented in Tables 10.5 to 10.7. The sex difference in the degree of infestation is believed to be related to differential habitat use - females using wetter areas than males (Chapter 4). In no case was unequivoval evidence found that either rumen or liver infestation had or would have been lethal.

TABLE 10.5: THE AGE-SPECIFIC FREQUENCY WITH WHICH DEGREES OF INFESTATION BY RUMEN (*Paramphistomum* spp.) AND LIVER (*Fasciola* spp.) PARASITES OCCUR IN LECHWE FEMALES

All numbers in percentages.

0 = no infestation 1 = slight
2 = moderate 3 = severe

AGE (years)	*Paramphistomum* spp.				*Fasciola* spp.			
	0	1	2	3	0	1	2	3
0 - 1	66,7	33,3	-	-	-	-	-	-
1 - 2	33,3	50,0	16.7	-	-	100.0	-	-
2 - 3	12,5	50,0	37,5	-	16,7	50,0	33.3	-
3 - 4	-	18,0	46,2	35,8	-	29,0	45,9	25,8
4 - 5	-	9,7	19,3	71,0	3,8	19,2	34,6	42,4
5 - 6	-	-	12,5	87,5	6,2	12,5	31,2	50,0
6 - 7	-	-	14,3	85,7	-	17,7	23,5	58,8
7 - 8	-	-	-	100,0	-	-	-	100,0
8+	-	-	-	100,0	-	-	25,0	75,0

TABLE 10.6: THE AGE-SPECIFIC FREQUENCY WITH WHICH DEGREES OF INFESTATION BY RUMEN (*Paramphistomum* spp.) AND LIVER (*Fasciola* spp.) PARASITES OCCUR IN LECHWE MALES

All numbers in percentages.

0 = no infestation
1 = slight
2 = moderate
3 = severe

AGE (years)	*Paramphistomum* spp.				*Fasciola* spp.			
	0	1	2	3	0	1	2	3
0 - 1	62,5	37,5	-	-	85,3	16,7	-	-
1 - 2	-	66,7	33,3	-	16,7	85,3	-	-
2 - 3	-	75,0	25,0	-	-	100,0	-	-
3 - 4	11,1	55,6	27,8	5,6	18,8	62,5	6,3	12,5
4 - 5	-	80,	15,4	3,8	10,5	63,2	21,1	5,3
5 - 6	-	44,4	33,3	22,3	-	57,1	28,6	14,3
6 - 7	20,0	20,0	60,0	-	-	75,0	25,0	-
7 - 8	-	25,0	75,0	-	-	25,0	50,0	25,0
8+	-	-	33,3	66,7	-	50,0	-	50,0

TABLE 10.7: THE DIFFERENCES BETWEEN MALES AND FEMALES IN THE EXTENT OF INFESTATION BY RUMEN (*Paramphistomum* spp.) AND LIVER (*Fasciola* spp.) PARASITES AND THE SIGNIFICANCE OF "t"-TESTS (Sokal & Rohlf, 1969)* OF THESE DIFFERENCES

Parasite	% with little or no infestation		% with moderate to severe infestation		% difference	Significance o differenc
	Male	Female	Male	Female		
Paramphistomum sp.	66,3	17,6	33,7	82,4	48,7	p< 0,001
Fasciola sp.	75,8	28,0	24,2	72,0	47,8	p< 0,001

* The equation of Sokal & Rohlf (1969) for a "t"-test involving proportions or percentages is:

$$t_s = \frac{\arcsin p_1 - \arcsin p_2}{\sqrt{820,8 \left(\frac{1}{n1} + \frac{1}{n2}\right)}}$$

Where p_1 and p_2 = proportions/percentages of respective samples in relevant category

n1 and n2 = respective sample sizes

820,8 is a constant

Three cases of what were probably accidental injuries (one broken hind leg, two dislocated carpal joints) were noted but it appeared unlikely that accidents were a significant mortality factor.

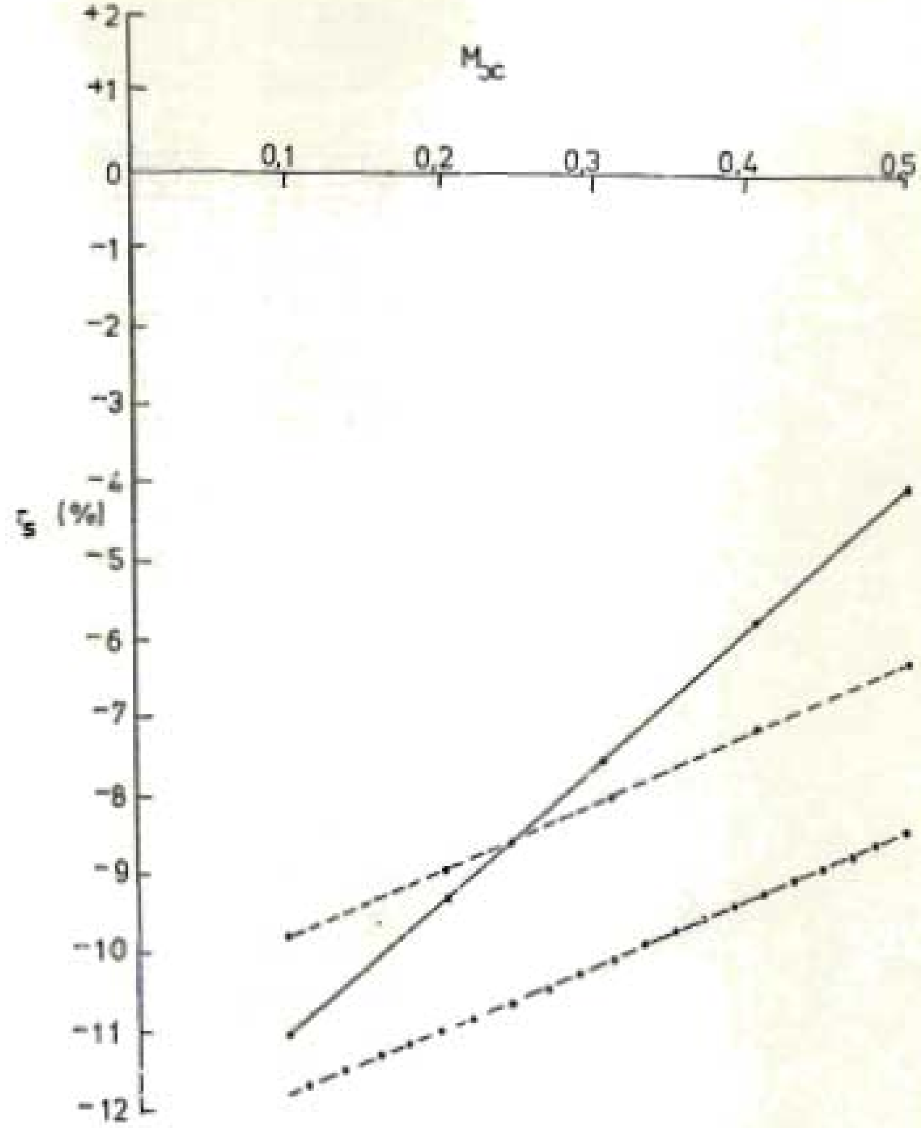
One factor which prevailed during this study, high water levels in the swamp, may have constituted a source of significant environmental stress. The influence of high water levels on juvenile mortality was indicated above and nutritional stress, caused by a reduction in the area of favoured habitat available to animals, may well have contributed to additional juvenile mortality. Nutritional stress may also have affected the fecundity of young females (Chapters 5 and 6). The ways in which variation in juvenile mortality and the fecundity of young females influences the population's rate of increase can be seen from the variation in "r_s" calculated from life-tables in which these parameters are varied.

Using the equation of Andrewartha & Birch (1954), r_s values were calculated for different yearling and 2 - 3 year old m_x values. The l_x schedule in Table 10.3 and the m_x values of animals older than three years were held constant. Where yearling fecundity was varied on its own, the observed m_x value for 2 - 3 year olds, 0,25, was used. Where 2 - 3 year old fecundity was varied on its own, yearling m_x was zero, as observed in the field.

The results of this exercise are illustrated in Figure 10.1. This shows that with the prevailing juvenile mortality rate (60%) increases in the fecundity of young females are not on their own sufficient to produce a positive rate of increase.

Figure 10.2 illustrates the effect on r_s of variation in juvenile mortality. Andrewartha & Birch's (1954) equation was again used to calculate a series of r_s values for different rates of juvenile mortality, with the mortality and fecundity of other age classes held constant.

From Figure 10.2 it appears that juvenile mortality is the major influence on r_s but clearly it is not the only important influence. It appears that with observed fecundity rates, the population would decline if juvenile mortality exceeded 30%. Comparable figures for other populations are 49% for Kafue lechwe (Grimsdell & Bell, 1975), 50% for wildebeest in



<u>Figure 10.1</u>: The relationship between yearling and 2-3 year old fecundity and the population's rate of increase.

——— = yearling and 2-3-year-old fecundity varied;

------ = yearling fecundity varied;

-·-·-· = 2-3-year-old fecundity varied.

Juvenile mortality held constant.

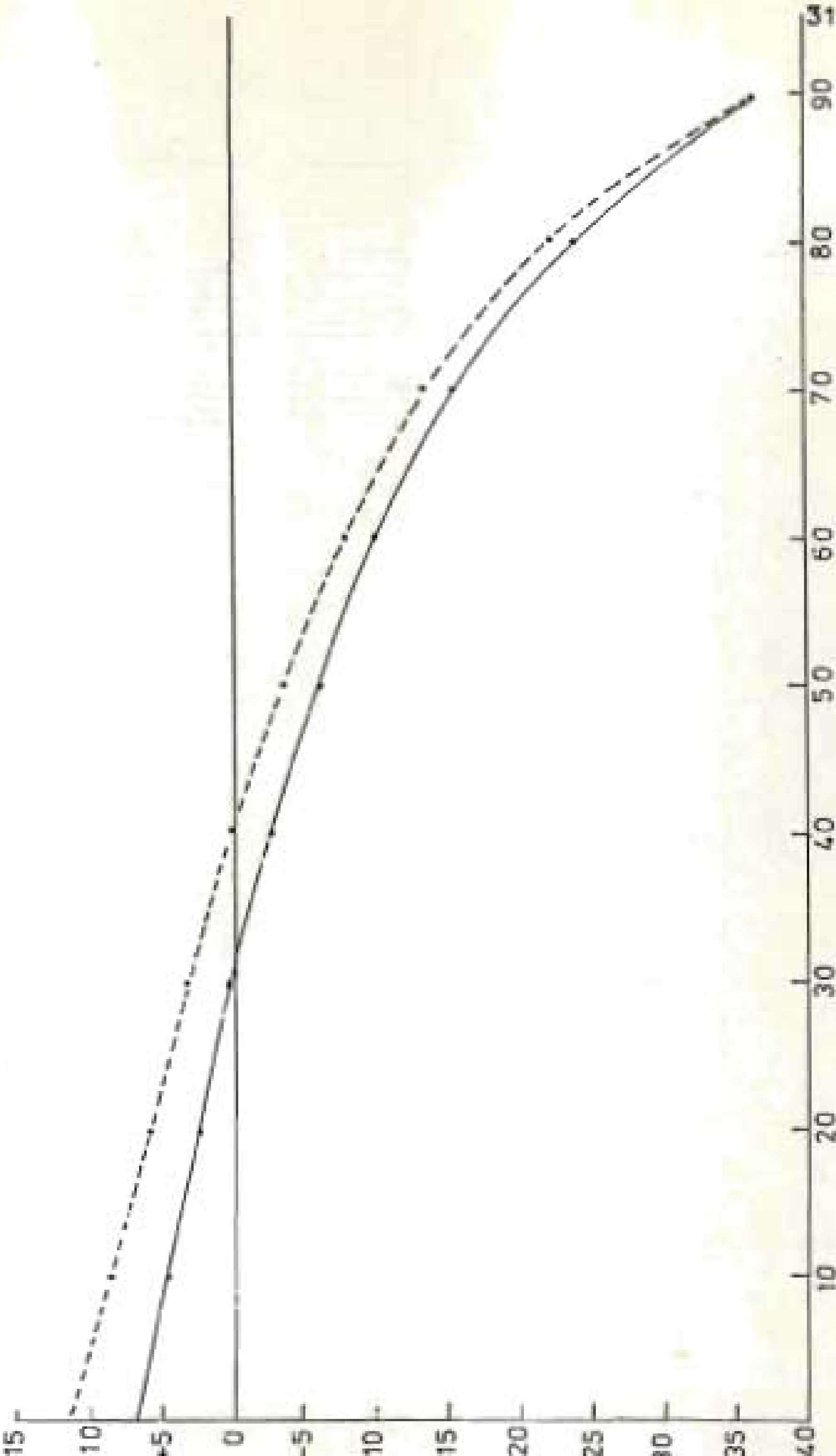


Figure 10.2: The relationship between the population's rate of increase and juvenile mortality. Solid line shows trend with prevailing fecundity rates. Dashed line shows trend when yearling fecundity is raised to $m_x = 0,25$.

Zululand (Attwell, 1977) and 75% for nyala in Natal (Anderson, 1978). Obviously the depressed fecundity of young animals in the Kwando population does have an important effect on r_s.

This effect is illustrated by the dashed line in Figure 10.2 which shows that when yearlings are given an m_x value of 0,25 the critical level of juvenile mortality rises to 40%. Further increases in yearling fecundity and improved fecundity of 2 - 3 year olds would no doubt bring the critical level of juvenile mortality into the range observed in other studies.

In the context of conservation it is of interest to have some idea of a population's ability to recover from a drastic decline in numbers. The intrinsic rate of increase "r_m" (Caughley, 1977) gives an indication of the maximum population growth to be expected under a given set of conditions. Estimates of r_m were made assuming a 30% rate of juvenile mortality and an m_x value of 0,5 for yearlings and all older animals (the latter values having been observed by Robinette & Child, 1964, in a captive herd of lechwe). Using Andrewartha & Birch's (1954) equation, these assumptions yield an estimate of r_m = 0,100. If yearlings are allocated an m_x value of 0,33 (the value observed in the field by Grimsdell & Bell, 1975), r_m = 0,08.

These values suggest a population doubling time of 7 - 9 years (Krebs, 1972). These rates of increase are neither unusual nor improbable for lechwe. Grimsdell & Bell (1972) found that the Busanga Plain lechwe population had been increasing at a rate which indicated an r value of 0,131, or a finite rate of increase of 14% per year. The captive herd referred to by Robinette & Child (1964) increased from 15 to 42 in three years, implying a rate of increase of 40%. Grimsdell & Bell (1975) calculated a value of r_m = 0,265 for Bangweulu lechwe, a finite rate of increase of 30% per year. The relevance of these figures is that they indicate that lechwe are capable of rapid population growth under favourable circumstances.

10.3.1.6

Conclusions on population condition

Although the rate of increase calculated from the aerial counts was of unknown accuracy, these counts provided no support for the suggestion (Child, 1975) of a rapidly declining population. The first Kwando survey (May 1975) found 1592 animals, the last (March 1979) 1907 animals and a reasonable conclusion to draw from the aerial work is that no drastic decline of the population is occurring. The findings in relation to foetal development and physiological condition are consistent with this conclusion.

Although there was no evidence of a drastic population decline, juvenile mortality appeared to be high and the fecundity of young females was definitely lower than that of young females in other populations (Chapters 5 and 6). Population models suggested that the combination of high juvenile mortality and reduced fecundity in young females could have resulted in a downward trend in the population. High flood levels, through their effect on mortality and fecundity (Chapters 5 and 6), are the likely explanation of any downward trend in the population and no indication of a long-term decline was found. The decline of the Chobe segment of the population is probably due to direct competition for the floodplain with an expanding human population (Von Richter, 1974). The present situation on the Kwando appears to be a neat illustration of Caughley's (1977) observation that "Should the decline be a consequence of reduced food supply or poor habitat the diagnostic feature is a rise in juvenile mortality, usually coupled with a decline in juvenile fecundity".

10.3.2

Harvesting Rate

This discussion will relate to only the Kwando side because ground counts did not extend to the Linyanti side of the swamp. The size of the Kwando subpopulation will be taken as 1651 animals, the mean of five aerial counts.

A total of 5942 animals were located during the six ground counts. The structure of this sample was as follows:
juveniles: 16,1%;
females over one year old: 45,9%;
subadult males: 22,2%;
adult males: 15,8%.

In the class of all animals older than one year the ratio of females: males was 1,21:1 (chi-squared with Yates correction = 44,331, $p < 0,005$). When this ratio is compared with the foetal sex ratio it becomes apparent that the sexes experience different rates of mortality. The sex ratio of foetuses that could be easily sexed was 34 females to 38 males. If four slightly doubtful determinations are added, the ratio becomes 35 females to 41 males, which is not significantly different from parity.

From data collected in this study the sustainable annual offtake would appear to be about 165 animals (10% of 1651). However, it would be inadvisable to allow this offtake at present because almost the entire offtake on the Kwando is by safari companies, which take only trophy males. With this selectivity in mind, it it recommended that the annual quotas for safari companies on the Kwando should not exceed 26 animals (15,8% Of 165).

It would seem sensible to reserve the quota of adult males for the safari companies because thwir value as trophy animals is much greater than it is as a source of subsistence. If the subsistence hunting demand for lechwe on the Kwando increases, which appears to be highly unlikely, this can easily be met by allocating up to 76 licences annually for females (45,9% of 165).

Superficially it may seem reckless to suggest any offtake from a relatively small subpopulation of a species which has been classified as endangered in terms of the Convention on International Trade in Endangered Species. Offtakes have been suggested both because they are, in my opinion, safe as this subpopulation is part of a much larger regional population, and also because there is a pressing need in Botswana to show economic benefits from wildlife conservation.

10.4

SUMMARY

The purposes of trying to assess the status of the Kwando lechwe population were:

(a) to establish whether or not there was any substance in suggestions that the population was declining rapidly;

(b) to determine sustainable offtake from the population.

No direct evidence of a serious decline in the population was found but population models indicated that at prevailing rates of juvenile mortality and of fecundity in young females the population may have been on a downward trend.

A low rate of offtake (26 adult males per annum) was recommended in view of the very selective harvesting that occurs at present and is likely to continue for the forseeable future.

CHAPTER 11

CONSERVATION AND MANAGEMENT

11.1

INTRODUCTION

The broad aim of the present study was to collect information that would facilitate the conservation and management of red lechwe in Botswana. To this end earlier chapters have outlined the ecology and behaviour of the lechwe population on the Kwando. The purpose of this chapter is to propose a management strategy for lechwe in Botswana which is based on the results of this study.

At this stage it is appropriate, for two reasons, to think in terms of a broad strategy rather than specific and detailed management plans. In the first place, the future of the population is clouded by political uncertainty . on the Namibian side and unsettled conservation status on the Botswana side (the Kwando is proposed as a wildlife management area but this proposal has yet to be accepted by government). Secondly, the population has never been actively managed and intensive management is at best a remote future prospect.

In designing a management strategy for the Kwando lechwe population it is important to view the management of this population in the context of the Department of Wildlife's overall management responsibility. This involves more than 20 ungulate species populations comprising one or two million animals which occupy more than 250 000 square kilometres of land. The burden of managing this enormous resource is aggravated by chronic staff limitations and the absence of good roads in most parts of the country. Given the magnitude of the task and the constraints of limited manpower and restricted movement it is obvious that only very limited management will be possible for the forseeable future.

11.2

THE OBJECTIVES OF MANAGEMENT

In formulating a strategy for management it seems logical to begin by articulating the objectives of management. This is important because wildlife occupies public land and its management requires the expenditure of public money, and unless the objectives of management are clear, it is difficult to judge whether or not it serves any valid purpose.

The objectives of managing the Kwando lechwe population will be decided by the management authority and my purpose here is merely to suggest what appear to me to be reasonable and attainable objectives. Later sections will outline possible ways of meeting these objectives.

It is suggested that management should have two primary objectives. The first, perhaps self-evident, should be the maintenance of a vigorous lechwe population in a stable and productive habitat. Other objectives are obviously dependent on meeting this precondition.

The second objective should be to strive to maximize economic returns from utilization of the population. This is extremely important because Botswana has severe problems of rural unemployment and poverty and there is growing insistence on the justification of setting aside land for wildlife by proving that it can produce economic benefits for the rural poor.

11.3

CONSERVATION OF THE POPULATION

The measures required to ensure the survival of a population depend on the species involved and the location of the population. Aspects of the ecology of the Kwando lechwe population that require particular consideration in the context of conservation are the status of the population and the animal's habitat use, food selection and movement patterns.

11.3.1

Consideration of the population status

The status of the population needs to be considered because there may be a need to augment or reduce its numbers. Reduction can be achieved rapidly by some form of harvesting. Augmentation can be achieved either by introduction of animals from another population or artificial rearing and subsequent release. The present status (Chapter 10) of the Kwando lechwe population does not seem to warrant these kinds of measures.

Aerial surveys on the Kwando and Linyanti sides of the swamp indicate a mean stocking rate of about one animal per 12,5 ha or 5,3 kilograms a ha. If this stocking rate is extrapolated to the entire wetland area in the system, a population of over 10 000 animals is indicated. There is no reason to doubt the viability of a population of this size.

There is also no reason to believe that the habitat is overstocked. Certain areas, for example, the intensive study area, are heavily used but in these areas grass cover is almost entirely of perennial species which are regenerating well, bush encroachment is minimal and there are generally few if any indications of habitat deterioration.

To guard against overstocking it is most important that a system of habitat monitoring should be instituted, perhaps along the lines indicated by Walker (1976). A habitat monitoring programme for all important wildlife areas in Botswana has been proposed (Williamson, 1979) and the range of the Kwando lechwe population is included in this.

To be in a position to prevent any serious decline of the population and to utilize the population efficiently it is also important that a population monitoring programme should be instituted. Table 11.1 outlines a possible monitoring system. Ideally this would cover the entire swamp and would begin as soon as possible with a survey of numbers and distribution in the whole area.

11.3.2

Habitat Protection

An animal's habitat must provide it with food and cover (Leopold, 1933). Because food and cover requirements vary from species to species it is necessary to make provision for the particular requirements of each individual species. Two stages can usefully be recognized in securing the habitat requirements of a given species. Firstly, there is the ecological problem of identifying the type and amount of habitat necessary to secure the survival of the particular species. Secondly, there is the problem of making and enforcing laws and regulations to protect the habitat so identified.

The type of habitat required is determined largely by food preferences and anti-predator behaviour. The amount of habitat required is determined by the size of the population and its degree of mobility. If a species migrates between widely separated winter and summer ranges both must be protected. Migratory species will obviously require larger areas than sedentary ones.

In this study it was found that lechwe were almost exclusively grazers, which appeared to select for new growth (Chapter 4). In respect of anti-predator behaviour they were found to be refuge users (Crook <u>et al</u>.,

TABLE 11.1: OUTLINE OF A PROPOSED MONITORING PROGRAMME FOR THE LECHWE POPULATION IN THE LINYANTI SWAMP

PARAMETER	METHOD	FREQUENCY OF OBSERVATION
(1) Population number	Aerial survey	Annually (February/March)
(2) Population distribution	Aerial survey	Annually (February/March)
(3) Population structure	Aerial photographs/ground counts	Annually (February/March)
(4)*Juvenile mortality	Female:fawn ratio from aerial photographs/ground count	Annually (February/March)
(5) Physiological condition of females	Fat indices, carcass mass index from shot sample of not less than than 30 animals	If population number changes drastically
(6) Fecundity of young females	Shot sample as in (5)	If population number changes drastically
(7) Female growth rate (see Chapter 5)	Shot sample as in (5)	If population number changes drastically

* assumes that the seasonality of reproduction will not vary greatly.

1976) which evaded predators by escaping into shallow water and/or emergent vegetation (Chapters 4 and 8). Observations on habitat use (Chapter 4) showed a marked preference for short-grass areas adjoining shallow water, where food quality was high and escape cover close at hand (Chapters 2, 4 and 8). Observed lechwe distribution (Chapter 4) was readily explicable in terms of these factors and was relatively stable, probably because of the relatively small fluctuations in water level (Chapter 2). Seasonal movements appeared to be small. On the basis of these observations it can be stated with some confidence that if areas of swamp and the adjoining floodplains are protected lechwe habitat requirements will be met.

Having established what type of habitat lechwe require it remains to determine the amount of habitat that should be protected. This depends partly on the minimum size of a viable population and partly on policy. Once the requirements of the smallest viable population are secured, how much more is set aside is a question of policy. My recommendation is that the entire Kwando floodplain from my intensive study area (known as James Camp area) to the Selinda Spillway should be protected. The animals contained in this area probably constitute a viable population.

In this area there are over 1 000 lechwe and at least two territorial breeding grounds. Judging by the history of the white rhino (<u>Ceratotherium</u> <u>simum</u>) conservation in Natal (Vincent, 1969 and 1970) a population of this size provides an adequate breeding nucleus to ensure the survival of the population. A population of about 1 000 rhino (which breed far more slowly than do lechwe) in the Umfolozi/Hluhluwe Complex is apparently viable and if anything difficulty has been experienced with disposing of surplus animals produced in this population (Vincent, 1970).

The nature of the legal protection that should be afforded to the habitat is open to debate. Von Richter (1974) suggests the creation of a lechwe sanctuary. This step would serve the purpose of protecting lechwe and would also protect sitatunga and ensure the conservation of a representative portion of a unique and rich ecosystem. Difficulties in the way of this option are the need to secure Namibian co-operation, the lack of a precedent in Botswana for a single species sanctuary and a growing antagonism towards the creation of further protected areas for .

wildlife. The form of legal protection that is eventually given to the area is a policy matter to be decided by the management authority and will not be further discussed here. The only further point that will be made in this regard is that some form of protection is urgently needed.

It is now virtually certain that an attempt will be made to eradicate tsetse fly from the Kwando. If this attempt is successful there is a very strong possibility that people will move onto the Kwando floodplain. Unless this movement is controlled lechwe and other wildlife populations will rapidly disappear, as is now happening in the Chobe segment of the population. The government has to decide whether people will be allowed to settle where they feel like doing so or whether settlement will only be tolerated in areas that have been investigated and zoned for human occupation. Unless the latter approach is followed any attempt at land use planning will be an exercise in futility.

11.4

GENERATING ECONOMIC RETURNS

In planning the economic exploitation of a species it is necessary to determine its monetary value. This varies with the way in which the animals are marketed. Three methods of marketing Kwando lechwe appear feasible at present. These methods and ways of promoting them are discussed below.

11.4.1

Non-consumptive Use

It is difficult to quantify the value of a lechwe in the context of game-viewing but this is not particularly important for the present purposes. What is important is that game-viewing is a potentially lucrative form of non-consumptive wildlife use. Low volume, high-cost camera safaris to the Kwando, capitilizing on the area's wilderness appeal, should be encouraged and assisted in all possible ways. The kinds of assistance that could be given include improvement of infrastructure, creation of small "no-shooting" areas and dissemination of information on the ecology and behaviour of important species. The latter is one way in which the data collected in the present study could be used.

11.4.2

Cropping for Meat, Hides and Horns

The prevalence of foot and mouth disease in Ngamiland precludes the export of fresh meat from the area. This problem and the remoteness of the Kwando mean that the only lechwe products that could be readily marketed at present are dried meat, salted skins and horns. In these terms the value of the average lechwe (Table 11.2) is approximately 11-14 Pula, depending on the sex. This is made up as follows:

dried meat (ca. 9 kg) : P9,00;
salted skin : P2,00;
horns : P3,00.

On this basis the quota of 165 animals (Chapter 10) from the Kwando would produce a gross revenue of just over 2 000 Pula. Because of transport costs, profits from a cropping operation on the Kwando would probably be very small. A detailed discussion of cropping is therefore unnecessary but because cropping may be more economically attractive in the Okavango Delta a few guidelines for harvesting lechwe, based on the results of this study will be suggested.

Cropping should not be allowed at certain times of the year. Stress around the time of mating can affect both conception and implantation (Skinner et al., 1974) and disturbance may lead to a reduced number of copulations (Geist, 1971). For these reasons there should be no shooting during the peak mating season (December to April). Around the time of birth, stress can lead to abortion (Skinner et al., 1974) and large scale disturbances during the peak birth period (August to November) should be similarly avoided.

Where a population is sedentary repeated disturbance is undesirable, inter alia because it may cause animals to abandon the area and will also make harvesting more difficult as animals become more and more wary. Areas in which repeated disturbance is particularly undesirable are the territorial grounds described in Chapter 9. In these areas high offtake by individual subsistence or sport hunters should not be allowed.

At present levels of management the numbers of each sex/age class to be removed should be in proportion to their contribution to the total population. In the interests of high productivity excessive removal of adult males must be avoided (Lynch, 1974).

TABLE 11.2: CALCULATION OF MEAN LECHWE MASS FROM GROUND COUNT DATA

Sex/age class	Number	Mean mass kg	Mean mass x number
Juveniles	959	32,1	30783,9
Females >1 year	2727	65,6	178891,2
Subadult males	1316	63,3	83302,8
Adult males	940	107,8	101332,0
TOTALS	5942	-	394309,9

$$\text{Mean lechwe mass} = \frac{\sum \text{Mean mass x number}}{\text{number}} = 66{,}4 \text{ kg}$$

In terms of condition and reproductive cycles, May would seem to be the ideal time to harvest lechwe in northern Botswana.

11.4.3

Trophy Hunting

The cost of a trophy licence provides a convenient measure of the value of trophy animals. It is a minimum value as species like lechwe attract hunters to Botswana and in this indirect way generate further revenue.

At present a trophy licence for a lechwe costs 75 Pula. Thus 26 animals from the Kwando generate an income of 1950 Pula. It is very likely that the cost of a trophy licence could be doubled without reducing the number sold. This is an obvious way of increasing income from lechwe.

With one exception the guidelines for cropping should also apply to trophy hunting. The exception is the duration of the period in which trophy hunting should be allowed. It is directed solely at adult males and could safely be allowed between April and December.

11.5

CONCLUSIONS ON MANAGEMENT

The present scope for management is not great because of organizational and logistic constraints. Consequently only modest benefits from management can be anticipated in the near future. This is unfortunate because, although in industrialized countries wildlife conservation (or preservation) is regarded as a self-validating activity, in the developing world there is a pressing need for it to produce tangible benefits. The enhancement of economic returns from wildlife should be a major preoccupation of managers in Botswana for the foreseeable future.

THESIS SUMMARY

The purpose of this study was to collect data that would facilitate the conservation and management of lechwe in Botswana. To this end continuous field work was undertaken on the western edge of the Linyanti Swamp from January 1975 to May 1977. Follow-up visits to the study area were made in February/March and October/November 1979.

Water levels in the main Kwando channel were monitored and it was found that there were two annual peaks in water levels. In order to describe the vegetation of lechwe habitat a collection of plant specimens was undertaken and an attempt was made to quantify the abundance of important plant species. Grasses appeared to be dominant in the areas most heavily used by lechwe.

Four methods of laboratory age determination (tooth eruption, tooth wear, and two ways of counting cementum annuli) were used to establish the ages of a shot sample of 231 animals. On the basis of the laboratory age determination field age determination criteria were established.

Habitat use was studied by intensive observations along an established circuit sampling all habitats used by lechwe. It was found that they favoured the ecotone between the perennial swamp and terrestrial communities. Observations on distribution at the population level indicated that variation in habitat use was not great and that the population was virtually sedentary.

Feeding style was studied by examining the stomach contents of autopsied animals and by direct observation. It was found that lechwe are predominantly grazers which appear to select for new growth.

Food selection was studied by direct observation and by examination of plants in areas used by lechwe in terms of the method developed by Walker(1976). Lists of plants taken by lechwe were produced and a quantitative assessment of the use of different grass species was made.

Fat indices and a carcass mass index (carcass mass/body length) were used to assess variation in the condition of lechwe and the possibility of using liver mass as an index of protein status was investigated. It was found that condition varied significantly with age, reproductive

status and season and that liver mass showed promise as an index of protein status. It was also found that the fecundity of females of all ages was affected by condition.

Theoretical Von Bertalanffy growth curves for growth in body mass, body length and girth, shoulder height and neck girth were produced for both males and females. There were strong indications that the growth rate of females was depressed. Equations to predict mass from measurements of length and girth were derived.

Females reached sexual maturity at over two years; later than in Zambian populations. There were indications that females may have to reach a critical weight before attaining sexual maturity. Lechwe may be polyoestrus, they were monotocous and implanted unilaterally in the right horn of the uterus. It was estimated that females were producing young about once a year. There were marked seasonal peaks in conceptions and births. Nutrition was believed to be the major factor influencing female reproductive seasonality.

In males spermatogenesis began at about 18 months, but it appeared unlikely that successful reproduction occurred before about 4,5 years of age. Possession of a territory was apparently essential for successful mating by males. There was no indication of a sexual cycle in males.

There were marked differences in the activity budgets of different sex/age and social classes. The activity patterns of lechwe were rather complex and the simple model of peaks of activity in the early mornings and evenings appeared to be inapplicable. It was found that there was normally a clear ecological separation between lechwe and most other ungulates but that this broke down during dry periods. Lechwe appeared to rely mainly on visual and auditory detection of predators and made use of shallow water and emergent vegetation as escape cover.

Lechwe social behaviour was found to be similar to that of other Reduncinae. Social organization was based on a territorial, polygamous mating system. Differences were found in the expression of territoriality in Kwando and Kafue lechwe. These differences were probably related to different ecological and demographic conditions.

Data on population numbers and density were obtained from aerial surveys. Three different methods were used to estimate juvenile mortality. Data on adult mortality and on fecundity were obtained from the shot sample. From data collected it was concluded that, although there was no evidence of a drastic decline in the population, at prevailing rates of juvenile mortality and fecundity in young females the trend of the population was probably downward. This was believed to be a temporary trend associated with the prevailing high water levels in the system.

On the basis of the findings of this study a strategy for the conservation and management of lechwe in the Linyanti Swamp is proposed. This makes provision for habitat protection, population monitoring and generating economic returns from the population. It is suggested that the enhancement of economic returns from wildlife should be a major preoccupation for managers in Botswana.

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APPENDIX

SYSTEMATIC LIST OF PLANT SPECIES

(The systematic order of families follows Biggs (1979))

ANGIOSPERMAE

DICOTYLEDONAE

Moraceae

Ficus burkei (Miq.) Miq.
Ficus sycamorus L.

Polygonaceae

Oxygonum alatum Burch.
Polygonym pulchrum Blume

Amaranthaceae

Achyranthus aspera L.
Aerva leucura

Nyctaginaceae

Commicarpus africanus (Lour.) Dandy

Nymphaeaceae

Nymphaea caerulea Sav.

Fabaceae (Leguminosae)

Mimosoideae

Acacia erioloba E. Mey
Acacia fleckii Schinz
Acacia hebeclada DC. subsp.chobiensis (.O.B.Mill) Schreiber
Acacia luderitizii Engl.

Acacia nigrescens Oliv.
Acacia tortilis
Albizia versicolor Welw. ex Oliver.
Dichrostachys cinerea L.

Caesalpinoidae

Bauhinia macrantha Oliv.
Colophospermum mopane

Papilionoideae

Indigofera astraglina DC.
Lonchocarpus capassa (Klotzsch) Rafle
Lonchocarpus nelsii
Peltophorum africanum Sond.
Sesbania bispinosa

Euphorbiaceae

Croton megalobotrys Muell. Arg.

Anacardiaceae

Sclerocarya caffra Sond.

Rhamnaceae

Ziziphus mucronata Willd.

Tiliaceae

Grewia spp.

Malvaceae

Abutilon angulatum
Hibiscus calyphyllus Cav.

Bombacaceae

Adansonia digitata L.

Sterculiaceae

Hermannia angolensis K. Schum

Guttiferae

Garcinia livingstonei T. Anders

Lythraceae

Nesaea crassicaulis
Nesaea radicans

Combretaceae

Combretum hereroense
Combretum imberbe
Terminalia sericea Burch, ex DC.

Ebenceae

Diospyros lycoides Desf. subsp. lycoides
Diospyros mespiliformis
Euclea divinorum

Periplocaceae

Tacazzea apiculata Oliv.

Asclepiadaceae

Gomphocarpus rostratus
Orthanthera jasminiflora

Boraginaceae

Heliotropum ovalifolium

Verbenaceae

Lantana angolensis
Phyla nodiflora

Labiatae

Leonotis nepetifolia

Campanulaceae

Lobelia nuda

Solanaceae

Solanum panduriforme

Scrophulariaceae

Ramphicarpa tubulosa
Striga asiatica
Striga bilabiata

Bignoniaceae

Kigelia africana (Lam.) Benth.

Lentibularaceae

Utricularia sp.

Acanthaceae

Monechma debile (Forsk.) Nees

Compositae

Bidens schimperi Schultz Bip.
Eclipta prostrata (L.) L.
Nidorella resedifolia
Pluchea leubnitziae

MONOCOTYLEDONAE

Typhaceae

Typha latifolia

Potomogetonaceae

Potomogeton thunbergii

Palmae (Arecaceae)

Phoenix reclinata
Hyphaena sp.

Commelinaceae

Commelina imberbis

Liliaceae

Gloriosa superba L.

Agavaceae

Sansevieria sp.

Amaryllidaceae

Crinum crassicaule Bak.
Haemanthus multiflorus Mort.

Poaceae - Gramineae

Oryzeae

Oryza longistaminata
Leersia hexandra

Arundineae

Phragmites sp.

Aristideae

Aristida congesta Henrard.
Aristida meridionalis
Aristida pilgeri Henrard.

Stipagrostis hirtigluma

Eragrostideae

Dactyloctenium aegyptium
Eragrostis echinochloidea
Eragrostis inamoena
Eragrostis lappula
Eragrostis pallens
Eragrostis superba
Eragrostis trichophora
Pogonarthia squarrosa
Trichoneura grandiglumis (Nees) Ekman

Sporoboleae

Sporobolus iocladus (Trin.) Nees
Sporobolus spicatus
Sporobolus sp.

Chlorideae

Chloris gayana Kunth
Chloris dactylon

Paniceae

Panicum coloratum
Panicum dregeanum Nees
Panicum maximum
Panicum repens L.
Setaria anceps
Setaria sphacelata
Setaria verticillata (L.) Beauv.
Echinochloa stagnina
Brachiaria deflexa
Brachiaria dura
Brachiaria humidicola
Paspalidium platyrrhacis
Paspalum orbiculare
Sacciolepis typhura (Stapf.) Stapf.
Rhynchelytrum repens

Andropogoneae

Elionurus argenteus
Elionurus trapnelli C.E.Hubbard
Hemarthia altissima
Heteropogon contortus
Sorghastrum friesii (Pilg.) Pilg.
Vetevaria nigritana
Vossia cuspidata
Imperator cylindrica
Miscanthidium sp.
Cymbopogon excavatus
Hyperthelia dissoluta
Schizachyrium jeffreysii (Hack.) Stapf.
Trachypogon spicatus
Andropogon eucomis

Arundinelleae

Tristachya nodiglumis

Zoiseae

Perotis patens Gand.

Cyperaceae

Scirpus rogersii
Scirpus uninodis
Fuirena pubescens
Fuirena umbellata
Fimbristylis ferruginea (L.Vahl.)
Fimbristylis sp.
Cyperus articulatus
Cyperus denudatus
Cyperus longus
Cyperus papyrus
Mariscus squarrosus
Pycreus flavescens
Pycreus lanceus
Pycreus polystachyos

Rhynchospora holoschoenoides

Cladium mariscus

Juncaceae

Juncus rigidus