THE POPULATION DYNAMICS AND SOCIAL BIOLOGY OF BUSHBUCK (*Tragelaphus scriptus* Pallas)

by

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A thesis submitted in partial fulfillment for the degree of Master of Science in the University of Nairobi,

February 1971.

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SUMMARY

Bushbuck is a member of the little known sub-family Tragelaphinae.

This study was conducted in two areas of Kenya. Bushbuck were collected from Study Area A for population dynamics data and Study Area B was used for observing social biology.

Aspects of growth and development are given in preparation for the later chapters on reproduction and population dynamics. All foetuses collected from Study Area A were aged according to their weights. Post natal growth and development is concerned with those characteristics that can be used as ageing criteria. The forty six females collected were aged according to the state of tooth eruption and wear and placed into Age Groups I - VIII. These groups were assigned chronological ages using changes in dentition and eye lens weights as further criteria.

Female bushbuck mature at an average age of 21.7 months and males after one year. There is a high rate of reproductive success and calving is synchronised to the period of maximum rainfall. The gestation period is one hundred and eighty days with lactation lasting six to seven months after parturition. Although the

post partum interval may be short there is an average of three to four months between successive births.

Natality, mortality and survivorship are discussed with the results being summarised in a female life table. Life expectancy for females in Age Groups I - VIII is calculated. Using the life table data together with the female age specific fecundity the mean generation time is given as [illegible] 116 years and the net reproductive rate as 0.940. The population in Study Area A is therefore declining in numbers.

Eighty individual bushbuck were recognised in Study Area B and their distribution recorded. This distribtion indicates possible 'family groups' which may consist of adult males, sub adult males, females and youngsters.

Although bushbuck are mainly solitary, associations between female and young; female and male; male and male are not uncommon. Associations with other species such as impala or baboon are recorded. Red billed oxpeckers are not encouraged and bushbuck do not remain in the vicinity of buffalo, Predators in Nairobi National Park include leopard, cheetah and Martial eagle.

There is considerable tolerance between male bushbuck except when in the presence of an oestrous female. No territorial area is defended but rather an adult male will form, and defend, an association with an oestrous female.

The home range of sub adult males is approximately twenty thousand square metres. This is considerably larger in area than the ranges of adult males or females which are about five thousand six hundred and two thousand five hundred respectively.

ACKNOWLEDGEMENTS

I am deeply indebted to the Ministry of Overseas Development, Great Britain and the East African Agriculture and Forest Research Organisation for sponsoring this study.

Without the help of a grant for travel and equipment from Ford Foundation the study would have been far more limited.

The Kenya Game Department and Kenya National Parks have both been most helpful and I am extremely grateful for their permission to collect animals for the study and to carry out observations in Nairobi National Park. I must also thank the managers of Kiambogo Estate, Prospect Farm and Ndabibi Estate for permission to shoot over their land.

I was most fortunate to be helped by the Center for Prehistory in preparation of skulls, the Kenyatta Hospital Medical School for histological preparations and the Kenyatta Hospital Radiography Department who supplied and processed X - ray negatives. The staff of the Zoology, Botany and Veterinary Departments of University College Nairobi were a constant source of help and encouragement. Mr.W.F.H. Ansell kindly supplied the data on distribution of bushbuck and Mr.T. Smith helped considerably with field work.

Finally I would like to acknowledge my particular appreciation to Dr.R.M. Watson for his help with the population dynamics data, Dr.W.Swank for criticising the manuscript and Mr. and Mrs. R.L. Courreges for their untiring help throughout the study period.

CHAPTER 1

INTRODUCTION

Introduction

Large mammals are a dominant feature of the African Continent. They represent on one hand a potential source of protein for human consumption and on the other a possible reservoir for parasitic diseases affecting both humans and domestic stock. At present their major economic importance lies in their attractiveness to tourists.

In East Africa they are a major natural resource and will undoubtedly be exploited to greater degrees in the future years.

This economic importance together with the great biological interest they generate has attracted numerous research workers, particularly of the zoological and veterinary disciplines. If these animals are to be most beneficially exploited such research is a necessary requirement.

Many antelopes have been studied in East Africa and other parts of the continent, but the emphasis has been very much on plains game. The more secretive bush and forest dwelling antelopes which are less frequently observed do nevertheless occur widely throughout Africa. Their habits and population statistics still remain virtually unknown.

Such a group of animals is the sub-family Tragelaphinae which includes some of the rarest and least known animals in East Afric , i.e. bongo. (Boocercus eurycerus). Bushbuck are probably the most numerous and widespread species of this group and as such present the best opportunity for study.

This study was therefore an attempt to determine aspects of the population ecology of bushbuck. It was not possible to cover the entire ecology and behaviour in the time allotted, and so the study was restricted to population dynamics and social biology with the emphasis, in the latter case, being on local distribution and associations rather than behaviour.

Nairobi National Park was chosen as study area since its proximity to University College, Nairobi, made regular visits possible. Bushbuck are present in sufficient numbers for observation to be made with reasonable certainty. For population dynamics a number of animals needed to be collected, and since National Park policies do not allow this another area had to be found for this data. It was discovered that bushbuck were being shot on control on several estates in the Central Rift Valley Province. Permission was sought and granted from the respective estate managers and the Kenya Game Department to participate in the control work and use the material for this study.

Previous Work

Since first recorded in 1766 by Pallas bushbuck have been described several times as new, or suspected new, species have been discovered. Thomas (1905), Rothschild (1906), and later Dollman (1929), Schwartz (1938), and Babault (1947), described such 'subspecies' as Barker's, Menelike's and Reid's bushbuck.

The ferocity shown by bushbuck when fighting seriously has prompted such descriptions as 'Fighting

Fury The Bushbuck' Jackson (1955), and 'Solitary But Brave' Patterson (1969). Serious research is, however, sparse. Verheyen (1955) describes aspects of behaviour observed during a short study of bushbuck in Albert National Park, and Wilson and Child (1964) record data collected during shoting of bushbuck for tsetse control operations in Zambia.

Reference can be found to bushbuck in more general books such as Prichett (1963), Walker (1963) and Stevenson - Hamilton (1947).

Description of Animals

Bushbuck show considerable sexual diamorphism as adults, but are indistinguishable up to the age of about ten to twelve months. They are born with the rufous pelage of adult females only being more downy than the sleeker, older animals. The flanks and hind quarters of both adults and young alike are marked with spots and occasionally stripes. There is considerable variation in the number and intensity of these spot patterns between local populations and more noticably between sub-species. From observations made over the course of the study period and from old photographs these spot patterns do not appear to change with time.

The most characteristic morphological feature of both male and female bushbuck is the collar of short velvety hair covering the neck for a few inches above the shoulders. The size of the collar varies and may extend to just below the head. The chest and throat of both sexes are adorned with narrow white bands, as also seen in other members of the sub-family Tragelaphinae. The neck of the female is thin and dainty compared with that of the male. Although the males lack the heavy mane of nyala (*Tragelaphus angasi* Gray) and the dewlap of eland (*Taurotragus oryx* Pallas) they do, when fully adult, have a thick, sturdy neck.

Facial markings are again similar for male and female. Each cheek has a white patch, sometimes divided into two smaller patches, running diagonally downwards and forwards from below the eye. Between the eyes are two small white crescents and beneath each nostril a small white patch. Variations in these facial markings are very characteristic of the Tragelaphinae.

(see Plate 1)

PLATE 1

The adult male (upper) is considerably darker than the female. Both have white spots on the side and flanks; white patches on the throat, chest and legs and white under the tail. Females are hornless.

Adult Male Bushbuck

Adult Female Bushbuck

All four legs of both sexes have two inner white patches, one high just beneath the trunk and another at the wrist or ankle joint. On the front of each foot immediately above the hoof are two white ovals.

After approximately one year of age, the youngsters begin to assume their sexual characteristics. The back of the male becomes much straighter and the profile more square than that of the female. A dorsal crest of longer hair, though present in the female, becomes far more pronounced in the male and tipped with white. Females remain hornless, but the males develop the twisted horns characteristic of the sub-family (see plates 3 & 4). Male colour becomes darker and subject to greater variation. Although it is not possible to generalize there does seem to be a tendency for males to darken with age. Young males can, however, be seen which are almost black in appearance. The darkening tends to exaggerate the numerous white patches and spots etc. giving the male a more striking appearance than the female which shows very little variation in the chestnut colouring.

The ears of both sexes are similar in length remaining at about thirteen cms. throughout life. The females are smaller in body size and therefore the ears seem proportionally larger. The tail is of medium length (25 cm) and very bushy with a white underside.

A young hornless male (10 months) will weigh in the region of 26 kilograms with a total length from nose to tip of tail of approximately 115 cm. A female of about the same age would be approximately the same length, but somewhat lighter in weight, 15 to 20 kilograms. An adult male would be 50 kilograms and 160 cm in length compared with an old female of about 35 kilograms, 135 cm long.

Both sexes have inguinal glands and two pairs of mammae. Preorbital and pedal glands are absent.

Taxonomy

Order Artiodactyla

Family Bovidae

Sub-family Tragelaphinae

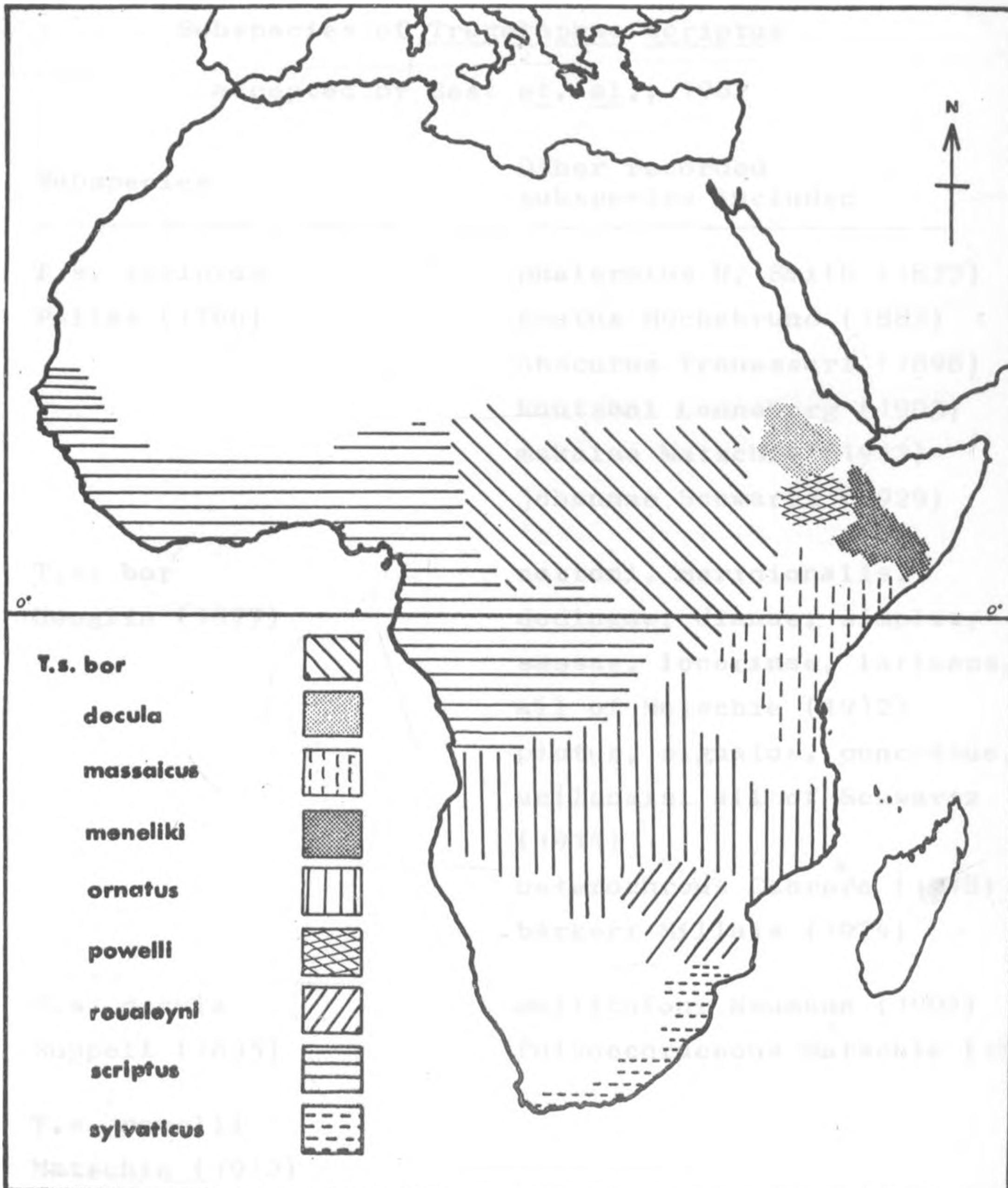
Genus Tragelaphus

Species scriptus


T.s. bor
decula
massaicus
meneliki
ornatus
powelli
roualeyni
scriptus
sylvaticus

FIG. 1

Distribution of the nine subspecies of *Tragelaphus scriptus* accepted by Best et. al. (1962) (After Ansell 1968).



Distribution of subspecies of <u>Tragelaphus scriptus</u> in Africa.

Subspecies of *Tragelaphus scriptus* accepted by Best *et. al.*, 1962

Subspecies	Other recorded subspecies included
T.s. scriptus Pallas (1766)	phaleratus H. Smith (1827) gratus Rochebrune (1882) obscurus Trouessart (1898) knutsoni Lonneberg (1905) makalae Matschie (1912) johannae Schwartz (1929)
T.s. bor Heuglin (1877)	cottoni, meridionalis, dodingae, dianae, simplex, sassae, locorinae, laticeps, all of Matschie (1912) pictus, signatus, punctatus, uellensis, all of Schwartz (1914) heterochrous Cabrera (1918) barkeri Millais (1924)
T.s. decula Ruppell (1835)	multicolour Neumann (1902) fulvoochraceous Matschie (1912)
T.s. powelli Matschie (1912)	
T.s. meneliki Neumann (1902)	nigrinotatus Neumann (1902) fasciatus Pocock (1900)

Subspecies	Other recorded subspecies included
T.s. delameri Pocock (1900)	roualeyni Noack (1899) massaicus Neumann (1902) dama Neumann (1902) haywoodi Thomas (1905) meruensis Lonneberg (1908) tjaderi Allen (1909) brunneus Matschie (1912) olivaceous Heller (1913) reidae Babault (1947) insularis Zukowsky (1961)
T.s. ornatus Pocock (1900)	
T.s. roualeyni Gordon-Cumming (1850)	typicus Sclater & Thomas (1900)
T.s. sylvaticus Sparrman (1780)	

Methods in Brief

This thesis is the result of studies conducted in two areas in Kenya. Study Area B is one square mile in Nairobi National Park and Study Area A is approximately 32,000 hectares of land surrounding Mt. Eburu in the Central Rift Valley Province.

Observations on the social biology of bushbuck were recorded mainly in Study Area B due to its proximity to University College, Nairobi. These were largely conducted from a vehicle using 7 x 50 binoculars. In order to determine home ranges it was necessary to identify individuals of the population. Within the one square mile area it was possible to become acquainted with all the regular inhabitants using spot patterns and horn characteristics for purposes of identification. As individuals became indentifiable their location was recorded and ultimately the distribution pattern of males and females together with the home ranges of selected animals could be mapped out. In addition the associations with conspecifics and with other species were noted together with aspects of social behaviour.

Since animals cannot be shot in national parks Study Area A was used for collecting specimens for population dynamics data. One or two trips were made each month from October 1968 to August 1969, two to five females and one to two males being collected each trip. A Winchester .264 was used to collect the animals and all shooting was done after dark. Eye lenses, ovaries, foetuses, skulls and skins were collected from females and eye lenses, testes and skins for males. Other material was collected for research not concerned with this study.

Study Area A will henceforth be referred to as S.A.A. and Study Area B as S.A.B.

CHAPTER 2

STUDY AREAS

Study Area A

Situated in the Central Rift Valley Province of Kenya, see Fig.2, S.A.A. comprises some 32,000 hectares. The three estates making up the area surround the Mt. Eburu Forest Reserve and lie between altitudes 6000 and 9000feet above sea level.

The estates are cut by deep valleys running down fron Mt. Eburu and these form the major daylight retreats of the bushbuck. All three estates, viz. Kiambogo, Ndabibi and Prospect, raise cattle but also grow such crops as maize, wheat and oats. Where these crops border valleys or patches of thicket bushbuck are invariably found.

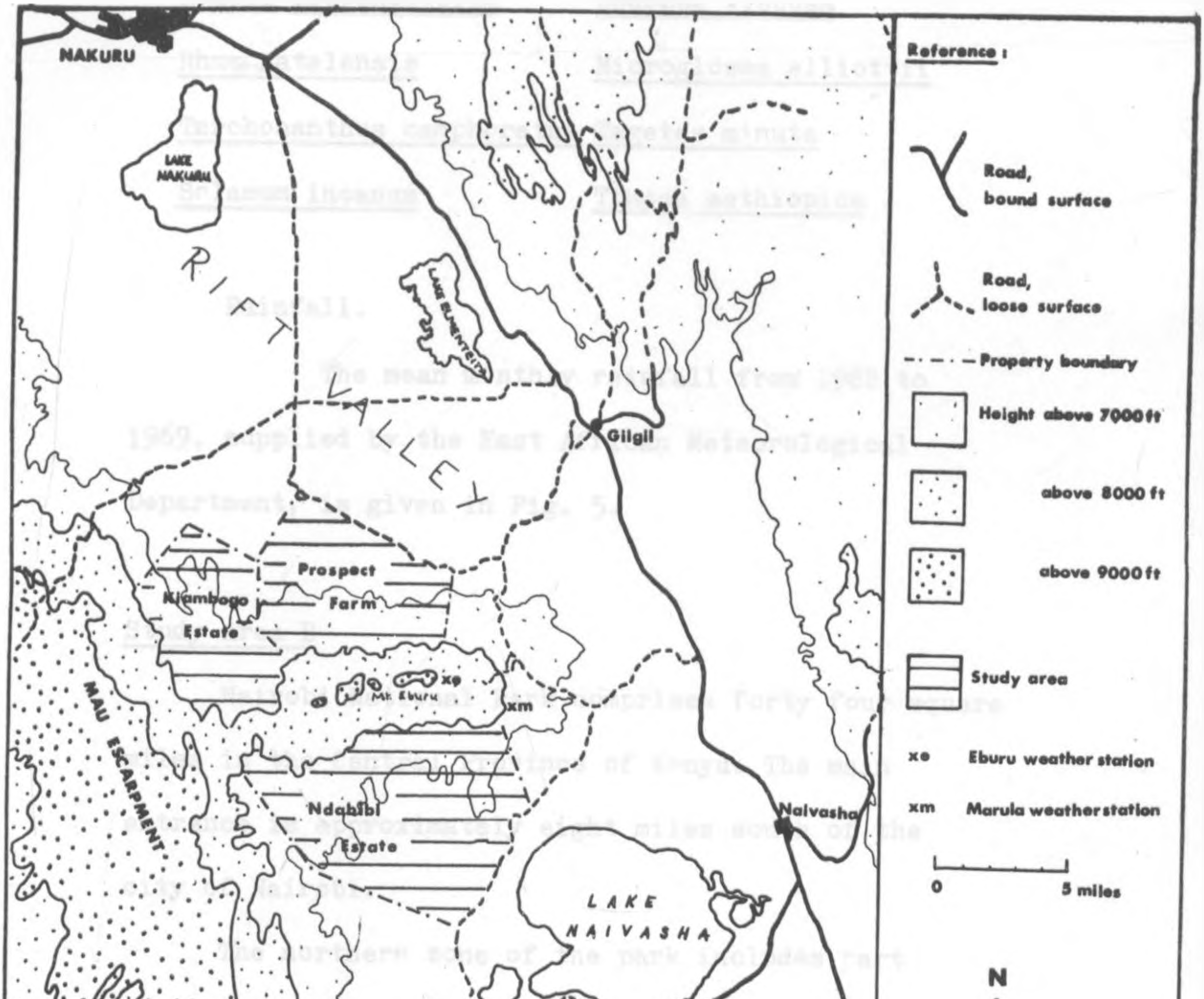
Vegetation.

The Mt. Eburu Forest Reserve, a mixed upland forest, is not included in the S A.A. The majority of the area is cultivated but large areas, particularly in the valleys, remain wild. The vegetation collected from these valleys was identified by the East African Herbarium and includes:

Abutilon longicuspe _Ricinus communis_

FIG. 2

Study Area A composed of Ndabibi Estate, Kiambogo Estate and Prospect Farm in the Central Rift Valley Province of Kenya.


NAKURU
LAKE NAKURU
RIFT VALLEY
Gilgil
Prospect
Farm
Kiambogo
Estate
MAU ESCARPMENT
xe
xm
Ndabibi
Estate
Naivasha
LAKE NAIVASHA
Reference :
Road, bound surface
Road, loose surface
Property boundary
Height above 7000 ft
above 8000 ft
above 9000 ft
Study area
xe Eburu weather station
xm Marula weather station
0
5 miles
N

Acacia drepanolobium	*Dodonea viscosa*
Rhus natalensis	*Microglossa elliottii*
Tarchonanthus camphoratus	*Tagetes minuta*
Solanum incanum	*Tinnea aethiopica* .

Rainfall.

The mean monthly rainfall from 1962 to 1969, supplied by the East African Meteorological Department, is given in Fig. 5.

Study Area B

Nairobi National Park comprises forty four square miles in the Central Province of Kenya. The main entrance is approximately eight miles south of the city of Nairobi.

The northern zone of the park includes part of the Langata Forest and S.A.B. is a one square mile area in this forest section.

S.A.B. lies at an elevation above sea level of 5600 feet.

Vegetation.

The soils and vegetation of Nairobi National Park have been described by Heriz-Smith and Verdcourt (1962).

FIG. 3

Nairobi National Park
showing location of Study Area B.

FIG. 3

Nairobi National Park

showing location of Study Area B.

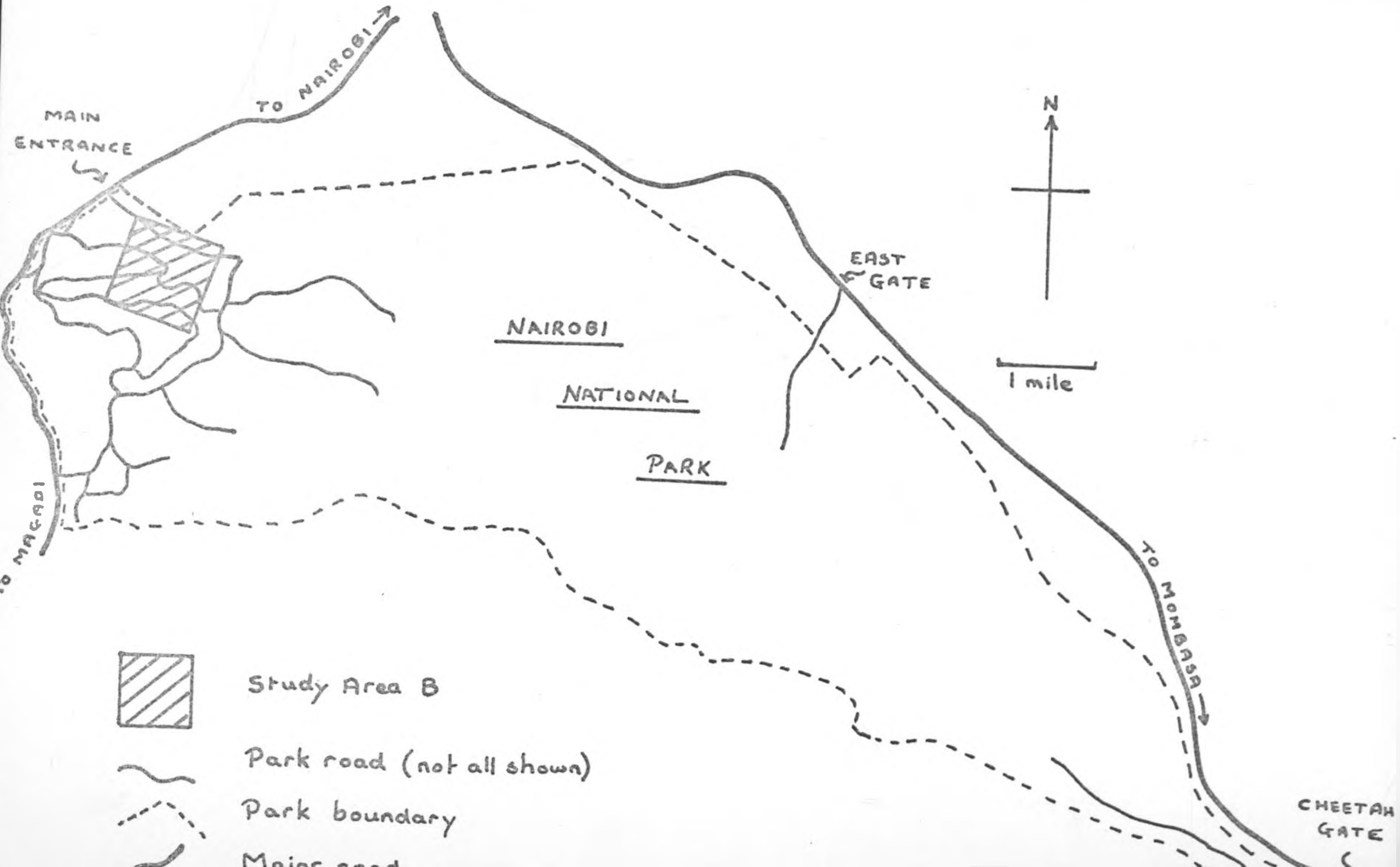
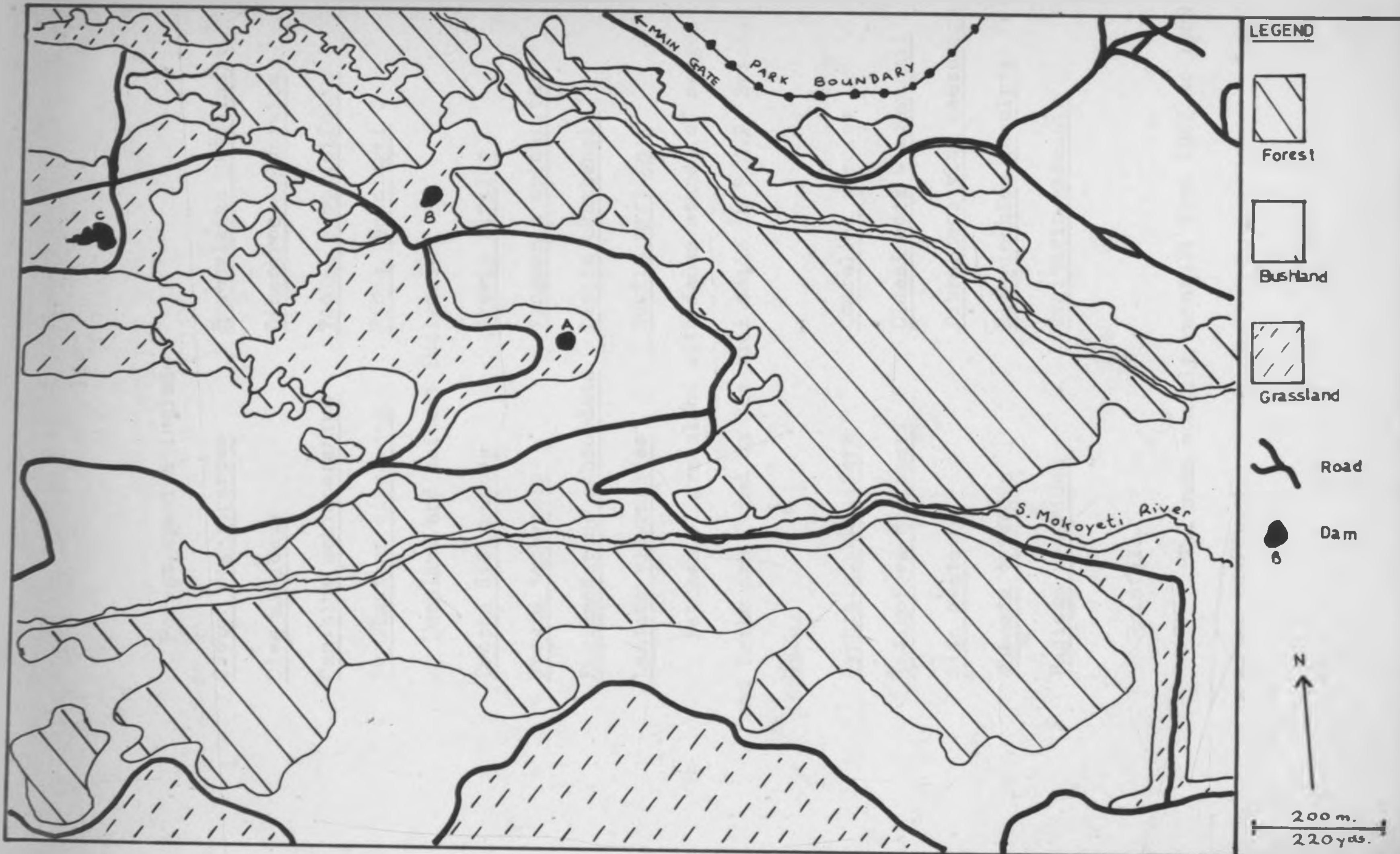

TO NAIROBI
MAIN ENTRANCE
N
EAST GATE
1 mile
NAIROBI
NATIONAL
PARK
TO MAGADI
TO MOMBASA
Study Area B
Park road (not all shown)
Park boundary
Major road
CHEETAH GATE

FIG. 4

Study Area B in Nairobi National Park.

One square mile in area.

Study Area B.


LEGEND
Forest
Bushland
Grassland
Road
Dam
B
N
200 m.
220 yds.
← MAIN GATE
PARK BOUNDARY
S. Mokoyeti River
A
B
C

Forest species include:

Croton megalocarpus	Brachylaena hutchinsii
Olea africana	Diospyros abyssinica
Canthium schimperanium	Teclea simplicifolia
Phyllanthus discoides	Ficus thonningii .

Bushland and thicket includes:

Croton dichogamous	Grewia similis
Grewia tembensis	Vangueria apiculata
Englerodaphne subcordata	Lippia ukambensis
Lantana viburnoides	Scutia myrtina

Patches of grassland with dense stands of sedges and herbs are found on the vlei soils in S.A.B. Species include:

Cyphia glandulifera	Commelina species
Indigofera schimperi	Oldenlandia wiedemannii
Sida ovata	Dibrachnostylus kaessneri
Themeda triandra	Bothriochloa insulpta
Panicum poaeoides	Digitaria gazensis

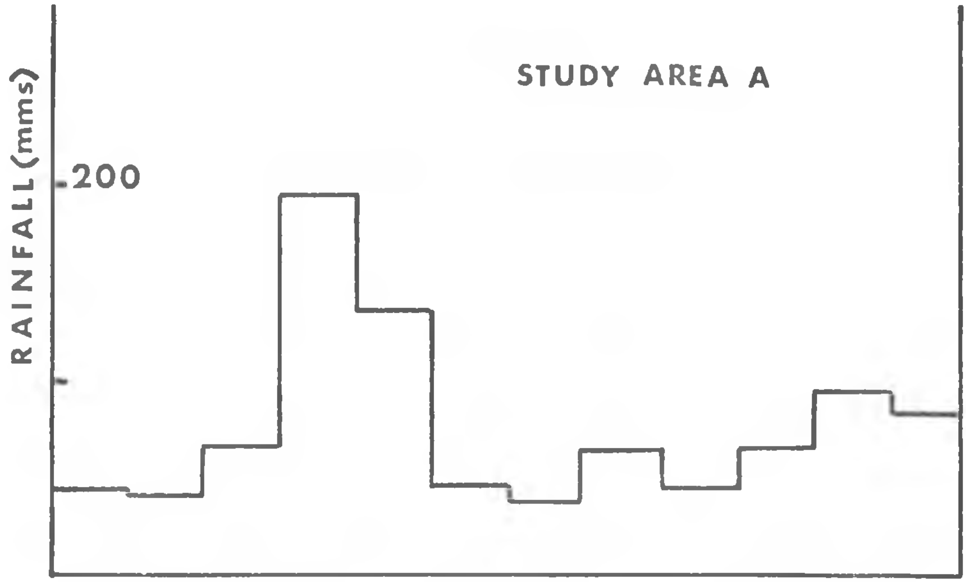
Rainfall.

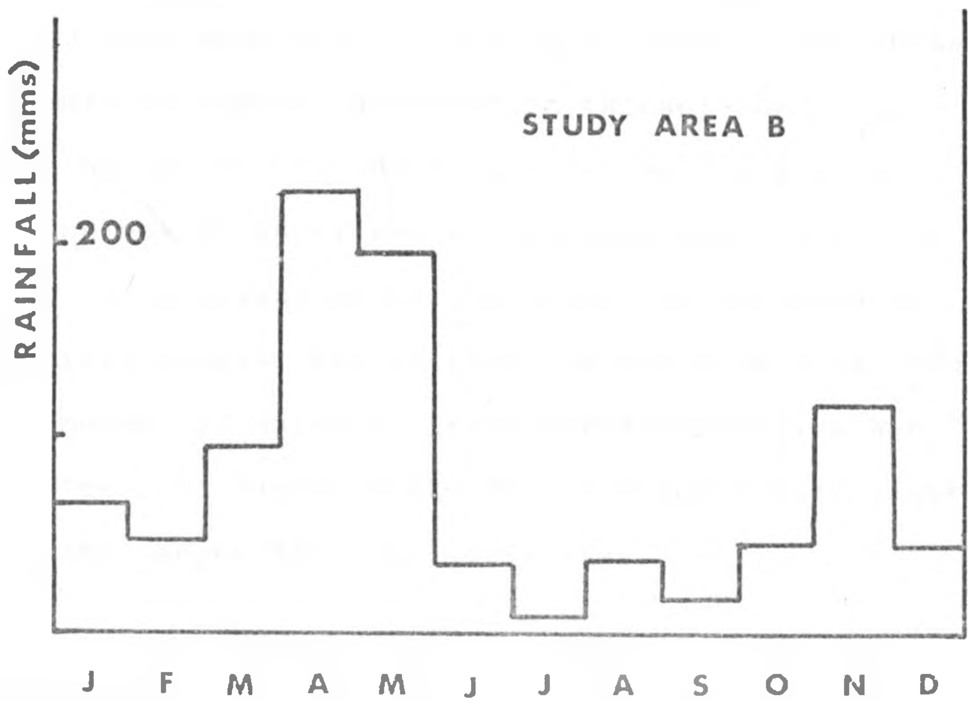
The mean monthly rainfall from 1962 to 1969 is given in Fig. 5.

STUDY AREA A
200

FIG. 5

Rainfall in Study Area A and Study Area B.


STUDY AREA A
RAINFALL (mms)
200


STUDY AREA B
RAINFALL (mms)
200
J F M A M J J A S O N D

CHAPTER 3

GROWTH AND DEVELOPMENT

Method

During the period October 1968 to August 1969 47 females and 16 males were collected from S.A.A. with the permission of the respective estate managers and the Kenya Game Department (see Acknowledgements). Early attempts to collect during daylight hours were unsuccessful due to a tendency for these animals to remain concealed in thickets until late evening and night. Shooting after dark using an iodine quartz spotlight proved much more effective with the greatest number of sightings recorded on moonless nights. Two to five females were collected per month and males at irregular intervals. A Winchester .264 Magnum rifle with x 2 telescopic sight was the weapon used for collecting.

It was assumed that all animals collected belonged to the same population. Females were usually alone when sighted and were shot whenever the opportunity arose. If in groups of two or more the animal on the left of the first group, right of the second etc. was collected irrespective of size. It was hoped that by shooting in this way a random sample of the population with respect to age would be collected.

After noting the state of lactation in females the reproductive tract with ovaries and foetuses when present were placed in 4% formol saline. Testes were removed from males and similarly preserved. Skins were removed immediately and salted prior to handing in to the Game Department. Blood samples and intestinal tracts were occasionally collected for research not connected with this thesis, otherwise the remaining intestine was discarded. Heads were placed in a cold storage room for one to two days after which time the eye lenses were removed for fixing in 10% formalin. Skulls were cleaned by the Department of Prehistory (see Acknowledgements).

After seven days in formalin the eye lenses were cleaned of all extraneous tissue and placed in an oven at 110°C - 120°C for drying. Drying time varied but always exceeded seven days. The temperature also varied because the oven was in constant departmental use. The lenses were cooled to room temperature in a desicator before weighing. Weights were taken at intervals of several days until constant to 0.001 gms. All uteri except obviously non-parous ones (see Reproduction) were examined for foetuses. The foetuses were then weighed alone, i.e. without membranes or fluids, to 0.5 gms and the crown rump length measured with the animal in the inter uterine position. The left eye lens was removed from each and treated as those above. A number of ovaries were sectioned and stained with H & E in order that corpora albicantia could be counted. It was found that these were persistent for too short a time and therefore this line of research was abandoned.

a) Growth - prenatal

Foetal development will be discussed in greater detail in the section headed 'Reproduction' with regard to calving.

During the eleven months of collection 24 foetuses were obtained ranging in weight from 7 to

4030 gms. The larger, fully formed foetuses agreed closely with the birth weights quoted by Hanover Zoo of 3375 gms for females and 4175 gms for males.

Foetal sex ratio was unity, 12 males to 12 females.

Using the method of Huggett and Widdas (1951) an estimate of foetal growth rate can be calculated for comparison with other mammals. The method requires a known birth weight and gestation period and those supplied by Hanover Zoo (see Gestation) were used. It assumes that during the latter part of pregnancy when the foetus has acquired environmental stability due to placental circulation there is a linear relationship between the cube root of weight and the time from conception. As well as giving an estimate of the growth velocity therefore this method also enables an estimate of foetal age to be calculated.

Specific foetal growth velocity: $a = \frac{W^{\frac{1}{3}}}{(t-t_0)}$

W = weight at birth

t = time in days from conception

t_o = numerical value, of no biological significance, estimated from analogy with other mammals of which known age foetuses are available. For mammals with gestation period 100 - 400 days t_o = gestation period x 0.2.

At birth: $a = \frac{16.10}{180 - 36}$ $= 0.112$

W = 4175 gms
t = 180 days
t_o = 180 x 0.2
= 36 days

This constant is low in the range of known values for Bovidae (sheep 0.147, eland 0.17, 'deer' 0.14, goat 0.12) according to Huggett and Widdas, and wildebeest 0.128 for 1965, 0.124 for 1964, Watson (Ph.D. thesis, 1967).

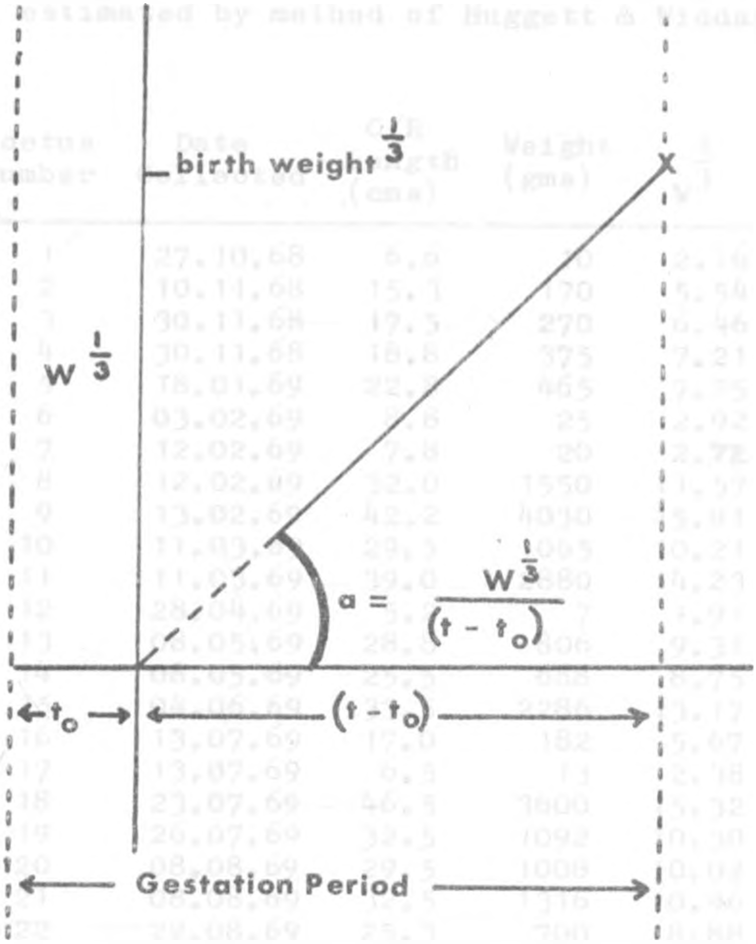
Ages calculated by the same method are given in Table 1. For this calculation male and female foetuses were grouped together because of the small sample being considered.

TABLE 1

FIG. 6

Illustration of way in which birth weight and gestation time can be used to determine a, specific foetal growth constant, and fowtal age. After Huggett and Widdas (1951).

See text for details.



birth weight $^{\frac{1}{3}}$
$W^{\frac{1}{3}}$
X
$a = \frac{W^{\frac{1}{3}}}{(t - t_o)}$
t_o
$(t - t_o)$
Gestation Period

TABLE 1

Foetus data collected from Study Area A with ages estimated by method of Huggett & Widdas (1951)

Foetus Number	Date Collected	C/R Length (cms)	Weight (gms)	$W^{\frac{1}{3}}$	Age (days)
1	27.10.68	6.6	10	2.16	55.28
2	10.11.68	15.3	170	5.54	85.46
3	30.11.68	17.5	270	6.46	93.68
4	30.11.68	18.8	375	7.21	100.37
5	18.01.69	22.8	465	7.75	105.19
6	03.02.69	8.8	25	2.92	62.07
7	12.02.69	7.8	20	2.72	60.28
8	12.02.69	32.0	1550	11.57	139.30
9	13.02.69	42.2	4030	15.91	178.05
10	11.03.69	29.5	1065	10.21	127.16
11	11.03.69	39.0	2880	14.23	163.05
12	28.04.69	5.2	7	1.91	53.05
13	08.05.69	28.8	806	9.31	119.12
14	08.05.69	25.5	668	8.75	114.08
15	04.06.69	33.5	2286	13.17	153.58
16	13.07.69	17.0	182	5.67	86.62
17	13.07.69	6.5	13	2.38	56.71
18	23.07.69	46.5	3600	15.32	172.78
19	26.07.69	32.5	1092	10.30	127.96
20	08.08.69	29.5	1008	10.02	125.46
21	08.08.69	32.5	1316	10.96	133.85
22	22.08.69	25.3	700	8.88	115.28
23	22.08.69	18.0	168	5.52	85.28
24	22.08.69	45.0	3500	15.18	171.53

b) Growth - postnatal

The aspects of growth and development considered were those that would be relevant in constructing age schedules. Previous work on ageing mammals has utilized changes in dentition, eye lenses, epiphyseal cartlidges, reproductive organs etc. Body weights and gross size are confused by ecological and genetical factors and are therefore seldom used. For this study changes in dentition and eye lens weight were recorded plus horn size in males.

(i) Horn size.

Data on horn eruption and change in size and shape with age has been supplied by Hanover Zoo. Personal observations in Nairobi Orphanage and S.A.B. support these data.

The horns first appear at 10 to 12 months and grow to a maximum of about 50 cm. The longest recorded by Rowland Ward was 22 inches (55 cm). They remain circular in cross section up to about 8 cm, 15 months of age, and then a ridge begins to develop along the length. When approximately 20 cm long, 18 months of age, the horns begin to twist in a manner characteristic of the tragelaphids. At 25 months when approximately 25 cm long the horns have undergone half a twist and they are fully tortile by 30 to 36 months when greater than 30 cm in length.

PLATE 2

Illustrating horn shape and size

For Male Age Groups (1) and (2).

PLATE 2

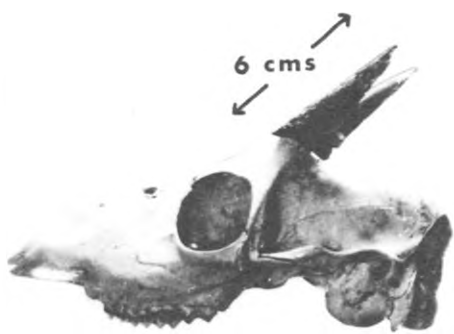
Illustrating horn shape and size

for Male Age Groups (1) and (2).

PLATE 2 ILLUSTRATING MALE HORN SIZE AND SHAPE.

Age Group (1)	Age Group

Cross section of horn sheath circular. No ridges or signs of torsion.



(2)

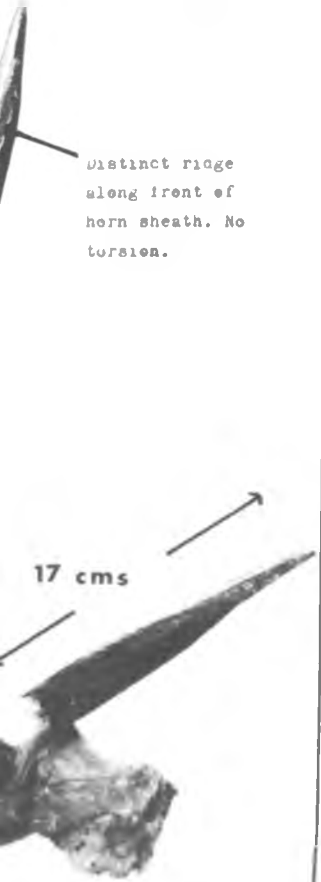


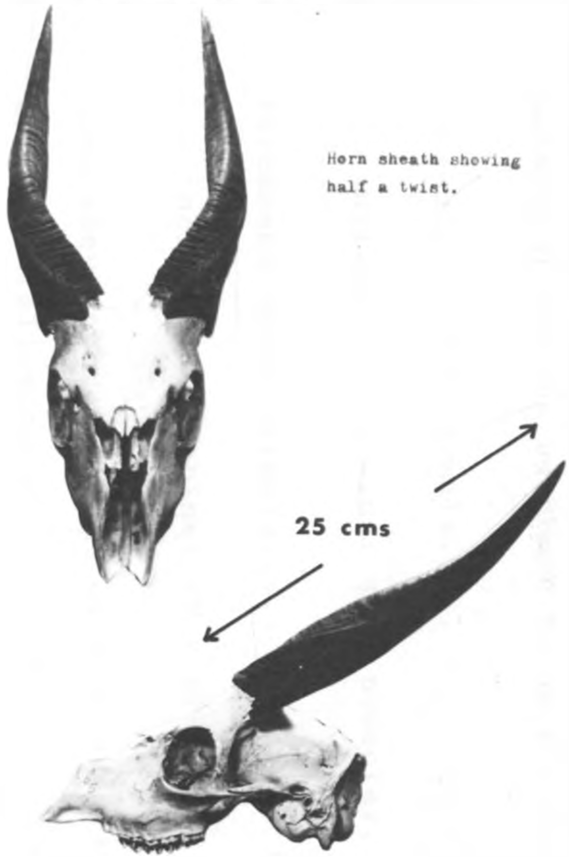
PLATE 3

Illustrating horn shape and size

for Male Age Groups (3) and (4).

PLATE 3 ILLUSTRATING MALE HORN SIZE AND SHAPE.

Age Group (3)	Age Group (4)



Horn sheath showing half a twist.

Torsion complete. Horn sheath showing one full twist.

Males can therefore be placed in age groups (0) to (4) according to horn size (see plates 2 & 3).

TABLE 2

Changes in horn length with age

Age Group	(0)	(1)	(2)	(3)	(4)
Length (cm)	0	1 - 8	9 - 18	19 - 30	30 +
Age (months)	0 - 12	13 - 15	16 - 20	21 - 30	30 +

Dentition

Dentition for the bushbuck is as follows:

Deciduous tooth formula..... $i\ \frac{0}{3}$; $c\ \frac{0}{1}$; $pm\ \frac{3}{3}$

i = incisor; c = canine; pm = premolar.

Permanent tooth formula..... $I\ \frac{0}{3}$; $C\ \frac{0}{1}$; $PM\ \frac{3}{3}$: $M\ \frac{3}{3}$

I = incisor; C = canine; PM = premolar; M = molar.

(The above abbreviations will be used throughout. (E) following any such abbreviation infers that the tooth in question is in a state of eruption).

The state of eruption and consequent wear of the teeth of females collected in S.A.A. is shown in Table 3. Using these changes in dentition the 46 animals have been placed in age groups I to VIII.

TABLE 3

Radiographs were taken of incisors, molars and whole mandibular dental arches. It proved easiest to X-ray the incisors and all measurements were recorded as ratios in order to eliminate discrepancies due to differing distances between subject and negative. This way measurements from different radiographs could be compared.

It was found that the pulp cavity decreases in width with age. The ratio of the outer tooth diameter (OW) to the diameter of the pulp cavity (IW) was therefore used as a second criterion for ageing. These measurements were taken at the waist between root and crown.

Attempts were made to obtain known age skulls or radiographs of them. This would have provided a method of accurately assigning chronological ages

TABLE 3

The state of dental eruption and consequent wear has been used to separate the females collected in Study Area A into the Female Age Groups I to VIII.

TABLE 3

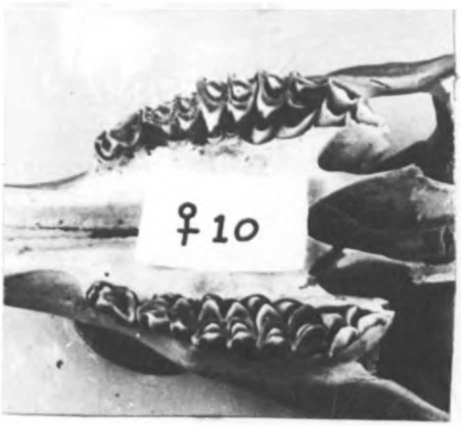
Number in sample	ERUPTION Premolars I 2 3 — Molars I 2 3	Age group
1	pm pm pm — M	I
3	pm pm pm — M M(E)	II
4	pm pm pm — M M	
I	pm pm pm — M M M(E)	
3	PM pm pm — M M M	
I	PM pm PM — M M M	III
I	PM PM pm — M M M	
	WEAR	
7	Negligible wear on any teeth.	
7	Infundibula on all molariform teeth. Cusps prominent on molars	IV
9	Infundibulum gone from Ist. premolar. Wear considerable on all premolars.	V
4	Infundibulum on Ist. molar reducing from crescent to a spot. Cusps flattening on all molars.	VI
4	Front infundibulum on Ist. m molar gone	VII
I	Both infundibula on Ist. molar gone.	VIII

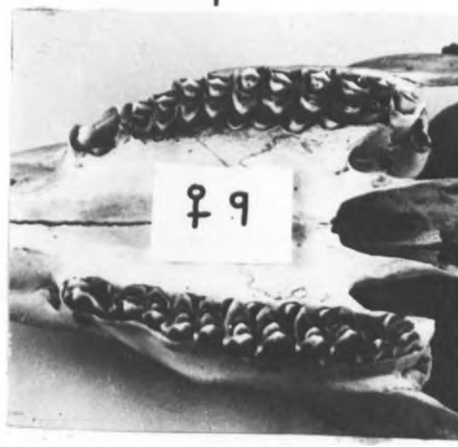
PLATE 4

Showing state of eruption and wear in maxillary dentition of females in Age Groups I - IV.

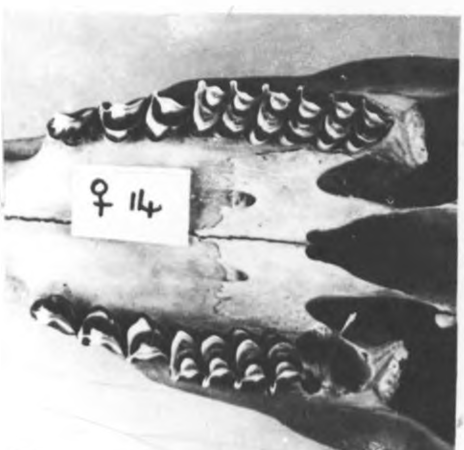
MAXILLARY DENTITION OF FEMALE AGE GROUPS II - IV

AGE GROUP II





AGE GROUP III



AGE GROUP IV

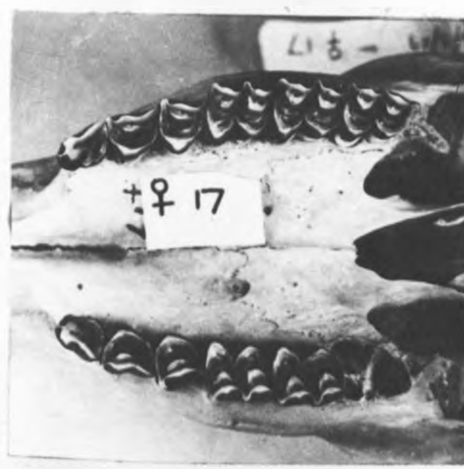
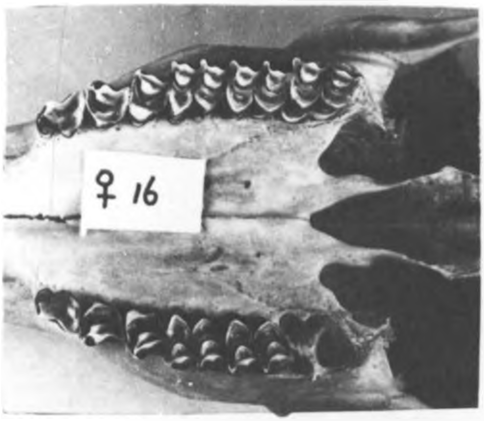


PLATE 5

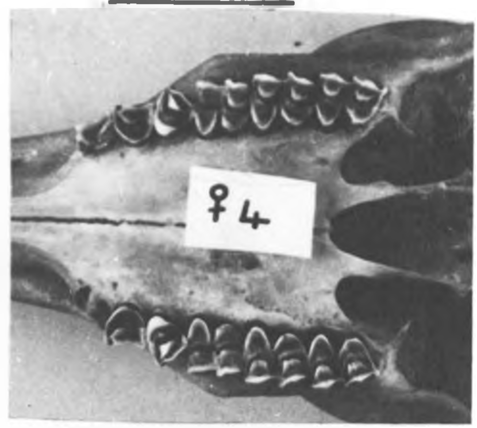
Showing state of eruption and wear in maxillary dentition of females in Age Groups V - VIII.

MAXILLARY DENTITION OF FEMALE AGE GROUPS V - VIII

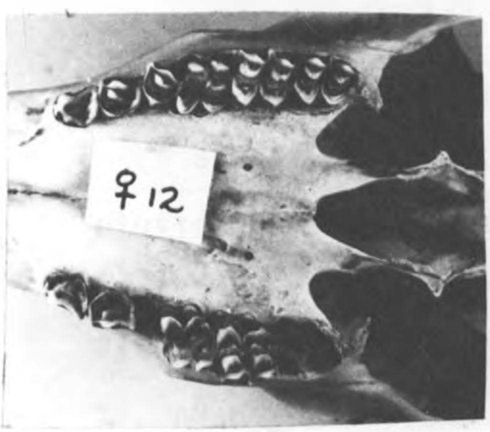
AGE GROUP V



AGE GROUP VI



AGE GROUP VII



AGE GROUP VIII

to the skulls collected. The only skull obtained was 16 days and therefore too young to be of any real value. If such skulls become available at a future date radiography would be a method of ageing live, tranquilised animals.

TABLE 4

TABLE 5

Mean $\frac{OW}{IW}$ ratio for male age groups (1) - (4)

Age group	(1)	(2)	(3)	(4)
Mean $\frac{OW}{IW}$	1.573	1.822	2.558	2.874

See also Fig. 7 showing the female $\frac{OW}{IW}$ ratio plotted against the female age groups. This shows a steady increase in the ratio up to age group IV after which the pulp cavity width decreases rapidly. Assuming the curve continued as shown in Fig. 7 the ratio would reach infinity soon after age group VIII, indicating closure of the root. If root closure cause loss of teeth this would impose a physiological logevity on the animals, corresponding

TABLE 4

Mean $\frac{OW}{IW}$ ratio for female age groups II - VIII

Age group	II	III	IV	V	VI	VII	VIII
Mean $\frac{OW}{IW}$	1.688	2.119	2.413	3.477	5.261	7.289	10.04
Standard deviation	0.164	0.394	0.520	1.449	1.964	1.52	-
No. in sample	8	7	7	9	3	2	1

FIG. 7

Ratio of measurements of female insicors taken from radiographs plotted against female age groups.

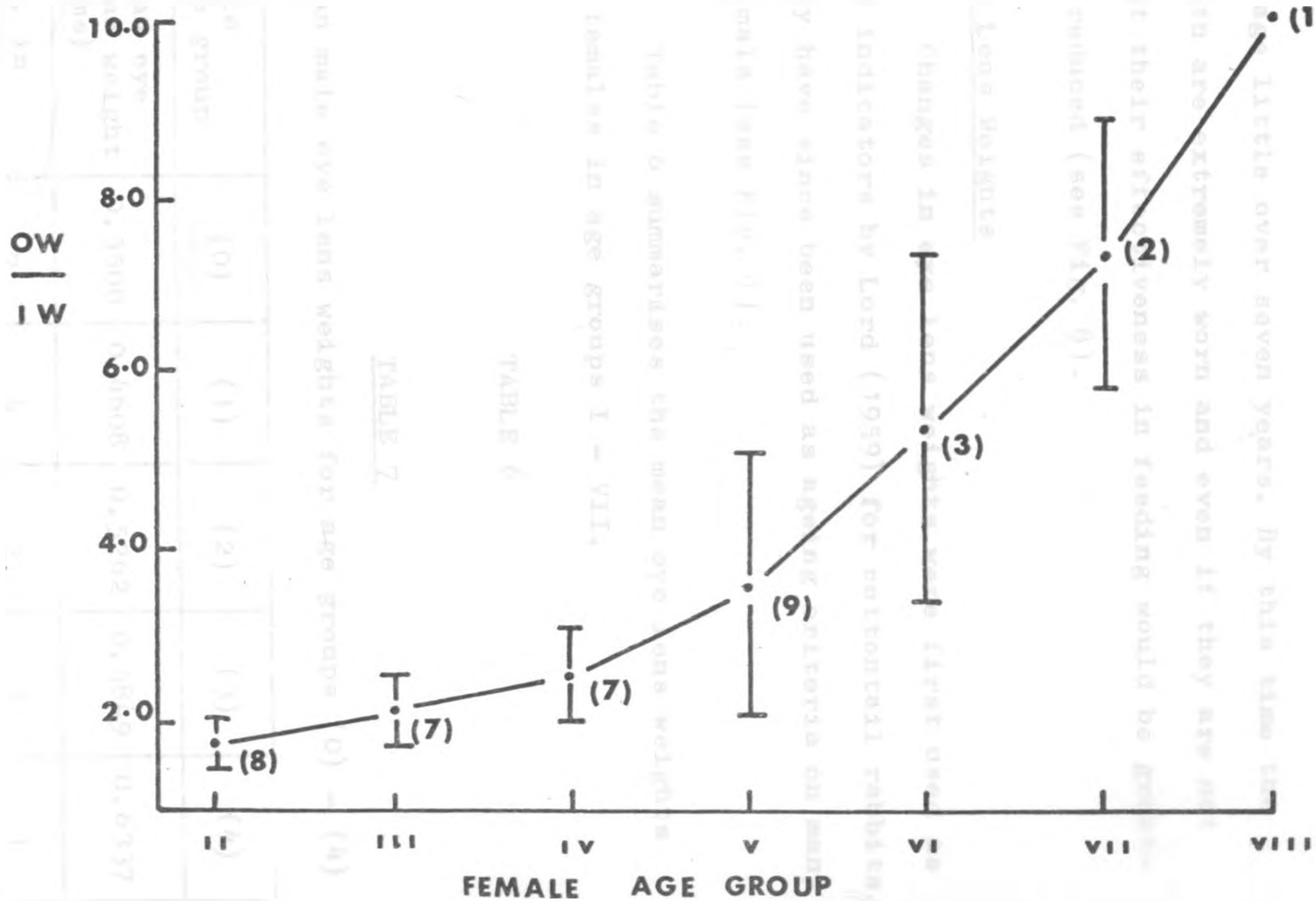
Outer diameter of insicor ... OW

Inner diameter (diameter of pulp cavity) ...IW

OW remains fairly constant through life. IW decreases proportional to age.

$\frac{OW}{IW}$ increases proportional to age.

The standard deviation for each mean ratio is indicated and also the number in parenthesis in each sample.



OW
IW
10·0
8·0
6·0
4·0
2·0
(1)
(2)
(3)
(9)
(7)
(7)
(8)
II
III
IV
V
VI
VII
VIII
FEMALE AGE GROUP

to age little over seven years. By this time the teeth are extremely worn and even if they are not lost their effectiveness in feeding would be greatly reduced (see Fig. 8).

Eye Lens Weights

Changes in eye lens weights were first used as age indicators by Lord (1959) for cottontail rabbits. They have since been used as ageing criteria on many animals (see Fig. 9).

Table 6 summarises the mean eye lens weights of females in age groups I - VII.

TABLE 6

TABLE 7

Mean male eye lens weights for age groups (0) - (4)

Male age group	(0)	(1)	(2)	(3)	(4)
Mean eye lens weight (gms)	0.3500	0.4608	0.5262	0.5849	0.6337
No. in sample	7	4	2	1	1

TABLE 6

Mean eye lens weights for female Age Groups I - VIII

Female Age Group	I	II	III	IV	V	VI	VII	VIII
Mean eye lens weight (gms)	0.2348	0.4652	0.5656	0.6157	0.6337	0.7072	0.7491	-
Number in sample	1	11	9	7	9	4	4	-

FIG. 8

Measurement of female insicors taken from radiograph plotted against female age groups.

Root length (cms.) ... R

Crown height (cms.) ... C

A – B ... Crown and root both growing

B – D ... Root constant in length

B – C ... Crown increasing in length

C – D ... Crown decreasing through wear

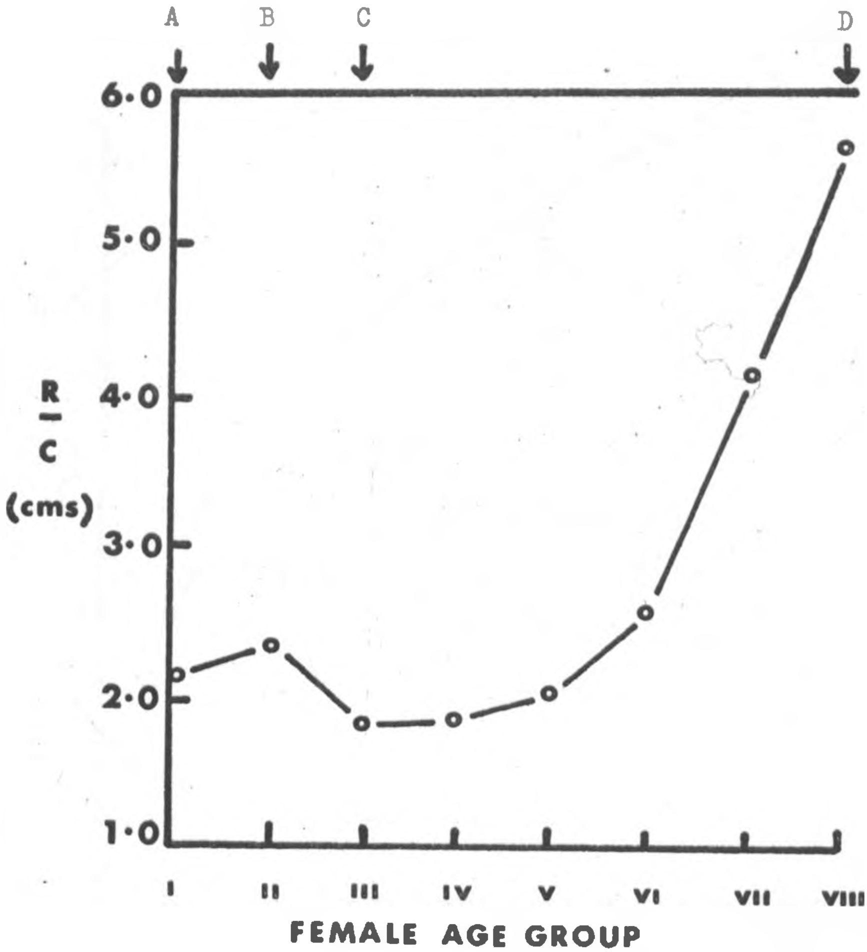

A
B
C
D
6·0
5·0
4·0
3·0
2·0
1·0
R
C
(cms)
I
II
III
IV
V
VI
VII
VIII
FEMALE AGE GROUP

FIG. 9

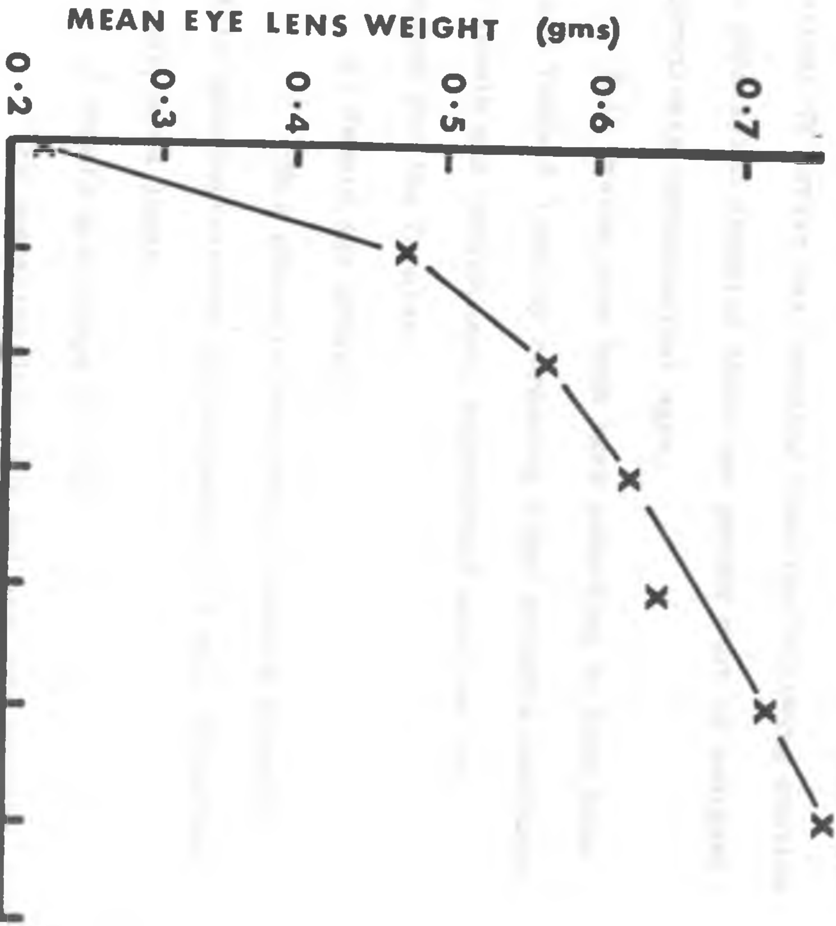
Changes in female eye lens weight plotted against female Age groups.

FIG. 9

Changes in female eye lens weight plotted against female age groups.

I II III IV V VI VII

FEMALE AGE GROUP


MEAN EYE LENS WEIGHT (gms)
0·2
0·3
0·4
0·5
0·6
0·7

Ageing

The animals collected from S.A.A. have been placed in age groups according to dental and eye lens characteristics. To derive real meaning from the following section on population dynamics these age groups must be assigned approximate chronological ages.

Male groups have been aged according to horn size (see Table 2) and by comparing other criteria mentioned in Growth and Development, approximate ages can be deduced for the females.

a) Female Age Group I

This group is composed of newborn animals and is underrepresented in the sample. It will therefore be calculated later.

b) Female Age Groups II - IV

By comparing dentition and eye lens measurements for males and females it is apparent that there is greatest similarity between female Group II and male Group (1); female Group III and male Groups (2) and (3); female Group IV and male Group (4).

TABLE 8

TABLE 8

Comparing eye lens weights and dental characteristics of female Age Groups II—IV with male Age Groups (1)-(4) ($\frac{OW}{IW}$ see text and Fig. 7)

Female			Male			
Age Group	Mean eye lens weight (gms)	Mean $\frac{OW}{IW}$	Age Group	Mean eye lens weight (gms)	Mean $\frac{OW}{IW}$	Chronological age (years)
II	0.4652	1.688	(1)	0.4608	1.573	$\frac{1}{2}$ - $1\frac{1}{2}$
III	0.5656	2.119	(2&3)	0.5555	2.180	$1\frac{1}{2}$ - $2\frac{1}{2}$
IV	0.6157	2.413	(4)	0.6337	2.874	$2\frac{1}{2}$ - $3\frac{1}{2}$

c) Female Age Groups V - VIII

Chronological ages can be derived for these groups by extrapolation in Figs. 7 and 9. The graphs show reasonably smooth curves of $\frac{OW}{IW}$ and eye lens weights both plotted against female age groups. By assigning the derived pivotal ages 1,2 and 3 years for female Age Groups II, III and IV in Figs. 7 and 9 the suggested pivotal ages for Age Groups V, VI, VII and VIII are 4, 5, 6 and 7 years respectively.

TABLE 9

Suggested chronological ages for females collected in Study Area A.

Female Age Group	I	II	III	IV	V	VI	VII	VIII
Pivotal Age (yrs)	0	1	2	3	4	5	6	7
Number in sample	1	11	9	7	9	4	4	1

Although considerable effort was spent trying to obtain known age skulls only one, aged sixteen days, was found. Attempts to devise a definitive ageing method were therefore abandoned and the age categories used here are only approximate. The Age Groups I -IV are

c) Female Age Groups V - VIII

Chronological ages can be derived for these groups by extrapolation in Figs. 7 and 9. The graphs show reasonably smooth curves of $\frac{OW}{IW}$ and eye lens weights both plotted against female age groups. By assigning the derived pivotal ages 1,2 and 3 years for female Age Groups II, III and IV in Figs. 7 and 9 the suggested pivotal ages for Age Groups V, VI, VII and VIII are 4, 5, 6 and 7 years respectively.

TABLE 9

Suggested chronological ages for females collected in Study Area A.

Female Age Group	I	II	III	IV	V	VI	VII	VIII
Pivotal Age (yrs)	0	1	2	3	4	5	6	7
Number in sample	1	11	9	7	9	4	4	1

Although considerable effort was spent trying to obtain known age skulls only one, aged sixteen days, was found. Attempts to devise a definitive ageing method were therefore abandoned and the age categories used here are only approximate. The Age Groups I -IV are consequently left at pivotal ages 0 - 3 years since this is adequate for this thesis Subdivision of these groups would require a selection of known age skulls.

Wilson and Child (1964) record a nineteen month old female having well developed third molars and deciduous premolars. This would be placed, according to the above method, in Age Group III which includes animals from eighteen to thirty months.

Longevity

Crandall records the age at death of a female bushbuck at Chicago Zoo as twelve years, seven months and ten days.

Flower records the age at death of a female at London Zoo as nine years, three months and fourteen days.

The decreasing pulp cavity width mentioned previously under Dentition suggests a possible physiological longevity in the wild of little more than seven years.

CHAPTER 4

REPRODUCTION

Due to lack of data this section remains rather hypothetical. An attempt has been made to estimate lactation, gestation, post partum periods and age at maturity but these times are based on only limited observations and records.

Gestation

Kenneth (1947) recorded the gestation period of bushbuck as 214 to 225 days. This period has since been quoted by Zuckerman (1953) and Asdell (1947). A figure of seven months was suggested by Stevenson-Hamilton (1947).

According to records of births supplied by Bindernagel (pers. comm.) in Nairobi Orphanage the reproductive history of one female bushbuck was:

1st. calf ....March 18. 1965

2nd. calf ....Sept. 1965

3rd. calf ....May 23. 1966

The exact date of the second calving is not known but assuming it occured at the end of Sept. the maximum gestation period possible would be 197 days minus the post partum interval. This suggests a gestation period in the region of 6 months with a short post partum interval.

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Other records from Nairobi Orphanage supplied by the rangers include the approximate dates at which the only male in the bushbuck enclosure was seen mounting a female. This was apparently repeated several times over a few days around Aug. 15th 1968. A calf was born Jan. 29th 1969 and assuming these two occurences are related the gestation period would be in the region of 165 days.

Dr. Dittrich (pers. comm.) states that the gestation period is 179 to 180 days from records of reproduction in Hanover Zoo.

From the information available a figure of 180 days appears to be a reasonable estimate of the gestation period and this figure will be used for any calculations in this thesis.

Calving

Whilst collecting foetuses in SAA no occurence of twins were recorded.

Brand (1963) suggests that calving occurs all year round. Seasonal distribution of pregnant females gives no indication of any seasonal cycle but more detailed analysis of foetal size does.

Using the method of Huggett and Widdas (1951) (see Growth and Development) to estimate foetal age, the number of foetuses conceived or born each month in S.A.A. can be calculated, see Fig. 10

Being on the equator, seasonal differences in day length and temperature are unimportant. Rainfall shows a marked seasonality and so in Fig. 10 mean monthly rainfall from 1962 to 1969 are shown along with the frequency of births and conceptions.

Peaking occurs in births just before the long rains of April and again before the short rains in November. This would give the newborn calves maximum available protein in the herbiage at the time they begin feeding on vegetation.

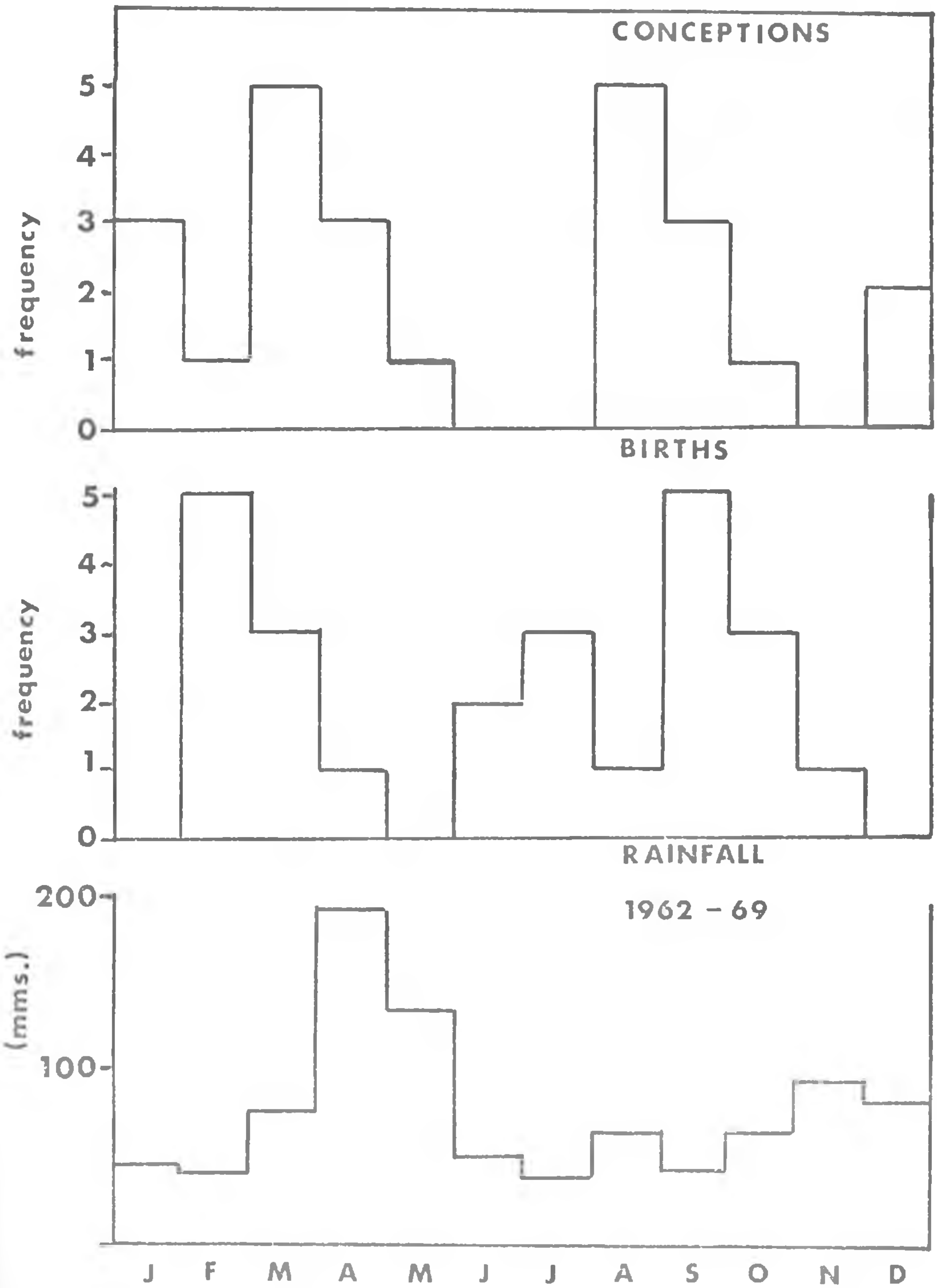
If the same treatment is applied to the data of Wilson & Child (1964), who state that bushbuck are non seasonal, peaks occur for frequency of births in December and to a lesser extent April.

The restricted season is less marked than in some domesticated animals or wildebeest (Connochaetes taurinus) where growth velocity has been calculated by Huggett and Widdas, and Watson. As mentioned previously, (see Growth & Development) the foetal growth rate of bushbuck is lower than sheep and wildebeest. This rate may reflect the seasonality of mammals by increasing to accomodate the environmental conditions when birth at a particular time of year is most

CONCEPTIONS
BIRTHS

FIG. 10

Relation of conceptions and births to mean monthly rainfall in Study Area A.


CONCEPTIONS
frequency
5
4
3
2
1
0
BIRTHS
frequency
5
4
3
2
1
0
RAINFALL
1962 - 69
(mms.)
200
100
J F M A M J J A S O N D

suitable. If this were the case, the foetal growth constant would be greater for seasonal animals than non seasonal ones. A markedly non seasonal animal would be expected to have a foetal growth rate less than that calculated for bushbuck.

Using the data of Robinette and Child 1964 for lechwe, (Kobus leche Gray) [illegible] seasonal, a foetal growth constant of 0.098 can be calculated. This agrees with the above hypothesis.

Lactation

The oldest calf seen suckling in Nairobi Orphanage was 5 months and 8 days old.

J.W.A. Brook (Johanesburg Zoo, pers.comm.) states that suckling lasts approximately 8 months.

Since these are the only records available, a lactation time derived from them would be suspect. They suggest a duration of 6 to 7 months.

TABLE 10

The mature females collected in S.A.A. were in varying stages of pregnancy and/or lactation.

	Lactating	Non lactating	Total
Pregnant	9 (25.7)	15 (42.8)	24
Non pregnant	8 (22.9)	3 (8.6)	11
Total	17	18	35

(25.7) represents the number, 9, as a percentage of the total mature females.

From Table 10, it is evident that 68.5% of the mature animals collected were pregnant, and 22.9% were non pregnant but lactating, thus indicating that 91.4% of the mature animals had been successfully mated within a year of the date of collection.

Post partum interval

Of the 24 foetuses collected in S.A.A., the largest found in a lactating female was 355 gms, 100 days old. Assuming a lactation period of 6 to 7 months, the post partum interval in this animal would have been 80 to 110 days. The mean age of all foetuses collected from simultaneously pregnant and lactating females was 75 days giving a mean post partum interval of 105 to 130 days.

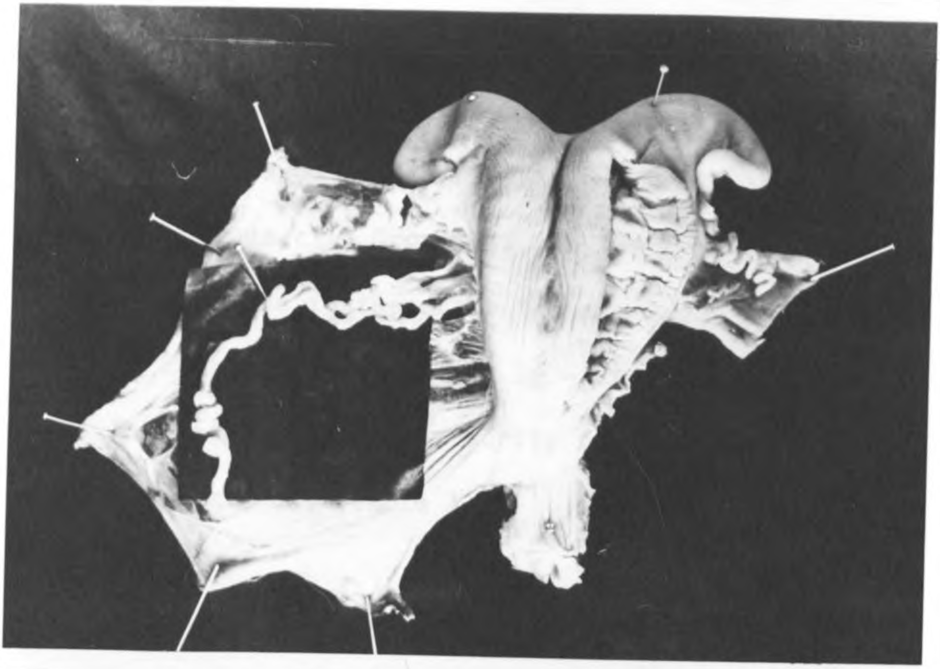
This interval can be shorter as evidenced by the record of two births within 197 days from the same animal in Nairobi Orphanage (see Gestation). The average minimum time between birth and the next conception would, however, appear to be in the region of 3 to 4 months.

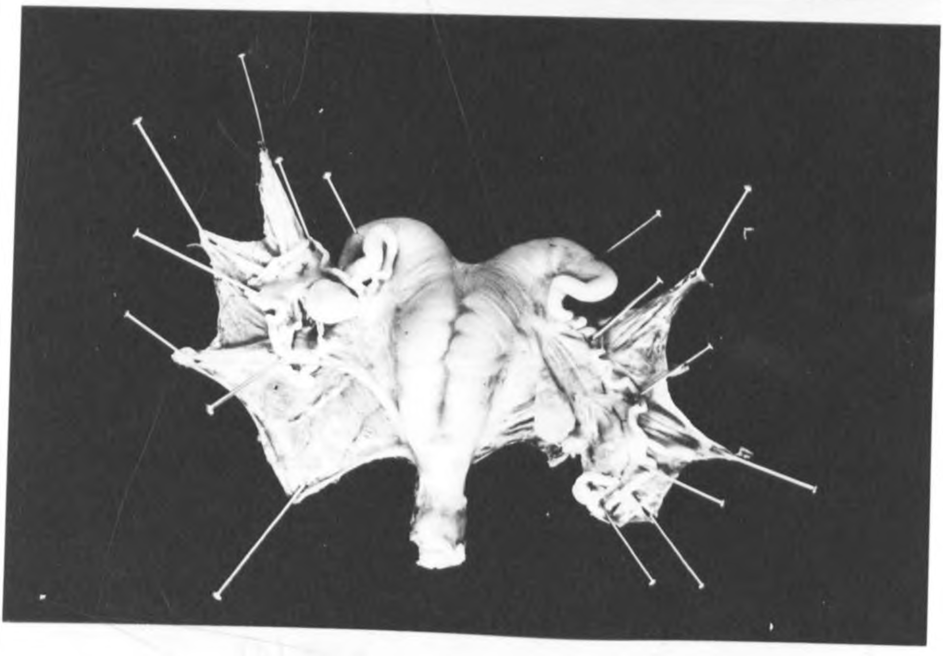
Maturity (a) Female

Females collected were examined for the presence of foetuses. When absent the state of the uterus and uterine arteries indicated whether the female had previously been pregnant or not. Non parous uteri (see Plate 6) are smooth walled and small, whilst after pregnancy and

PLATE 6

Uteri from a non parous female and (above) a female previously pregnant.
The non parous uterus is small and smooth walled whereas after pregnancy the walls become creased and the blood vessels convoluted.





consequent stretching they do not return to their original size but remain enlarged and show evidence of their post partum shrinkage in the wrinkled walls and convoluted arteries.

Only one Group II female was pregnant, the rest being non parous. In Group III all the females had been pregnant and this is therefore the age group during which maturity is reached, i.e. from 1½ - 2½ years.

Estimates of age at maturity received from other sources are given in Table 11.

TABLE 11

Some estimates of maturing age of female bushbuck.

Source of information	Birth date	Date of first calf	Age at first calving (months)
Frankfurt Zoo	27.8.1964	28.5.1967	27
Hanover Zoo	-	-	19
Nairobi Orphanage	18.3.1965	Feb. 1967	17

Taking a mean of all estimates of age at maturity, including the mean age of Age Group III i.e. 24 months, the figure derived is 21.7 months (S.D. 4.48).

(b) Male

Testes lengths and widths were recorded for all males collected in S.A.A. The contents of each vas deferens consequent stretching they do not return to their original size but remain enlarged and show evidence of their post partum shrinkage in the wrinkled walls and convoluted arteries.

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(b) Male

Testes lengths and widths were recorded for all males collected in S.A.A. The contents of each vas deferens was squeezed out and examined for sperm content. The presence of spermataozoa was taken to indicate sexual maturity.

From Age Group (1) onwards, sperm were found in all testes examined. At the same age there is a marked increase in testis size. It is assumed therefore, that males may be sexually mature from Age Group (1) i.e. approximately one year old.

The potential to breed at this early age does not necessarily mean that the possibility occurs. As shown later in Social Biology, the older males tend to prevent younger ones from mating. By maturing early the young males could supply a reservoir of breeding potential which might prevent possible wastage if an oestrous female were not detected by an adult male.

Early maturing is not uncommon in antelopes and cannot therefore be taken as a specific feature of bushbuck. The solitary nature of bushbuck may place greater importance on this feature since the possibility of an oestrous female escaping detection is probably higher than it would be for a more gregarious species where a male is constantly accompanying the females, for example, impala (Aepyceros melampus Lichtenstein).

TABLE 12

Condition of testes from male bushbuck collected in Study Area A.

Age Group	Mean testis measurement (cms)		Number in sample	Number with sperm +ve.
	length	width		
(0)	3.33I	I.448	7	0
(I)	5.272	2.404	4	4
(2)	6.I62	2.870	3	3
(3)	6.2I2	2.928	I	I
(4)	7.050	3.43I	I	I

CHAPTER 5

POPULATION DYNAMICS

A sample of 46 female bushbuck was collected from S.A.A. between Oct. 1968 and Aug 1969. By shooting all solitary females as they were encountered, regardless of size, it was hoped to acquire a random selection of the population with regard to age. To eliminate any behaviourism with mother and young the left animal was collected from the first group, the right from the second and so on alternately, again disregarding size.

The skulls have been aged and they represent the age structure of the female population.

Age Group	I	II	III	IV	V	VI	VII	VIII
Number in sample	1	11	9	7	9	4	4	1

A few males were collected but the numbers were insufficient to estimate male dynamics.

Due to the habit of female bushbuck of concealing their young for the first few weeks of life, the newborn age group in under-represented and must be calculated (see Recruitment).

Recruitment

The female age specific fecundity will be calculated later (see Population Parameters). The results will, however, be used here in order to calculate the number of newborn animals expected from the sample, taking this sample as a cohort. The female age specific fecundity m_x multiplied by the number in each mature group will give the number of newborn expected from each group. Summing these gives the total expected natality.

Age Group	I	II	III	IV	V	VI	VII	VIII
m_x	0.00	0 091	0.777	0.428	0.555	1.000	0.750	1.000
No. in sample l'_x	1	11	9	7	9	4	4	1
$l'_x m_x$	0.00	0.993	6.993	2.996	4.995	4.000	3.000	1.000

$$\sum l'_x m_x = 23.977$$

Assuming a stable population, the number of newborn expected from this cohort is 24.

The final age distribution would include one very young animal from the collected sample in Age Group I leaving eleven in Age Group II.

Age Group	I	II	III	IV	V	VI	VII	VIII
Number in sample	24	11	9	7	9	4	4	1

The total number in the cohort is therefore 69.

Mortality

To attain the age distribution above, a certain number of animals must die between age groups leaving the number surviving to each successive group. Mortality is therefore proportional to age distribution. From a knowledge of mortality the female life table for the population in S.A.A. has been constructed.

It is usual to construct a life table assuming a cohort of 1000 so the number dying d_x in each age group from a cohort of 1000 would be:

Age Group	I	II	III	IV	V	VI	VII	VIII
d_x	348	159	131	101	131	58	58	14

The mortality rate, i.e. the fraction of those living at the beginning of each age interval that die during the interval, is q_x. Expressed on 1000 basis, $1000\, q_x = \frac{1000\, d_x}{l_x}$

Survivorship

Survivorship data assumes that all animals in the cohort have reached age 0 i.e. birth. The number d_x dying in successive age groups are then subtracted to give the numbers surviving at the beginning of each group l_x.

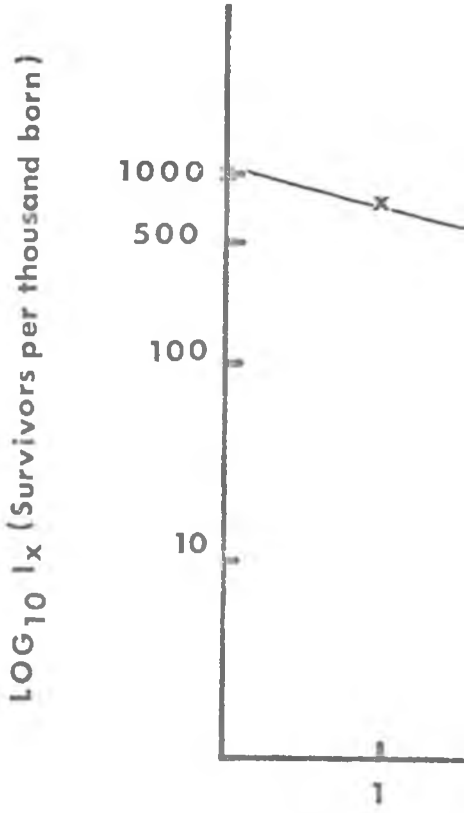
Age Group	I	II	III	IV	V	VI	VII	VIII
l_x	1000	652	493	362	261	130	72	14

A survivorship curve is obtained by plotting log l_x against pivotal ages 1, 2, 3, etc.. The curve in fig. 11 shows an even mortality rate from birth to Age Group V. From this age of four years onwards, there is a decreasing chance of survival with very heavy mortality after six years.

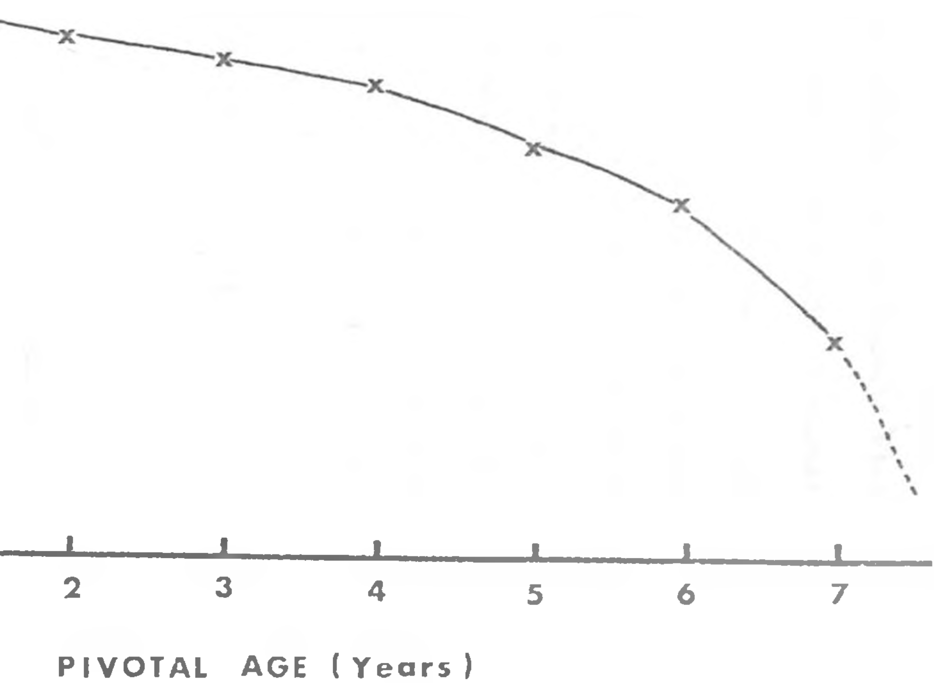
Survivorship curves have been constructed for Dall Sheep (<u>Ovis dalli</u>) Murie (1944) and wildebeest Watson (1967). Both of these show an initial period of heavy mortality amongst the calves. Bushbuck tend to show greater parental care than either of these other two animals. This, together with cryptic colouration as a predator escape mechanism, may account for the relatively low calf mortality. Concealment would be as effective with youngsters as with older animals, if not more so, due to the smaller size.

FIG. 11

Female survivorship curve obtained by plotting $\log_{10}$ values of surviving animals from original cohort of 1000 against pivotal age of female age groups.


LOG10 lx (Survivors per thousand born)
1000
500
100
10
1

FEMALE SURVIVORSHIP (l_x) CURVE



Dall Sheep escape their predators, mainly wolves, by herding, where all individuals stand an equal chance of being selected, or by flight to higher elevations where wolves are unable to follow. This latter escape mechanism may be the cause of calf mortality since the younger animals would have neither the experience nor the ability of the older sheep.

Wildebeest populations show a high degree of synchronisation in calving. The result is that many calves are present at the same time in a migrating herd. The greatest factor in calf mortality is abandonment; a calf that becomes separated from its mother has little chance of survival.

From birth to about five years there is a fairly constant survival ratio in bushbuck with an increasingly heavy mortality after this. This compares with Dall Sheep which suffer a drastic mortality rate after 9 years of age. Wildebeest show a fairly constant mortality rate throughout life after the initial heavy calf mortality.

Life expectancy

The mean life expectancy remaining for animals that have attained a given age x, can be calculated by measuring the area under the survivorship curve beyond x and dividing by the number of survivors. This gives the number of animal years remaining.

This can also be calculated from the life table by compiling an age structure Lx where:

$$Lx = \frac{l_x + l_{(x+1)}}{2}$$

By summing the animal years, i.e. successive values of Lx from older groups to younger giving successive values of Tx then life expectancy e_x is given by:

$$e_x = \frac{Tx}{l_x}$$

Age Group	I	II	III	IV	V	VI	VII	VIII
e_x	2.477	2.532	2.188	1.861	1.306	1.123	0.690	0.500

The female life table showing the entire dynamics is given in TABLE 13.

TABLE 13

Life table for female bushbuck in Study Area A (1968 / 69)

Age group	Pivotal age (years)	d'_x	l'_x	l_x	d_x	$1000q_x$	e_x
I	0	24	69	1000	348	348	2.477
II	1	11	45	652	159	244	2.532
III	2	9	34	493	131	266	2.188
IV	3	7	25	362	101	279	1.861
V	4	9	18	261	131	502	1.306
VI	5	4	9	130	58	446	1.123
VII	6	4	5	72	58	806	0.690
VIII	7	1	1	14	4	1000	0.500

d'_x is the number of bushbuck dead at pivotal age x
l'_x is the number of bushbuck alive at pivotal age x
d_x is the probable number of bushbuck dead at pivotal age x from a cohort of 1000
l_x is the probable number of bushbuck alive at pivotal age x from a cohort of 1000
q_x is the fraction af animals living at beginning of age interval x that die during the interval - i.e. mortality rate, expressed here on a basis of 1000
e_x is the probable future life expectancy, in years, of animals in age group x

Population parameters

The parameters considered are:

(a) female age specific fecundity m_x

(b) mean generation time T

(c) net reproductive rate (or finite rate of increase) Ro

(a) Female age specific fecundity

This is the mean number of female offspring produced in the period of time x.

The total number of offspring produced in time x can be represented by the relationship,

$$\text{total number of offspring} = \frac{A}{B} \times \frac{C}{100}$$

$$A = \frac{\text{number of pregnant females in age group x}}{\text{total number of females in age group x}}$$

$$B = \frac{\text{number of pregnancies expected in age group x}}{\text{total number of females in age group x}}$$

The gestation period of bushbuck is half a year. Since each age group represents one year, B would be the number of offspring expected, assuming one birth per gestation period per year, if all pregnancies were successful and all females monotocous.

C = percentage of mature females in age group x.

Since foetal sex ratio is unity (see Growth & Development) the number of female offspring is:

$$\frac{\text{total number of offspring}}{2}$$

Therefore $m_x = \frac{A}{B} \times \frac{C}{100} \times \frac{1}{2}$

For groups consisting of mature animals only, viz. Age Groups III to VIII: $m_x = \frac{A}{B} \times \frac{1}{2}$

The values of m_x are given in TABLE 14

(b) Mean generation time T

The mean generation time is calculated from the relationship $T = \frac{\sum x.l_x m_x}{\sum l_x m_x}$ after Birch (1948).

From TABLE 14 T is seen to be 3.116 years.

(c) Net reproductive rate, Ro

This is the rate of reproduction in one generation, Lotka (1945), expressed as the ratio of total female births in two successive generations.

This parameter is obtained by summing the products

TABLE 14

Continuation of female life table for bushbuck in Study Area A showing derivation of some population parameters.

Age group	Pivotal age(yrs)	l_x	m_x	$l'_x m_x$	$x.l'_x m_x$
I	0	1000	0.000	0.000	0.000
II	1	652	0.091	0.059	0.059
III	2	493	0.777	0.383	0.766
IV	3	362	0.428	0.155	0.465
V	4	261	0.555	0.145	0.580
VI	5	130	1.000	0.130	0.650
VII	6	72	0.750	0.054	0.324
VIII	7	4	1.000	0.014	0.098

$$\Sigma\, l'_x m_x = 0.940$$

$$\Sigma\, x.\, l'_x m_x = 2.929$$

l_x is the probable number surviving at pivotal age x from a cohort of 1000.

m_x is the mean number of female offspring produced in the period of time x which is the female age specific fecundity.

$l'_x m_x$ is the product of m_x and $l_x/1000$ the sum of these terms being the net reproductive rate Ro. = 0.940

T the mean generation time $= \frac{\Sigma\, x.l'_x m_x}{\Sigma\, l'_x m_x}$

$= 3.116$ years.

of l'_x and m_x for successive age groups:

$$Ro = \sum l'_x m_x$$

From TABLE 14 Ro = 0.940

The population in S.A.A. is therefore multipying at the rate of 0.94 times per generation time T. This is obviously a declining population decreasing at the rate of 60 per 1000 per generation time of 3.116 years.

Discussion of population parameters

It is apparent from the figures obtained for Ro and T that the population in S.A.A. is decreasing at a rate of about 2% per year.

It was shown in CHAPTER 4 that there is a high reproductive success with 91.4% of the mature females having shown evidence of calving within the year.

Bushbuck tend to be ecotone animals and derive benefit by occurying a habitat that is dynamic. The estate managers in S.A.A. are constantly clearing new ground as much of the land is wild. They would appear to be providing the habitat bushbuck prefer. The population has adjusted to cultivation of the estates since animals are regularly seen in these areas; hence the need for control.

It is unlikely therefore that food and habitat scarcity is causing the decline of the population. Most probably the active course of game control together with private hunting over the past years accounts for the decreasing population figures.

CHAPTER 6

SOCIAL BIOLOGY

Methods

During the fifteen month period from April 1968 to June 1969 visits were made to S.A.B. in Nairobi National Park for the purpose of observing aspects of the social biology of the bushbuck population. Policies of the National Park restricted the freedom in research method and the time was spent merely observing the animals from a vehicle using 7 x 50 binoculars.

In order to record intra specific associations some form of individual recognition was a prior requisite and the natural markings of these animals proved adequate for this. The spot patterns on the sides and rear quarters appear to be persistent as, for over a year, no change in these patterns was observed in known animals. These characteristics were therefore assumed to be reliable criteria for individual recognition. In addition to these spot patterns the males could also be identified from variation in coat, colour, horn shape, and size. Males below one year of age do not possess horns and their pelage is indistinguishable from that of females. Young animals were therefore all classed together.

Photographs of bushbuck were taken using a Pentax 35mm. camera and Novoflex 400mm. telephoto lens. Since many sightings were obtained during times of poor light quality the photographs were not always useable for recognition purposes. At such times morphological charasteristics were sketched onto data sheets.

Females proved more difficult to photograph than males and although many prints were obtained only fifteen were adequate for recognition purposes. The female population estimate was therefore based mainly sketches of lateral spot patterns.

Youngsters were not frequently seen and the estimate of their numbers was based on a few easily recognisable ones and others that were associatedwith known females or specific localities.

The population estimate was therefore derived as follows:-

Males - 31 photographed and sketched
Females - 15 photographed, 18 sketched
Youngsters - 14 estimated from association with females or locality.

The number of positive individual identifications varied from three to ten with better known individuals as many as sixteen.

No regular time was allotted to visiting the park and during the course of the fifteen months observations were made at all times of day from dawn to dusk. Nocturnal activity was never recorded in Nairobi Park but data on aspects of behaviour after dark were collected during shooting excursions in S.A.A.

The activity of every bushbuck seen in S.A.B. was recorded along with the location. Notes were taken of association between sexes, between males of different age groups and with other species.

Males were placed into age groups according to horn size. No attempt was made to age living, wild females.

Activity Patterns

Stereotyped activity patterns are not the general rule during daylight hours, although individuals may feed or rest in the same place for several consecutive days. Feeding or moving has been observed at all times of day.

Considerable time may be spent in the area without seeing any bushbuck. This is particularly so during the early morning and early to mid afternoon when they retreat from the more open areas to the thickets where they lie or stand for long periods.

Individuals are seldom seen lying in open grassland but prefer to rest in concealment. This is not, therefore, a frequently observed activity but sightings, when recorded, were mostly in the early afternoon. The place in which they lie is usually well chosen for all round vision and ease of escape. Such places may be used at different times by many individuals of the area.

Greatest diurnal activity occurs in the area between forest or bush and grassland. Being a more dynamic environment the ecotone may provide, in greater abundance, the forbs and small shrubs that appear to be the prefered diet of bushbuck. Evening is the time of day when most animals are seen. Males and females leave the seclusion of the thickets and venture out more into the open, sometimes in small groups. When in such groups it is usual for all members to be performing the same activity.

Daily activities expressed as a percentage are shown in TABLE 15 below. Four activities are considered, Feeding, Ruminating, Standing and Lying. The figures were obtained by summing the activity noted on any one sighting over a period of nine months.

TABLE 15

Common daily activities of bushbuck expressed as percentages.

Activity	Percentage of time spent in activity		
	Male	Female	Male and female
Feeding	46.07	33.84	39.65
Ruminating	1.68	6.06	3.98
Standing	47.19	58.08	52.92
Lying	5.06	2.02	3.45

TABLE 15 shows that by far the greatest time is spent feeding or merely standing. The latter activity may be an anti predator mechanism. When disturbed a bushbuck will often stand motionless for a considerable time before fleeing, relying on its colouration and immobility for concealment. Lying and ruminating may be under represented because, as mentioned above, lying is usually carried out in concealment and it is probably during this time that the animal ruminates.

Nocturnal activity was observed in S.A.A. whilst on shooting excursions. Both sexes are extremely active throughout the night although this is less noticeable on bright moonlight nights. They venture further out into open areas after dark, particularly on cloudy or moonless nights. Feeding is a major nocturnal activity and almost every bushbuck collected after dark had a full stomach. Animals have been shot at all times between dusk and dawn.

Grouping is more frequently observed during the night than the day and calves are often seen accompanying females.

Distribution of bushbuck in Study Area B

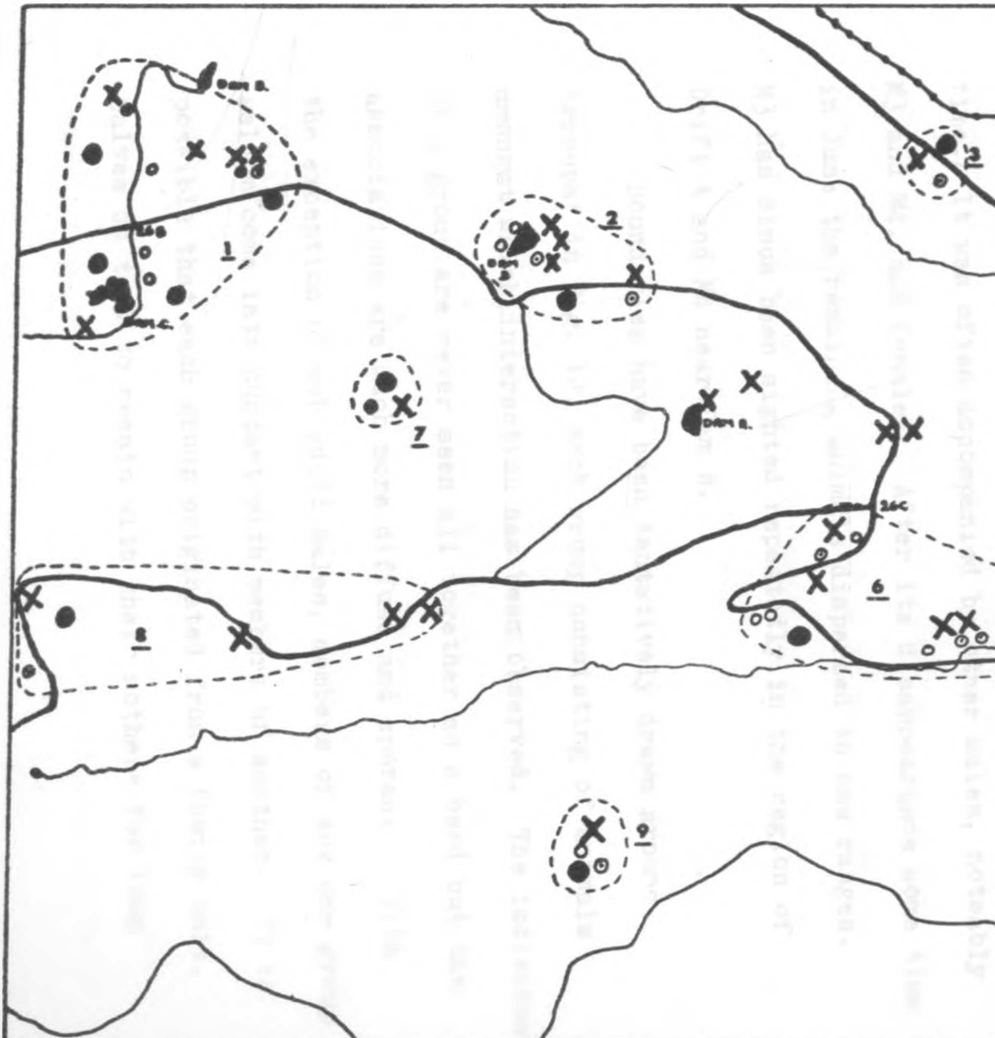
A total of eighty bushbuck have been recognised in S.A.B. In June 1969 they were distributed as shown in Fig 12. This distribution has remained essentially the same throughout the year.

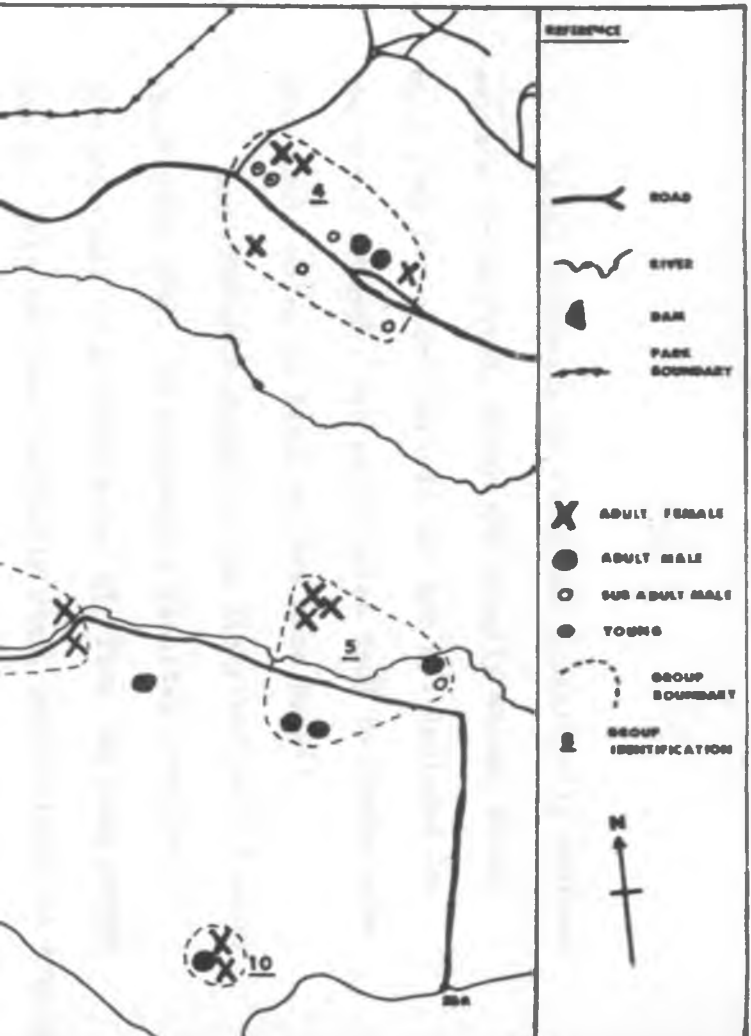
Eighty is the number of animals that can be individually recognised and are considered resident in the area. Since parts of the area such as forest and river valleys are inaccessible, there are probably other animals that have not been seen regularly and will not be included in the total figure. Eighty must therefore be regarded as a minimum figure.

Game census figures, Foster and Kearney (1968), give an average number of 14.3 bushbuck for the entire forty four square miles of Nairobi National Park from counts taken between 1961 and 1966. This reflects the secretive nature of these animals.

FIG. 12

Study Area B showing distribution of adult male, sub adult male, female and young bushbuck. Boundaries are drawn around possible discrete groups.


DAM B.
26B
1
DAM C.
2
DAM B.
7
26C
6
8
9


REFERENCE
ROAD
RIVER
DAM
PARK BOUNDARY
ADULT FEMALE
ADULT MALE
SUB ADULT MALE
YOUNG
GROUP BOUNDARY
GROUP IDENTIFICATION
N
4
5
10

Local movements do occur and occasionally unknown animals are sighted. These are usually males which only stay for short periods and are not included in the total figure. Sub adult males tend to wander more than adult males or females (see Home Range).

One notable change in the distribution did occur about June 1968. It apparently resulted from the disappearance of a large male, M1. from the area around Dam A. This male was regularly seen, particularly at evening time. It was often accompanied by other males, noteably M3 and M4, and females. After its disappearance some time in June the remaining animals dispersed to new ranges. M3 has since been sighted repeatedly in the region of Drift A and M4 near Dam B.

Boundaries have been tentatively drawn around 'groups' in Fig. 12, each group consisting of animals amongst which interaction has been observed. The individuals of a group are never seen all together as a herd but the associations are much more diffuse and sporadic. With the exception of sub adult males, members of any one group seldom come into contact with members of another. It is possible that each group originated from a family unit. Calves do tend to remain with their mothers for long periods and what may appear to be three adult females could in fact be one adult female with two calves. Young males (1) have a very restricted home range and probably remain in the immediate locality of their mothers. This extended mother/young relationship and the tolerance (see Territoriality) between males would make the formation of family groups quite plausible. It is impossible to state that this is the case until observations over a longer period of time have been carried out. An alternative explanation for 'grouping' would be that these are neutral associations. The larger groups in Fig. 12 are in areas such as Dam B, Dam C or along the Mokoyeti River, i.e. where there is permanent water. However, the group associated with M1 was in such a favoured area until its disappearance after which they all moved away to take up residence in new areas.

Age and sex composition

The population can be divided into males, females and young with the males being further subdivided into age groups (1), (2), (3), and (4) (see Ageing) according to horn size. Although there is considerable change in coat colour and body shape with ageing males no such change occurs with females. Young females reach adult size during their second year and even if size differed considerably with age this characteristic alone would be inadequate as a field ageing technique. Due to the similarity between the females of different ages no attempt was made to place them in age groups.

Up to the age of one year males and females are identical in appearence. Males of this age are hornless and their coat colour is indistinguishable from that of a similarly aged female. Testes are very small and held close to the body so that even if a young male were in a position to expose the scrotum it would still be difficult to see. All animals less than a year old are therefore classed together as immatures.

The composition of 'groups' shown in Fig. 12 is given in TABLE 16.

TABLE 16

Associations

(a) Intra specific

TABLE 17

(i) Solitary. The associations shown in TABLE 17 indicate that for the majority of time bushbuck are alone during daylight hours. As mentioned under Activity Patterns, this may not be the case during the night. Nocturnal associations were not quantified but there did seem to be far greater occurrence of grouping.

TABLE 16

Composition of the groups tentatively outlined in Figure 12.

Group Number	Adult Male	Sub adult Male	Female	Young
1	4	3	5	3
2	1	2	4	2
3	1	-	1	1
4	2	3	4	2
5	3	1	3	-
6	1	4	6	3
7	1	-	1	1
8	1	-	4	1
9	1	1	1	1
10	1	-	2	-
Total	16	14	31	14
Individuals	1	-	4	-

Males 31

Females...35

Young 14

Grand total 80

TABLE 17

Intrespecific associations recorded with frquency greater than one occurence.

Association	Number of sightings	Percentage
M	II2	28.0 *
MM	2I	5.2
MMM	7	I.7
F	95	23.7 *
FF	2I	5.2
FFF	5	I.2
MF	32	8.0 **
MFF	I4	3.5
MMF	6	I.5
FY	58	I4.5 ***
Y	8	2.0
MFY	7	I.7
FFY	8	2.0
FFFY	3	0.7
FFFFY	2	0.5
	400	I00.0

* Single animal 5I.7%

** Commonest adult association.....8%

*** Commonest association of two or more....I4%

(M=Male, F=Female, Y= Young unsexed)

Greatest diurnal grouping activity is seen in the late evenings which supports the subjective impression that nocturnal grouping is relatively more common.

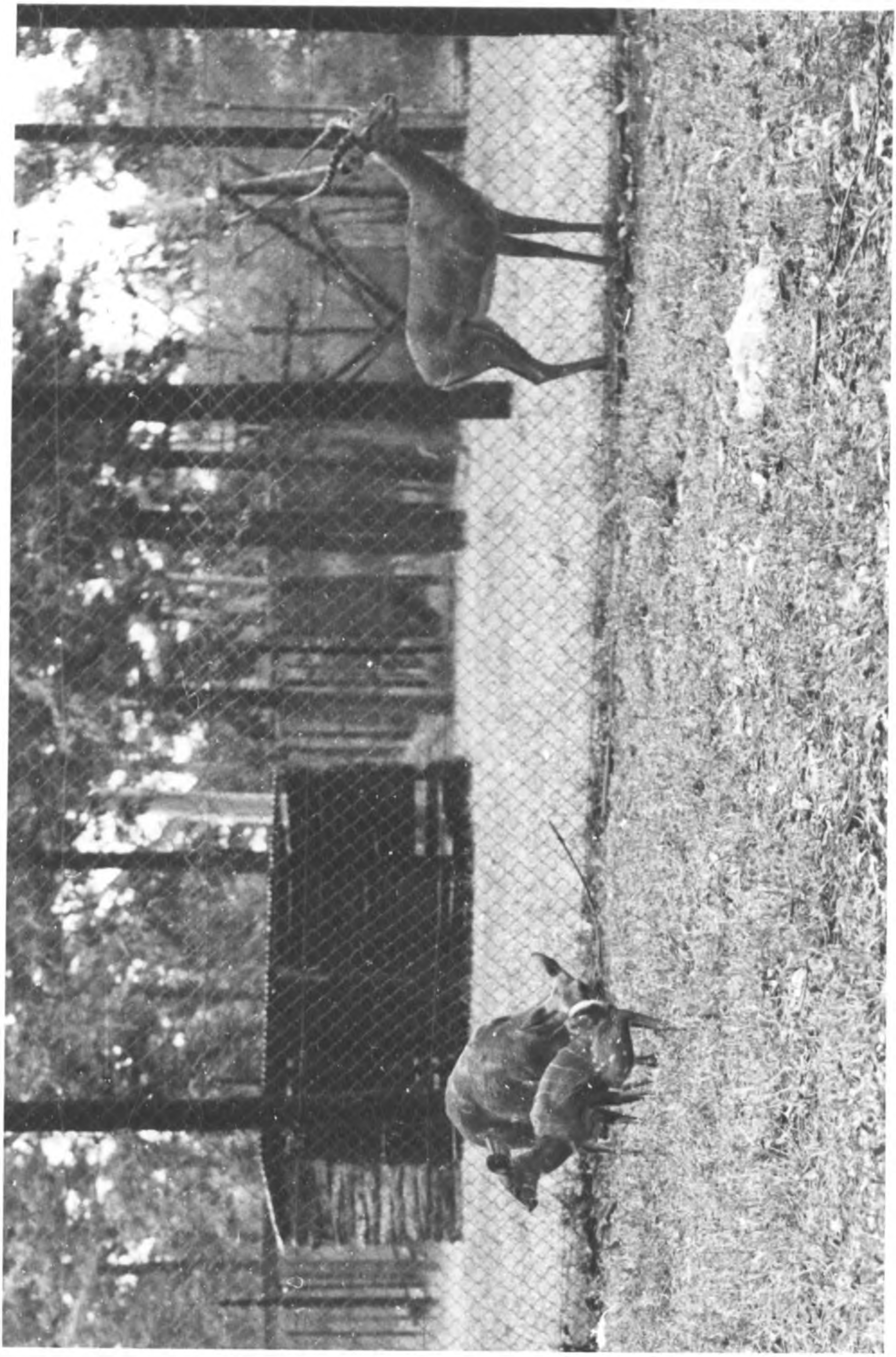
The solitary nature of bushbuck together with their reliance on camouflage as a main anti-predator device suggest that much of the behaviour of these animals is geared to avoidence of predators. When surprised, bushbuck freeze into immobility. They are able to remain completely still for long periods of time, then if the stimulus becomes too great they will run. From the open they immediately make for the bush and once under cover are able to move through the vegetation with great rapidity. During the day, when cryptic colouration is their main defence against predators, it would be disadvantageous to associate in groups. At night this is of less value in concealment and the animals move more into the open, relying on the combined senses of a group to detect danger.

The associations most frequently observed during the day are those in which maternal and sexual instincts override the avoidence of predators, viz. female/young and male/female.

(ii) Female/young. There is considerable attempt at concealment of the young by mothers. This may take the

PLATE 7

Female consuming the droppings of its calf.



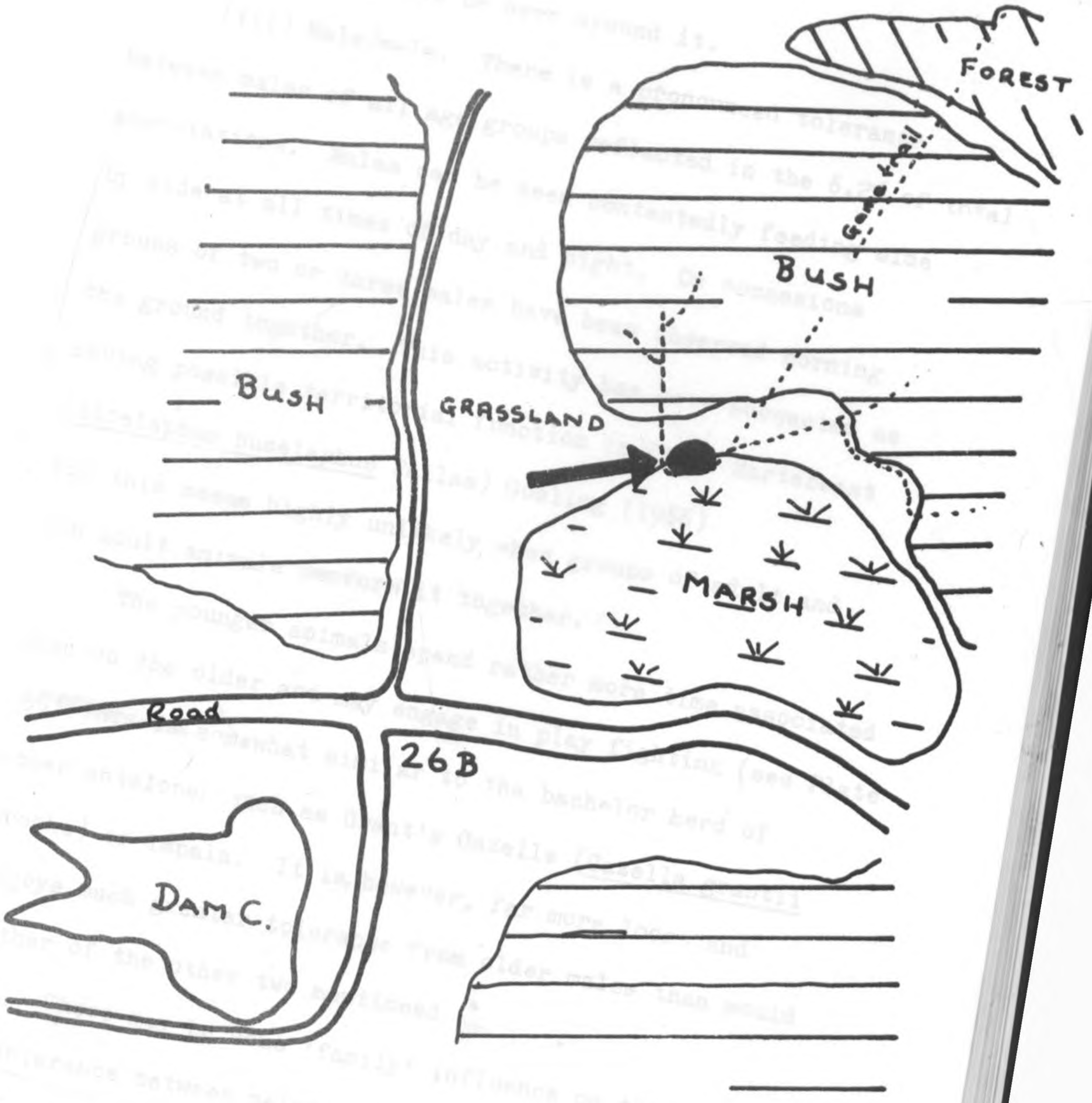
form of consuming dropping. (see plate 7) or leaving them alone in long grass during feeding periods. Very young calves, up to about two months of age, are very seldom seen in the wild. From four to five months onward the youngsters spend an increasing amount of time feeding alongside the female. Many of the sightings of two females are probably in fact of one adult female and a full size youngster.

One female regularly seen with its calf fed in the same area for six days between 1100h to 1400h. For this period of time the youngster would appear when the female was first sighted but would immediately make for a particular bush on the edge of a marshy open grassland. The bush, see Fig. 13, was extremely well sighted having an unobstructed view on all sides. There were numerous exits from within the bush which led to a large area of thicket about ten to fifteen yards away. The female wandered several hundred yards away from the bush whilst feeding and at times disappeared completely into the thicket for as much as forty minutes. At about 1300h to 1400h the female would approach the bush and enter, staying there for the longest recorded time of almost two hours. After six days this regular behaviour terminated. Other bushbuck, usually males, have been seen using the same bush and

BUSH
BUSH
MARSH

FIG. 13

Diagram of area in which a regular mother/young association was observed. Bush under which youngster spent many hours in concealment is arrowed. Several game trails lead to this bush which has no visual obstruction, thicket etc., less than ten yards away.


FOREST
Game trail
BUSH
BUSH
GRASSLAND
MARSH
Road
26B
DAM C.

footprints can always be seen around it.

(iii) Male/male. There is a pronounced tolerance between males of all age groups reflected in the 6.2% of total associations. Males can be seen contentedly feeding side by side at all times of day and night. On occassions groups of two or three males have been observed horning the ground together. This activity has been suggested as having possible territorial function in Cokes Hartebeest (Alcelaphus buselaphus Pallas) Gosling (1966) but this seems highly unlikely when groups of adult and sub adult animals perform it together.

The younger animals spend rather more time associated than do the older and may engage in play fighting (see Plate 8) This is somewhat similar to the bachelor herd of other antelopes such as Grant's Gazelle (Gazella grantii Brooke) or impala. It is, however, far more loose and enjoys much greater tolerance from older males than would either of the other two mentioned.

There may be some 'family' influence on the degree of tolerance between males. In any one area certain males can be expected most of the time and may be part of a family group. Males from other areas are tolerated but the individual distance between strange males and males of the same area is much less. When in the presence of a

PLATE 8

Sub adult males engaged in play fighting.

strange male there may be some display usually in the form of an agonistic posture (see Plate 9). On one occasion four males were feeding in the same area as a troupe of baboons (Papio ursinus Elliott). Each appeared oblivious of the presence of the others until their feeding movements brought them fairly close together. Then all feeding stopped and they assumed much greater awareness of each other. The three older animals assumed agonistic postures and eventually began prancing around each other leaping into the air with arched backs and finally began clashing heads together. The actual contact lasted only for a few seconds each time then they would resume the 'excited' leaping and short chases. The whole episode lasted less than five minutes when they each began to move away in a different direction. The dorsal crests remained raised for several minutes after they had parted but were eventually lowered and as they wandered slowly away intermittent feeding was again carried out. This particular group of animals was never seen together again.

On another occasion two males appeared together and fed side by side for two hours. They slowly moved along whilst feeding until they approached within 50 yards of two females that had been in the area throughout the time. For no apparent reason other than the proximity of the

PLATE 9

Two adult males displaying the agonistic posture. Note particularly the ears flattened back, the raised dorsal crest and the erected tail.

females the two males suddenly began fighting very fiercly. The fighting consisted mainly of locking horns in headlong clashes and then twisting in an apparent attempt to overbalance the opponent. This continued in a very spirited fashion until one broke away and fled with its tail raised high. The victor gave chase and fighting commenced again several hundred yards away after they had circled each other displaying the agonistic posture. The same animal broke away again and after another long chase the victor returned to the area of the females. No actual contact was seen between this male and the females.

The suggestion here is that males are mutually tolerant, but only up to a point. There is a threshold individual distance between strange males and if this is encroached it elicits agonistic display and possibly fighting. Female presence may also cause this reduction in individual distance between males, but as males and females have been seen together quite frequently there must be some special condition causing this. It may be that this other condition is a female in oestrous. This is substantiated by observations of male/female associations which constitute 8% of the total observed.

(iv) Male/female. Invariably when single male/single female observations are made the male is seen following the female. Wherever the latter chooses to go the male will follow behind, never allowing too great a distance between them. The male makes no attempt to control the movements of the female as is frequently seen with impala etc. Similar behaviour has also been recorded in Lesser Kudu (Tragelaphus imberbis Blyth) by Leuthold (per. comm.).

The male/female association is by no means a permanent relationship but usually lasts only a few days. During this time the male allows no other males in the proximity. An incident illustrating this occured between two males that have before and since been seen together. M23 had been accompanying F29 for several days. On one occasion when they were feeding together M28 appeared several hundred yards away. M23 immediately ceased feeding and watched the intruding male constantly. M23 began to walk toward M28 the latter making no sign that he acknowledged the presence of the other. Approaching within five yards of M28, M23 assumed the agonistic posture still without reply from M28 which merely walked slowly past M23. When M28 was fifteen to twenty yards away from M23 the latter turned to face it, this time M28 fled into the bush. M23 made no attempt to follow but immediately ran back to the female.

(b) Interspecific

There may be a positive reaction between bushbuck and other species such as antelopes or a negative reaction as with predators.

(i) Positive reaction

TABLE 18

Common associations of bushbuck with other species

Species	Number of sightings	Percentage of sightings
Impala	51	47.7
Baboon	39	36.4
Warthog	9	8.4
Waterbuck	8	7.5
Total	107	100%

The associations shown in TABLE 18 concern only those most frequently seen.

Impala, waterbuck (<u>Kobus ellipsiprymnus</u> Ogilby) and warthog (<u>Phacochoerus aethiopicus</u> Pallas) probably form neutral associations with bushbuck. This would occur

PLATE 10

Adult male bushbuck 'horning the ground' in the presence of impala and baboon.

if there were a common preference for some type of vegetation etc.. The animals would therefore come together purely by chance and not by any design of their own. During the association bushbuck would passively share in the benefits afforded by the herd structure and it's greater ability to detect danger.

With baboons the associations appears to be positive. Since their diets are considerably different it is unlikely that bushbuck and baboons should come together through a food preference. The younger, more nervous baboons spend much of their time high in the trees where they would have a commanding view of the surroundings (Altman pers.comm.). They are probably very efficient sentinels and it may be for this security that bushbuck associate with them. The predators most frequently seen in S.A.A. are leopard (Felis pardus Linnaeus) which are probably the greatest predator of both bushbuck and baboon. It may be because of this common enemy that the association originally formed.

(ii) Negative reaction. Apart from predators, bushbuck also avoid red billed oxpeckers (Bugaphus erythrorhyncus) (compare Verheyen 1955) and buffalo (Syncerus caffer Sparrman). The latter may be a consequence of the former. Oxpeckers are notoriously noisy birds and often give away the presence of buffalo and rhino long before they are seen. This may be the reason why bushbuck do not allow them to alight on them to remove ticks as they do with many other animals. It may be a consequence of chasing away tickbirds that bushbuck invariably have these parasites infested around the neck and ears. The accompaniment of tickbirds with buffalo and the subsequent vocalisation of their presence may be the reason why bushbuck tend to leave the vicinity when buffalo move in.

(iii) Predators. The recorded bushbuck kills in Nairobi National Park from April 1968 to June 1969 are cheetah (_Acinonyx jubatus_ Schreber) 4 (R.T. McLaughlin pers. comm.); leopard 1; Martial eagle (_Polemaetus bellioosus_) 1.

Only the leopard and eagle kills occured in S.A.A.

The Martial eagle was seen feeding on a very young calf, the umbilical cord of which was present but dried. The calf had therefore not been just born but was perhaps a few days old. The female was still present and ran away as I approached giving an alarm bark. The rump and tail of the calf were badly mauled, the latter having been stripped from the bone. The skull had been cracked open and parts of the head and forelegs eaten. It appeared that the eagle had taken the calf from behind pulling off the tail in the process, it had then killed the animal by cracking open the skull with its beak. The condition of the carcase suggested strongly that the eagle had actually killed the calf and was not merely scavenging.

The single leopard kill was suggested by a ball of hair regurgitated by an adult male leopard. The hair was indentified as that of a female bushbuck.

Records from Kruger National Park (Van Pienaar 1963) show bushbuck to be the preferred prey of leopard at 2.27% compared with waterbuck and reedbuck (Redunca redunca Pallas) at 2.20%. Over twenty-five years lion have been seen on 80 bushbuck kills, leopard on 564, cheetah on 31 and wild dog (Lycaon pictus Thomas) on 68.

Territoriality

Male bushbuck have never been seen defending an area in the fashion of classical territoriality as described by Burt (1943). The associations described above suggest a different type of territorial behaviour.

To briefly summarize the relevant observations, males are mutually tolerant except on few occasions when it the presence of a female, not any female on any occassion but what has been assumed as a female in oestrous. Single male/single female associations are not uncommon and during this time males actively chase away other males.

The suggestion is that male bushbuck do not defend an area but rather an association with a female. The oestrous female may be detected during the late evening or night when grouping is more common. The association is then defended against other males and just as a Uganda Kob (Kobus kob Erxleben) could be displaced from its territorial ground by a stronger male so could the bushbuck be replaced. Impala show a similar form of 'territoriality' only the number of females defended by a male is much larger and the association is continuous until the male is replaced. Much of the behaviour of bushbuck is geared to avoidence of predators and this may explain why the territorial association is much looser and concerns single females only.

As the oestrous female must first be detected by a mature male, one might expect that some allowance is made to prevent wastage of breeding potential. This may be provided by the early maturation of male bushbuck, (see Reproduction). All males examined for presence of sperm in the vas deferens showed positive from Age Group (1) onwards.

No form of territorial marking has been observed for male bushbuck. Preorbital and inter digital glands are absent and the inguinal glands are present and active in adult, sub adult and females. Defecation is not confined to a specific area forming dung piles as in Diddik (Madoqua species) or Thomson's gazelle (Gazella thomsoni Gunther) and horning the ground may be carried out simultaneously by males of all age groups. Males have been seen rubbing their horns vigorously amongst small branches on bushes. This is not confined to specific bushes and does not appear to leave any mark or scent. It may be an attempt to remove ticks which abound around the neck and ears of bushbuck, a condition exaggerated by their reaction against oxpeckers.

This form of territorial behaviour would have the advantages of territoriality in other antelopes such as utilisation of the best genetical strain and prevention of wastage of germ cells. Other advantages associated with spacing out through territoriality are intrinsic in the general behaviour of bushbuck, Errington (1946 'threshold concept'), and therefore are not a territorial requirement. In addition the possible internecine consequences of grouping during daylight hours are reduced.

Home range

By recording sightings of known animals in S.A.B. , the approximate area of their home range has been calculated. The boundaries tentatively drawn in Figs. 14,15, and 16 enclose sightings of known individual bushbuck and represent their minimum home ranges.

Recording home ranges in this way shows considerable variation in the areas utilized by adult males, sub adult males and females. The approximate area of home range of females is two thousand five hundred square metres, for an adult male, five thousand six hundred square metres and for a sub adult male, twenty thousand square metres.

The young males range over by far the largest area. Burt (1943) suggests that animals can only be said to have a home range after they have established themselves and that the wanderings of young animals are in a different category of movement. Using Jewell's (1968) definition of home range as, "the area over which an animal normally travels in pursuit of its routine activities" it may be be more correct to assign different types of home range to different age group animals. Contrary to Burt the area

FIG. 14

Study Area B showing home ranges of known adult male bushbuck M1, M6 and M27.

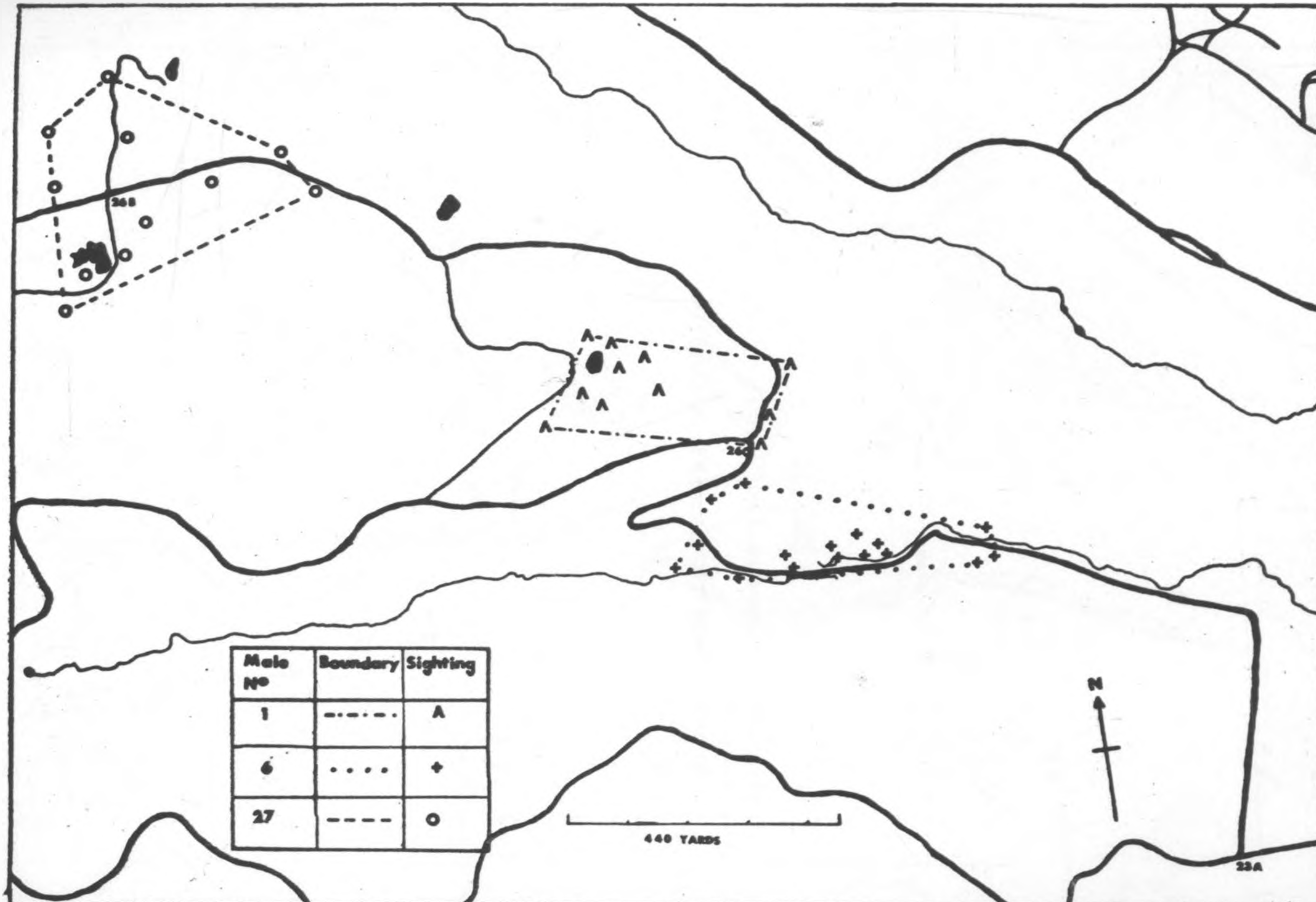
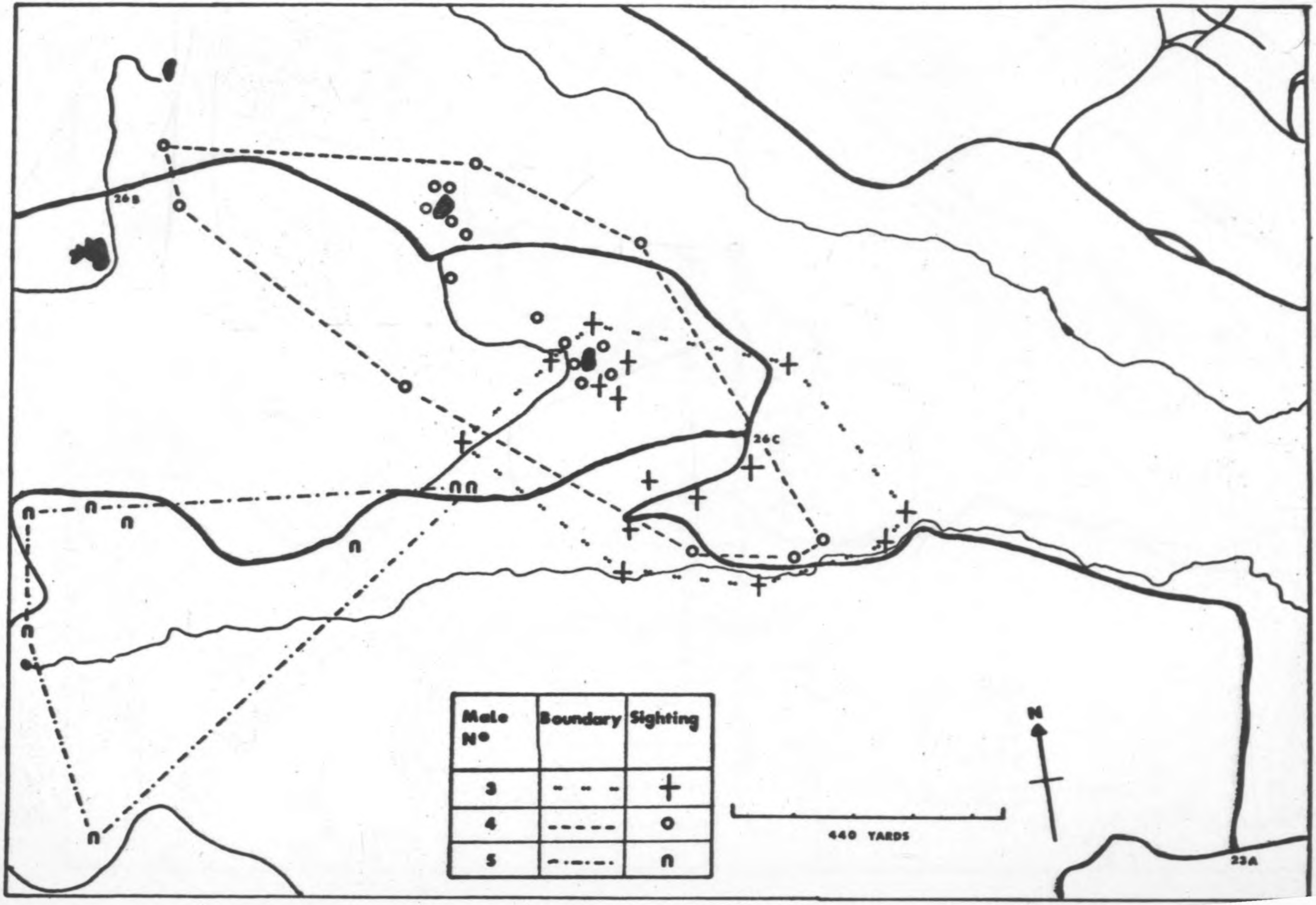

Male No
Boundary
Sighting
1
A
6
+
27
o
440 YARDS
N
23A

FIG. 15

Study area 2 showing home ranges of known sub adult male raccoons M3, M4 and M5.

FIG. 15

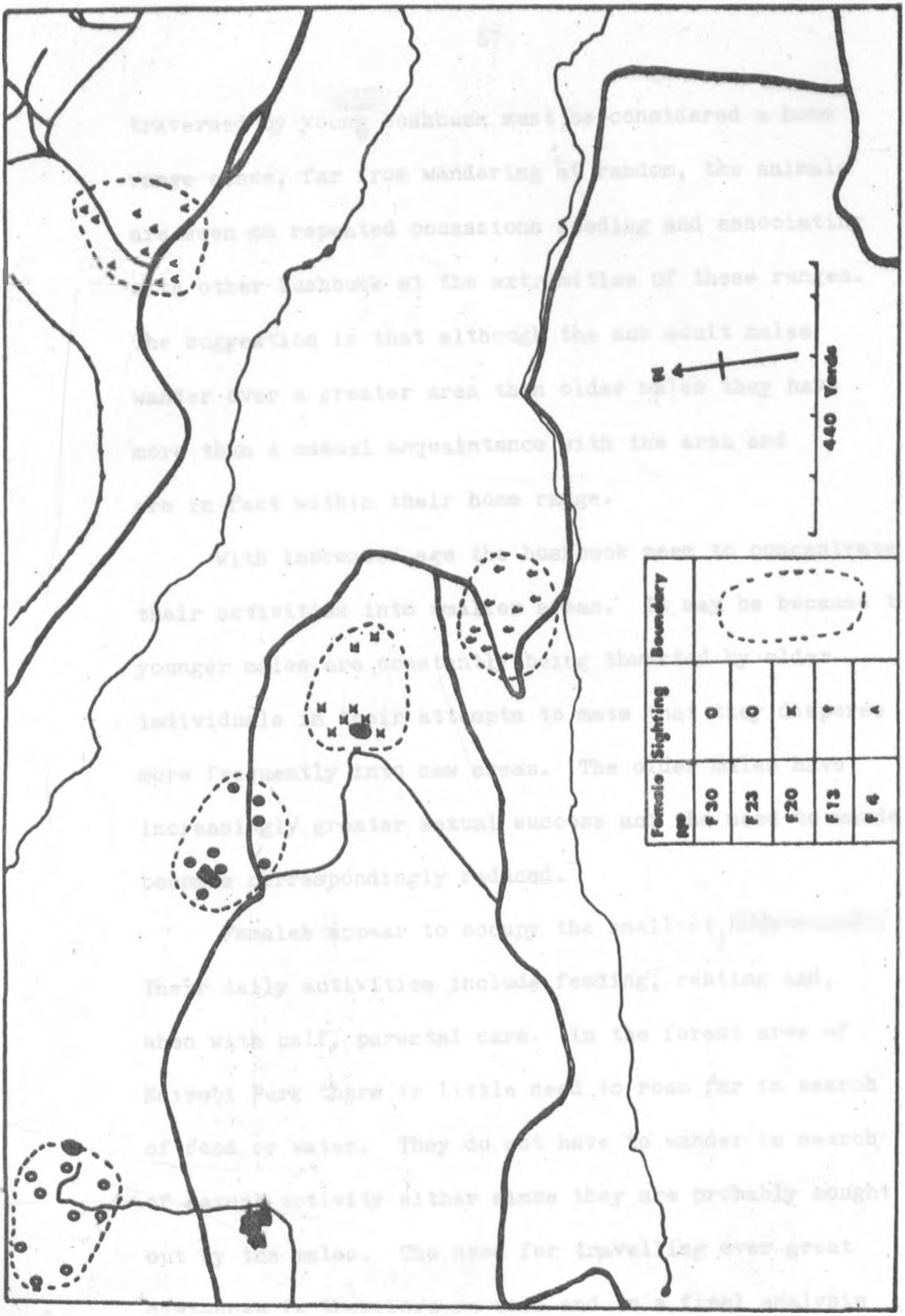
Study Area B showing home ranges of known sub adult male bushbuck M3, M4 and M5.



26B
26C
23A
Male N°
Boundary
Sighting
3
4
5
440 YARDS
N

FIG. 16

Study Area B showing home ranges of known female bushbuck F30, F23, F20, F13 and F4.


N
440 Yards
Female No
Sighting
Boundary
F30
F23
F20
F13
F4

traversed by young bushbuck must be considered a home range since, far from wandering at random, the animals are seen on repeated occassions feeding and associating with other bushbuck at the extremities of these ranges. The suggestion is that although the sub adult males wander over a greater area than older males they have more than a casual acquaintance with the area and are in fact within their home range.

With increased age the bushbuck seem to concentrate their activities into smaller areas. It may be because the younger males are constantly being thwarted by older individuals in their attempts to mate that they disperse more frequently into new areas. The older males have increasingly greater sexual success and the need to wander becomes correspondingly reduced.

Females appear to occupy the smallest home ranges. Their daily activities include feeding, resting and, when with calf, parental care. In the forest area of Nairobi Park there is little need to roam far in search of food or water. They do not have to wander in search of sexual activity either since they are probably sought out by the males. The need for travelling over great distances is therefore reduced and in a final analysis the home ranges of old males and females are probably very similar, their smaller size being dictated by food availability.

Discussion.

Several points of interest arise from the study of bushbuck in Nairobi National Park. The solitary nature and great tolerance between males is probably characteristic of bushbuck in general. The high density of the Park population is, however, specific to the unnatural conditions pertaining there, being a reflection of the boundary fencing and provision of artificial dams.

As mentioned previously seclusion and lack of territoriality are probably behavioural adaptations to predator avoidance. Cryptic colouration is logically associated win non gregarious behaviour, this being exemplified at many levels of animal life. For mating success at least grouping together should occur at some time; indications are that this occurs after dark with bushbuck when camouflage is ineffective.

The great diversity of Ungulates probably expanded during the climatic and vegetational changes which took place between the late Miocene and Pleistocene (Moreau 1952). The formation of a social structure based on the herd was necessary in the more exposed grassland habitat where safety in numbers was more effective in defence against predators. Grouping together does, however, create its own problems of social strife and over taxation of the available habitat. The evolution of territoriality, with dominant males defending specific areas against use by other males eased this problem by spacing out elements of the population. Utilization of the preferred area by females and young, that is the breeding stock, buffered them against the hazards of over crowding. Sub-dominant males would have to move onto less favourable habitats so expanding the population boundary. They may also suffer greater mortality but in either case the result is a lessening of the population density.

Bushbuck have remained in the forest and have not undergone these social advances. Anchorism remains the ideal predator escape mechanism. Territoriality, in the classical form, has not developed since it is not to their advantage to associate in conspecific groups or to mark boundaries. The solitary nature of bushbuck reduces the need for spacing out of the population and the dangers of social strife are insignificant unless density increases to a point where individual distances can no longer be maintained. The territorial system of bushbuck as it exists, and if in fact it can be called such, consists of an association between a single male and a single oestrous female. Defence of this association is understandably fierce since both males would be competing for an oestrous female and hence in a state of high excitement. As their horns have not undergone the adaptations related to ritualised display such as seen in gazelles, these territorial conflicts could well result in mutilation or death.

Charles Darwin in the Origin of Species first recognised that populations do not increase without limit but are controlled by such factors as shortage of food, predation and disease.

During the period of observation in Nairobi Park nothing was seen to indicate that the population was unhealthy. Sick animals and carcasses were never found. This lack of obvious mortality also suggests that predation is light. Dead animals may have been overlooked in the forest and bush, particularly since vultures are not often seen in these areas. Lions and cheetah occasionally venture into the forest area but their style of hunting is more suited to the plains. Leopard, though seldom seen, are probably the most common predator in the area. Little is known of their numbers, home range size, etc. and so it is difficult to surmise about the pressures they exert. On the whole predation does not appear to be heavy.

With the construction of artifical dams a year round water supply is assured in addition to the standing pools that remain in the North and South Mokoyeti Rivers. In the forest, bush and grassland there is no shortage of food and the Park's staff even cut the grass in some areas so maintaining the more palatable new growth.

Control factors do not therefore appear to be seriously limiting this population. If breeding success is similar to that indicated for the species in Study Area A and ecological mortality is low the population will increase. Since the boundaries are limited and social behaviourisms such as territoriality do not tend to encourage dispersion, any expansion must be internal; thus increasing density. If the population is increasing, density dependant factors must eventually exert their effect and cause a population decline. Since bushbuck are seldom seen in large numbers by visitors to the Park or by the Park's staff this would probably go unnoticed.

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