REPRODUCTION IN THE IMPALA (Aepyceros melampus
Lichtenstein), WITH PARTICULAR REFERENCE TO
THE POPULATION IN MKUZI GAME RESERVE, ZULULAND.

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by JOHN VINCENT.

CHAPTER 1:

INTRODUCTION.

It has long been recognised that a knowledge of
reproductive processes is an essential prerequisite in the
management of animals. In the case of domestic animals
such a knowledge has been taken for granted in enabling
breeders most efficiently and economically to produce
maximum yields under different conditions. This implies,
not only a foreknowledge of the mechanisms of reproduction,
but also of the effects of varying environmental factors
on them.

Sadleir (1969) has very adequately reviewed the
ecology of reproduction in many mammals but, on account of
the comparative paucity of information on wild species, has
perforce had to concentrate to a very large extent on
domestic animals in order to formulate general principles
which may have an application elsewhere.

Leopold (1933) lists some of the reproductive
attributes of game animals which are important in understandi
their management. His principles remain sound, and have
since been added to in the general upsurge of interest in all
aspects of the biology of large wild ungulates.

This interest has, in the past decade, centred very
largely around the wide range of species in Africa, where an
awareness of the importance of herbivores in the overall
ecology of the continent was initially stimulated by the
conference of the International Union for the Conservation of
Nature in Arusha in 1963.

It goes without saying that a good deal of the efforts of wildlife research workers in Africa today is concentrated on studies on reproduction, simply because it is basic to the understanding of population dynamics, on a thorough knowledge of which are founded efficient management technique: An excellent example of this is to be found in the work of Watson (1969), who illustrates very clearly the application of reproductive research in the management of the wildebeest (<u>Connochaetes taurinus</u>). In deriving the parameter "r" (the intrinsic rate of natural increase) he very concisely sums up the important role of studies on reproduction when he says, "A knowledge of the mechanisms of reproduction, both behavioural and physiological, enables one to view with some degree of insight the changes wrought in 'r' by natural and man-made environmental changes. A comprehensive under-standing of reproduction would allow accurate prediction and, ultimately, control of the value of this parameter."

It is important to note that Watson mentions both the behavioural and physiological approaches to studies on reproduction. For management purposes, a knowledge of one is valueless without a knowledge of the other.

The present study sets out to review the literature on reproduction in African ungulates on a broad basis, with particular emphasis upon that of the impala (one of the most numerous and widespread of African herbivores), and contribut some original results from a study of an impala population in Mkuzi Game Reserve in Natal.

CHAPTER 2:

THE STUDY AREA.

2.1. Location.

Mkuzi Game Reserve is situated in north-eastern Zululand, in the province of Natal. It is part of the extensive southern extension of the Mocambique coastal plain, and has faunal and floral affinities with the tropical eastern lowlands, as well as with the more temperate zone of Zululand proper. Poynton (1961) has shown that the floral and amphibian forms are still largely tropical in nature, whilst Winterbottom (1962) has demonstrated that the birds also have a similar affinity. However, because of the comparative ease with which more western and southern forms may reach this southern portion of the coastal plain, strong intrusions of less tropical forms are evident.

The reserve is bounded on the north and east by the Mkuze river. The western boundary, situated in the eastern foothills of the Lebombo mountain range, is an artificial one, whilst the southern boundary consists of a small seasonal drainage line which feeds into a large seasonal pan filled by the flooding of the Mkuze river. South of the reserve, composed as it were of a large "bite" into the reserve, and ecologically a logical extension thereof, is an area of State Land known as Nxwala Estate.

Mkuzi Game Reserve is approximately 24 300 ha. in size, whilst Nxwala Estate comprises a further 8 000 ha

2.2. Topography.

For the most part the reserve is comparatively flat, particularly in the eastern sector. The central region consists of three low ridges orientated in a north-south direction, whilst the western sector, situated in the Lebombo foothills, is fairly broken.

The streams are all seasonal, and run mainly from west
to east, while the few drainage lines in the central
and eastern parts run north-south or vice versa.
The Dagela stream, comprising the southern boundary,
also runs eastwards to join up with the Mkuze river
in the south-eastern corner of the reserve, after
passing through Nsumu pan.

2.3. Geology.

Most of the flatter parts of the reserve were, during
Cretaceous times, part of the sea bed. With the
recession of the coastline, the Cretaceous deposits
have been covered by recent sands, derived partly
from beach formation, and partly from the parent
material of the Lebombo range.   In the north-central
part of the reserve, on a fairly high promontory
overlooking the Mkuze river, the Cretaceous beds lie
on the surface.

The Lebombo mountains are of volcanic origin,
composed mainly of basalt, overlaid by a thick
succession of rhyolite and pyroclastic material.
These latter rocks are thought to have been extruded
as lava through a series of dykes which are now filled
with rhyolitic breccia (Van Wyk, 1963).

2.4. Soils.

The dominant soil type throughout the reserve is
sand, which varies considerably in structure from
area to area.   Pure sand, found in a central north-
south belt, changes through varying degrees of loamy
sands to almost pure loam in the west, and deep, dark
clayey alluvium along the river.   The soils in the
foothills are very stony, whilst those of the flood-
plain of the Mkuze river have been derived from the
predominantly Karroo System sandstones, shales and
basalt of the catchment area.

2.5. Water.

The game reserve is almost devoid of any natural

surface water in the dry months of the year - from
about May through September, whilst even during the
rest of the year a great deal depends upon the
incidence of rain.   The Mkuze river is very seasonal
in nature, and has surface flow only after heavy rain
in its catchment.   There is however, a fair amount
of underground water movement in the very deep, sandy
bed.   All the streams and drainage lines contain
flowing water only after heavy rain, although odd
pools may persist for a short while thereafter.

There is only one natural source of near-permanent
water: it is a deep hole, known as Nkazeni,
situated in the south-eastern corner of the reserve,
which is fed by an underground stream.   Even this
has been known to dry up.   Surface pans are numerous,
and vary in size from the very extensive Nsumu pan to
small ones, a few metres in diameter.   These latter
are found scattered over the whole area, and are filled
only by rain.   The larger ones are not far from the
river and are filled by overflow therefrom during
flood periods.

Two small pans in the centre of the reserve are
maintained artificially throughout the year for the
benefit of the animals and for the enjoyment of
visitors.

2.6.   Climate.

2.6.1.   Rainfall.   The rainfall in the reserve is influence(
primarily by its location on the western edge of the
coastal plain.   The rain-bearing southerly winds are
intercepted by the coastal dunes or by the Lebombo
range, so that there is a subtraction eastwards and
westwards of rainfall.   Mkuzi therefore falls within
a rain shadow, and its erratic precipitation is
largely in the form of thunderstorms.   The average
rainfall for the reserve is about 700mm.

2.6.2. <u>Temperature</u>.   On account of its situation on the southern end of the tropical coastal plain, Mkuzi is subjected to high summer temperatures. No figures are available, but extrapolation from nearby stations suggests a mean summer (October - March) temperature of 24,5°C, a mean winter (April - September) temperature of 19,5°C, and a mean annual temperature of about 22°C.

2.6.3. <u>Wind</u>.   The prevailing winds are northerly and southerly, blowing in about equal proportions throughout the year.

2.7.   <u>Vegetation</u>.

Generally speaking, the vegetation depends upon the topography, with variations according to soil types.

In the Lebombo foothills the dominant vegetation is characterised by <u>Combretum apiculatum</u> as a medium-sized (5-7m) tree, in an open grassed woodland, with <u>Themeda triandra</u> the dominant grass.   On the lower slopes, and forming a belt around the bases of the ridges, is an <u>Acacia nigrescens</u> association. This extends eastwards on some of the lower foothills, and the grass cover is sparser on account of the apparent preference of game to use this zone.

Along the streams in the foothills is a narrow strip of largely deciduous woodland, dominated by such trees as <u>Schotia brachypetala</u>, <u>Spirostachys africana</u>, and <u>Acacia robusta</u>.   Where the streams converge on the flat, low-lying country, they tend to open out and give rise to low-lying plains composed of dark clay soils on which the dominant plants are <u>Acacia luederitzii</u> and <u>Euclea divinorum</u>. The ground cover in these areas is very poor. Stands of <u>Acacia xanthophloea</u> are frequent and are associated with slightly elevated areas with less clayey, and presumably deeper, soils.

Most of the flatter parts of the reserve consist
of mixed _Acacia_ woodland, with _A. nilotica_ most
frequent on the shallower, loamy soils of the central
parts, and _A. tortilis_ on the deeper loamy soils of
the eastern parts. A large portion of the south-
east is composed of a dense thicket of _Acacia
luederitzii_ and _Euclea_ spp., with occasional large
specimens of _Spirostachys africana_ and _Schotia
brachypetala_.

The belt of pure sand in the centre of the reserve
supports a fine stand of xeric sand forest in which
Newtonia hildebrandtii, _Cleistanthus schlechteri_,
and _Pteleopsis myrtifolia_ are dominant. This gives
way, around the edges, to a marginal form of woodland
with considerable local variation in composition, but
containing, inter alia, such species as _Spirostachys
africana_, _Acacia burkei_, _A. grandicornuta_, _Combretum
molle_, and _Strychnos_ spp. Another sandveld
association, found in the region of the rest camp, and
south of the game-viewing hides, is dominated by
Terminalia sericea, whilst other species present are
Combretum molle, _Zizyphus mucronata_ and _Strychnos
spinosa_.

A riparian fringe, varying in width from a few to
several hundred metres, is found along most of the
Mkuze river. The vegetation here is dominated by
Ficus sycamorus, some of the trees attaining enormous
proportions. Other trees present include _Trichilia
emetica_ and _Rauvolfia caffra_. Generally there are
large specimens of _Acacia xanthophloea_ also present,
but these often form a fringe to the forest proper.
A dense tangle of _Acacia ataxacantha_ comprises the
undergrowth to the riverine forest, whilst the most
characteristic climber is _Combretum microphyllum_.

Generally speaking, but with the possible exception
of parts of the seasonally flooded areas, and in the
foothills, the grass cover is poor. This is however,
largely a secondary condition resulting from heavy

grazing pressures in the past. Much of this has improved in recent years, although large areas are almost denuded of ground cover in the drier months.

2.8.   Fauna.

The characteristic species of large mammal in Mkuzi is the impala, of which there are at present (April, 1971) an estimated 10-12 000. This figure is based on the results of a census carried out by helicopter in 1970, together with the estimated recruitment during the 1970 breeding season. (Natal Parks Board, unpublished records.)

Other large mammal species present, and estimates of their populations, are:

Wildebeest	Connochaetes taurinus	2 500
Zebra	Equus burchelli	150
Nyala	Tragelaphus angasi	1 500+
Kudu	T. strepsiceros	500
Bushbuck	T. scriptus	Few
Black Rhinoceros	Diceros bicornis	35
Square-lipped Rhino	Ceratotherium simum	8
Warthog	Phacochoerus aethipicus	1 500
Reedbuck	Redunca arundinum	250
Mountain Reedbuck	R. fulvorufula	25
Grey Duiker	Sylvicapra grimmia	Numerous
Steenbok	Raphicerus campestris	Numerous
Giraffe	Giraffa camelopardalis	30

Such a spectrum is typical of the lowveld habitats of southern Africa, particularly since it is known that such species as elephant (Loxodonta africana), buffalo (Syncerus caffer), roan (Hippotragus equinus), tsessebe (Damaliscus lunatus), and waterbuck (Kobus ellipsiprymnus), used to occur in the past.

As has been mentioned before, the small mammals of Mkuzi Game Reserve have strong tropical

affinities with elements of more temperate forms also
present.   Those species which have been recorded from
the reserve have been described by Dixon (1964).

CHAPTER 3:

REPRODUCTION IN AFRICAN UNGULATES.

3.1.   A brief history of research.

Studies on the reproduction of African ungulates
have shown an interesting, but perhaps not
unexpected, evolution from the comparatively crude
and simple observations on mating behaviour to
highly sophisticated laboratory, chemical techniques
aimed at the understanding of reproductive
physiology.   This evolution is typical of most
scientific doctrines in which a high degree of
specialisation in a particular topic is becoming
evident.   It is symptomatic too of the ever-
increasing numbers of wildlife research workers who
find it necessary to expand on the basic facts
gleaned by non-specialists.   An example of such
unspecialised work is that of Stevenson-Hamilton
(1947), who covers a vast field of natural history,
but who also includes many very pertinent
ecological principles.

It is really only in the last 10 years that
scientists have recognised the potential of African
wildlife as a source of research, and have begun to
exploit its possibilities.   As broad bases for such
research, the applied work of agricultural
scientists on domestic stock, and the research on
American game animals in particular, have served as
very stable "launching pads" for the veritable
explosion of data coming out of Africa.

One of the earliest reproductive studies on
African ungulates, and one which showed a high
degree of refinement, was that of Kellas (1955)
on the dik-dik (Madoqua kirkii).   More typical of
the rather naturalistic studies carried out in the
early stages are those of Bourliere and Verschuren
(1960) and of Brooks (1961), the latter a specific

study on the Thomson's gazelle (Gazella thomsonii).
All these works mention the seasonality or otherwise
of breeding in the various species, and the ages of
sexual maturity are quoted in each case. Similarly,
Riney and Child (1960) describe seasonality in the
duiker (Sylvicapra grimmia) and establish the age of
sexual maturity. Their work may perhaps be
considered as the start of the more specialised
studies on ungulate reproduction. Other similar
studies on African ungulates may be found in Dasmann
and Mossman (1962a), Talbot and Talbot (1963),
Fairall (1968), and Brand (1963).

The next stage in reproductive studies was
initiated by Buechner's (1961) discovery of the
phenomenon of territoriality in Uganda kob (Adenota
kob). This led to a spate of research projects
directed at understanding the spatial distribution of
individuals within populations. Such studies
included further work on kob (Leuthold, 1966), on
wildebeest (Estes, 1969), and on impala (Leuthold,
1970; Schenkel, 1966). This in turn produced, as
"by-products", several works on mating and post-natal
behaviour (Kiley-Worthington, 1965; Buechner and
Schloeth, 1965; Spinage,1969a).

The latest trend in reproductive studies was
initiated by Cheatum (1949) in a study of fertility
in white-tailed deer in America. The technique
described by him has since been used extensively both
in America (Golley, 1957; Morrison, 1960; Teer
et al, 1965) and latterly in Africa. Ovarian
analysis in Africa has been used in studies on
hippopotamus (Hippopotamus amphibius) (Laws and
Clough, 1966), on waterbuck (Spinage,1969b), on
wildebeest (Watson,1969), and on Uganda kob
(Buechner et al,1966).

Apparently the first histological study on female
reproductive organs of an African ungulate was that
of Kayanja (1969). Skinner and Van Zyl (1970) and

Skinner (1971) have carried out both histological and histochemical studies on male reproductive organs in an effort to understand the mechanism of the male reproductive cycle.

Mentis (1970) has recently reviewed many of the known life history phenomena of African ungulates pertinent to their productivity. Therefore the following discussion will be limited largely to aspects of reproductive biology not covered in his review.

3.2. Behaviour.

The many aspects of behaviour associated with breeding in African ungulates have received a good deal of attention from the rather broader considerations of sociology to the detailed ethological studies of pre- and post-coital displays exhibited by some species. These aspects will be briefly covered under their various headings in the light of information contained in the literature.

3.2.1. Sociology in the non-territorial context.

As will shortly be shown, territorial behaviour has some general functions in a fairly wide range of species, but there are those animals in which this form of organisation does not appear to be prevalent.

There is very little information in the literature about non-territorial species, although Robinette and Child (1964) simply state that in lechwe (Kobus leche), no indications of territoriality were found, although observations were made in the breeding season. This may perhaps be considered somewhat anomalous if behaviour is any indication of taxonomic relationships, as has been suggested by Estes (pers. comm.). Territorial behaviour has been observed in an animal belonging to the same genus, namely the waterbuck (Kobus defassa and K. ellipsiprymnus).

Klingel (1969) describes the social organisation of
the zebra (Equus burchelli) in terms of family units
containing one adult male. If the viewpoint of
Schenkel (1969) is to be accepted, this may in fact be
a form of territoriality in that the male defends a
mobile territory dependent on the presence of the
females.

Other than this evidence, one can but speculate
on what other species may not be territorial, and
in this category must be placed such ungulates as the
elephant, hippopotamus, warthog and the giraffe. None
of these has, as far as is known, been studied from
the sociological point of view.

3.2.2. Territoriality.

The phenomenon of territoriality amongst
African ungulates has been shown to be far more
widespread than was at first supposed, and the
sociological advantages of this habit are possibly
closely bound to the need for an orderly pattern
amongst individuals in a population. It ensures a
minimum of intraspecific fighting by means of highly
specialised ritualistic displays. This in turn is
probably a survival mechanism.

However, the chief function of territoriality
is probably related to breeding. Estes (1969) points
out that in several northern temperate ungulates,
territorial behaviour is limited to the rutting season,
e.g. red deer. In most of the East African ungulates
which exhibit territoriality, with the exception of
the wildebeest, there is no marked rutting or breeding
season. Estes (op.cit.) also goes on to say that all
these species, including wildebeest, are territorial
throughout the year. This coincides with year-round
breeding recorded in many species, e.g. Thomson's
gazelle (Brooks, 1961; Hvidberg-Hansen,1970), Uganda
kob (Buechner,1963), and impala (Kayanja,1969;
Leuthold,1970). The reason for the anomaly displayed
by wildebeest is not clear, although it may

be related to the fact that there appear to be no
cyclical changes in testicular activity as manifest
in testis weights (Watson, 1969). Nevertheless it
remains true to say that territoriality is most
closely related to breeding.

Hvidberg-Hansen (1970) has shown that, although
Thomson's gazelles show spermatogenesis at a fairly
early age, the males do not take part in the breeding
until much later. The onset of active reproductive
behaviour coincides with the attainment of full
physical maturity. It is at this time too that the
first overt signs of territoriality are displayed.
Similarly, Buechner et al. (1966) have noted that,
although spermatogenesis may occur in the Uganda kob
at 14 months of age, the minimum effective breeding
age is about $3\frac{1}{2}$ years. They go on to say, "Only
when a male has established himself firmly in the
territorial system, can he contribute successfully
to the reproduction of the species."

The establishment of territories is often preceded
by a good deal of fighting amongst contending males,
but in many species, the incidence of such fighting
is reduced by the development of elaborate rituals,
such as have been described for wildebeest by Estes
(1969).

What now of the strictly seasonally breeding African
ungulates, such as the many that are to be found in
southern Africa? This phenomenon is recorded in the
earliest biological writings, such as that of
Stevenson-Hamilton (1947), and indeed, it is such a
notable and typical feature of animals in this part
of the continent that no naturalist could fail to
observe it. Unfortunately, no detailed observations
on breeding behaviour have been noted, but certainly
personal observations on such species as wildebeest
and impala (both seasonal breeders) point to a marked
seasonal incidence of territorial behaviour.

Correlated with this is an apparent seasonal cycle in
testicular activity, as noted in impala by Anderson
(1965) and Skinner (1971), in the springbok
(Antidorcas marsupialis) by Skinner and Van Zyl (1970),
and in the wildebeest by Vincent (unpubl.)   The peak
of this activity coincides in each case with the
presumed height of the mating season. Skinner and
Van Zyl (1970) postulate that the seasonality is due
largely to the physiological status of the female.
However, this does not account for the synchronisation
of ovulation, and the possibility is here put forward
that the onset of territorial behaviour in males acts
as a stimulus to the synchronous, overt reproductive
reactions of the females in the form of ovulation.

Perhaps in confirmation of this theory is the
data presented by Kellas (1955) on the dik-dik. In East
Africa this species is quoted as having two breeding
peaks, correlated with two peaks in the activity of
the testes and male accessory glands. Further
confirmation comes from evidence cited by Sadleir
(1969), quoting authors who had worked on experimental
populations of domestic sheep, goats and cattle. In
these animals, the mere introduction of males brought
on a synchronous oestrous in the females. Watson and
Radford (1960 - quoted in Sadleir, op.cit.) went
further to show that the mere sound and smell of rams
was sufficient to cause synchronization of oestrous
in ewes.

It is obviously difficult to apply such
experimental methods to natural populations of wild
animals, but not improbable to assume that some similar
psychosomatic influence could affect synchrony in
ovulation through behaviour patterns associated with
territorial behaviour.

3.2.3.   Pre-coital behaviour.

In many species, an elaborate ritual of

pre-copulatory displays is evident. These have been
most intensively studied in the Uganda kob (Buechner
and Schlooth, 1965), in the waterbuck (Spinage,1969a
and Kiley-Worthington, 1965), and in the reedbuck
(Redunca arundinum) (Jungius, 1970). In general,
these displays appear to be mutually exciting on the
part of both male and female, and to synchronise the
actual mating with the period of maximum receptivity
in the female.

Insufficiently detailed work has been carried
out on most species for any significant trends to have
emerged, but it is possible that future studies will
reveal similar behaviour patterns, or at least
similarly orientated patterns, in other species as well.

3.2.4. Post-coital behaviour.

The only species in which this phase of mating
has been carefully documented is the Uganda kob
(Buechner and Schlooth,1965), but this may possibly
be because it is most obvious in this animal, and is
explained by these authors as being a consequence of
the very highly developed form of territoriality.

Buechner and Schlooth (1965) make comparisons
of the Uganda kob's display rituals with those of
other species. They qualify these comparisons by
adding that insufficient is known of the mating
ceremonies of other antelope in Africa.

It would seem that, in view of the basic
similarities of the display elements in many species,
there may be reason to expect that phylogenetic
similarities will be demonstrated following comparisons
once more is known.

3.2.5. Behaviour during parturition.

During this phase of reproduction, there are
definite patterns which have emerged from observations
on a fairly wide range of species, and it becomes
necessary to subdivide the phase further:

3.2.5.1. <u>Pre-parturition.</u>   In the very strongly
gregarious species such as wildebeest (Watson,1969),
females remain together in herds, to such an extent
that calving barely interrupts their social
organisation.   Watson (1969) speculates that
labour in a group of females may be psychosomatically
induced by its advent in one of the individuals,
giving this as a possible explanation of the
synchronous calving within the group.   In this
species, such a phenomenon may have a survival
value on the principle that "there is safety in
numbers".   On the other hand, he suggests that
this could also be on account of a prior "sorting
out" of cows at the same stage of pregnancy into
groups.

Most species however, become solitary at the
time of parturition and females leave the herds
temporarily in order to give birth.   This has
been observed in waterbuck (Spinage, 1969a), in
the reedbuck (Jungius, 1970), in the Grant's
gazelle (<u>Gazella granti</u>) (Walther, 1965), and
in the impala (Schenkel, 1966a).   It probably also
occurs in many other species, but has not yet been
documented.   The reedbuck, although not strictly
gregarious, nevertheless moves to a secluded spot
in the home range in order to give birth (Jungius,
1970).

3.2.5.2.   <u>Parturition.</u>   This has not often been
described for wild animals, and it is perhaps
significant that, because of its habits, the
wildebeest is probably the species in which it has
been most commonly observed.   Talbot and Talbot
(1963), Estes (1964), and Watson (1969) all
describe this feature.   On the other hand,
Spinage (1969a), although several times seeing
new-born young, did not witness the actual birth
in waterbuck.

Probably the most likely explanation for this
dearth of records is that most species give birth
during the hours of darkness. This does not appear
to have been documented, but personal observations
of known groups of animals do indicate such an
occurrence. Spinage (1969a) mentions that in
waterbuck most births seem to take place "in the
early morning".

3.2.5.3.   Post-parturition.   In this phase of breeding
there seem to be distinct trends, which are
associated with the habits of the species concerned.
In highly gregarious species such as the wildebeest,
the young is mobile within minutes of birth, and
able to keep up with the dam within hours (Talbot
and Talbot, 1963).

In those species which are gregarious, but which
secrete themselves during parturition, the young
are not quite as precocious, but are usually quite
mobile within one or two days of birth.   Into
this category would fall the giraffe, buffalo and
gazelles.   The former two have been personally
observed in company with adult females in the herds
at obviously very young ages.

Finally there are those animals which have the
habit of secreting their young for varying periods
after birth, before any attempt is made to incorporate
them in the normal social units.   Spinage (1969a)
gives the period of such hiding in the waterbuck
as from two to four weeks, whilst Jungius (1970)
gives it as one and a half to two months, possibly
even three months, in the case of the reedbuck.

The correlation here is between the period of
time from birth to incorporation in the social
unit, and the extent to which the species is bound
to the home range;   there is also some influence
by the extent to which the species is gregarious.
The two extremes are shown by the wildebeest (which

at least in East Africa is highly nomadic), and the
reedbuck in which a family unit is restricted to a
territory (Jungius, 1970).

Walther (1958),(in Jungius, 1970), recognises only
the two extreme conditions which he called
"Nachfolgertyp" and "Abliegetyp" respectively.
Unfortunately there has been insufficient work on
the intermediate types to establish a definite
progression, but it is likely that most species will
not fall into either of Walther's categories.

3.3. Male reproductive physiology.

Many species, particularly those which exhibit
seasonal breeding, also show a marked peak in
testicular activity, manifest in the testis weight.
In addition to this, it has been shown that an
increase in seminiferous tubule diameter accompanies
the onset of breeding activity. Furthermore, in
animals with no apparent peak in testicular weights,
e.g. wildebeest in East Africa (Watson, 1969), there
is no increase in the diameter of seminiferous tubules.

Of particular interest are the observations of
Clough (1966, in Spinage, 1969b) that the testis
weight in hippopotamus fluctuated randomly, but that
there was a correlation between peaks of conceptions
and testicular activity as determined by studies on
spermatogenesis. Spinage (1969b) found no apparent
seasonal changes in testis weights or tubule diameter,
yet there was a significantly higher proportion of
conceptions in the dry season, resulting in more
births in the wet season.

Skinner and Van Zyl (1970) and Skinner (1971) have
shown that in the springbok and impala there is a
close correlation between peaks of testis weight and
tubule diameter, both occurring at a time immediately
preceding the main mating season. These authors have
further shown that certain other parameters, viz.
the weight of the seminal vesicles, weight of the

epididymides, epididymal sperm numbers, and particularly the percentage of motile sperm, are also correlated with the breeding season. Their histochemical studies also indicate a similar cyclical change in concentrations of fructose and citric acid in the seminal vesicles. From these latter observations they conclude that, because of the correlation found in ruminants between testicular testosterone and vesicular fructose and citric acid, the production of androgens is also of a cyclic nature, declining only after the mating season.

Such studies as these may well, in due course, throw light on the fundamental reasons for the seasonal incidence of mating and reproduction. Many theories have been put forward by Sadleir (1969), amongst which are the influences of light and photoperiod.

3.4. Female Reproductive Physiology.

More work has been done on this probably than on any other aspect of reproduction. Authors who have carried out such work include Watson (1969) on wildebeest, Laws and Clough (1965) on hippopotamus, Spinage (1969a) on waterbuck, and Buechner et al (1966) on the Uganda kob.

3.4.1. Oestrous. The detection of an oestrous cycle in wild animals is very difficult on account of the fact that there is usually no control, and most females in a natural population are probably fertilised very soon after exhibiting overt oestrous behaviour. Nevertheless, various workers have postulated on the length of the cycle. In wildebeest, Watson (1969) suggests a cycle of 15 days, whilst in Uganda kob it appears to be from 21-26 days (Buechner et al, 1966).

The situation is further confounded by the observations on both these species that an oestrous period appears to precede the one in which fertilisation takes place. Watson (1969), on the evidence of the presence of regressing corpora lutea of the cycle in

most instances studied, goes so far as to say that
this condition may be a prerequisite to successful
oestrous behaviour.   Buechner et al (1966) found
that two to three ovulations may occur before
fertilisation.   This phenomenon has been termed
"silent ovulation" (in preference to "silent heat",
which implies overt behaviour) by Fraser (1968), who
also quotes numerous authors who have observed it in
domestic ungulates.   Spinage (1969b), on the other
hand, suggests that in waterbuck there is no pre-
conception oestrous.

Several workers quoted by Fraser (1968), notably
Lagerlof (1951), suggest that the occurrence of these
"silent ovulations" may be hereditary, at least in
domestic stock.   This may account for differences
between and within wild ungulate species.   Fraser
(1968) states that the female sex drive is dependent
upon the presence in the ovary of a ripe follicle,
and is therefore of short duration.   Male sex drive,
on the other hand, is dependent upon the secretion of
testosterone, and is very prolonged, if not
permanently evident, in non-seasonally breeding species.
It is this fact which ensures the generally high
incidence of successful ovulations encountered in
wild animals.

The duration of oestrous is not well established,
although Buechner et al (1966) cite evidence for a
period not exceeding 24 hours.   Fairall (1970) quotes
the duration of oestrous as varying from 24 hours in
some species to 9 days in the zebra.

3.4.2.   Ovulation.   There appear to be considerable
differences in the pattern of ovulation in various
species.   Watson (1969) found that in wildebeest a
significantly larger number of successful first
ovulations take place from the right ovary than from
the left;   thereafter both ovaries contribute at
random.   Buechner et al (1966) record random release
of ova from left and right ovaries.   On the other hand,

Robinette and Child (1964) found that a significantly
larger number of successful ovulations had occurred
from the left ovary than from the right (57:33) of the
red lechwe and Spinage (1969b) found that the left
ovary of waterbuck was 1,2 times more active than
the right.

3.4.3.   Implantation.   The interesting phenomenon of
unilateral, or nearly so, implantation has been found
in most ungulate species that have been studied.
This was first reported by Kellas (1954) for the dik-
dik (right uterine horn), and subsequently
implantation has also been found in the right horn
in impala (Mossman and Mossman 1962),in Uganda kob
(Buechner, 1961) and in the waterbuck (Spinage 1969b).

In the wildebeest, Watson (1969) found almost
perfect homolateral correlation between ovulation and
implantation.   Nevertheless, although not significantly
different in frequency at the 5% level, there appeared
to be a tendency to favour the right horn for
implantation - 33:19.   This he broke down to 11:2
for non-parous females, and 22:17 for parous females,
the former difference being significant.   This ties
up with his observation that the first successful
conception occurred from the right ovary.

The reasons for unilateral implantation have
never been investigated (Skinner, pers.comm.) and
the mechanism is not understood.   The work of
Buechner et al (1966) suggests that there may be a
genetic fixation of symmetry at least in Uganda kob,
as they found that even in foetal uteri, there was a
tendency for the right uterine horn to be larger.

3.4.4.   Gestation.   No effort will be made to cite
recorded gestation lengths, as these have been
adequately dealt with by Kenneth and Ritchie (1953)
and by Mentis (1970).   However the physiological
and somatic changes taking place during pregnancy
will be briefly reviewed.

Watson (1969) reports that in early pregnancy, two corpora lutea may be present in the wildebeest, one derived from the preconception oestrous cycle, and the other being the corpus luteum of pregnancy. The former disappears after about 90 days, but can at no stage be confused with the latter or with corpora albicantia on account of its much lighter colour. Personal data on the same species from Zululand confirms this finding, and notes were made at the time of this observation to the effect that such corpora lutea would not have left.a pigmented scar typical of the corpora albicantia. This phenomenon has not yet been recorded for any other species.

Laws and Clough (1965) report that in the hippopotamus, follicles develop throughout, pregnancy and give rise to "accessory corpora lutea" through becoming luteinised. However, it may be significant that they also note that in some cases there was no other luteal material present in the ovaries, particularly in the later stages of pregnancy. Spinage (1969b) states that in the waterbuck there are no accessory corpora lutea, and the fact that their presence has not yet been recorded for other African artiodactyls seems to imply that it may be peculiar to the hippopotamus and the equines.

The technique of ovarian analysis as a possible means of determining the breeding history of an individual was first described by Cheatum (1949), who concluded that it was adequate for estimating ovulation rates in the immediate past season. He did go further to say that pigmented scars from luteinised follicles could be distinguished from those of corpora lutea of pregnancy in white-tailed deer (Odocoileus virginianus). Golley (1957), using the same method on black-tailed deer (O. hemionus), arrived at the same conclusion.

Morrison (1960) concluded that in elk (Cervus

canadensis) the occurrence of pigmented scars could
in no way be correlated with past productivity,
particularly since they were also formed from
accessory corpora lutea that developed during
pregnancy.   Haugen and Trauger (1962), whilst
finding no corpora albicantia in white-tailed deer
that had not previously bred, could not correlate
the number of corpora albicantia with age of older
animals.

It would appear from evidence from north-temperate
species that corpora albicantia in that region are
not as persistent as they are in some African
antelope, and that the ovarian cycle during pregnancy
may vary in some respects, particularly with
regard to the development of accessory corpora lutea.

In some species, the corpus luteum increases in
size with duration of pregnancy, decreasing in the
last stages.   This has been recorded for
hippopotamus (Laws and Clough, 1965), in which this
is also manifest in changes in the weight of the
ovary containing the corpus luteum.   In the
wildebeest (Watson, 1969) there is an increase in size,
followed by a slight decrease and then a further
increase, whilst in the waterbuck (Spinage, 1969b)
the corpus luteum achieves maximum size at about 30
days post-conception, and thereafter remains constant
in size until parturition.

These observations are generally contrary to the
situation in sheep (Short and Moore, 1959, cited in
Watson, 1969) in which the corpus luteum decreases in
size in later pregnancy, as its function of
progesterone production is partly taken over by the
placenta (Fraser, 1968).   In fact there is as yet
no evidence from wild animals that this function is
at any stage performed by the placenta. If corpus
luteum size is any criterion, it would seem doubtful.

3.4.5. <u>Post-partum period.</u>   After parturition, the
corpus luteum degenerates rapidly, and gives rise
to a corpus albicans.   This structure is
persistent for varying periods, and it is seen as
a "pigmented scar".

Watson (1969) found a fairly close correlation
between the number of corpora albicantia present
and the expected number of pregnancies experienced.
At no stage did this number exceed the number
expected.   Spinage (1969b), on the other hand,
found that there was no correlation, and in some
cases the number present exceeded the expected
number of pregnancies.

In species with no fixed breeding season, i.e.
continually breeding species, there generally is
a post-partum oestrous cycle in which conception
may or may not take place.   Buechner et al (1966)
suggest that in the Uganda kob the period between
parturition and first oestrous corresponds
approximately to the length of the oestrous cycle
(21-26 days).   However they also say that the
post-partum interval varies between 21 and 64
days, suggesting that two or more cycles may
elapse before conception.   Spinage (1969b) found
that fertilisation may occur at the first ovulation
after parturition, or later, in the waterbuck.

This variation may in part be due to the
plane of nutrition, and could account (in essentially
non-seasonal breeders) for the observed peaks in
parturition recorded in some species.   The
phenomenon of a lactation anoestrous would appear
not to be manifest in wild ungulates anyway, for
even in seasonally-breeding populations, many
females are still lactating at the time of
oestrous (Watson, 1969).

Most animals suffer varying degrees of neonatal
mortality, yet no instance of mastitis - so

prevalent in dairy cows which are not milked
properly - has been reported for wild animals.
Spinage (1969b) records this fact, in spite of the
incidence of regressing mammary glands due to calf
loss in waterbuck.

3.5. Fertility and fecundity.

Most African ungulates have a very high rate
of fertility in individuals that have reached
breeding age. In most species there is a certain
segment of the population which matures earlier
than the rest, and the proportion which does so
varies within a species according to conditions. The
high fecundity is perhaps not surprising in view of
the high degree of social organisation attained by
many species during the breeding season or, in
non-seasonal breeders, throughout the year.

In East Africa, where most species are non-
seasonal in their breeding activities, workers have
tacitly assumed an almost continuous breeding, and
no evidence has been put forward of marked deviations
from this in the form of populations showing any
degree of temporary cessation of breeding.

It is easier to establish fecundity rates for
seasonal breeders, and in this most authors agree
that they are very high. Watson (1969) gives a
fertility rate of 96% for wildebeest females over
three years old, and during a period of four years,
37% of yearlings conceived and 83% of two-year old
animals did so. Talbot and Talbot (1963) obtained
figures of 83% for yearlings and 95% for older
animals, whilst Estes (1966) found 75% of yearlings
to be pregnant.

Simpson (1968), working on greater kudu
(Tragelaphus strepsiceros) in Rhodesia, concluded
that "middle-age" adults showed 100% effective
fertility whilst "young adult" and "old adult" animals

showed 80% and 85% fertility respectively.   The
"young adult" group included animals that had recently
attained full permanent dentition.   He also found
that 25% of yearling females and 63% of two year-old
females were fertile.

Robinette and Child (1964) found that 40% of
yearling lechwe bred, whilst the figure for older
animals was between 93% and 96%.

For many of the larger animals, it is often
difficult to establish fertility rates.   For instance,
Laws and Parker (1968), working on elephant in East
Africa, concluded that fertility is widely variable
from year to year - the mean calving interval varying
from four to nine years in two separate populations.
This variation is evidently dependent upon nutritional
effects.   Hanks (1970), cited in Fairall (1970),
describes a decline in fertility rate with increase
in density of elephant in Zambia.

In the case of the buffalo, Fairall (1970) states
that fecundity may be modified by nutritional
conditions.   In hippopotamus, Pienaar et al (1966)
found 22 out of 36 (61%) adult females to be either
pregnant or lactating, and quotes Bere (1959) who
found 67% to be pregnant and/or lactating in East
Africa.   Laws and Clough (1965) report finding 77%
of 649 female hippopotamus to be pregnant and/or
lactating, whilst a further 6% had recently ovulated.

3.6.   Sexual maturity.

The age at which sexual maturity is achieved in
both males and females is adequately reviewed by
Mentis (1970).   There does seem to be some
correlation between the size of the animal and the
age at maturity, particularly in the case of the female.
This may be as young as seven to eight months, as
in the springbok (Bigalke, 1970) and grey duiker (Child
and Wilson, 1964) and as old as eight to fifteen years

in the elephant (Laws,1966; Laws,1970; Hanks,1970).

There is however, a modifying effect on the basic age of maturity, namely the plane of nutrition. It is this, probably more than anything, that results in such variation in the age of sexual maturity within a species as is outlined for several species by Mentis (1970). Another factor which cannot be overlooked is seasonality: an animal may be potentially capable of breeding earlier than it in fact does because of the apparent need to await the next breeding season.

3.7. Foetal growth.

The rate of foetal growth of most mammals studied follows the pattern of the curve of exponential growth, but modifications to this curve have been made to assist in the prediction of conception age of a foetus of known mass or size. The simplest of these modifications is the logarithmic curve which, as in the case of an exponential growth curve, is a straight line.

However, greater use of the method devised by Huggett and Widdas (1951) has recently been made in the prediction of age from mass. This method however, depends upon the establishment of an age at which the straight line intercepts the age (X) axis. The Y-axis is the cube root of the mass, whilst a further constant is the so-called instantaneous growth rate in the formula $W = k(t-t_0)$, where k is the constant, t is the gestation period, and t_0 the X-intercept.

Buechner et al (1966) were in the fortunate position of knowing the exact age of 13 foetuses of Uganda kob, and fitted these to a regression line of age on mass with a very close correlation. They state further that the confidence limits of this regression are considerably narrower than those

obtained by the method of Huggett and Widdas (1951).
The derivation of an identical regression for impala
foetuses by the Huggett and Widdas method in two
separate studies will be discussed in more detail
in a later section.

CHAPTER 4:

REPRODUCTION IN THE IMPALA: OTHER STUDIES.

4.1.   Seasonality.

Sadleir (1969) discusses at some length the
literature pertinent to seasonal breeding in many
mammals. Most of this discussion deals with the
various factors - both inherent (genetic) and
environmental - which play a part in determining
seasonality of reproduction in mammals.

The evidence appears to indicate that different
factors act in different ways in different parts
of the world to achieve the same.end, but the main
question remains unresolved, i.e. at what stage in
the reproductive cycle the various factors play the
most significant role. Is the cycle arranged so
that the peak of parturition occurs at a time when
the food resource is most abundant, or does some
other environmental factor such as photoperiod act
to cause synchronisation of oestrous and testicular
activity? No attempt will be made to answer this
question here, but it is important to realise that
it underlies the whole concept of seasonal breeding.

It should perhaps further be pointed out that
there are two main variables in considering the
subject of seasonal breeding, namely the timing of
the peak of behavioural oestrous or overt
reproductive activity, and the duration of this peak.
Consideration of the incidence of seasonality in
different parts of the range of the impala in Africa
clearly demonstrates that it is chiefly
environmental influences rather than genetic ones,
which have been instrumental in achieving the end.

In East Africa, where the impala occurs in a
somewhat discontinuous distribution, the evidence
points to a double peak of breeding behaviour,
resulting in peaks of parturition coinciding with
the two annual rainy seasons: April-May and
October-December.   Haltenorth (1963, in

Kayanja, 1969) states that the main peak of parturition occurs in April and May, whilst Kayanja (1969) goes farther to say that a second peak is evident in the last three months of the year, i.e. during the "short rains". Both these authors are referring to populations in Kenya, Kayanja more specifically quoting the area around Lake Elmenteita (36°14'E, 0°26'S) where he worked on the subspecies <u>Aepyceros melampus rendilis</u> Lönnberg. Leuthold (1970), working in Nairobi National Park, states "...impala breed throughout the year; reproductive peaks may be correlated with the rainfall pattern."

Schenkel (1966b) gives data for breeding peaks in south-western Kenya, and is more specific about peaks in Nairobi National Park. In the former area he quotes evidence for a mating "peak" in "...January to March and sometimes early April", suggesting a lambing peak between August and October. In Nairobi National Park, in 1963, rutting peaks were observed from February to April, and August to October, which would give peaks of lambing from September to November and March to May.

According to Pearsall (1957) the rains in the Serengeti area occur in the form of "short rains" in December and as main or "long rains" in April-June. Darling (1960), on the other hand, states that in the adjacent Mara plains, there is a short rainy season in November and December and a main rainy season from March to May.

These rainy seasons do not quite coincide with the impala lambing peaks as described by Schenkel (1966b). The short rains in the Nairobi National Park also occur in November and December, whilst the long rains occur in March to May (Foster and Kearney, 1967). Thus, in this area anyway, there is a closer correlation between the peak of parturition and the rainy seasons, as described by Kayanja (1969) and Leuthold (1970).

Jarman and Jarman (1969), working in the Serengeti National Park in Tanzania, describe two calving peaks in

a period of 18 months - July-October 1968 and June-August
1969 - but also state that the peaks varied in their
amplitude and incidence in different parts of the park.
There was a greater tendency for defined peaks in the
northern part of the park than in the west. Later, it
was reported from the same region that a small breeding
peak had occurred in the first quarter of 1970 (Jarman,
1970a).

Ansell (1960), gives the lambing season for impala
in north-western Zambia as September-October, whilst in
southern Zambia it is a month later - in October-November.
The latter area includes the middle Zambesi Valley in
which is situated the Kariba basin. It was here that
Child (1968) stated that the peak of parturition takes
place in December. However he quotes Dasmann and Mossman
(1962b) who worked mainly on the Henderson ranch in
south-western Rhodesia, and it is possible that he has
made the tacit assumption that the seasons are the same
in the two regions. In another paper Child(1964),
however, gives November as the lambing peak in the
Zambesi Valley from "records on hand"; it is the same
in south-eastern Rhodesia.

Dasmann and Mossman (1962b) state that in two years
(1959 and 1960), the peak of parturition took place in
the latter half of December. They also mention an
observation by Stevenson-Hamilton (1937) that some young
are born later than the rest. This they speculatively
attribute (as does Stevenson-Hamilton) to the two-year-old
females, which are bearing their first young, having a
slightly later period of parturition than the older
females. However, there is no evidence provided for this.

Whilst discussing impala breeding seasons in Rhodesia,
it is interesting to note that Wilson (1969), working on
animals in the Matopos National Park in central western
Rhodesia, noted an apparent peak of lambing about mid-
December (51 out of 62 births took place in December).
This appears to indicate a trend from north to south,

although Dasmann and Mossman (1962b) deny this in quoting
Stevenson-Hamilton (1937) and Rhodesian departmental
records. The danger of using departmental records
is evident, particularly in an area the size of Rhodesia
which seems to be an important intermediate zone: the
breeding season to the north is earlier than it is to
the south of Rhodesia.

Farther south, notably in the Kruger National Park,
authors such as Pienaar (1963) and Fairall (1968)describe
a lambing season which begins during the first week of
November and extends through until late December.
Stevenson-Hamilton (1937), referring mainly to the
Kruger National Park population, states that impala
lambs are usually born from about the middle (sic) of
November until the end of December. He goes on to
provide two further qualifications to this general rule,
namely that the actual time of parturition may vary by
as much as a "couple of weeks according to the lateness
or otherwise of the season"; and secondly suggests that
the two-year-old females may parturate several weeks
later than the older ones.

As far as the second of these statements is concerned,
there is again no evidence, other than circumstantial,
to suggest that this is a general rule. However, the
comment that the peak of lambing may vary from year to
year according to the season is more significant.
Fairall (1968) also mentions this phenomenon, stating
that in some years the lambing appears to be concentrated
over a short season, whilst in others the season is more
prolonged. Furthermore, more lambs are born "out of
season" during abnormal years or in areas where grazing
conditions have been disrupted". Unfortunately, there
is no reference made to any possible variation in the
actual mating season as a result of drought or other
factors, and the inference by both authors is that the
actual gestation period may be prolonged somewhat under
drought conditions. It is of course not as easy to
detect the peak of oestrous or mating behaviour without

examination of ovarian material, as it is to record a peak
in parturition, so that slight variations in the time of
mating are likely to go undetected.

In Zululand, as elsewhere in eastern South Africa,
there is again a very marked seasonal peak in breeding
behaviour which has been documented by Anderson (1965).
He describes a peak of rutting in Hluhluwe Game Reserve
during the latter half of May, 1963.   Assuming a gestation
period of 200 days, this would give a peak of parturition
about mid-December, which is in accordance with
observations for most years in the region.   In the Mkuzi
Game Reserve, perusal of unpublished records of Natal
Parks Board indicates that the normal peak of lambing takes
place over a two to three week period from the last week
of November until mid-December.

Farther west, in Botswana, Robbel and Child (1969)
describe a peak in the rut in 1969 between about 12th
May and 16th May, giving a lambing peak at the end of
November and the beginning of December.   Thus, if the
discussion on a possible north-south gradient in central
Africa is to prove significant, the lambing peak in
Botswana ($19^\circ 05$'S, $23^\circ 44$'E) falls between that for the
Zambezi Valley population and the Matopos National Park
population.

In South West Africa, the situation approximates
that in Zambia, with a lambing season in September-October
(Shortridge, 1934).   This is confirmed by Gaerdes (1965)
who says that the rutting season of impala in South West
Africa is dependent upon the season, but normally occurs
in February-March, with parturition taking place in
September-October.

Finally, some data obtained from captive animals in
Pretoria (Brand,1963) show that there is a very marked
peak of births during the first half of December.   The
interesting point about the information provided in
that source (which is a well-controlled one) is that there
is a greater tendency for births to tail off after the

peak then to build up prior to it, i.e. it is a
markedly skewed distribution. This indicates a
significant feature of the female reproductive
cycle which will be dealt with later.

Fig. 1 summarises all the data in this section as
a map which shows the distribution of lambing
peaks in different parts of Africa.

4.2. Sociology.

The phenomenon of territoriality has been
recorded for impala (Kayanja, 1969), and its prime
function is probably one associated with breeding.
It was however, not until quite recently (Leuthold,
1970) that the existence of territorial behaviour
in the species was unequivocally recognised.

Prior to this, there had appeared in the
literature some suggestions that this may be the
case. Dasmann and Mossman (1962b) recorded what
they somewhat apprehensively termed rutting
behaviour. They went on to mention that during
the peak of this activity "lone males were widely
spaced in areas that appeared to be breeding
territories", whilst other males were associated
with groups of females. The latter observation
may be interpreted as merely a further manifestation
of the territorial behaviour, in that such males
could have simply been accompanying the females
whilst remaining within their territories.
Unfortunately no mention is made by these authors
of prolonged observations of males which might have
clarified the situation, although later in the paper
(p.390) they provide further circumstantial
evidence in the form of dung-piles which were found
only during the mating season, and the fact that a
single male may be seen repeatedly in the same
location, only leaving it to drink.

Schenkel (1966a), apparently unaware of the work
of Dasmann and Mossman in Rhodesia, worked on

social behaviour of impala in Kenya, primarily in
the Nairobi National Park, and either assiduously
avoided any mention of territoriality, or failed to
interpret some of his observations as manifestations
of this form of behaviour. Although not described
in any detail, the behaviour noted on page 181 of
his work is certainly in keeping with that to be
expected of territorial animals. In several other
situations his descriptions can also be interpreted
as behaviour associated with territoriality.

The underlying theme of Schenkel's paper is one
in which the dominance of one male over others is of
paramount importance: this dominance takes the
form of "possession" of a female herd.

At a later stage, Schenkel (pers.comm.,1969)
reiterated that he did not recognise the behaviour
of impala as territorial, sensu stricto, but that
he did agree that the situation as noted by him
could have been a transitional stage of behaviour.
He clarified the position, explaining that a male
dominates a female herd, in the immediate vicinity
of which he is intolerant of other males. However,
this intolerance is "...focussed on the female herd,
and not on his home range..."

Leuthold (1970) takes up the cudgels against
Schenkel by saying (p.717) the problem resolves
itself into one of semantics: "The argument is
thus reduced to the question of what the difference
is between a male that is dominant in a certain
location but not in another, and a territorial male.
If there is any difference at all, it would appear
to be one of degree rather than of absolute
categories." He points out that Schenkel is
perhaps too dogmatic in his definition of a
territory when he says (Schenkel, 1966c, in Leuthold,
1970) "...that an area can only be called a true
territory if the occupant has the entire area under
sensory control at all times and can confront and

ward off any intruder immediately." The generally
accepted definition of territoriality is one which
implies "...defensive behaviour or intolerance towards
conspecifics within a given area." (Leuthold,1970:
704). Thus Schenkel's observations fall within this
acceptable definition and should be construed as true
territoriality.

Leuthold (1970) concludes that impala are
territorial, at any rate in the Nairobi National Park,
and that females do not attach themselves to any
particular male. One male occupied a territory for
35 consecutive weeks, but it must be remembered that
this observation was made in a population with no true
seasonal breeding peak. He also tentatively states
that any apparent variations in social behaviour may be
due to different environmental conditions and features
of the habitat.

With regard to the social behaviour of impala other
than territoriality, most authors agree that there is
no rigid herd organisation, but that the various social
units are highly flexible in their nature. Dasmann
and Mossman (1962b) describe briefly the seasonal
changes in group composition from the large "ewe-lamb"
herds at the end of the lambing season, through
smaller groups during the rut, to mixed groups in
the dry season.

Schenkel (1966b) recognises two main groupings:
the female or breeding herds, and the male or bachelor
herds. He evidently did not recognise the dynamic
aspect of impala herds, changing in size as they do
with the different seasons.

Leuthold (1970), working in the same area as
Schenkel, did however note this aspect of group
formation and concluded that:

"1. The female herds are unstable in number
        and composition.

2.   Thĕre are no stable social units, with the
      poɔsible exception of small (sic) mother-
      young associations.

3.   Female herds or individual females are not
      permanently attached to a particular
      adult male."

He nevertheless qualified these conclusions with the
observation that in one part of the study area
(Somali Ridge) the pattern is not as variable, probably
on account of its lesser suitability as a habitat.

4.3. Age at sexual maturity.

   4.3.1.   Males.

         The only really definite information on the
age at which impala males achieve sexual maturity is
that provided by Kerr (1965).   Using a simple technique
of sperm smears, he detected the presence of
spermatozoa in the epididymus of impala 13 months old,
concluding that the males are physiologically capable
of taking part in breeding at this age.   He supports
his contention by quoting an instance that occurred in
Natal in which a number of juvenile impala introduced
to a farm, and isolated from other populations,
produced their first progeny at two years of age.   Thus
the males must have bred at 17-18 months of age.

         Whilst breeding may take place amongst
yearling animals, full adult testis mass is not
achieved until considerably later, as showh by Kerr
(1965) and Child (1968).   It would appear, from
incomplete evidence that full adult testis mass is
reached at the age of about 27-30 months, but it should
be remembered that there is also a marked seasonal
change in testis mass (see later) which tends to mask
the attainment of adult mass.   Unfortunately, both
Kerr's and Child's samples were taken during the same
period of the year, and both omitted animals between
17 and 22 months old, and between 29 and about 34
months old.

In spite of maturing at a comparatively
early age, it is unlikely that young males, up to the
age of about three to four years, take part in the rut
under natural conditions. This is because they would
be what may be termed "psychologically unprepared" for
assuming territories. Physically too, they are not
as robust as older animals, and would not be able to
compete with them in fighting.

4.3.2. Females.

Most authors agree that the majority of
females produce their first young at the age of two
years.

Using the instance cited earlier, Kerr
(1965) reasonably concludes that females are capable
of producing young when two years old, whilst Skinner
(1969) quotes an instance of a semi-tame animal which
also produced its first young at two years of age.
These examples do not, however, preclude the
possibility that females may give birth at the age
of one year: there is in fact a good deal of evidence
that in a small proportion of cases this does take
place.

Dasmann and Mossman (1962a), working on a
population in south-western Rhodesia, found no animals
of less than one year old to be pregnant, whilst 11
out of 13 yearlings were pregnant.

Child (1968), studying populations in the
Zambezi Valley, found that seven out of eight yearlings
had conceived, and again that no juveniles had done so.

In Zululand, I.B.Stewart (Unpublished data,
Natal Parks Board) has recorded that in 1965, 16 of 20
(80%) of "subadults"(one to two years old) were pregnant,
whilst only one of 26 juveniles was pregnant, and seven
of 20 (35%) "subadults" were lactating, indicating that
they had conceived as juveniles.

The explanation for this apparent early

maturity in a fairly large proportion of the population
of females presumably lies in the plane of nutrition.
It is possible that under Zululand conditions, with
a somewhat extended summer (rainy) season, the herbage
remains nutritious enough to influence follicular
development in time **for** the first mating season after
birth, whereas in Rhodesia, with a relatively early
cessation of the rainy season, this is not the case.

Up till now consideration has only been
given to animals in populations with a clearly defined
breeding season, but what of those with a protracted
breeding season, as in Kenya. The only available
information on these animals is that supplied by
Kayanja (1969). He cites Haltenorth (1963) who
suggested that females probably mature at about 18
months, but in his study, found that the minimum age
at conception was closer to 12 months. This is
surprising in the light of the information obtained
from Zululand, where the animals could not have been
more than six months old at the time of conception.

Mentis (1970) discusses Stevenson-
Hamilton's (1947) statement that "young" females give
birth later than "older" females, in the light of the
inability to age females in the field by the end of
their second year. He concludes that Stevenson-
Hamilton's "young" females are therefore just over
one year old, and that they must have conceived as
juveniles. This argument presupposes that Stevenson-
Hamilton did not simply assume that it was only the
younger females that gave birth after the main peak of
parturition. If it was by direct observation, then
it would be true to say that juveniles also conceive
in the Kruger National Park.

4.4. Sex ratios.

The sex ratio of any wild animal at birth is a
difficult parameter to determine at the best of times,
and it can usually only be done indirectly by working

on the sex ratio of foetal material.

There is, however, one useful source for the sex ratio at birth, namely the data provided by Brand (1963): of 120 impala of known sex born in the National Zoological Gardens, 50 were males and 70 were females, i.e. a sex ratio of 1:1,4. Mossman and Mossman (1962) recorded 25 males and 34 females in a sample of foetuses old enough to be sexed in a population in Rhodesia, i.e. 1:1,4. Neither of these samples, taken separately, shows a significant difference from parity, although Mentis (1970) points out that if they are lumped together, the combined ratio does so.

With regard to the adult sex ratio, there is a good deal of information available. This is summarised in tabular form in Table 1.

All the sex ratios in Table 1 are for animals over one year of age, and it is clear that the approximate average ratio is 1 male:2 females. What is particularly interesting is that all the large samples are particularly close to such a ratio.

A good deal of speculation as to the cause of the disparate sex ratio in many ungulates has taken place, but it seems to be generally agreed that it is due to a heavier mortality amongst young males than among females of the same age, e.g. Taber and Dasmann (1954) in the black-tailed deer in America. The evidence of Robinette et al (1957) seems to contradict this theory however, as does a fair amoung of evidence on the sex ratios of juvenile animals.

Pienaar (1969) attributes the disparity in the sex ratio of several species in the Kruger National Park to differential predation on the sexes. Indeed, the data he provides on recorded kills of impala by predators reveal that between 1966 and 1968, a total of 850 were males and 964 were females. If there is a factor of sex linked mortality as well, then such a differential kill ratio could further enhance the effect.

Table 1.   Sex ratios of impala populations from
different parts of the species' range.

AREA	SOURCE	SAMPLE SIZE	SEX RATIO ($\male$: $\female$)		
Nairobi N.P.	Leuthold (1970)	300-350	1	:	2
Zambia	Mentis (1970)	459	1	:	1,5
Rhodesia:					
Fort Tuli	Dasmann & Mossman (1962b)	1986	1	:	2,1
Limpopo River	" "	107	1	:	2,6
Central Estates	" "	88	1	:	1,8
Wankie N.P.	" "	327	1	:	1,2
Kariba	" "	333	1	:	2,6
Henderson Ranch	" "	2864	1	:	2,1
Kariba	Child (1968)	800	1	:	2
South Africa:					
Kruger N.P.	Pienaar (1969)	?	1	:	2,4
Timbavati G.R.	Hirst (1969)	14319	1	:	1,8
Mkuzi G.R.	Stewart & Stewart (1966)	3921	1	:	1,9
Mkuzi G.R.	Anon. (1968)	2511	1	:	1,9
Unknown	Mentis (1970)	50	1	:	2,1

Dasmann and Mossman (1962b) describe a small
sample of impala from Kariba in Rhodesia, in which
a ratio of juveniles changed from 1 male:0,9 female
in February-May, to 1 male: 1,6 females between June
and September. The conditions pertaining at the time
would have placed the animals under some degree of
stress. They add that, "Under conditions of
overcrowding and inadequacies in the habitat, ...
a higher percentage of male lambs succumb during the
early months of life, whereas under better conditions,
....the sexes survive in a more equal proportion."

In Zululand, Stewart and Stewart (1966) recorded
a sample of 833 11-month-old animals. (They called
these individuals "subadults"). Of these, 433 were
males and 400 were females - a sex ratio of 1: 0,9.
Such a preponderance of males is rather surprising in
the light of what has already been said, but it can
only be added that, in the author's experience, it is
extremely difficult accurately to distinguish juvenile
females from older animals in the field from the age
of about eight to nine months. It is very likely
therefore that Stewart and Stewart (1966) under-
estimated the number of 11-month-old females in their
sample, confusing this class with adults.

In the Eastern Transvaal, Hirst (1969) obtained
several samples of "partly grown" impala, i.e. animals
10-12 months old, over a period of three years. The
sex ratio of this age class varied from 1:1,3 to
1:5,5, but if all his samples are lumped together, the
ratio becomes 1:2,2. The same comments must apply to
these results as were made in respect of Stewart and
Stewart's (1966) sample, except that it seems probable
that Hirst's figures are biased in favour of the female
class, i.e. some adult females could have been
mistakenly classified as "partly-grown".

4.5. Male reproductive cycle.

As has been described earlier, males achieve
sexual maturity at the age of about 13 months (Kerr,
1965), and in seasonally breeding populations are
physiologically capable of mating with females in
their second year of life. However, in regard to
the cycle in males, the only information available
is from seasonal populations, and does not therefore
reflect the age at which sexual maturity is
attained. **Anderson (1964) reports** on a peak of
testis mass in February-March, coinciding with a
peak in kidney fat mass, which has been used
extensively as a condition index (Riney, 1955).

A similar pattern has emerged from work by Kerr
(1965), who found a pronounced increase in testis
mass of impala in Rhodesia in March. This was
confirmed by the findings of Child (1968) at Kariba.
A peak of testis mass occurred there in April, just
prior to the rut, although it must be pointed out
that the samples examined by both Kerr (1965) and
Child (1968) were incomplete in that no animals were
collected after March and April respectively.

Fairall (1968) briefly reviews the situation,
adding the comments that impala testes are active
throughout the year, sperm being present at all
times, but that the degree of activity may vary a
good deal during the course of the year. He also
mentions that he has evidence of a decrease in the
viability of the sperm during the period outside
the mating season.

Skinner (1971) has carried out fairly intensive
histochemical investigations on a series of impala
testes from the western Transvaal. His findings
are very much in keeping with what may be inferred
from gross examinations of testis mass, and perhaps
the most significant of his conclusions may be

summarised as follows:

1.   There is a pronounced peak in all morphological, histological, and chemical activity in the testes during the rut, although spermatogenic activity did not altogether cease at any stage.

2.   Testes mass and seminiferous tubule diameter attain maximal values prior to the rut.

3.   There is a decline in body mass, starting prior to the rut, and presumably resulting from increased activity in establishing territories.

4.   The production of androgens declines after the rut, presumably resulting in a lowered sex drive. This feature may result in the reduced territorial activity after the rut, noted by Dasmann and Mossman (1962b).

Finally, Skinner (1971) speculates on the possible role of the male in stimulating oestrous behaviour in the female, and tentatively suggests that "...the mating season is partly dependent on the physiological status of the male at the time."

4.6.   **Female reproductive cycle.**

Very little work on the cyclic nature of ovarian activities in the impala has been carried out, and the only work of any real consequence is that provided for East Africa by Kayanja (1969). His observations however, can be applied to other populations. Kayanja (1969) described the histological changes in the developing follicle, until its rupture at what he assumes to be a mean diameter of 8mm. At or near oestrous, he notes that there are areas of the ovary in which all follicles are atretic. At ovulation he states that there was little or no haemorrhage into the spent follicle, although he does mention that an estimated eight-day old corpus luteum was very vascular. The corpus luteum increases in volume until a foetal crown-rump length of about 400mm is reached at about 170 days, according to Fairall (1969).

After parturition, the corpus luteum is rapidly invaded by connective tissue, before degenerating into a corpus albicans. In Kenya, Kayanja (1969) reports an almost immediate post-partum oestrous.

According to Kayanja (1969), ovulation occurs with almost equal frequency from both ovaries (13 from the left and 15 from the right), as evidenced by the presence of corpora lutea. This observation is supported by data from Mossman and Mossman (1962) from Rhodesia, where the figures obtained were 28 from the left and 27 from the right. In contrast however, is some information from Zululand, in which I.B.Stewart (Unpublished report, Natal Parks Board) found 19 ovulations from the left ovary and 34 from the right. This is a significant departure from random ovulation ($X^2 = 4,28$: d.f. $1, p < 0,05$).

Fairall (1968), reporting briefly on an intensive study of impala reproduction in the Kruger National Park, states "..., it seems as if the female has more than one oestrous cycle only in exceptional cases." This implies a highly successful social system, in which there is no wastage of ova, but does conflict with the theory that late conceptions are due to failure to conceive in the first or later oestrous cycles.

Lactation appears to be a fairly prolonged process, and Dasmann and Mossman (1962b) report that lactating females were found in Rhodesia as late as August. Child (1968) notes that at Kariba lactation ceased shortly after the rut. I.B. Stewart (Unpublished report, Natal Parks Board) records lactating females in late June in Zululand, and that by July "...most females' udders are drying up".

Jarman (1970) estimates that eight per cent of females in the Serengeti conceive whilst they are still lactating, bringing the situation closer in line with that farther south.

4.7. Foetal implantation.

Mossman and Mossman (1962) were the first to point out that the phenomenon of unilateral implantation is evident in the impala. They report that all of the 58 gravid tracts they examined contained the foetus in the right horn of the bicornuate uterus, despite the fact that ovulation took place randomly from both ovaries. A similar observation is made by Hofmeyr and Skinner (1969) who found that all seven pregnant females examined from a Rhodesian ranch had the foetus implanted in the right horn. I.B.Stewart (Unpublished report, Natal Parks Board) reports one "definite record" of implantation having taken place in the left horn, this being a female with the "left horn enlarged from previous calf." This would appear to be a somewhat dubious record.

4.8. Gestation period.

On this subject there has been some controversy, on account of the difficulty of establishing exact dates for individual animals. The generally recognised authoritative work on gestation periods (Kenneth and Ritchie, 1953) merely quotes Stevenson-Hamilton (1947) and Wilhelm (1933), who give periods of 195-210 and 150-180 days respectively. These two sources obviously cannot be reconciled. Most other authors however, estimate the gestation period as between 195 and 205 days. Brand (1963), from animals in a zoo, gives it as "approximately 196 days" - a figure which agrees with that calculated by Fairall (1969) on a population basis, and from 379 foetuses examined at all stages of development. In a footnote to his paper, Fairall (1969) mentions that his assumed period of 196 days was confirmed by two captive animals.

On the other hand, Basch (1964) quotes two established incidences of a gestation period of 204

days in the Transvaal. It is not beyond the realms
of possibility that the period of gestation may be
affected by the plane of nutrition. Several
species of mammal (but only one ungulate) have also
been shown to exhibit delayed implantation (Sadleir,
1969), and this could well account for some of the
variations in recorded gestation period.

Dasmann and Mossman (1962b) arrive at a figure of
180-210 days, also obtained on the basis of
observations on peak rutting and peak parturition
in Rhodesia. Gaerdes (1965) suggests that the
length of the gestation period may possibly depend
to some extent upon the age of the female, and this
theory too may account for some of the variability.
In this context, it is interesting to note that
a gestation period of 204 days was reported for each
of two impala females experiencing their first
pregnancy (Basch, 1964).

4.9. Foetal development.

There are two works dealing with the prenatal
development of impala: Fairall (1969) for a sample
from the Kruger National Park, and Roettcher et al
(1970) for a sample in East Africa.

Fairall (1969) provides detailed data on the
morphological characteristics of foetuses at
different ages right through the period of gestation,
from an age of about three weeks. He also provides
various measurements and the mean mass of foetuses week
by week. The table of masses and measurements
shows some minor inconsistencies, but this is to be
expected in view of the latitude in the timing of
conceptions on either side of the peak.

Roettcher et al (1970) also present data on
masses and measurements in graphic form. However
their task was complicated by the fact that the
foetuses were in various stages of development at
any one time, because of the absence of a strict
breeding season.

It is of particular interest to note that, by using two different methods, and without reference to one another, both the above authors derive an identical formula for the prediction of conception age from known mass.   Such a formula was first derived by Huggett and Widdas (1951), with the general form of $W^{1/3} = a(t-t_o)$, where $W^{1/3} =$ the cube root of the mass, a = a constant, t= the conception age, and $t_o =$ the intercept of the regression line on the X (time) axis. In the case of the impala, both authors derive the formula $W^{1/3} = 0,11(t-39)$, and this enabled Roettcher et al (1970) to illustrate foetal development and to predict the conception age.

Fairall (1969) notes that foetal growth seems to be divided into two periods, separating at about 10 weeks.   It is at this time that the foetus starts growing much faster, in accordance with any typical growth curve.

4.10. Number of young.

As has been stated earlier, the impala is a . strictly seasonal breeder over most of its range, so that the rule is only one birth per female per annum.   However in East Africa, where there is no strict season of breeding, a post-partum oestrous has been recorded (Kayanja,1969).   This means that the impala there have the potential for producing about seven young in every five years - assuming a calving interval of about seven months.

Jarman and Jarman (1970) noted that there was an interval between peaks of parturition in impala in the Serengeti National Park in Tanzania, which was some two and a half months longer than the gestation period, implying an oestrous cycle about two and a half months after parturition. Jarman (1970) states that the calculated breeding rate is 1,17 pregnancies per female per annum, and that in most animals the first successful post partum oestrous is delayed until the previous lamb is weaned or dies.

There has been only one recorded, substantiated
instance of impala having twins. Kayanja (1969) reports
that, in a sample of 25 pregnant females, one contained
two foetuses. In this case there was only one corpus
luteum, suggesting that they were "identical" twins.
Stevenson-Hamilton (1947) comments that reports were
received from time to time of twin impala in the
Kruger National Park, but says that "...it must be
a very unusual occurrence." All other authors who
have dealt with foetal material, agree that the
animal is monotocous, while Brand (1963) notes the
same for captive impala over a period of more than
50 years.

4.11. Breeding behaviour.

This section will deal only with those aspects
of behaviour directly related to breeding, namely
copulation and immediate pre-and post-parturient
behaviour.

Very few direct observations of copulatory
behaviour seem to have been recorded, although
Schenkel (1966a) observed the process on four
occasions. He describes three pre-copulatory phases
of behaviour, characterised by chasing, genital
licking, and mounting without copulation. The
actual intromission, he states, is achieved very
rapidly and "...does not last longer than one second,"
with the male not in contact with the female's rump
(in the normal quadruped fashion), but standing
unsupported on his hind legs. Thereafter the female
walks forward, and the male resumes his normal position
on four legs, and usually exhibits a sudden outburst
of "snorting and roaring" in apparent aggression.

Robbel and Child (1969) record a very similar
behaviour to the above, with the male approaching
the female, attempting to smell and lick her vagina.
They also note several "attempts" at mounting before
achieving intromission, followed by "...a few rapid

pelvic thrusts", and lasting for "...as little as 10 seconds".

Elsewhere, the reports of copulatory behaviour are very fragmentary, and Child (1968) mentions that it was twice observed, without giving details. Dasmann and Mossman (1962b) describe an "attempt" at copulation, but in the light of Schenkel's description, this may well have been a successful attempt.

Pre-parturient behaviour of females seems to be characterised by individuals, or small groups of two or three splitting off from the herds (Schenkel, 1966b). Parturition itself then takes place in isolation, usually in some thick bush. Thereafter, when the new-born young is able to keep up with its mother (probably within 24 hours) both animals then rejoin a herd. (Stevenson-Hamilton,1947).

Schenkel (1966b), on the other hand, states that in East Africa, the young are hidden in undergrowth for some days before they link up with other mother-young pairs to form small, discreet nursing groups. He also remarks that the mother-young relationship is essentially a silent one, with no evident vocalisations as means of communication.

CHAPTER 5:

REPRODUCTION IN THE IMPALA: MKUZI POPULATION.

5.1.   Materials and Methods.

During 1970, as part of the routine management
programme for Mkuzi Game Reserve, a total of 379
impala was destroyed.   Of these 285 were males
and 94 were females.   In addition to these
animals, which were hunted on foot and shot, a
further 1 374 impala were caught alive for
distribution to farmers.   The catching method is
briefly discussed by Oelofse (1970).

The animals which were shot were transported to
a base as soon as possible, where they were
weighed on a Salter spring balance to the nearest
pound.   These masses were subsequently converted
to kilograms, and recorded to the nearest 0,5 kg.

In the case of males, the testes were removed,
and each pair was weighed, complete with epididymis,
to the nearest 0,1g on an Ohaus triple beam
balance.   Prior to weighing, and in order to
achieve a standardised mass, the tunica vaginalis
was removed, and the spermatic cord severed at a
point as close to the head of the epididymis (which
is contiguous with the testis) as possible.   The
testes were not preserved for histological analysis.

In the case of females, the complete reproductive
tract was removed and preserved in 10% formalin
for future analysis.   Later-term foetuses, which
were too large to preserve, were removed from the
uterus, weighed to the nearest gram, and measured
along the mid-dorsal line to obtain the dorsal
curvature length (D.C.L.) as described by Ansell
(1965).   Large foetuses were not preserved.   For
purely ethical and humane reasons, very few female
impala were shot during the last two and a half
months of pregnancy (from early in October), and the

bias at this time was towards males.

The lower jaws were removed, suitably numbered with serial numbers on metal tags wired to them, and dried for subsequent ageing on the basis of the state of eruption and attrition of teeth.

In the laboratory the female reproductive tracts were examined as follows:-

1. The site of implantation was recorded as to left or right uterine horn.

2. Small foetuses were weighed to the nearest 0,05g and measured using the method described by Ansell (1965) for small foetuses and embryos, viz. sitting height (S.H.), by means of vernier calipers.

3. Non-gravid tracts were recorded, with notes on which of the two uterine cornua showed greater swelling.

4. Ovaries were weighed to the nearest 0,05g and measurements made of the length, width and thickness. The point of attachment to the Broad Ligament (hilum) is elongate and was used as a means of orientation.

5. Each ovary was then sectioned by hand with a razor blade, into sections about 0,5mm thick, and the following features recorded: (a) Number of follicles greater than 2mm in diameter, (b) number of follicles less than 2mm in diameter, (c) diameter of the corpus luteum of pregnancy, and (d) number of corpora albicantia. In each case the site was also recorded, namely whether the above structures were situated in the left or right ovary.

Ageing of the lower jaws was carried out, for ages up to about two years, on the same basis as that described by Child (1964) and by Dasmann and Mossman (1962a). It was not possible however to obtain

many specimens of animals less than about 6 months
old due to shooting bias against this age-class.
The results described by the above authors were used to
assign ages to animals up to about 30 months of age.

For animals greater than two years of age, wear on
the molar teeth was used as a criterion for assigning
individuals to arbitrary age classes. This was done
on the basis of a consistent pattern of wear which
resulted in the disappearance of the infundibula of
the molar cusps in a regular order. In addition, a
quantitative measure of wear on the first permanent
incisors was recorded. By means of vernier slide
calipers, the "width" of each incisor (bucco-
lingually at right angles to the length of the
mandibles) and the "length" of the worn surface
(proximo-distally, in the direction of the length of
the mandibles) were measured. These parameters were
added together for each animal, and the product of the
two measurements used as an index of area, corresponding
to the "incisor area" of Vincent et al (1968).

Similar criteria as this have been used by Roettcher
and Hofmann (1970) and Roettcher et al (1970), who
also assigned definite chronological ages to the
various wear classes. Their method was based on
relative degrees of wear on the incisiform and
molariform teeth, and has been used in this study to
assign approximate ages to some of the material
obtained,

5.2. Results and Discussion.

5.2.1. Ageing.

No known-age skulls were available from the
study population, and the methods of Child (1964)
and of Roettcher and Hoffman (1970) were found to be
applicable for animals with incomplete dentition.
For animals with complete permanent dentition, a
uniform method of assigning animals to different
classes on the basis of wear was devised. This was

rendered possible by the fact that the cusps of the
molars exhibit a definite sequence whereby the
infundibula wear away to leave a smooth surface to
the cusp.

A summary of the sequence of eruption of
permanent teeth, together with the duration of time
over which this takes place in each tooth, is provided
in Fig. 2. However it must be pointed out that this
summary is based on the assumption that impala in
Mkuzi Game Reserve are strictly seasonal breeders. This
has been discussed in section 5.2.2., and in
instances which appear obviously to represent
significant deviations from such a pattern, this
is indicated.

Table 2 shows the various wear classes that
have been used for assigning older animals to their
respective categories, together with the definitions
that have been used. In each case, but for the last
two classes, if a particular tooth was smooth on one
side, and not on the other, this was interpreted as
having been smooth, and the individual assigned to
its respective class.

The sequence of wear may be compared with that
of Roettcher and Hoffman (1970), who also assigned
chronological ages to their wear categories. These
authors did not have any known-age material from
which to work, and it must be assumed that their
chronological ages were mere calculated estimates.
On their basis, ages which could be assigned to wear
classes in the current study are shown in Table 3.
They qualify their conclusions by saying that up to
an age of eight years, the assigned ages are
"tentatively considered to have an accuracy of $\pm$ 6
months," and thereafter of about one to two years.

It is interesting to note that Roettcher and
Hoffman report that the posterior cusp of M_3 shows
advanced attrition at a much later stage than that
indicated in the present study. Amongst animals

Table 2.   Definition of the "adult" tooth wear classes
used for impala in Mkuzi Game Reserve,
together with the number of individuals
assigned to each class during the study period.
The definitions assume a sequence in which
the various cusps are worn smooth (See text.)

WEAR CLASS	CODE	DEFINITION	NO.OF ANIMALS
Nil	Nil	No cusps worn smooth.	$30\,\male + 12\,\female = 42$
Light	L	Ant.cusp of M_1 smooth.	$42\,\male + 14\,\female = 56$
Light–moderate	L/M	Post.cusp of M_1 smooth.	$52\,\male + 22\,\female = 74$
Moderate	M	Post.cusp of M_3 smooth.	$18\,\male + 1\,\female = 19$
Moderate–heavy	M/H	Ant.cusp of M_2 smooth.	$14\,\male + 6\,\female = 20$
Heavy	H	Post.cusp of M_2 smooth.	$17\,\male + 6\,\female = 23$
Very heavy	V.H.	Ant.cusp of M_3 smooth.	$0\,\male + 2\,\female = 2$
Extra heavy	E.H.	Mid.cusp of M_3 on one side smooth	$17\,\male + 4\,\female = 21$
Extra heavy plus.	E.H.+	Mid.cusp of M_3 on both sides smooth.	$8\,\male + 8\,\female = 16$

Table 3.   Chronological ages corresponding to the
            molariform teeth wear classes of impala
            in Mkuzi Game Reserve on the basis of
            the data of Roettcher and Hoffman (1970).

WEAR CLASS	AGE IN YEARS (according to Roettcher and Hoffman (1970)
Nil	2-3
L.	4
L/M	5-6
M.	7* (by inference)
M/H	8-9
H.	9-10
V.H.) E.H.) E.H.+)	11+

*   This class is not reflected in Roettcher
     and Hoffman's work, and the assigned age
     is assumed on the basis of those
     preceding and succeeding it, and of the
     fact that wear is consistent.

from Mkuzi Game Reserve, only two had this cusp
wearing smooth out of the sequence given.

Of those authors who have described tooth
eruption and replacement, Child (1965) is probably
the most reliable. Dasmann and Mossman (1962b)
worked with too small a sample, whilst Roettcher and
Hoffman (1970) had the disadvantage of working
on a non-seasonally breeding population and, not
having any known age animals, had to guess the ages
at which events took place.

The present study differs in the following
respects from the results of Child (1965):

1. Child embraces all incisiform teeth in saying .
that replacement takes place between 17 and 22 months.
In this study, there is a definite progression of .
replacement from the median incisors to the canines,
with I_4 and C replacing almost simultaneously.

2. No sufficiently young animals were collected to
compare Child's estimate of two months as being the .
age by which all milk premolars have erupted. However,
it will be seen that in the Mkuzi impala, replacement
takes place over a much more contracted period of
five months, as opposed to Child's observation of 11
months (19-29 months of age).

3. Eruption of the molars agrees very closely with
the Rhodesian impala, the only variations of any note
being the fact that in this study M_1 has completed
eruption by six months (seven in Rhodesia), and M_3
is still erupting at 32 months (26 months in
Rhodesia) in a few animals.

5.2.2. Seasonality.

It requires little more than direct observation to establish that breeding of impala in Mkuzi Game Reserve follows a seasonal pattern.

During 1970, overt reproductive behaviour was exhibited by males as early as February. This activity was manifest in the roaring displays described by Schenkel (1966) in the context of herding of female groups by individual males. It increased in activity over the next few months, accompanied by changes in sociology (described in a later section) until the peak of the rut. The precise timing of this peak was not easy to determine on the basis of behaviour, and results from ovarian analysis have provided a further key thereto.

The first corpus luteum, indicating that fertilisation had taken place, was found in an animal shot on 18th May. Thereafter, all potentially productive animals were found to be pregnant, with the exception of a very few whose cases will be discussed in a later section. Evidence will also be provided in due course supporting the observation that the peak of conceptions occurred during the latter half of May, 1970. In fact, the date chosen as the approximate midpoint of this peak is 20th May.

It was further estimated, by direct observation, that most births took place during the second week of December. At this time, several after-births were found which had not yet been consumed by scavengers, and females with obviously very new-born young were in evidence everywhere.

The season in 1970 was in fact considered by most people with experience of the area to be rather later than usual. The reason for this is not clear, but it is here postulated that it may have been a result of unfavourable environmental conditions which adversely affected the habitat, and which could have

influenced ovulation incidence through the nutritional plane.

Whilst no direct evidence is available, and the observations may have been due to some other factor, it appeared that the rut in the eastern part of Mkuzi Game Reserve was farther advanced than it was in the west. This was not evident from observations during the season of parturition however. It is hoped that the continuation of the study will clarify the position and that this theory will be tested further.

As will be shown later, the rutting period is very brief, but the fact that obvious out-of-season lambs are occasionally observed indicates that a very small percentage of females ovulate later than the majority. Although no figures are available, there does appear to be a slightly higher proportion of such late births during January and February. After that it is very rare to see new-born young, although they have been recorded as late as May.

5.2.3. Territoriality.

Whilst not directly concerned with breeding behaviour, territoriality in the Mkuzi Game Reserve population is very evident. The view has long been upheld that impala males take "harems" of females during the rutting season, and that the antagonistic behaviour between males, which usually takes the form of displays and occasionally of direct conflict, is merely a manifestation of the right of possession by a dominant male. This too is the impression gained by reading Schenkel's (1966a) account of sociology.

In fact, as has now been shown by Leuthold (1970), the "possession" of a female herd by a "dominant" male may be only a transitory phenomenon in that the male is bound by the social organisation to a particular piece of ground. The female herd, apart from being more wide-ranging, is a comparatively

stable unit, and generally speaking, it is uncommon
for a male to be accompanied by a single female, as
has been described by Buechner & Schloeth (1965) for
the Uganda kob.   The view here upheld is that the so
called "harems" are in fact only temporary associations
between a territorial male and a breeding herd, and
that once the herd moves on, it is "taken over" by
 another male.

    Such a "takeover" was witnessed on one
occasion on open ground.   The male in whose territory
the herd was first seen, accompanied the herd to the
territorial boundary.   An adjacent male advanced to
meet the herd, before stopping and waiting.   This
second animal showed no apparent interest in the
females, but eventually entered into a low intensity
conflict with the first male.   Only when the whole
female herd had passed the scene of the conflict, did
the males break off fighting;   the first male then
simply stood, whilst the second one joined the herd.
It was quite clear from the nature of the fighting,
which involved alternate domination by first one male
and then the other, that it took place at a territorial
boundary, which it was possible to demarcate to within
a metre or two.

    A further point, which compares in some
respects to the leks or "territorial grounds" in
Uganda kob (Buechner, 1963), is the apparent choice
by territorial males of certain areas in which several
such males may be found.   This observation may be
directly related to the presence of favourable habitat,
but it is more likely that the relationship is
indirect in that the territories are established in
the vicinity of one or more large breeding herds,which
in turn are present because of the habitat.   Prior to
the rut, some of these breeding herds may achieve
considerable size, but they become fragmented during
the rut.   In this context it is interesting to
reiterate the findings of Jarman (1970) who concludes

that female herds in particular become very attached
to a particular area.

Further evidence for territoriality comes
from Oelofse (pers. comm.) who notes that, whilst
driving impala with a helicopter in order to catch
them, the males are very reluctant to be driven during
the rutting season.   The herds of females are amenable
to being driven for up to 5 km, but the males
invariably break away after very short distances.

Finally, Fig. 3 shows how the incidence of
single or territorial males recorded as a percentage
of all adult males and total animals counted, varies
during the course of the year.   These results were
extracted from figures obtained in a series of sample
counts carried out regularly from mid-1969 to mid-1971.

Clearly the highest incidence of lone males
is in May, which coincides with the main rutting period.
This too is clear evidence of the important role played
by territorial behaviour in the breeding of the impala.

The other high incidence of lone males - in
September - is inexplicable on any positive basis.
It could be a figment of inadequate sampling, but may
also be the result of an incipient bi-annual breeding
season, in which the flush of new grass and the
prevailing photoperiod stimulate some basic breeding
behaviour in the males.

5.2.4. Rutting.

Signs of rutting or at least of overt breeding
behaviour in males, were observed to take place quite
early in the year, and certainly three or more months
prior to the peak of mating.   This behaviour took the
form of roaring displays which were initially of a
low intensity, and uttered at seemingly infrequent
intervals by males still in the company of other males.
The roaring display is described by Schenkel (1966)
as being performed in several situations, and that
which fits this context is given as "showing off",

which may take place between males in a bachelor herd.

Towards the peak of the mating season, the frequency with which the roaring display is uttered increases markedly, and the context in which it is uttered changes to become associated with the presence of a female herd, or with territoriality. During the stages at which territories become established a good deal of fighting takes place between rival males, and by the time of the peak rut the social organisation among the males is such that little or no time is occupied by this activity, and all efforts can be directed towards the females.

At this stage, a high proportion of adult males occupies territories, and the activity of the males produces considerable disruption amongst the female herds. This is shown by the marked changes in female herd sizes as the rut approaches its peak. Several instances were observed in which the chasing behaviour of males resulted in a female being widely separated from the remainder of the herd. In some cases this female made an effort to return, but in others she did not and frequently was herded by another male into his territory. It is possible, in view of the intense interest shown in such a female by more than one male, that these individuals were in oestrous. It is presumed that these separations of females from herds is a temporary phenomenon for Jarman (1970) has shown how impala may become attached to a home area. Thus the chances of a female rejoining the herd are improved.

It has further been observed that territorial males actively chase out yearling males from the breeding herds. This has also been witnessed on several occasions, and is borne out by the observation at the peak of the rut that this class of individuals forms discrete groups on the fringes of breeding herds, or is found in twos or threes in fairly close proximity to what are presumed to be the herds from

which they have been "ejected". They were seen on
a few occasions in the company of a single male, and
again, accompanied by juvenile(five month-old)males.
Although not actually witnessed, it is possible that
these juveniles may also be temporarily ejected from
breeding herds.

The subject of young males taking part in the
rut, or at least in mating, has been discussed in
section 4.3.1., and it is generally agreed that it is
physically possible in yearling animals, but socially
unlikely. Nevertheless, at the peak of the rut in
1970, both yearling and juvenile males were seen to
attempt copulation with presumably oestrous females.
Whilst perhaps not being surprising in the case of
yearling males, it is particularly interesting to note
that even five month-old males will at least attempt
couplation. All evidence indicates that
spermatogenesis in impala at this stage is undeveloped,
so that it must be concluded that the production of
androgens is nevertheless at a high enough level to
induce at least a low plane of libido under the stimulus
of females in oestrous.

Finally, in the context of rutting, it is of
interest to note that there is a sharp decline in
the overt behaviour after the rut, which coincides with
a similar decline in the number of large follicles
present in the ovary of females. This is to be
discussed more fully under the subject of the female
reproductive cycle, but at this stage it should be
mentioned that there is a slow increase in the number
of ripe follicles from January onwards. This too,
coincides with the already described gradual build-up
in sexual displays by males. It is possible that the
presence of follicles in varying stages of development
may act as a stimulus to the increased gonadal activity
and sexual behaviour of males, through the action of
hormones.

The "silent ovulations", or, as they have

sometimes been called, "silent heats", which have been
observed in other species, but not hitherto in impala,
will be discussed in a later section. Their
significance in the stimulation of overt behaviour
is not clear.

5.2.5.   Sociology, and behaviour associated
          with breeding.

The disruption of the female social system
during the time of the rut was described in the
previous section. At this time, the breeding herds of
females and juveniles are considerably broken up,
and yearling males are temporarily separated from
these herds.

The process of copulation has been observed
on several occasions. It may be preceded by the
preliminary mounting attempts described by Schenkel
(1966a) and by Robbel and Child (1969), but intromission
has been seen in certain circumstances to be achieved .
only after brief smelling. Contact is extremely brief,
lasting for as short a time as two seconds. The
chasing, of Schenkel (1966a), does not seem to be a
necessary preliminary, but is of frequent occurrence.

After the rut the breeding herds reform
for the duration of pregnancy, whilst the immature males
may form loose aggregations either consorting with
mature males, or rejoining the breeding herds.

At the approach of parturition, the gravid
females separate from the main herds as individuals or
groups of two or three, as reported by Schenkel (1966).
This author then describes how the young may remain
in hiding for some days before joining their mothers
and regrouping into herds. Personal experience, and .
that of others, in the study area of Mkuzi Game Reserve,
contradicts this observation, but only circumstantially.
In an area with a density as high as in Mkuzi, it would
be expected that the new-born lambs would be encountered
fairly frequently on their own if such were the case.

This is not so, and to the author's knowledge, this
has very seldom been observed: all contacts of new-
born impala have been in the presence of the dam.
This contrasts with nyala which are frequently found
as new-born lambs, hidden in thickets. Parturition
itself has not been observed, and the majority of
births is presumed to take place at night. After-
births are most frequently encountered in the early
morning.

For some weeks after birth, groups which
have been termed "nursery" herds" are a common sight.
Fraser (1968: 134) described these nurseries as
manifestations of a "highly developed behavioural
system", but it is doubtful whether this is the case.
Such herds have been seen in the process of formation,
and the mechanism appears simply to be one whereby,
following a period of browsing or grazing, the young
may be nursed by their mothers, and then settle down
in groups to rest. The grouping may be a
manifestation of the gregarious instinct, but there
appears to be no conscious effort on the part of any
individual(s) to organise a nursery group. At this
time, the remainder of the herd may move off, feeding,
and the observation that one or more adult females
remain behind to "look after" the lambs is really
no more than a coincidence of seeing such females in
close proximity. Usually too, the lambs remain at
rest until the return of the females, whereupon they
make contact with their dams by a vocalisation, which
can only be described as an "abbreviated bleat",
uttered by both parties.

Thus the so-called nursery herds are no
more than groups of lambs which, on account of their
lesser need for forage and because they are still
suckling, take the opportunity of resting whilst the
females feed in the vicinity.

Suckling may take place at any time when the
mother and young are together, but each nursing period
is generally of short duration - no more than 30 seconds.

Lactating females have been observed well into August, and lactation may thus last for 8 months or more. There is however, a marked decline in their incidence from May or June onwards.

5.2.6. Male reproductive cycle.

The basis for discussion on this aspect of reproduction is a series of testis masses from 285 animals obtained during the study period, including all age classes, from three months to adult.

The mean paired testis mass of animals from the various age classes - less than 12 months, 12-24 months, 24-30 months, and older than 30 months (aged on the basis of tooth eruption and replacement as described in section 5.2.1.) are set out in Table 4 for each month.

Beyond the age of 30 months, accurate ageing is not possible, due to the limitations of ageing by means of molar wear; all the animals over this age have therefore been lumped together. Further . analysis on the basis of wear classes will, however, be presented later in this section.

A graph to show the progressive increase of mean testis mass of animals up to 30 months of age is presented in Fig.4, in which the various significant seasons are also indicated.

Clearly, there is a progressive increase in the mass, as shown by the dotted line, which serves to smooth the curve drawn from comparatively small monthly samples. Nevertheless a peak in testis mass in the 12-24-month-old group is evident, and coincides with the observed peak of the rut. Closer inspection, however, reveals that the peak in this group actually falls somewhat later than the rut, whilst the peak in 24-30 month old animals falls just prior to the rut. This latter situation is, as will be shown later, typical of that to be found in older

Table 4. Mean paired testis mass of impala in
Mkuzi Game Reserve, arranged according to
age classes, for 1970.

Month	0-12 months		12-24 months		24-30 months		>30 months	
	n	mass(g)	n	mass(g)	n	mass(g)	n	mass(g)
Jan	0	—	0	—	1	100,0	4	92,1
Feb	0	—	0	—	12	62,3	20	95,4
Mar	1	32,3	3	27,2	7	69,1	14	117,1
Apr	0	—	4	32,7	5	90,1	7	118,3
May	1	25,5	4	44,4	12	93,1	11	108,5
Jun	0	—	7	56,2	1	71,1	7	104,5
Jul	0	—	1	48,4			15	79,2
Aug	0	—	4	35,1			12	66,3
Sep	6	19,4	7	48,7			27	61,7
Oct	0	—	5	35,7			20	59,6
Nov	1	15,1	5	67,9			13	78,0
Dec	0	—	4	66,6			13	89,3

animals. The reasons are not entirely clear, but it is hoped that a continuation of the present study will indicate whether it is an artefact brought about by the comparatively small size of the sample (58, of which 23 were collected in the period March-July). In the meantime, it is suggested that the peak of testis mass in older animals is due to physiological factors, whilst that in the younger group is brought about through psychosomatic influences of the overt behaviour of the adult males.

Alternatively, it could be explained by the fact that the onset of oestrous in females stimulates the production of androgens which in turn results in increased testis mass. This phenomenon has not, as far as is known, previously been reported.

Upon further analysis of the testis mass, it was found possible to separate certain of the younger "adult" tooth wear classes from others. This analysis is presented in Table 5, the tooth wear classes referring to those described in Table 2.

From the results shown in Table 5, it is possible to conclude that, for the purposes of showing how the testis mass of younger adults behave differently from older adults, separations may be made in accordance with Table 6.

For the months of July-November inclusive, the criteria for separation have been drawn from extrapolation, since during this stage of regression and dormancy in the testes, the masses all drop to a basically similar level. Nevertheless, differences were found to be significant at the 5% level between the wear classes as shown in Table 6 for all months except August.

The mean paired testis masses for all "adult" wear classes are shown in graphic form in Fig.5, while the separated ones are shown in the refined form of Fig. 6.

Table 5. Means and Student's t tests for differences in means, of testis mass (expressed in grams) of the two youngest tooth wear classes and all older tooth wear classes of impala in Mkuzi Game Reserve.

	WEAR CLASS						STUDENT'S t.	
	Nil		L		L/M+		Nil-L	L-L/M+
Month	mean	n	mean	n	mean	n		
Jan	109,0	1	-	0	86,4	3	Sample too small.	
Feb	63,2	5	76,8	6	103,3	14	1,728 d.f.=9	$^{+}$4,12 d.f.=1 
Mar	77,2	4	93,9	4	126,3	10	0,698 d.f.=6	$^{+}$3,77 d.f.=1 
Apr	93,5	4	74,1	1	125,7	6	Nil & L -L/M	$^{+}$2,34 d.f.=9
May	81,4	5	106,3	6	116,6	11	$^{+}$2,91 d.f.=9	1,13 d.f.=1 
Jun	71,1	1	98,1	1	105,6	6	$(X^2 =^{+}4,28)$	0,314 d.f.= 
Jul	48,2	2	95,6	2	78,4	6	$^{+}$13,7 d.f.=2	$^{+}$5,25 d.f.=6
Aug	64,4	3	66,3	5	65,1	3	No significant difference	
Sep	58,0	2	66,1	10	59,4	15	.No significant difference	
Oct	51,3	3	61,4	6	60,8	11	0,595 d.f.=7	0,335 d.f.=1
Nov	-	0	65,6	2	80,2	11	-	1,17 d.f.=1 
Dec	128,3	1	62,4	3	93,9	9	Sample too small	$^{+}$2,96 d.f.=1 

n = number in sample

+ indicates significance at the
   5% level

Table 6.   Mean paired testis mass of younger and older
           adult tooth wear classes of impala in Mkuzi
           Game Reserve, separated in accordance with
           data derived from Table 5, together with
           tests of their significance of difference.

Month	"Young adults"		"Old adults"		Student's t
	Wear class	Mean	Wear class	Mean	
Jan	Nil	109,0	L/M+	86,4	—
Feb	Nil & L	70,6	L/M+	103,3	8,65 (d.f.23)P<0,0005
Mar	Nil & L	85,6	L/M+	126,3	11,4 (d.f.16)P<0,0005
Apr	Nil & L	89,6	L/M+	125,7	20,6 (d.f.9) P<0,0005
May	Nil	81,4	L & L/M+	113,0	14,1 (d.f.20)P<0,0005
Jun	Nil	71,1	L & L/M+	104,5	7,75 (d.f.6) P<0,0005
Jul	Nil	48,2	L & L/M+	82,7	10,8 (d.f.8) P<0,0005
Aug	Nil	64,4	L & L/M+	67,2	0,93 (d.f.9) P<0,15
Sep	Nil	53,0	L & L/M+	62,4	3,23 (d.f.25)P<0,005
Oct	Nil	51,3	L & L/M+	60,9	3,83 (d.f.18)P<0,005
Nov	(nil)	—	L & L/M+	78,0	3,41(d.f.13) P<0,005
Dec	Nil & L	78,9	L/M+	94,0	8,45 (d.f.11)P<0,0005

In order to take this analysis further, and
in view of the fact that ages of animals with full
permanent dentition are not definitely known, it is
necessary to assume the actual ages of animals with
no wear (Nil) and with light wear (L). These assumed
ages are set out in Table 7 for each month. The
assumptions are not unrealistic when it is considered
that full permanent dentition may be achieved at the
age of 26 months.

It is to be concluded therefore, from the
data presented in Tables 6 and 7 and Fig.6, that full
adult testis mass is not reached until the animals
are over three years old.

The general picture of cyclical changes in
testis mass of animals over 24 months of age is
clear from Figs. 5 and 6. A peak is reached some   .
two months prior to the rut. This peak is maintained,
but nevertheless shows a slight drop by the time of
the peak rut.

The reason for this appears to be fairly
evident: the period from February to June is one in
which the nutritional value of the fodder is
declining (Linton & Abrams, 1950: 161) and rutting
activities induce a form of self starvation (Nordan
et al, 1968). In male impala, Anderson (1965) has
shown that there is a drop in condition, as shown
by kidney fat mass as an index, between March and May.
Such a drop in condition due to reduced intake of
nutrients, might reasonably be expected to result in
the drop in testis mass at the time of the rut in May.
In other words, most of the energy in males is
required during the pre-rut preparations in the form
of territorial behaviour.

The time of lowest testis mass (October)
coincides with the onset of summer, and thereafter
they start to show a fairly rapid increase again.
It is not possible to separate the two factors of

Table 7.   Assumed ages (in months) of Mkuzi impala
             showing no molar wear (Nil), light molar
             wear (L), and of older animals.

             Evidence for these assumptions is drawn
                        from Table 6.

| MONTH | AGE | | Wear |
	Wear class(Nil)	Wear class(L)	Classes(L/M+)
Jan.	37	37	49+
Feb.	26	26	38+
Mar.	27	27	39+
Apr.	28	28	40+
May	29	41	53+
June	30	42	54+
July	31	43	55+
August	32	44	56+
Sept.	33	45	57+
Oct.	34	46	58+
Nov.	35	47	59+
Dec.	36	36	48+

nutrition and photoperiodism as affecting this
increase, but in the latter stages, the period of
light is decreasing, although testis mass continues
to increase. This suggests that the production of
androgens may initially be stimulated by both
nutrition and increased photoperiod, but that there-
after it is a self-inducing process which eventually
becomes retarded due to nutritional factors.

The anatomy of the male reproductive tract is
illustrated in Fig.7, and it is clear that it resembles
closely that of other ungulates, vide Skinner (1971).

5.2.7. Female reproductive cycle.

Evidence for cyclical changes in the
reproductive physiology of the female has been
obtained from a series of ovaries of animals of all
age classes from 6 months upwards. Totals of 66
left ovaries and 66 right ovaries were obtained and
examined, although these were not all paired, and came
from 70 animals. Unfortunately, due to a misunder-
standing during the collection of specimens,
reproductive tracts were not preserved from any
animals after August, when foetuses were weighed and
the tracts discarded.

5.2.7.1. Anatomy. An overall view of the female
reproductive tract is shown in Fig. 8. It is
typical of the bovine tract, and the characteristic
feature of the adult uterus is the greater size of the
right uterine horn. This is brought about by previous
implantations. Both horns are of equal size in
the virgin uterus.

The point of attachment of the ovary to the
broad ligament of the uterus is elongated, and this
feature was used in the orientation of the ovary for
purposes of measurement. Three measurements were
taken of the ovary: length - in the plane of the
long axis of the point of attachment; thickness -

across the long axis of the point of attachment; and
width - from the point of attachment to the opposite
surface. These measurements are shown in Table 8 for
virgin ovaries, and for "bred" ovaries, the latter
being defined by the presence of a corpus luteum or of
one or more corpora albicantia. The masses of the
respective ovaries are also shown, having been taken
to the nearest 0,05g.

Tests of significance of difference were
carried out between parameters of left and right
ovaries, and between those of virgin and bred ovaries.
There was no significant difference between left and
right ovaries in any respect, and the only one between
virgin and bred ovaries was the mass ($t = 6,38$,
$d.f. = 130$, $P < 0,0005$). This is due, not so much to
an inherent change in density, as to the cumulative
effect of slight changes in the dimensions.
Nevertheless, a "density index" was worked out
according to the formula:

$$\frac{\text{Mass}}{\text{Length x Thickness x Width}}$$

For virgin ovaries this index is 0,595 and for bred
ovaries it is 0,667. These are not significantly
different at the 5% level, but do however show what
would appear to be a slight increase in "density".

5.2.7.2. Graaffian follicles. During the sectioning
of the ovaries, Graaffian follicles were recorded as
to the number in the case of follicles less than two
millimetres in diameter, and as to the number and
diameter of those greater than two millimetres. The
diameter of the larger follicles was taken as the
mean of two measurements across the cut surface showing
the greatest size. Two millimetres was arbitrarily
chosen to separate the groups; Spinage (1969b) chose
five millimetres for waterbuck ovaries.

It is perhaps to be expected from the

Table 8.   Mean mass (in grams) and measurements
(in centimetres) of left and right,
virgin and bred ovaries, of impala in
Mkuzi Game Reserve.

	L E F T O V A R Y				
	n	Length	Width	Thickness	Weight
Virgin	12	0,98	0,77	0,74	0,33
Bred	55	1,07	0,75	0,88	0,46

	R I G H T O V A R Y				
	n	Length	Width	Thickness	Weight
Virgin	11	0,96	0,78	0,70	0,31
Bred	54	1,08	0,75	0,86	0,48

evidence of Spinage (1969b) for the waterbuck, that
the number of follicles increases at least until
conception, and then decreases with pregnancy. This
aspect was investigated during the present study, and
the results are presented in Fig.10.

Clearly, there is a definite trend in the
number of larger follicles, with a gradual increase up
to April, and thereafter a comparatively rapid decrease.
In the case of smaller follicles, no trend is evident.
When compared with age, there appears to be no trend:
animals less than 12 months old had means of 1,3 large
and 12,3 small follicles, 12-24 month old animals had
means of 1,0 and 10,8, whilst animals older than 24
months had 1,2 and 10,8 respectively. None of these
is significantly different.

The mean sizes of all follicles larger than
two millimetres and of the largest follicle in each
animal in each month are plotted in Fig.9. As with
the numbers of follicles, this parameter shows an
increase up to the time of mating, followed by a
decrease during pregnancy.

Possibly the reason for the decline both in
numbers and sizes of follicles in May represents a bias
in favour of animals that have already conceived. In
other words, both parameters should increase up to the
time of conception - the peak of which occurred on
about 20th May. It is significant that the results
obtained during the study period of 1970 compare very
closely with those obtained from a slightly smaller
sample collected during a pilot project in 1969. The
largest follicle seen was one of 6,5mm, from an animal
collected on 10th April - some five weeks before the
peak of the rut.

It is also pertinent at this stage to mention
that Cloete (1939), in quoting Hammond (1927), mentions
that follicular atrophy is more severe during
pregnancy than during the sexual cycle, in the domestic

cow. This fact results in a decrease in ovarian mass during gestation, especially in the case of the ovary not containing the corpus luteum. It also agrees with the observation noted above, that the number of larger follicles in the impala ovaries declines during pregnancy.

5.2.7.3. Ovulation. The observation regarding the largest follicle cited above, would appear to be exceptional, for no others larger than 5,5mm were seen, suggesting that this may be about the optimum size attained before ovulation occurs.

The site of ovulation (or rupture site) is characterised by a blister on the surface of the ovary, seemingly appearing only after the process has taken place.

There is no preference for which ovary is responsible for ovulation. In 20 corpora lutea examined, 10 were situated in the left ovary, and 10 in the right. Similarly, on the basis of the site of the largest follicle, there is again no preference; 24 such follicles were observed in the left ovary between February and May, and 18 in the right. This difference is not significant:X^2= 0,286, d.f.= 1, p >0,5.

The sample was too small to detect the phenomenon observed by Watson (1969) whereby the right ovary showed a tendency to produce the first ovum to be fertilised in each animal.

In the light of Watson's (1969) observation that a "silent ovulation" may be necessary in some animals to serve as a stimulus for overt oestrous, it is interesting to note that five of six impala in this study that had very recently ovulated or conceived (according to the presence of a lumen in the corpus luteum of pregnancy), also had a smaller luteinised structure which at the time was noted as a "luteinising follicle". This was paler in colour

and smaller than the corpus luteum of pregnancy, and
is thought to be a regressing, luteinised corpus
luteum of ovulation. However, in view of Fairall's
(1970) findings that impala have oestrous cycles of
12 or 29 days, it is surprising that not more than
one animal that had not yet conceived was found to
have a corpus luteum of ovulation. A larger sample
may reveal something more definite.

5.2.7.4. <u>Corpora lutea.</u> The first corpus luteum found
was from an animal collected on 18th May, and measured
7,6mm. Another from the same day measured 3,8mm,
but was accompanied, in the same ovary, by a smaller
luteinised structure. The next smallest corpus
luteum measured 4,8mm. As with the follicles, the
diameter of a corpus luteum was taken as the mean of
two measurements on the cut surface showing the
largest diameter.

The mean diameters of corpora lutea, together
with their standard deviations, are shown in Table 9
for each of the four months in which they were
examined.

There is a definite upward trend with
increasing pregnancy, as shown by other workers for
other species (Watson, 1969, Spinage,1969b), but
the sample does not extend far enough into pregnancy
for any later tendencies to show up. Nevertheless,
corpora lutea from the 1969 sample had mean diameters
of 7,35mm (n=20) and 7,91mm (n=16) for the months of
May and June respectively. (The peak of conceptions
took place some three weeks earlier in 1969 than it
did in 1970). This sample exhibits a similar
tendency.

As mentioned earlier, (Watson,1969) reported
slight changes in the size of the corpus luteum
with the advance of pregnancy in wildebeest, whereas
Spinage (1969b) reported no such change after the
initial increase to maximum size. Cloete (1939)

Table 9.   Mean diameters (in mm) and the standard
deviations of corpora lutea, observed in
ovaries of impala in Mkuzi Game Reserve.

MONTH	SAMPLE SIZE (n)	MEAN	RANGE	S.D.*
May	4	5,88	3,8 - 7,6	± 1,88
June	8	6,58	4,8 - 7,8	± 1,32
July	1	7,00	-	-
Aug.	7	7,52	4,9 - 8,2	± 1,09

*   S.D. = Standard Deviation

quotes evidence that the bovine corpus luteum does not
decrease in size, whilst Quinlan and Mare (1931) found
that the ovine corpus luteum does so from about the
end of the 4th month (in a five month pregnancy), i.e.
about four fifths of the way through pregnancy. The
inference here is that.the evidence for this phenomenon
is as yet inconclusive, or else there is wide variation
within the various groups.

The smallest corpus luteum seen in August
(4,9mm) was found in an animal which had an embryo
undergoing resorption. This fact probably accounted
for the small size of the corpus luteum, which was
2,1mm smaller than the next smallest. The mass of
the embryo could not be determined as it was already
merely an amorphous, bloody smear in the uterus.
Other embryos obtained in the same week had a mean
mass of 117,8g.

5.2.7.5. Corpora albicantia. Counts of corpora
albicantia were made in the hope that, as in wildebeest
(Watson, 1969), these might give some indication of
age. However, as will be seen from Table 10, the
mean number of corpora albicantia per pair of ovaries
(unpaired ovaries were omitted from the sample) shows
no trend whatsoever, and it must be concluded that
this feature in impala is unreliable as an indicator
of past breeding history.

There is a significant absence of corpora
albicantia in the juvenile (0-12 month) age class, and
the presence of one corpus albicans in each of seven
of the 12 animals in the 12-24 month class. This
latter suggests strongly that in the sample more than
half the juvenile animals bred. This will be discussed
in its proper context in a later section.

As has been noted by other workers (Watson,
1969) the corpora albicantia tend to become compressed
by follicles and corpora lutea of later pregnancies,
so that frequently they are seen as.mere thin brown
streaks. It is highly likely that, were two or more

Table 10.   Counts of corpora albicantia in impala

of all wear classes from Mkuzi Game

Reserve. (n = number of pairs of ovaries

in sample).

AGE/WEAR CLASS	n	No.OF C.A.	MEAN	RANGE
0-12 months	4	0	0	-
12-24 months	12	7	0,58	0-1
Nil	15	8	0,53	1
L	13	22	1,69	1-3
L/M	11	16	1,45	0-4
M	1	0	0	0
M/H	5	8	1,60	1-2
H	2	6	3,00	2-4
V.H.	2	5	2,50	2-3
E.H.	4	8	2,00	1-3
E.H.+	3	10	3,33	5

corpora albicantia to become adpressed, it would not
be possible to distinguish them from one another.
Similarly, it is not unlikely that the action of a
corpus luteum could split a corpus albicans, so that
it would appear as two. The first-mentioned fact
may account, at least in part, for the low counts
obtained in many specimens.

5.2.7.6. **Pregnancy and implantation.** Several authors
(Mossman and Mossman,1962; Stewart,pers.comm; and
Skinner, 1969) have recorded the phenomenon of
unilateral implantation in impala. The present study
confirms this in that in every case but one examined,
the right uterine horn was either enlarged - as a
result of previous pregnancies, swollen - in
preparation for receipt of the fertilized ovum, or
bore the embryo. The one exception was a specimen
collected in February with the left horn more
enlarged than the right. This can hardly be taken
as irrefutable evidence as it may have been due to a
pathological condition in the non-pregnant uterus.

No cases of twins were found, although, as
Kayanja (1969) has shown, this is not impossible in
impala.

5.2.8. **Gestation period and foetal growth.**

To establish the precise peak of conceptions
is not an easy matter on the basis of behaviour or of
general observation. However, it is possible from
the results of the present study, to deduce that the
optimum data in 1970 fell during the latter half of
May. None of the animals collected prior to 15th
May were found to have corpora lutea, although all
contained large follicles in one or other of their
ovaries. Those collected after that date however,
were found to have corpora lutea in various stages of
development.

Further evidence for such a timing is to be

found by establishing the peak parturition period,
and working back, assuming a known gestation period.
As described earlier, the gestation period of impala
has been shown by Fairall (1969) to be 196 days.
Basch (1964) however, puts it at 204 days. This
difference may be on account of the innate differences
between individuals - be they due to age or not -
or it may be an environmental factor influencing the
gestation period, as suggested by Watson (1969) for
wildebeest.

With a gestation period of 196 days, the conception
peak, based on a parturition peak between 6th and
13th December - which was the case in 1970, would have
been between 21st and 28th May. With a gestation
period of 204 days, on the other hand, the conception
peak would have been between 13th and 21st May. Both
these dates agree closely with the earlier deduction
made from the data obtained from ovarian analysis.

As a means of deriving a formula for the prediction
of conception age from the mass of the foetus, according
to the method of Huggett and Widdas (1952), the date
selected as the mean date of conception is 20th May.
This is a fair compromise in the light of the
arguments presented above.

The derivation of the sample regression coefficient
("b") is shown in Table 11.

The sample regression equation is therefore
calculated as follows (Snedecor, 1956; 124):

$$\hat{Y} - y = b (X - \bar{x})$$

$$\therefore \quad \hat{Y} - 7,15 = 0,102 (X - 107)$$

$$\hat{Y} = 7,15 + 0,102 (X - 107)$$

$$\hat{Y} = 3,75 + 0,102X$$

This sample regression is plotted in Fig.11,
together with the interval estimates at the 95% level
for the population regression, where $b - t_{,05}S_b \leqslant \beta \leqslant$
$b + t_{,05}S_b$. $t_{,05}$ with 16 degrees of freedom = 2,2120.
By calculation, $0,088 \leqslant \beta \leqslant 0,116$.

Table 11. Calculation of the sample regression coefficient of the cube root of the foetal weight ($W^{\frac{1}{3}}$) on the conception age of impala in Mkuzi Game Reserve.

(n = number in sample)

CONCEPTION AGE X(days)	n	MASS W	$W^{\frac{1}{3}}$ Y	DEVIATIONS x	DEVIATIONS y	SQUARES x^2	SQUARES y^2	xy
42	1	1,15	1,1	-65	-6,05	4225	36,60	393,3
63	1	9,40	2,1	-44	-5,05	1936	25,50	222,2
72	3	60,40	3,9	-35	-3,25	1225	10,65	113,8
77	1	114,8	4,9	-30	-2,25	900	5,06	67,5
78	1	139,9	5,2	-29	-1,95	841	3,80	56,6
90	4	113,6	4,8	-17	-2,35	289	5,52	40,0
91	4	122,0	5,0	-16	-2,15	256	4,62	34,4
101	1	355,8	7,1	- 6	-0,05	36	0,00	0,4
103	3	398,1	7,4	- 4	+0,25	16	0,06	-1,0
106	1	390,1	7,3	- 1	+0,15	1	0,02	-0,2
107	2	431,7	7,6	0	+0,45	0	0,20	0,0
108	3	183,2	5,7	+ 1	-1,45	1	2,10	-1,4
122	1	314,4	6,8	+15	-0,35	225	0,12	-5,3
128	2	411,0	7,4	+21	+0,25	441	0,06	5,3
142	1	1405	11,2	+35	+4,05	1225	16,40	141,8
151	1	1907	12,4	+44	+5,25	1936	27,56	231,0
161	1	2248	13,1	+54	+5,95	2916	35,40	321,3
185	1	3870	15,7	+76	+8,55	5776	73,10	649,8
Total 1924	32		128,7	- 1	0,0	22245	246,68	2269,5
Mean 107			7,15					

Sample regression coefficient, $b = \dfrac{\Sigma xy}{\Sigma x^2} = \dfrac{2269,5}{22245} = 0,102$

The sample regression line intercepts the X axis at
37,5 days, so that this figure can be inserted in the
general equation of Huggett and Widdas (1952), namely
$W^{\frac{1}{3}} = a(t - t_0)$, to give $W^{\frac{1}{3}} = 0,102 (t - 37,5)$.
This compares with the formula of $W^{\frac{1}{3}} = 0,11 (t - 39)$
obtained independently by Fairall (1969) and Roettcher
et al (1970). In view of the small size of the sample,
this is considered to be a very reasonable
approximation.

The confidence limits calculated above embrace the
sample regressions of Fairall (1969) and of Roettcher
et al (1970).

A calculation of "goodness of fit" (Snedecor,1966:
126) was then carried out according to Table 12.
With t = 15,65 and d.f. = 16, the regression is highly
significant (P<0,001).

The formula derived above was used to calculate
the theoretical mass at weekly intervals for comparison
with Fairall's (1969) masses. This comparison is
shown in Table 13.

These two studies reveal a very close similarity
up to the last two weeks of gestation. Thereafter,
Fairall's animals show a more rapid rate of development,
which may be due to the small size of the present
sample. Such a conclusion also implies that the
Huggett and Widdas formula may not be applicable in
late pregnancy.

It should also be pointed out that Cloete (1939),
whilst working on foetal development in sheep,
mentions that several factors may influence foetal
mass, amongst which are the following:

1.   Genetic influences of the dam, and possibly
also of the size.

2.   The size and condition of the dam. It is
possible that larger females produce larger neonates
(probably genetically controlled), whilst condition
of the dam seems to be effective only in extreme cases.

Table 12. Test of significance of the sample regression coefficients (b = 0,102) of the cube root of the mean foetal mass on the conception age (in days) of impala in Mkuzi Game Reserve.

CONCEPTION AGE (days)	MEAN MASS	EST. MASS	DEVIATIONS FROM REGRESSION $(Y - \hat{Y})$	SQUARES OF DEVIATION
X	Y	$\hat{Y}$	$d_{y.}$	$d_{y.x}^2$
42	1,10	0,45	0,65	0,4225
63	2,10	2,60	-0,50	0,2500
72	3,90	3,60	0,30	0,0900
77	4,90	4,03	0,87	0,7569
78	5,20	4,20	1,00	1,0000
90	4,80	5,43	-0,63	0,3969
91	5,00	5,54	-0,54	0,2916
101	7,10	6,55	0,55	0,3025
103	7,40	6,75	0,65	0,4225
106	7,30	7,06	0,24	0,0576
107	7,60	7,17	0,43	0,1849
108	5,70	7,27	-1,57	2,4620
122	6,80	8,70	-1,90	3,6100
128	7,40	9,32	-1,92	3,6864
142	11,20	10,74	0,46	0,2116
151	12,40	11,65	0,75	0,5625
161	13,10	12,67	0,43	0,1849
185	15,70	15,13	0,53	0,2809
			-0,20	15,1737

Mean square deviation from regression, $S_{y.x}^2 = d_{y.x}^2 / n-2 = \dfrac{15,1737}{16}$

$= 0,948$

Sample standard deviation from regression, $S_{y.x} = \sqrt{0,948} = 0,974.$

Sample standard deviation of regression coefficient, $S_b = S_{y.x.} / \sqrt{\sum x^2} = \dfrac{0,974}{149,2}$

$= 0,00652.$

Student's t = b/S_b = $0,102/0,00652$ = 15,65. d.f.16 P<0,001

This indicates a very significant "goodness of fit".

Table 13. Theoretical masses of foetuses of impala from Mkuzi Game Reserve at weekly intervals, derived from the sample regression coefficients of Fig.11, together with the corresponding masses and confidence intervals of Fairall (1969) for impala in Kruger National Park.

WEEK	MASS IN GRAMS (this study)	MASS IN GRAMS (Fairall,1969)	CONFIDENCE INTERVALS (Fairall,1969)	
4		0,4	0,3 —	0,5
5		1,9	0,0 —	3,8
6	0,9	2,9	1,8 —	4,0
7	1,6	12,2	8,3 —	16,1
8	6,8	10,6	2,3 —	18,9
9	17,6	28,9	19,9 —	37,9
10	36,6	45,4	34,8 —	56,0
11	65,4	56,5	47,5 —	65,5
12	106,5	105,8	103,4 —	108,2
13	162,8	111,0	86,5 —	135,5
14	234,9	150,6	90,6 —	210,6
15	327,1	320,8	150,8 —	390,8
16	439,0	395	330,0 —	460,0
17	573,9	340	275,5 —	404,5
18	736	855	705,0 —	1005,0
19	924	852	750,0 —	954,0
20	1141	1245	1093,0 —	1397,0
21	1395	1430	1317,0 —	1543,0
22	1677	2150	1935,5 —	2264,5
23	2000	1881	1710,0 —	2052,0
24	2358	2335	2141,0 —	2529,0
25	2762	2739	2307,0 —	3171,0
26	3203	3105	2680,0 —	3530,0
27	3688	4160	4086,6 —	4243,4
28	4228	5370	5334,0 —	5406,0

3. Age. Mature female sheep produce larger lambs than do younger animals, whilst aged females also tend to produce smaller lambs. This influence was found in sheep to obscure the effect of sex.

4. Sex of foetus. Male embryos tend to be heavier than females, even at a comparatively early stage of development.

In the light of this, the method of Roettcher et al (1970) for deriving a regression of foetal mass on conception age in impala with no fixed breeding season, would appear to be open to question. However, they had no means of allowing for differences as there were no foetuses of known conception age.

By the same token, the variation in foetal mass found in the present study could have been affected to some extent by differences in the foetal growth rate.

By calculating the standard deviation of the x values, i.e. estimated conception age, from the regression line, it is possible to deduce from the sample that about 70% of the observed pregnancies were conceived in an 18-day period: nine days on either side of the optimum conception date as discussed above. The standard deviation of the x values is calculated as 9,27 days.

At the 80% level the limits are 11 days on either side, whilst at the 95% level, the limits are 17 days on either side of the optimum conception date, for the sample examined.

5.2.9. Age-specific fertility.

Results of the present study show how in the sample of 57 females collected between May and September, seven were juveniles (0-12 months), seven were "immature" (12-24 months), and 43 were adult.

Of the adult animals, 38 were recorded as pregnant; a further three, collected in May, had either just ovulated or contained one large Graaffian follicle,

one (collected on 11th June) contained a small (2,5mm)
luteinising follicle and one large (4,0mm) follicle,
and the remaining one was apparently a barren female
in the E.H.+ tooth wear class.   This last-mentioned
animal had no Graaffian follicles whatsoever, the
ovaries being composed entirely of connective tissue.
If one assumes that the other four non-pregnant
females would have been fertilised, then 42/43
(97,7%) adults were fertile.

All seven of the 12-24 month-old females were
pregnant, i.e. 100% fertility, whilst one of the seven
juveniles (14,3%) was pregnant.   Thus for animals over
one year of age, the fertility rate in the sample was
98%.

As mentioned earlier, however, one of the 12-24
month-old females contained a foetus in the process
of being resorbed.   This reduces the fertility rate
to 96%.

In the 1969 sample there were no juveniles, but
all of the 39 animals collected were either pregnant
or had large developing follicles.   However, in the
1970 sample, six out of 20 (30%) animals between 12
and 24 months old had corpora albicantia, suggesting
that they had been pregnant in 1969.   This figure of
30% fertility in 1969 compares with that of 14,3% for
1970.

In 1965, I.B.Stewart (Unpublished report, Natal
Parks Board) reports that 38,5% of 26 "subadult" (12-24
month-old) animals from Mkuzi Game Reserve were
lactating, also indicating that they had given birth
as 12-month-old animals in 1964.   This figure is
surprisingly high, particularly when it is considered
that some of the 16 other females may have lost their
lambs and ceased lactating.   She also found that two
out of 27 (7,4%) juveniles were pregnant.

5.2.10.   Sex ratios.

Finally, in order to provide comparisons with other populations, the sex ratio of the study population has been determined from a series of sample counts carried out in connection with a separate investigation.

It is found impossible to separate mature females from juveniles in the field with any reliability after the juveniles have achieved an age of about nine months. Consequently, the sex ratios are derived from the animals over 12 months old, between January and September, and from animals over nine months old, between October and December.

Over a period of nearly two years, the mean of all samples taken reveals a sex ratio of the age classes described above of 1♂ : 1,71♀ or 58♂♂ : 100♀♀. The range of variation among these 13 samples is from 1♂ : 1,3♀ (76♂♂ : 100♀♀) to 1♂ : 2,3♀♀ (43♂♂ : 100♀♀).

The range of variation, which incidentally showed a progressive change with time, corresponds closely to the sex ratio observed in other areas by other workers, as outlined in an earlier section.

CHAPTER 6.

ACKNOWLEDGEMENTS.

CHAPTER 7.

SUMMARY.

This work reviews the literature on reproduction
in African ungulates, with particular emphasis on the
impala (Aepyceros melampus). Original research on a
population of this species occurring in Mkuzi Game
Reserve, Zululand, is reported upon.

The most overriding influence on this particular
population is the fact that it is seasonally breeding in
nature and, unlike other populations that have been
studied in East Africa, the reproductive processes
behavioural, anatomical, and physiological - exhibit a
regular cyclic pattern. This renders much of the data
a good deal easier to analyse and interpret.

As a means, primarily of establishing such
parameters as the age at which sexual maturity is
achieved, a method of ageing, initially on the basis of
tooth eruption and replacement and in older animals, on
molariform tooth attrition, was worked out. Results
indicate that females are capable of breeding at about
six months of age, whilst males, albeit potentially
capable at about 13 months, probably do not in fact take
part until they are at least three or four years old,
when they are socially and physically ready to compete for
territories.

The paired testes mass exhibits a peak during the
time of the rut in May; this is preceded by a prolonged
period during which it slowly increases, probably due to
increased testicular activity brought on by improved
nutrition, and is succeeded by a rapid decline in the
mass to its lowest point in the cycle in winter. This
cycle is closely followed by behaviour associated with
territoriality.

The ovaries also show increased activity with the
improved nutritional plane between October and May, during
which time follicular development takes place. Just

prior to the rut, a "silent" ovulation occurs, and this is
followed by overt oestrous which is synchronised to the
extent that nearly 80% of the conceptions are registered
in a period of 14 days. Ovulations appear to be in
equal proportions from the left and right ovary, as shown
by the presence of corpora lutea of pregnancy. The corpus
luteum of pregnancy is persistent, and appears to increase
slightly in diameter, at least up to the 4th month of
gestation. It also persists for some years after
fulfilling its function, as a corpus albicans or pigmented
scar; however it is not possible to use this feature as
a means of accurately assessing the breeding history of
an individual.

The gestation period, determined on a population
basis, is between 196 and 204 days, the peak of births in
1970 occurring in the second week of December. The
regression, the cube root of foetal mass on conception age,
is a straight line, and the relationship between the two
parameters is shown by the formula $W^{\frac{1}{3}} = a(t-t_o)$.

In 1970, 14,3% of the juvenile (0-12 month old)
females were pregnant, whilst counts of corpora albicantia
revealed that 30% of the juveniles in 1969 had been
pregnant. The sex ratio of males to females in the Mkuzi
population, which is artificially controlled numerically,
was found to be 1 : 1,7.

REFERENCES

Anderson, J.L.   1965.   Annual change in testis and kidney
fat weight in impala (Aepyceros m.melampus
Lichtenstein).   The Lammergeyer 3(2): 56-59.

Anon.   1968.   Some observations on the sex ratios and
occurrence at waterholes of the three main species
of game animals in Mkuzi Game Reserve, Zululand.
Mimeo., University of Natal Wild Life Society.

Ansell, W.F.H.   1960.   The breeding of some larger mammals
in Northern Rhodesia.   Proc. zool.Soc.Lond.134:
251-274.

─   1965.   Standardisation of field data on
mammals.   Zool. Afr. 1(1): 97-113.

Basch, W.S.B.   1964.   Gestation period of impala.   Afr.
Wild Life 18(2):   162.

Bere, R.M.   1959.   Queen Elizabeth National Park, Uganda.
The hippopotamus problem and experiment.   Oryx
5(3):   116-124.

Bigalke, R.C.   1970.   Observations on springbok populations.
Zool. Afr. 5(1): 59-70.

Bourliere, F. and J. Verschuren.   1960.   Introduction à
l'ecologie des ongulés du Parc National Albert.
Institut des Parcs Nationaux du Congo Belge.
158pp.   Brussels.

Brand, D.J.   1963.   Records of mammals bred in the National
Zoological Gardens of South Africa during the
period 1908-1960.   Proc.zool. Soc.Lond. 140(4):
617-659.

Brooks, A.C.   1961.   A study of the Thomson's gazelle
(Gazella thomsonii Gunther) in Tanganyika.
H.M. Stationery Office, London.   147pp.

Buechner, H.K.   1961.   Territorial behaviour in Uganda
kob.   Science 133: 698-699.

Buechner, H.K. 1963. Territoriality as a behavioural adaptation to environment in Uganda kob. Proc. XVI Intl. Congr. Zool.: 59-63.

Buechner, H.K. and R.Schloeth. 1965. Ceremonial mating behaviour in Uganda kob. Z. für Tierpsychol. 22(2): 209-225.

Buechner, H.K., J.A.Morrison, and W.Leuthold. 1966. Reproduction in Uganda kob with special reference to behaviour. Symp. zool. Soc.Lond. 15: 69-88.

Cheatum, E.L. 1949. The use of corpora lutea for determining ovulation incidence and variations in the fertility of white-tailed deer. Cornell Vet. 39(3): 282-291.

Child, G. 1964. Growth and ageing of impala, Aepyceros melampus. Occ. pap.Nat.Mus. S.Rhod. 27B: 128-135.

— 1968. Behaviour of large mammals during the formation of Lake Kariba. Kariba Studies, Nat. Mus. of Rhodesia. 123pp.

Child, G. and V.J.Wilson, 1964. Delayed effects of tsetse control hunting on a duiker population. J. Wildl. Mgmt. 28: 866-868.

Cloete, J.H.L. 1939. Prenatal growth in the Merino sheep. Ond. J. Vet. sci. and Anim. Ind. 13(2): 417-558.

Clough, G. 1966. Reproduction in the hippopotamus. Ph.D. thesis, Cambridge Univ.

Darling, F.F. 1960. An ecological reconnaissance of the Mara Plains in Kenya Colony. Wildl.Monographs 5. 41pp.

Dasmann, R.F. and A.S.Mossman. 1962a. Reproduction in some ungulates in Southern Rhodesia. J. Mammal. 43: 533-537.

— and — 1962b. Population studies of impala in Southern Rhodesia. J.Mammal. 43(3): 375-395.

Dixon, J.E.W.   1964.   Preliminary notes on the mammal
        fauna of the Mkuzi Game Reserve.   The Lammergeyer
        3(1): 40-58.

Estes, R.D.   1964.   Third Report, August-January.
        Antelope behaviour study.   Nat. Geogr. Soc./Cornell
        Univ. 43pp. mimeo.

  —   1966.   Behaviour and life history of the
        wildebeest (Connochaetes taurinus Burchell).
        Nature 212 (5066) :999-1000.

  —   1969.   Territorial behaviour in the wildebeest
        (Connochaetes taurinus Burchell 1823).   Z.
        Tierpsychol. 26 : 284-370.

Fairall, N.   1968.   The reproductive seasons of some
        mammals in the Kruger National Park.   Zool. Afr.
        3(2): 189-210.

  —   1969.   Prenatal development of the impala,
        Aepyceros melampus Lichtenstein.   Koedoe 12: 97-103.

  —   1970.   Research on the reproduction of wild
        ungulates.   Proc. S. Afr. Soc. Anim. Prod. 9: 57-61.

Foster, J.B. and D. Kearney.   1967.   Nairobi National
        Park census, 1966.   E. Afr. Wildl. J. 5: 112-120.

Fraser, A.F.   1968.   Reproductive behaviour in ungulates.
        Academic Press, London.   202pp.

Gaerdes, J.H.   1965.   The impala of South West Africa.
        Afr. Wild Life 19(2): 108-113.

Golley, F.B.   1957.   An appraisal of ovarian analysis
        in determining reproductive performance of black-
        tailed deer.   J. Wildl. Mgmt. 21(1): 62-65.

Haltenorth, T.   1963.   Klassifikation der Säugetiere:
        Artiodactyla Handb. Zool. 8(32): 96.

Hammond, J.   1927.   The physiology of reproduction in
        the cow.   Cambridge Univ. Press.

Hanks, J.   1970.   Elephant research project.   Black
        Lechwe 8(1): 14-18.

Haugen, A.O. and D.L. Trauger.   1962.   Ovarian analysis
        for data on corpora lutea changes in white-tailed
        deer.   Proc. Iowa Acad. Sci. 69: 231-238.

Hofmeyer, J.M. and J.D.Skinner.   1969.   A note on
        ovulation and implantation in the steenbok and
        impala.   Proc. S. Afr. Soc. Anim. Prod. 8: 175.

Hirst, S.M.   1969.   Predation as a regulating factor of
        wild ungulate populations in a Transvaal Lowveld
        nature reserve.   Zool. Afr. 4(2): 199-230.

Huggett, A.S. and W.F.Widdas.   1951.   A relationship
        between mammalian foetal weight and conception age.
        J. Physiol. 114: 306-317.

Hvidberg-Hansen, H.   1970.   Contribution to the knowledge
        of reproductive physiology of the Thomson's gazelle
        (Gazella thomsonii Günther).   Mammalia 34(4): 551-563.

Jarman, P.J.   1970a.   Impala ecology.   Progress report
        of the Serengeti Research Institute, January-March
        1970.

Jarman, M.V.   1970b.   Attachment to home area in impala.
        E. Afr. Wildl. J. 8: 198-200.

Jarman, P.J. and M.V.Jarman.   1969.   Impala ecology and
        behaviour.   Annual Report of the Serengeti Research
        Institute, Tanzania National Parks.

Jungius, H.   1970.   Studies on the breeding biology of
        the reedbuck (Redunca arundinum Boddaert,1785)
        in the Kruger National Park.   Z. für Säugetierk.
        35(3): 129-146.

Kayanja, F.I.B.   1969.   The ovary of the impala,
        Aepyceros melampus Lichtenstein 1812.   J. Reprod.
        Fert., Suppl. 6: 311-317.

Kellas, J.M.   1955.   Observations on the reproductive
        activities, measurements and growth rate of the
        dikdik (Rhynchotragus kirki thomasi Neumann).
        Proc. zool. Soc. Lond. 124: 751-784.

Kenneth, J.H. and G.R.Ritchie. 1953. Gestation periods:
a table and bibliography, 3rd ed. Commonwealth
Bureau of Animal Breeding and Genetics, Tech.Comm.
No.5. 39pp.

Kerr, M.A. 1965. The age at sexual maturity in male
impala. Arnoldia (Rhodesia) 1(24): 1-6.

Kiley-Worthington, M. 1965. The waterbuck (Kobus
defassa Rüppel 1835, and K. ellipsiprymnus
Ogilby 1833) in East Africa: spatial distribution.
A study of sexual behaviour. Mammalia 29(2):
177-204.

Klingel, H. 1969. The social organisation and population
ecology of the plains zebra (Equus quagga(sic)).
Zool. Afr. 4(2): 249-264.

Lagerlof, N. 1959. Hereditary forms of sterility in
Swedish cattle breeds. Fert. Steril. 2: 230.

Laws, R.M. 1966. Age criteria for the African elephant,
Loxodonta africana. E. Afr. Wildl. J. 4: 1-37.

―   1969. Aspects of reproduction in the African
elephant, Loxodonta africana. J. Reprod. Fert.,
Suppl. 6: 193-217.

Laws, R.M. and G.Clough. 1966. Observations on
reproduction in the hippopotamus Hippopotamus
amphibius Linnaeus. Symp. zool.Soc.Lond. 15: 117-
140.

Laws, R.M. and I.S.C.Parker. 1968. Recent studies on
elephant populations in East Africa. Symp. zool.
Soc.Lond. 21: 319-359.

Leopold, A. 1933. Game Management. Chas. Scribner's
Sons. 481pp.

Leuthold, W. 1966. Variations in territorial behaviour
of Uganda kob Adenota kob thomasi (Neumann,1896).
Behaviour 27: 214-257.

―   1970. Observations on the social organisa-
tion of impala (Aepyceros melampus). Z.Tierpsychol.
27: 693-721.

Mentis, M.T.   1970.   A review of some life history
        features pertinent to the productivity of the large
        herbivores of Africa.   139pp, mimeo.

Morrison, J.A.   1960.   Ovarian characteristics in elk of
        known breeding history.   J. Wildl.Mgmt.24(3):297-307.

Mossman, A.S. and H.W.Mossman.   1962.   Ovulation,
        implantation and foetal sex ratio in impala.
        Science 137: 869.

Nordan, H.C., I.McT.Cowan, and A.J.Wood.   1968.
        Nutritional requirements of black-tailed deer,
        Odocoileus hemionus columbianus, in captivity.
        Symp. zool. Soc.Lond. 21: 89-96.

Oelofse, J.   1970.   Plastic for game catching.   Oryx 10(5):
        306-308.

Pearsall, W.H.   1957.   Report on an ecological survey of
        the Serengeti National Park, Tanganyika: November
        and December,1956.   Fauna Preservation Society.

Pienaar, U.de V.   1963.   The large mammals of the Kruger
        National Park - their distribution and present-day
        status.   Koedoe 6: 1-37.

      —   1969.   Predator-prey relationships
        amongst the larger mammals of the Kruger National
        Park.   Koedoe 12: 108-176.

Pienaar, U.de V., P.van Wyk, and N.Fairall.   1966.   An
        experimental cropping scheme of hippopotami in the
        Letaba river of the Kruger National Park.   Koedoe 6:
        1-33.

Poynton, J.C.   (1961)   Biogeography of south-east Africa.
        Nature 189: 801-803.

Quinlan, J. and Maré.   1931.   The physiological changes
        in the ovary of the Merino sheep in South Africa,
        and their practical application in breeding.
        17th Rep. D.V.S. and Anim.Ind., Un.of S.A.:
        663-703.

Riney, T. 1955. Evaluating condition of free-ranging
red deer (Cervus claphus), with special reference
to New Zealand. N.Z. J. Sci. Tech. Sect.B, 36(5):
429-463.

Riney, T. and G.Child. 1960. Breeding season and ageing
criteria for the common duiker (Sylvicapra grimmia).
Proc. 1st Fef. Sci. Congr. (Salisbury, Rhodesia):
291-299.

Robbel, H. and G. Child. 1969. Note on the 1969 impala
rut in the Moremi. Botswana Notes and Records
2: 95-97.

Robinette, W.L. and G.F.T.Child. 1964. Notes on the
biology of the lechwe (Kobus leche). The Puku 2:
84-117.

Robinette, W.L., J.S.Gashwiler, J.B.Low, and D.A.Jones.
1957. Differential mortality by sex and age among
mule deer. J. Wildl. Mgmt. 18(3): 309-315.

Roettcher, D. and R.R.Hofmann. 1970. The ageing of
impala from a population in the Kenya rift valley.
E. Afr. Wildl. J. 8: 37-42.

Roettcher, D., R.R.Hofmann and F.I.B. Kayanja. 1970.
Ergebnisse der prae-und postnatalen Alterbestimmung
beim ostafrkanischen Impala (Aepyceros melampus
Lichtenstein, 1812). Z. Saugetierk. 35(5):289-305.

Sadleir, R.M.F.S. 1969. The ecology and reproduction in
wild and domestic mammals. xii + 321pp. Methuen,
London.

Schenkel, R. 1966a. On sociology and behaviour in impala
(Aepyceros melampus suara Matschie). Z. Saugetierk.
31(3): 177-205.

—   1966b. On sociology and behaviour in impala
(Aepyceros melampus Lichtenstein). E. Afr.Wildl.
J. 4: 99-114.

—   1966c. Zum problem der Territorialität und
des Markierens bei Säugern - am Beispel des Schwarzen
Nashorns und das Löwen. Z. Tierpsychol. 23: 593-626.

Short, R.V. and N.W.Moore. 1959. Progesterone in blood
V: Progesterone and 20α-hydroxypregn-4-en-3-oné
in the placenta and blood of ewes. J. Endocr. 19:288.

Shortridge, G.C. 1934. The mammals of South West Africa.
2 vols. W. Heinemann Ltd., London.

Simpson, C.D. 1968. Reproduction and population structure
in greater kudu in Rhodesia. J. Wildl. Mgmt. 32(1):
149-161.

Skinner, J.D. 1969. Lifetime production of an impala.
Afr. Wild Life. 23(1): 78-79.

—   1971. The sexual cycle of the impala ram,
Aepyceros melampus Lichtenstein. Zool. Afr. In press.

Skinner, J.D. and J.H.M. van Zyl. 1970. The sexual cycle
of the springbok ram (Antidorcas m. marsupialis
Zimmerman). Proc. S. Afr. Soc. Anim. Prod. 9:
197-202.

Snedecor, G.W. 1956. Statistical Methods. Iowa State
Univ. Press. 5th ed. 534 pp.

Spinage, C.A. 1969a. Naturalistic observations on the
reproductive and maternal behaviour of the Uganda
defassa waterbuck Kobus defassa ugandae Neumann.
Z. Tierpsychol. 26(1): 39-47.

—   1969b. Reproduction in the Uganda defassa
waterbuck, Kobus defassa ugandae Neumann. J. Reprod.
Fert., Suppl. 6: 287-310.

Stevenson-Hamilton, J. 1947. Wild Life in South Africa.
364pp. Cassell, London.

Stewart, P.G. and Iona B. Stewart. 1966. The use of age
and sex ratios in estimating the abundance and
productivity of impala. The Lammergeyer 6: 9-19.

Taber, R.D. and R.F.Dasmann. 1954. A sex difference in
mortality in young Columbian black-tailed deer.
J. Wildl. Mgmt. 18(3): 309-315.

Talbot, L.M. 1965. A survey of past and present wildlife
research in East Africa. E. Afr.Wildl.J.3:61-85.

Talbot,L.M. and M.H.Talbot. 1963. The wildebeest in western Masailand, East Africa. Wildl.Monographs 12. 88pp.

Teer, J.G., J.W.Thomas and E.A.Walker. 1965. Ecology and management of white-tailed deer in the Llano basin of Texas. Wildl. Monographs 15. 62pp.

Van Wyk, W.L. 1963. Ground water studies in northern Natal, Zululand and surrounding areas. Geol. Surv. Mem. 52. Dept.of Mines, R.S.A.

Vincent, J., P.M.Hitchins, R.C.Bigalke and A.J.Bass. 1968. Studies on a population of nyala. The Lammergeyer 9: 5-17.

Walther, F. 1958. Zum Kampf- und Paarungsverhalten einiger Antilopen. Z. Tierpsychol. 15: 340-380.

Watson, R.H. and H.M.Radford. 1960. Influence of rams on the onset of oestrous in Merino ewes in the spring. Aust. J. agric.Res.11: 65-71.

Watson, R.M. 1969. Reproduction of wildebeest, Connochaetes taurinus albojubatus Thomas, in the Serengeti region, and its significance to conservation. J. Reprod. Fert., Suppl. 6: 287-310.

Wilhelm, J.H. 1933. Das Wild des Okavangogebietes und des Caprivi Zipfels. J.S.W.Afr.Sci. Soc. 6: 51-74.

Wilson, V.J. 1969. The large mammals of the Matopos National Park. Arnoldia (Rhodesia) 4(13): 1-32.

Winterbottom, J.M. 1962. A note on the zoogeographical limits in south-east Africa, as suggested by the avifauna. Ann. Cape Prov. Mus., II:152-154.

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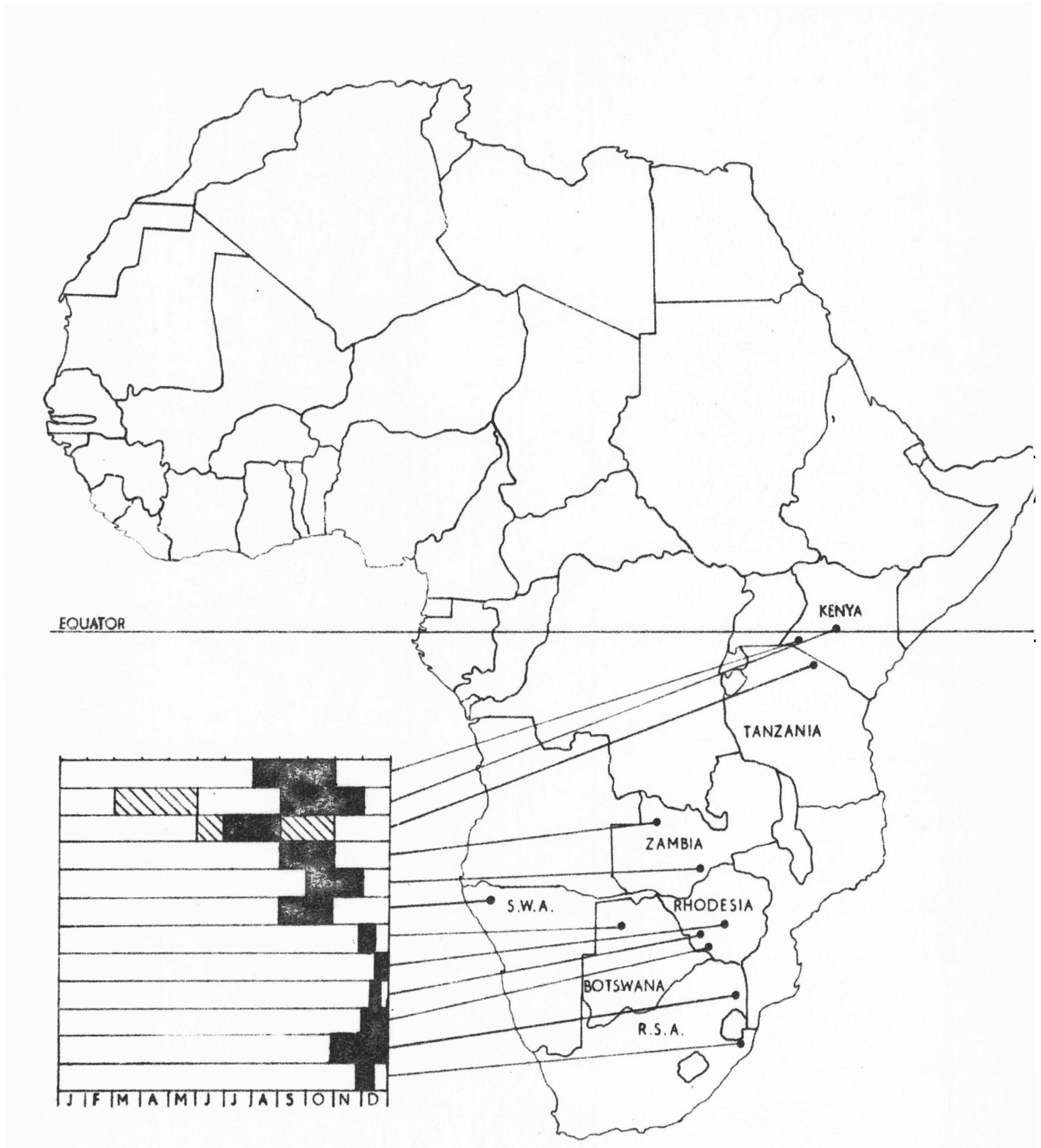
Fig. 1. Seasons of peak births in impala in various parts of the species'
range, showing an apparent tendency for the peak parturition period
to be later and more abbreviated towards the southern end of the
range. Cross hatching represents less marked parturition periods.
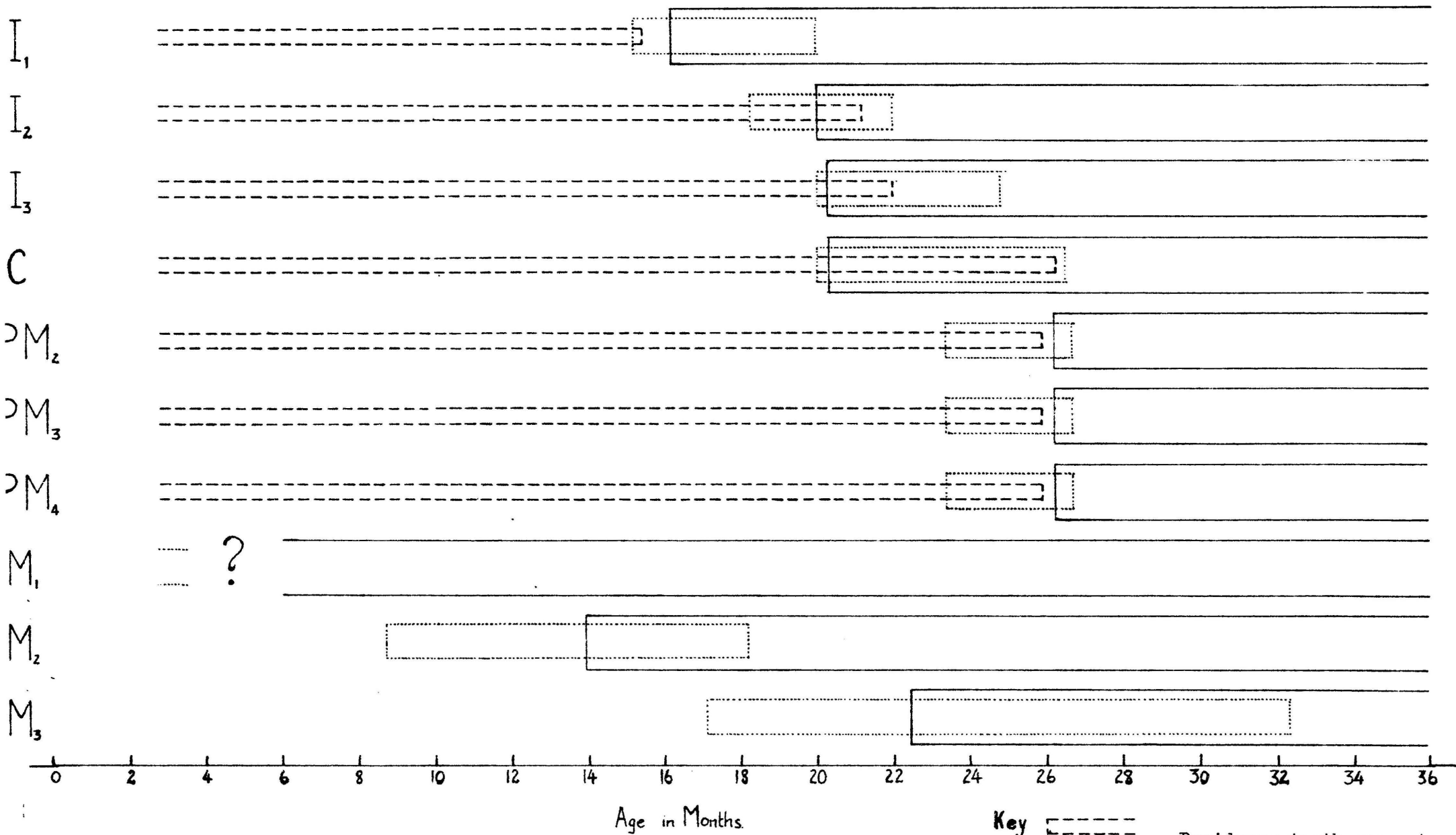
Fig. 2. The sequence and timing of eruption and replacement of deciduous and permanent teeth in the lower jaw of impala in Mkuzi Game Reserve.
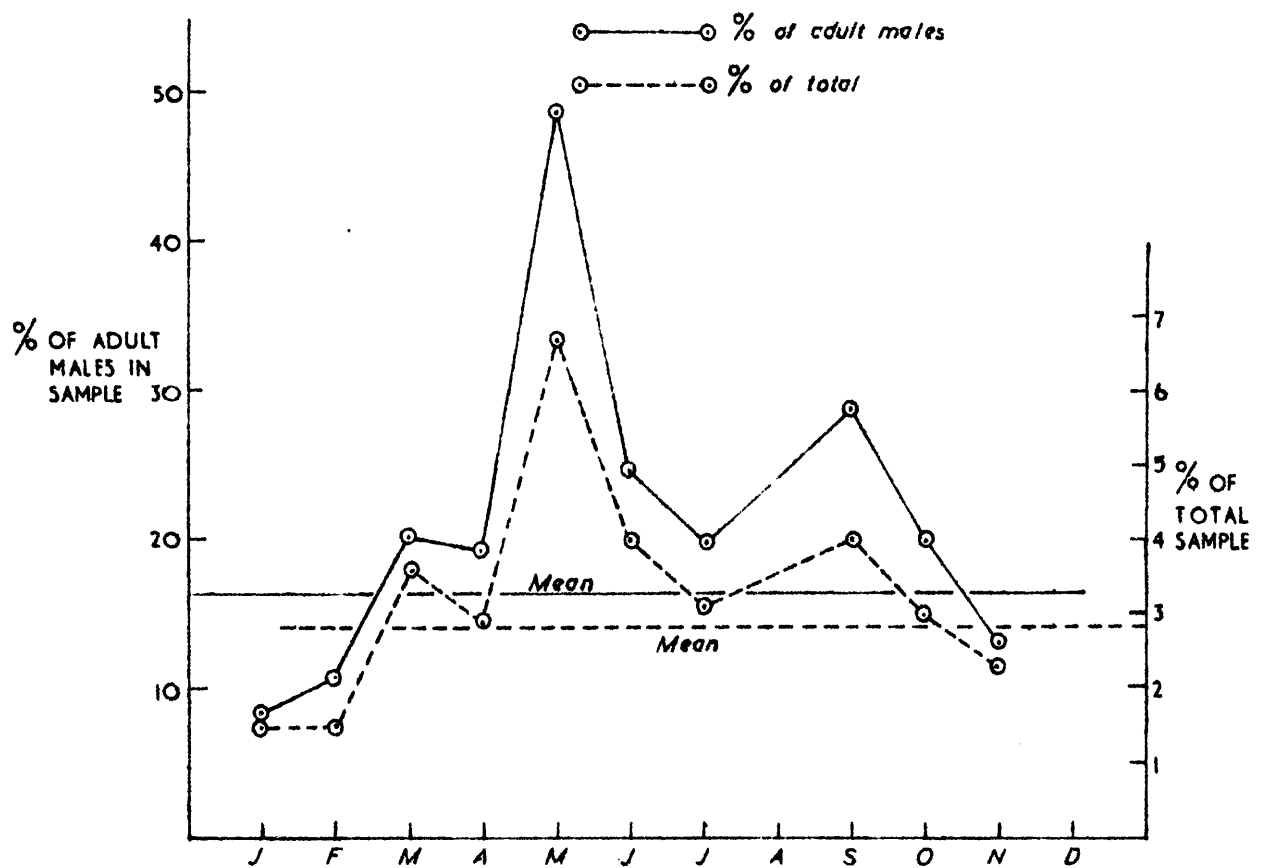
Key

- - - - - Deciduous tooth present

.... Permanent tooth erupting/replacing

Permanent tooth present

Fig. 3. Incidence of single adult males throughout 1970 in
Mkuzi Game Reserve, expressed as a percentage of all
adult males and of the total population.
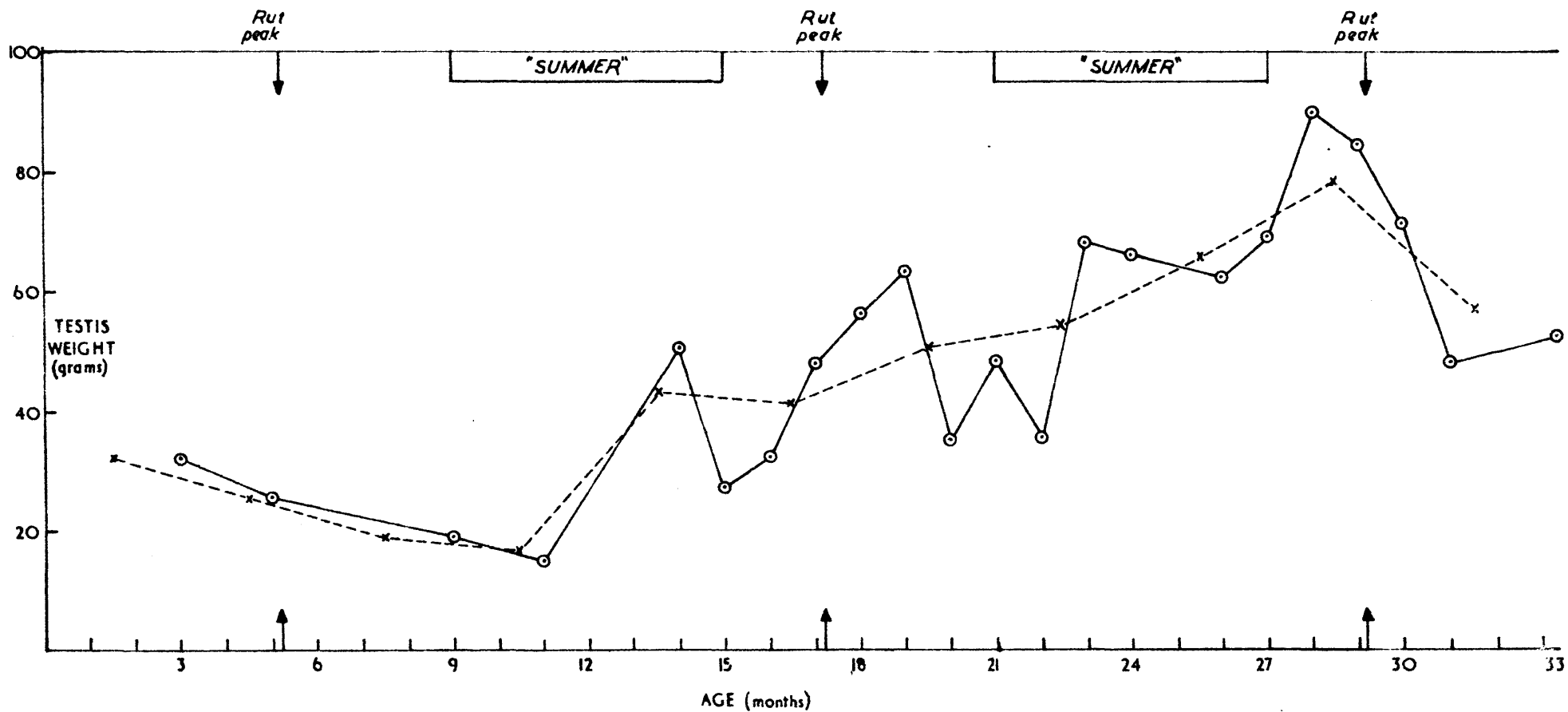
Fig. 4. The progressive increase in mean paired testis mass in impala in Mkuzi Game Reserve up to the age of 33 months, showing also fluctuations relative to significant seasons of the year. The solid line shows the mean mass at monthly intervals, whilst the dotted line shows the mean mass at three-monthly intervals.
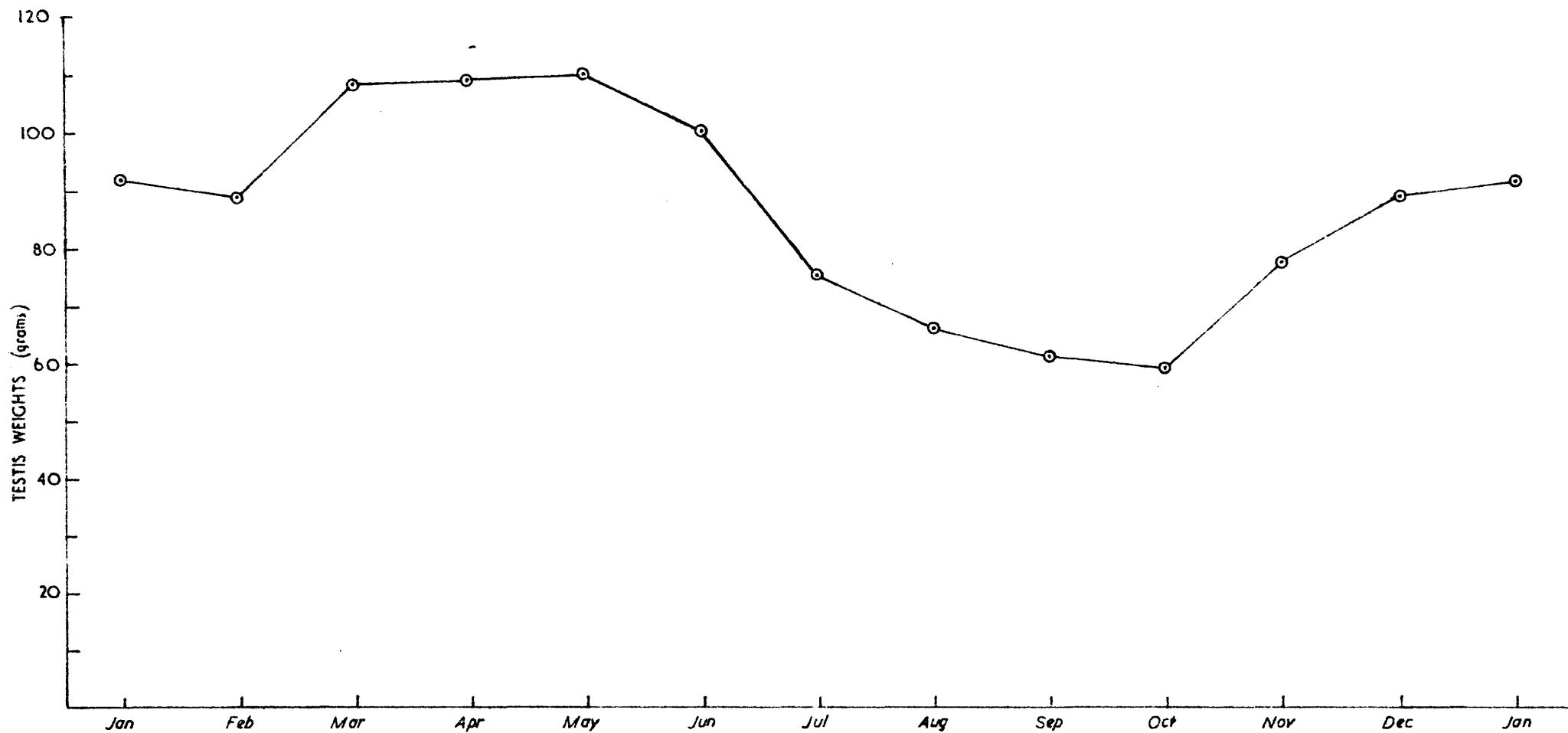
Fig. 5. The mean paired testis mass at monthly intervals of all animals in which full permanent dentition was recorded.
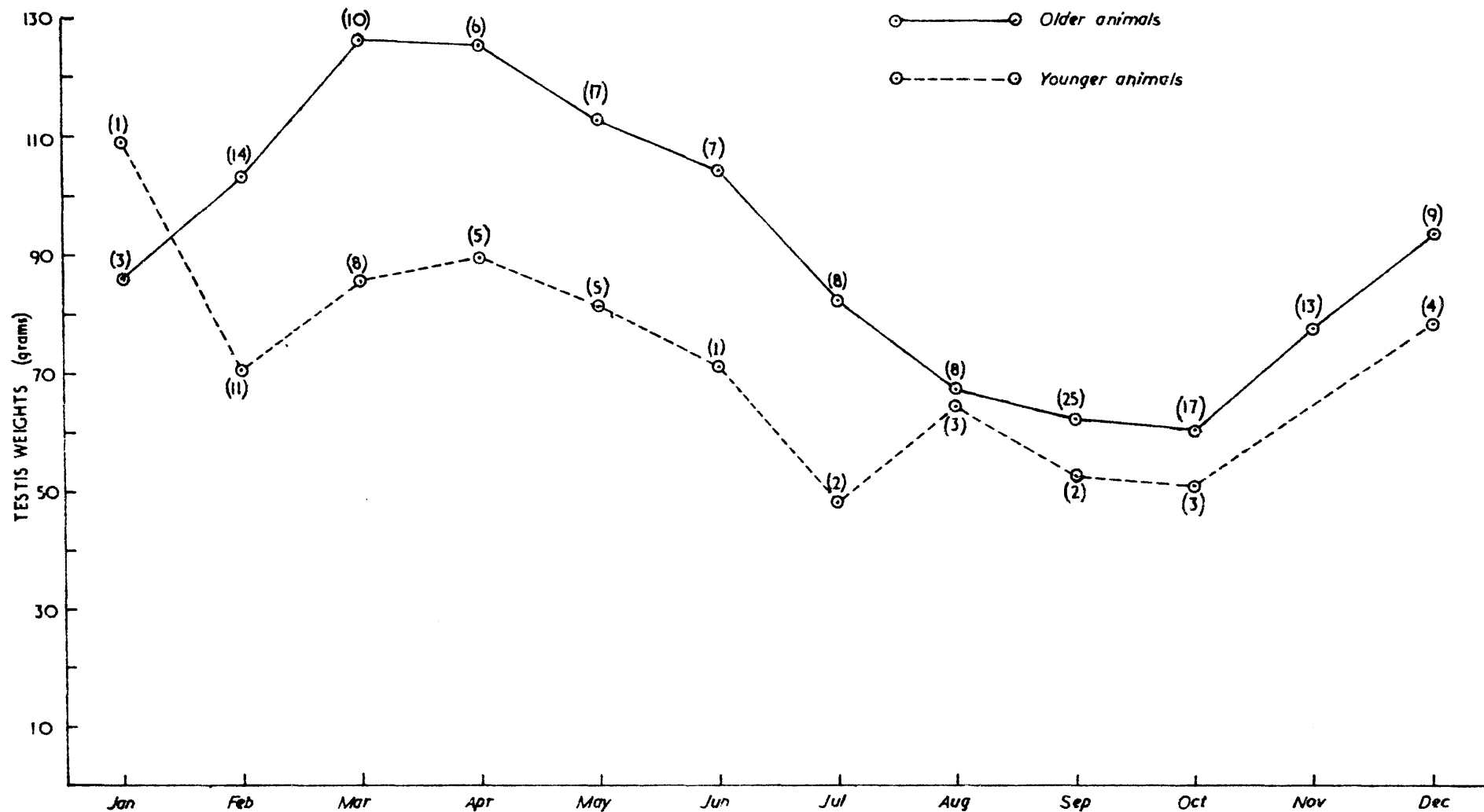
Fig. 6. The monthly mean paired testis weights of "young adults" and of "old adults", separated in accordance with the analysis shown in Table 6. The figures in brackets are the sample sizes.
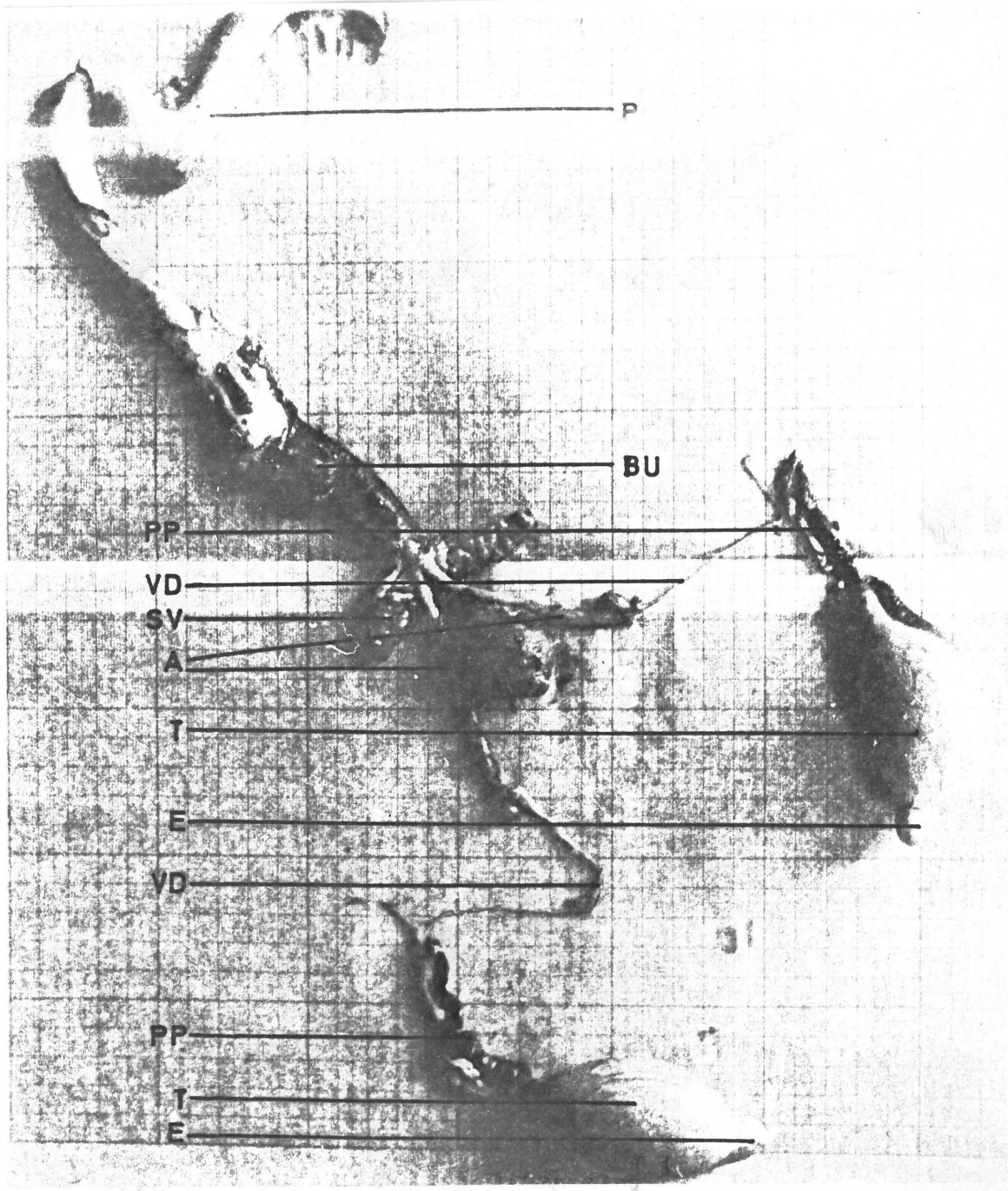
Fig. 7.   General view of the complete male
reproductive tract of impala.

T	=	Testes	A	=	Ampullae
E	=	Epididymides	SV	=	Seminal vesicles
PP	=	Pampiniform plexus	BU	=	Bulbo-urethral glands
VD	=	Vasa deferentia	P	=	Penis
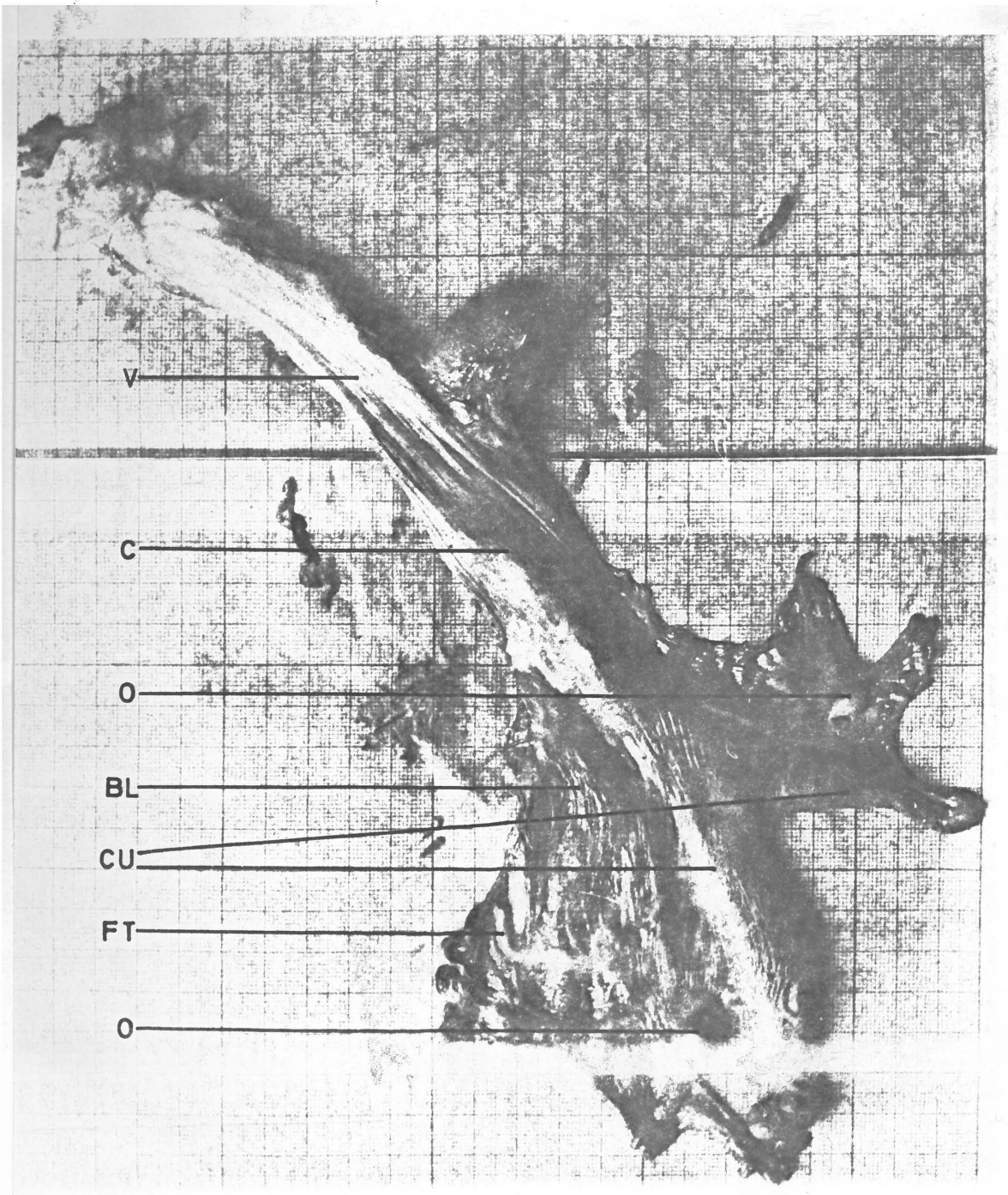
Fig. 8.   General view of the complete female
reproductive tract of impala.

FT = Fallopian tubes   O   = Ovaries
CU = Uterine cornua   BL = Broad ligament
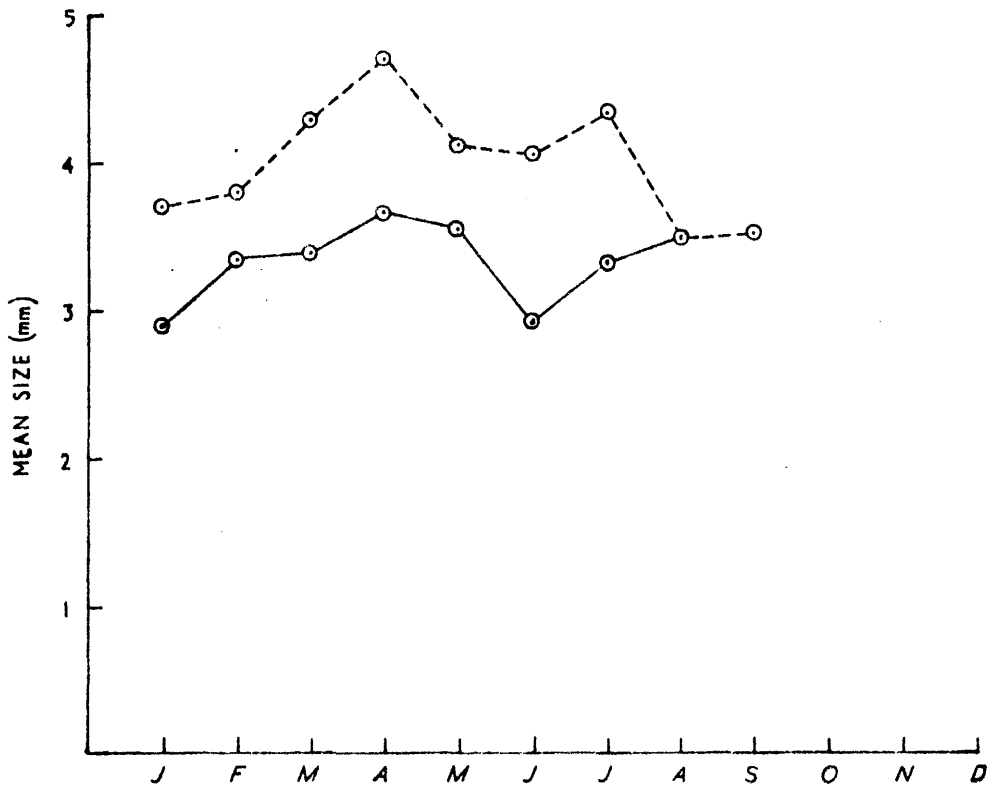 C = Clitoris   V   = Vagina

Fig. 9. The mean diameter of all follicles larger than 2mm in diameter (o———o) and of the largest follicle in each pair of ovaries (o———o), plotted against time.
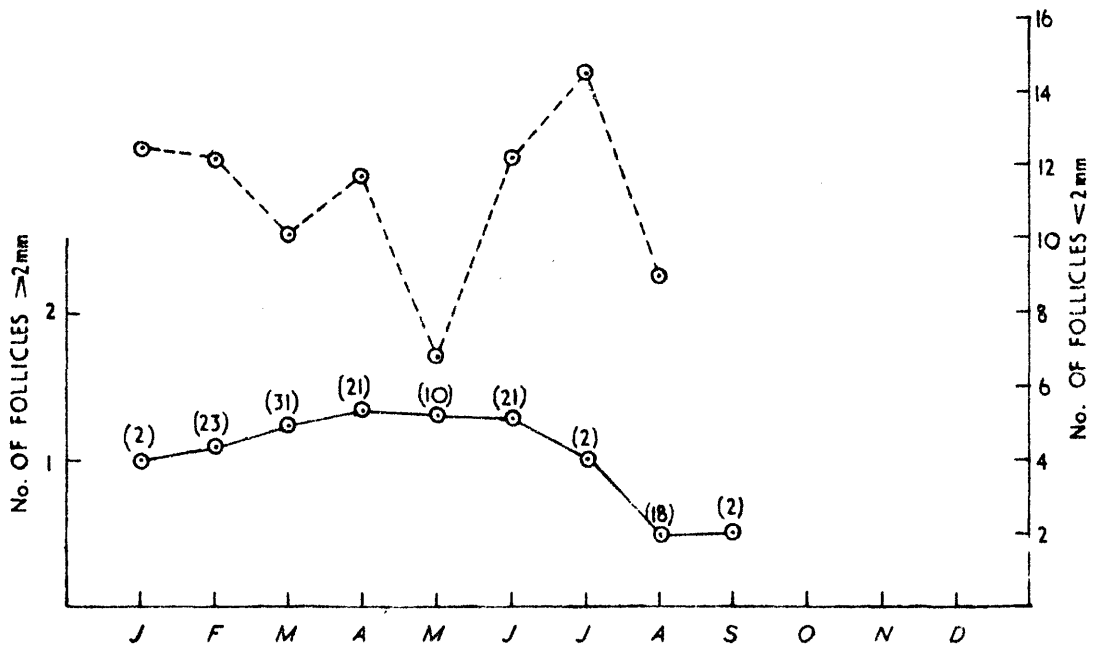

Fig. 10. The mean number of follicles greater than 2mm in diameter (o———o) and of those less than 2mm in diameter (o———o) in all the ovaries examined, plotted against time. The figures in brackets denote the number of ovaries examined.
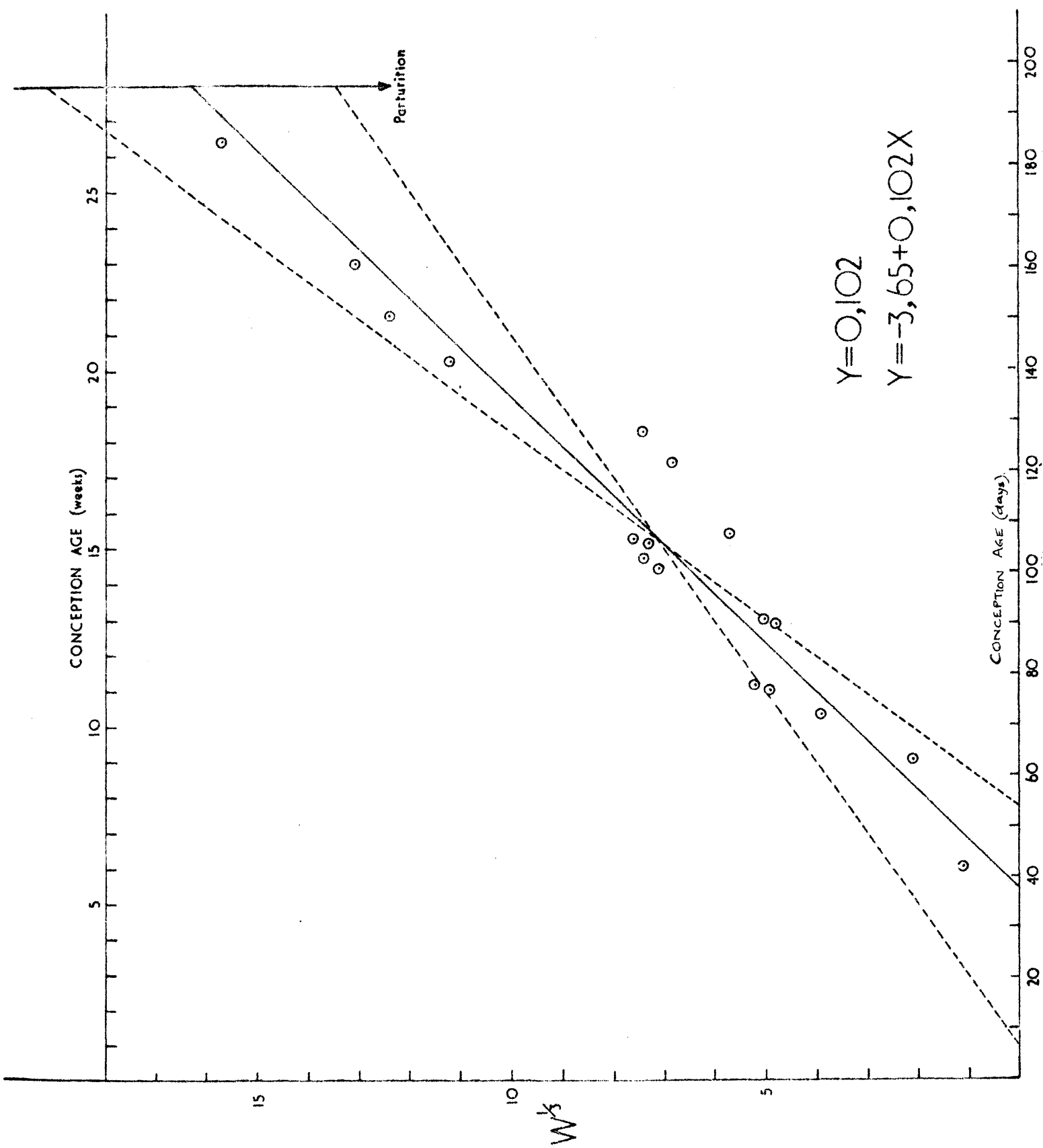
Fig. 11. Sample regression of the cube root of foetal mass ($W^{\frac{1}{3}}$) on conception age in days of impala in Mkuzi Game Reserve, with the calculated 95% confidence limits for the population regression shown as dotted lines.