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STUDIES ON THE BIOLOGY AND ECOLOGY OF THE WARTHOG *PHACOCHOERUS AETHIOPICUS SUNDEVALLI* LÖNNBERG, 1908 IN ZULULAND

by

DARRYL RAYMOND MASON

Submitted in partial fulfilment of the
requirements for the degree of

D.Sc. (Wildlife Management)

in the
Faculty of Science
University of Pretoria
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"This day I pursued several pigs with the old sows, with a view to shoot one of them, but in vain, however, the chase of them afforded me a singular pleasure. In fact, the heads of the old ones, which were before of a tolerable size, appeared to have suddenly grown still larger and more shapeless than they were before; which momentary and wonderful change surprised me so much the more, as riding hard over a country full of bushes and pits, I had hitherto been prevented from giving sufficient attention to the manner in which it was brought about. The whole of the mystery, however, consisted in this; each of the old ones, during its flight, took a pig in its mouth; a circumstance that also explained to me another subject of my surprise, which was, that all the pigs which I was just before chasing along with the old ones, suddenly disappeared. But in this action we find a kind of unanimity among the wood-swine, in which they resemble the tame species, and which they have in a greater degree than many other animals; it is also very astonishing, that the pigs should be carried about in this manner between such large tusks as those of their mothers, without being hurt, or crying out in the least. I saw the same thing done, however, on two other occasions, as I was chasing them. The cry of these young ones was like that of our common pigs, as I found in some we afterwards caught."

A. Sparrman, 1789. "A voyage to the Cape
of Good Hope, towards the Antarctic Polar
Circle, and round the world: but chiefly
into the country of the Hottentots and
Caffres, from the year 1772, to 1776."

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by

D.R. MASON

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ABSTRACT

Warthog biology, population structure and behavioural ecology were studied over a two-year period in the Hluhluwe-Corridor-Umfolozi Game Reserve complex, Natal. Age-specific stages of tooth replacement, eruption and attrition were described and incremental layers in the cementum were evaluated as correlates of age. Criteria for distinguishing between three age classes of warthogs in the field were described. Carcass yield, physical condition, postnatal and allometric growth were investigated and body mass measurements were compared with data for other warthog populations. Parameters of male sexual function were correlated with age and a seasonal fluctuation was found. Breeding was seasonal with a peak in conceptions during May and peak farrowing in November early in the wet season. Mean prenatal litter size was 3,21 foetuses per female and the prenatal sex ratio was not significantly different from unity. A minimum farrowing rate of 95,5 % was recorded during the study period. Lactation endured for about five months and the post partum reconception interval was slightly longer. Habitats with short grass areas were preferred and the availability of holes was not a population limiting factor. The highest local seasonal density exceeded 35 warthogs per km² and the population age structure was characterised by a large base of juveniles. Recruitment into the yearling age class was substantial. The disparate sex ratio of 1♂ :2,18♀♀ among adults was found to generally agree with ratios from other warthog populations, but

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had probably been exaggerated by male-biased culling. Grasses constituted the bulk of warthog food throughout the year but there was a dry season change in emphasis towards more grass rhizomes, which were dug up with the rhinarium. Holes were very important in warthog welfare although adult warthogs particularly were not absolutely dependent on holes for their survival. Thermoregulatory behaviour was a conspicuous feature of warthog activities. Mean group size was 3,28 and social structure was based on four main types of sounders: solitary adult males, bachelor sounders, heterosexual sounders of yearlings and matriarchal sounders. Warthogs were sedentary and lived in small overlapping home ranges but territorial defence was absent. Agonistic displays between mature males appeared to be related to dominance mostly in respect of mating priority. Scent marking behaviour was observed and other forms of communication were outlined. Some generalisations were made regarding the adaptive significance of the tusks and warts and the mode of fighting. Courtship behaviour was described and observations of mating season activities showed that warthogs are polygamous. The sows of matriarchal sounders were generally solitary when about to farrow and the piglets were born underground. Piglets started emerging from the hole and grazing before the age of one month, but were almost two months old when they started accompanying their mothers throughout the day. Yearling progeny may rejoin their mothers after the latter have farrowed. A combination of the warthog removal programme and an increasing lion population appeared to have inhibited the rate of increase of the warthog population. Findings are related to suggested management of the warthog population.

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her dedication and unselfish involvement made an invaluable contribution to this study and I owe her eternal gratitude. My appreciation is expressed to Dr. J. Labuschagne of the Animal and Dairy Science Research Institute, Irene, for analysis of warthog milk samples; Ms. E. van der Hoven of the Veterinary Research Institute, Onderstepoort, for identifying internal parasites; Dr. J.A. Ledger who arranged for external parasites to be identified at the South African Institute for Medical Research, Johannesburg; Mr. P. du Toit of the Botanical Research Institute, Pretoria, for plant identifications; Mr. J.V. Ludbrook of the Natal Parks Board for assistance with the analysis of warthog bone marrow samples; and Mr. P.F. Retief of the National Parks Board for advice on statistical analyses. Dr. D.H.M. Cumming of the Department of National Parks and Wildlife Management, Zimbabwe, kindly contributed known-age warthog teeth.

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Finally, I acknowledge my own foolhardy courage for continuing this enterprise while paying a brutal price in stress, and I acknowledge Carolyn, who suffered greatly but succeeded in alleviating the burden and in typing the rough manuscript. I extend my heartfelt gratitude to her and to my parents, and I wish warthogs well.

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CHAPTER 1

GENERAL INTRODUCTION

INTRODUCTION

Warthogs, *Phacochoerus aethiopicus*, have a wide geographical range throughout the African savanna biome and, with their prolific reproductive propensity, are a potential source of red meat. They are also important both as hosts for African swine fever virus and tsetse flies (*Glossina* spp.), the vectors of trypanosomiasis. Thomson, Gainaru & van Dellen (1980) point out that African swine fever is "probably the most serious disease confronting the pig-producing areas of the world" although the conditions of transmission to domestic pigs are not clearly understood. A better understanding of the biology, ecology and behaviour of warthogs is therefore important for their management and utilisation.

Overgrazing by ungulates in the Hluhluwe-Corridor-Umfolozi Game Reserve complex resulted in the Natal Parks Board instituting a programme of population control, which provided an opportunity for collecting data on warthogs. Observations in the field provided complementary information on warthog behaviour and population ecology. Fieldwork commenced in May 1973 and terminated in June 1975.

STUDY METHODS

COLLECTION OF POST-MORTEM MATERIAL

Most warthogs were shot in the Umfolozi and Hluhluwe Game Reserves, which together with the intervening state land known as the Corridor form a single unit (hereafter referred to as the Complex.) A small sample was collected over a limited period in Mkuzi Game Reserve. Although it is possible that major rivers might delimit fairly discrete sub-populations of warthogs within the Complex, there are no other barriers preventing movements of game populations between the Hluhluwe, Corridor and Umfolozi sections. Thus, for the purposes of this study, the sample of warthogs from the Complex is considered to represent a single population.

The monthly distribution of post-mortem material collected was not evenly spread regarding sample size and sex and age composition, nor was it a random sample. For purposes of comparison between different classes of animals, it has been assumed that the frequency of occurrence of a particular characteristic within the sample reflects its distribution within the population. The methods used for the various investigations are described in the appropriate chapters.

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FIELD OBSERVATIONS

In between collection of material from cropping, surveys were made every month, using a motor vehicle and on foot, to examine warthog population structure and aspects of their ecology and behaviour. Because the author resided in Hluhluwe Game Reserve (HGR) during the first year of the study, field observations were concentrated here. The base was subsequently resited in Umfolozi Game Reserve (UGR), where the vegetation is generally more open and observation of live warthogs proved easier, from May 1974 until the end of the study in June 1975.

With certain exceptions such as during game capture operations, driving off roads and tracks in the Complex is generally not permitted, to prevent damage to the vegetation. Subject to this limitation, and although some areas were necessarily traversed more frequently, it was attempted to make field observations throughout the Complex, in order to study the warthog population over its entire range. Warthogs were classified every month according to sex and age on a random basis for as many individuals as possible. However, time taken up by post-mortem work, and the size of the area (897,3 km^2), permitted only portions of the Complex to be surveyed each month. Moreover, particular individuals or groups were sometimes observed for periods of several hours, to record behaviour. In addition, some time was spent classifying warthogs at waterholes during the dry season to examine their population sex and age structure.

Except for certain areas, warthogs often reacted uneasily to the presence of a vehicle, and departed, which did not facilitate observation in the predominantly wooded habitat. Warthogs usually fled when they detected the presence of an observer on foot. Information was recorded by notebook and included the general location of the warthogs (according to a 1:50 000 topographic map), their sex and age categories, activities in relation to time of day and weather, and interactions between animals. Observations were made using Pentax 7x35 binoculars and supplemented by still photography with a Pentax Spotmatic camera and a 135 mm or 400 mm lens. A telescope proved useful for long distance observation from a vehicle.

STUDY AREA

LOCATION

The Hluhluwe-Corridor-Umfolozi Game Reserve complex is located between latitudes 28° 0'S and 28° 6'S and longitudes 31° 42'E and 32° 9'E, in the Zululand region of the province of Natal, Republic of South Africa (Figs. 1 & 2). The Corridor comprises 189,1 km^2 of state land north of the Black Umfolozi River, bordered on the north-east by Hluhluwe Game Reserve (230,7 km^2) and on the south-west by Umfolozi Game Reserve (477,5 km^2). Passing through the Corridor from south-east to north-west is the main road from Mtubatuba to Hlabisa and Nongoma.

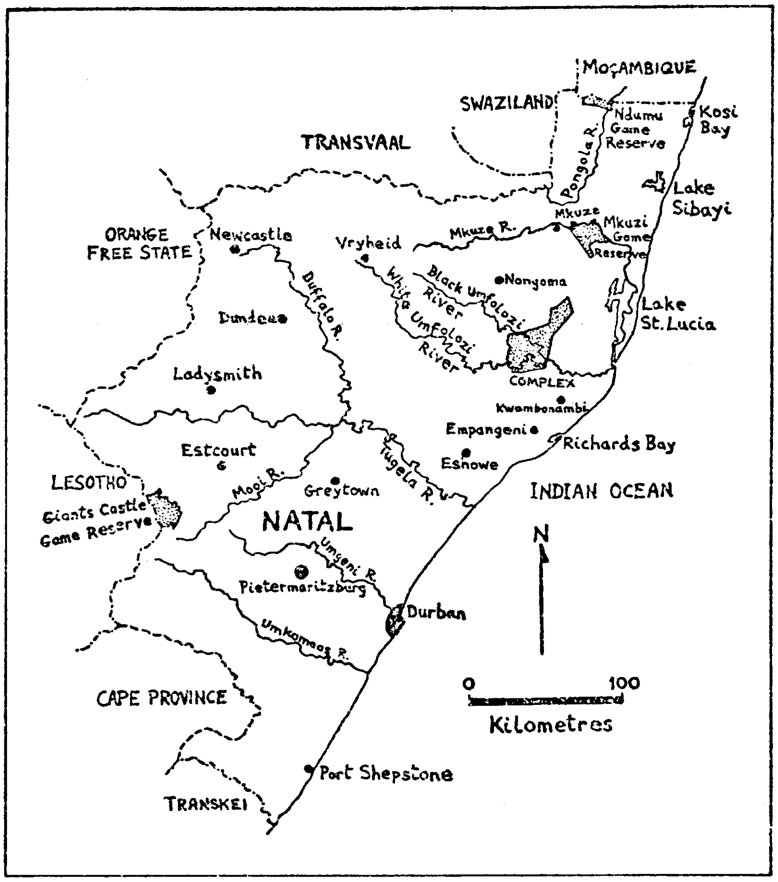

FIG. 1. Location of the Hluhluwe-Corridor-Umfolozi Game Reserve complex and Mkuzi Game Reserve in the province of Natal, Republic of South Africa.

Although the Corridor does not have legal status as a game reserve, no hunting or settlement is allowed here and the area is patrolled and managed like the rest of the Complex by the Natal Parks Board. There are no fences separating the Corridor from the Hluhluwe and Umfolozi sections, so that as far as the wildlife populations are concerned the Complex forms a single unit. A game-proof perimeter fence separates the Complex from the densely settled, surrounding country where the Zulu people carry out traditional pastoralism and cultivation.

Post-mortem material from 27 warthogs shot during July, August and September of 1973 was collected during cropping operations in Mkuzi Game Reserve (MGR), and has some value for comparison with material from the Complex. Some sample classifications of warthog population composition were also undertaken at waterholes in MGR during this same period.

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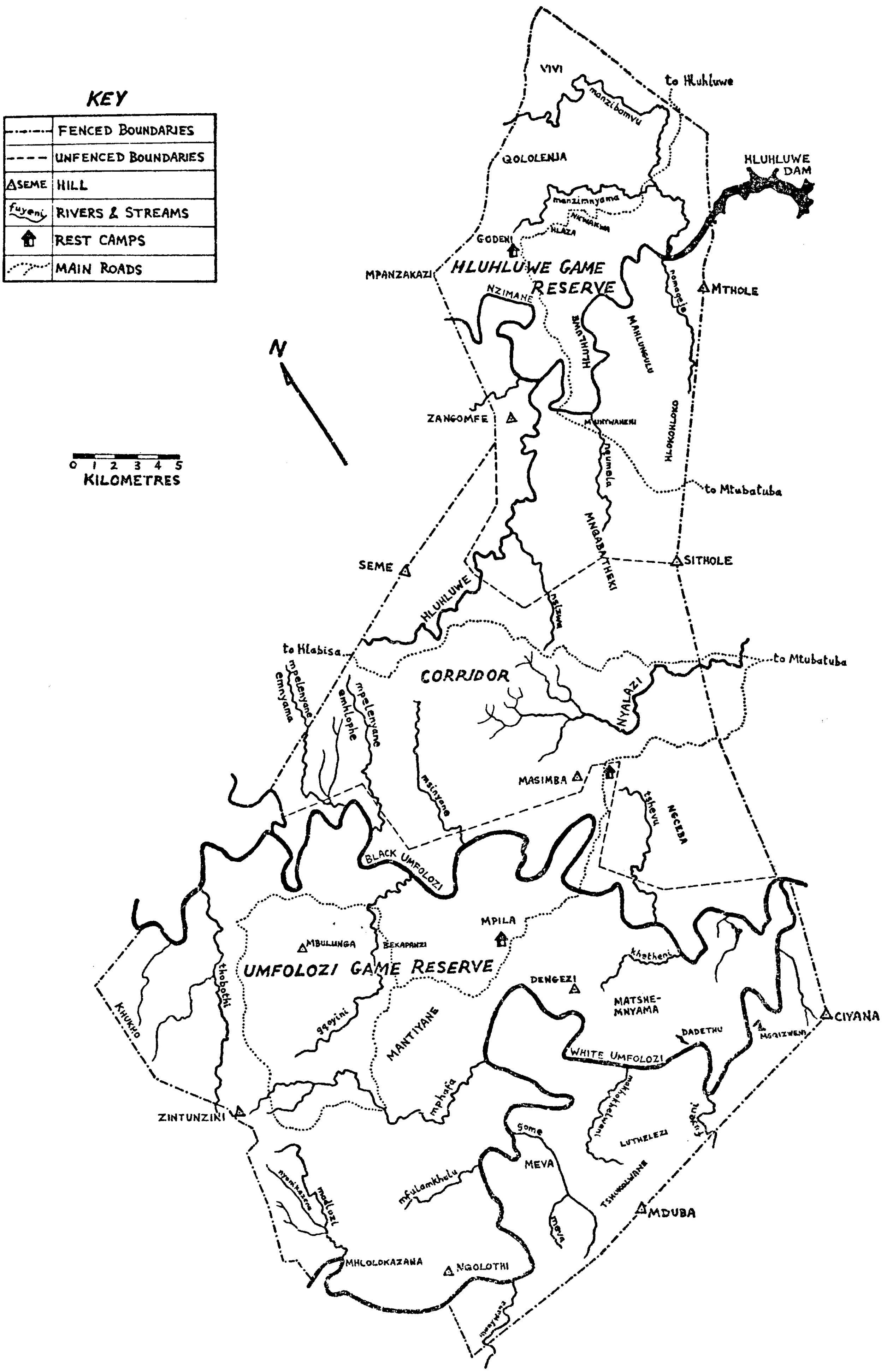

FIG. 2. Map of the Hluhluwe-Corridor-Umfolozi Game Reserve complex showing the main topographical features.

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Mkuzi Game Reserve is some 30 km north-east of the Complex (Fig. 1) and covers approximately 243 km^2, although a further 80 km^2 of adjoining state land known as Nxwala Estates are available to the Reserve's animals. Although climatically similar to the Complex, MGR is a generally drier locality with little permanent surface water. The terrain is comparatively flat except along the eastern foothills of the Lebombo mountain range, where the vegetation is predominantly *Combretum apiculatum* open woodland. The remainder of the Reserve is largely wooded with *Acacia* spp. dominant. Features of the vegetation were outlined by Moll (1968), and the mammal fauna, which is very similar to that of the Complex except for the absence of lions (*Panthera leo*), waterbuck (*Kobus ellipsiprymnus*) and buffalo (*Syncerus caffer*), has been described by Dixon (1964).

CLIMATE

The prevailing climatic regime of the Complex comprises moist hot summers extending from October to March inclusive and mild dry winters from April to September. Summer temperatures commonly exceed 35^{0} C, especially in the low-lying valleys. During winter, days are characteristically clear and sunny but nights are generally cold. Temperature inversion associated with cold air drainage into the valleys is common on winter nights, resulting in radiation fog which persists as valley mist during the early morning. Heavy dews are deposited mainly during autumn and winter, but frost rarely occurs.

The prevailing fine weather breeze is northerly, but intermittently during August and September warm, dry winds blow strongly from the north, usually or west. However, winds approaching gale force very rarely occur. Rain-bearing winds are mainly from the south and south-west. The rains normally commence in September or October, and during the spring are mainly soft and spread over several consecutive days. Mists occur frequently on the higher hills during periods of light rain. Heavy afternoon thunderstorms are usual during late summer (January to March), but hailstorms are infrequent.

Rainfall patterns vary considerably from year to year, but records from two stations within the Complex show that UGR is drier than the northern section of HGR (Figs. 3 & 4). The mean annual rainfall recorded over a period of 44 years (1932 - 1975) at Godeni Camp (altitude 457 m a.s.l.) in HGR was 953,6 mm. At Mpila Camp (altitude 290 m a.s.l.) in UGR, the mean annual rainfall measured over a 17 year period (1959 - 1975) was 694,7 mm. Comparing mean monthly rainfall between the HGR and UGR stations, the higher average in UGR for July arises from a most exceptional rainfall of 325,2 mm during July 1963, including a deluge of 281,5 mm on 73-07-04.

During 1973 and 1975, rainfall at Godeni Camp was above average by 179,9 mm and 376,0 mm respectively, while the 1974 rainfall was 199,2 mm below

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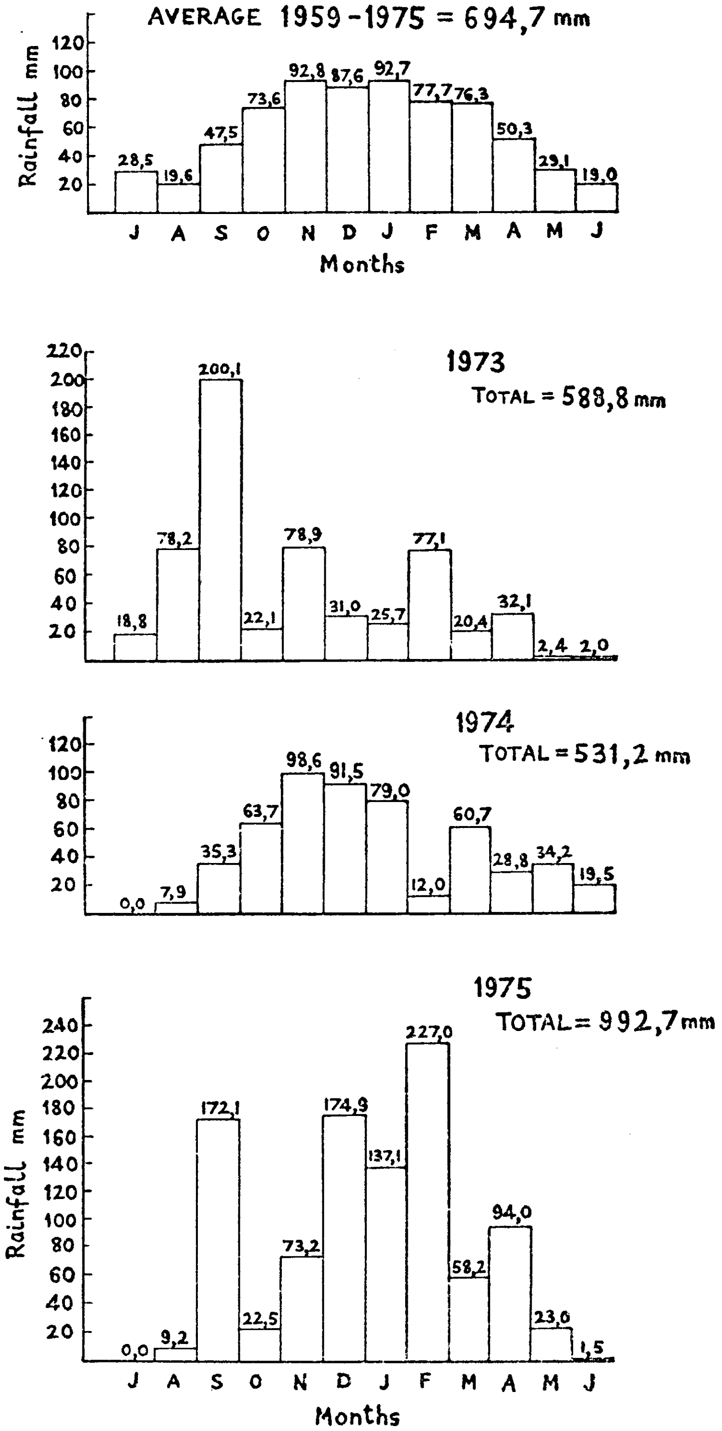

FIG. 3. Rainfall patterns at Mpila Camp (altitude 290 m a.s.l.), Umfolozi Game Reserve (data from Natal Parks Board records).

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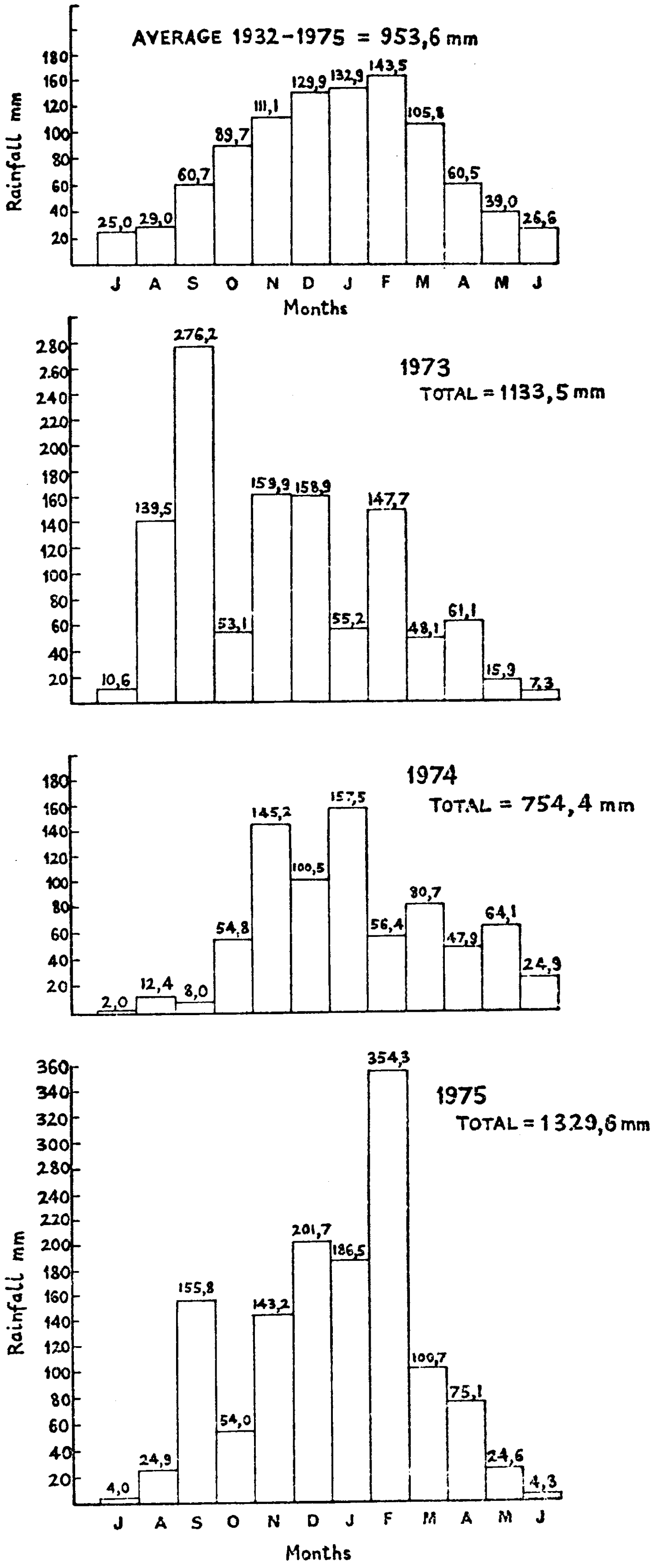

FIG. 4. Rainfall patterns at Godeni Camp (altitude 457 m a.s.l.), Hluhluwe Game Reserve (data from Natal Parks Board records).

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average. Rainfall at Mpila Camp during 1973 and 1974 was respectively 105,9 mm and 163,5 mm below average, but 298,0 mm above average during 1975. Judging by evidence of a succession of above and below average rainfall cycles at intervals of about 10 years in the summer rainfall region of South Africa (Dyer 1975, 1976, Tyson & Dyer 1978, Gertenbach 1980), the study period apparently corresponded with a wet phase in Zululand. Cyclical rainfall patterns will influence environmental conditions and so may be correlated with natural fluctuations in wild animal populations.

Temperatures and relative humidities recorded at Godeni Camp during 1974 and 1975 are depicted in Figs. 5 & 6. During 1974, the maximum daily temperature recorded at Mpila Camp was 40,6° C and the minimum temperature 6,7° C. Temperatures recorded at Mpila Camp from April 1960 to March 1963 and from September 1966 to September 1970 ranged from 6,7° C to 43,3° C, and mean monthly temperatures varied from 19,3° C to 27,2° C; the mean daily maximum temperatures for July and January were 25,3° C and 32,6° C respectively, compared with corresponding mean daily minima of 13,2° C and 21,8° C (Downing 1972). Absolute temperature ranges at Mpila and Godeni Camps appear very similar, but these represent hill locations, and greater temperature extremes have been found at lower altitudes. Downing (op. cit.) reports that maximum temperatures at Thobothi (approximately 183m a.s.l.), in the western section of UGR, were usually about 3° C higher than those at Mpila Camp (290m a.s.l.), and minima about 3° C lower.

GEOLOGY AND SOILS

The major geological strata underlying UGR are Ecca sandstones and shales. Sandstones, shales and mudstones of the Stormberg series occur in the eastern section of UGR, while in limited areas, e.g. on the western slopes of the Madlozi Valley, Dwyka tillite occurs near the surface. Dolerite intrusions through the sedimentary strata are numerous, outcropping as localised dykes which have an almost ubiquitous distribution in UGR, and fairly extensive sills. There are also localised exposures of Table Mountain sandstone, notably the scarp above the White Umfolozi river in the Mhlolokazana area. The basic geology of UGR has been mapped by Downing (1972). In HGR and the Corridor Table Mountain sandstone, and in some localities basement granite, are commonly found at or near surface level (Owen-Smith 1973).

Downing (1972) has classified the soils of UGR into upland, bottomland or riverine associations, according to their topographic situation. Upland soils are derived *in situ* from the underlying parent rock, and are usually stony, shallow (less than 50 cm deep) and leached, with a low moisture storage capacity. Transported soils of bottomlands, where water run-off drains away slowly or tends to accumulate, have good fertility and depth; their "B" horizons

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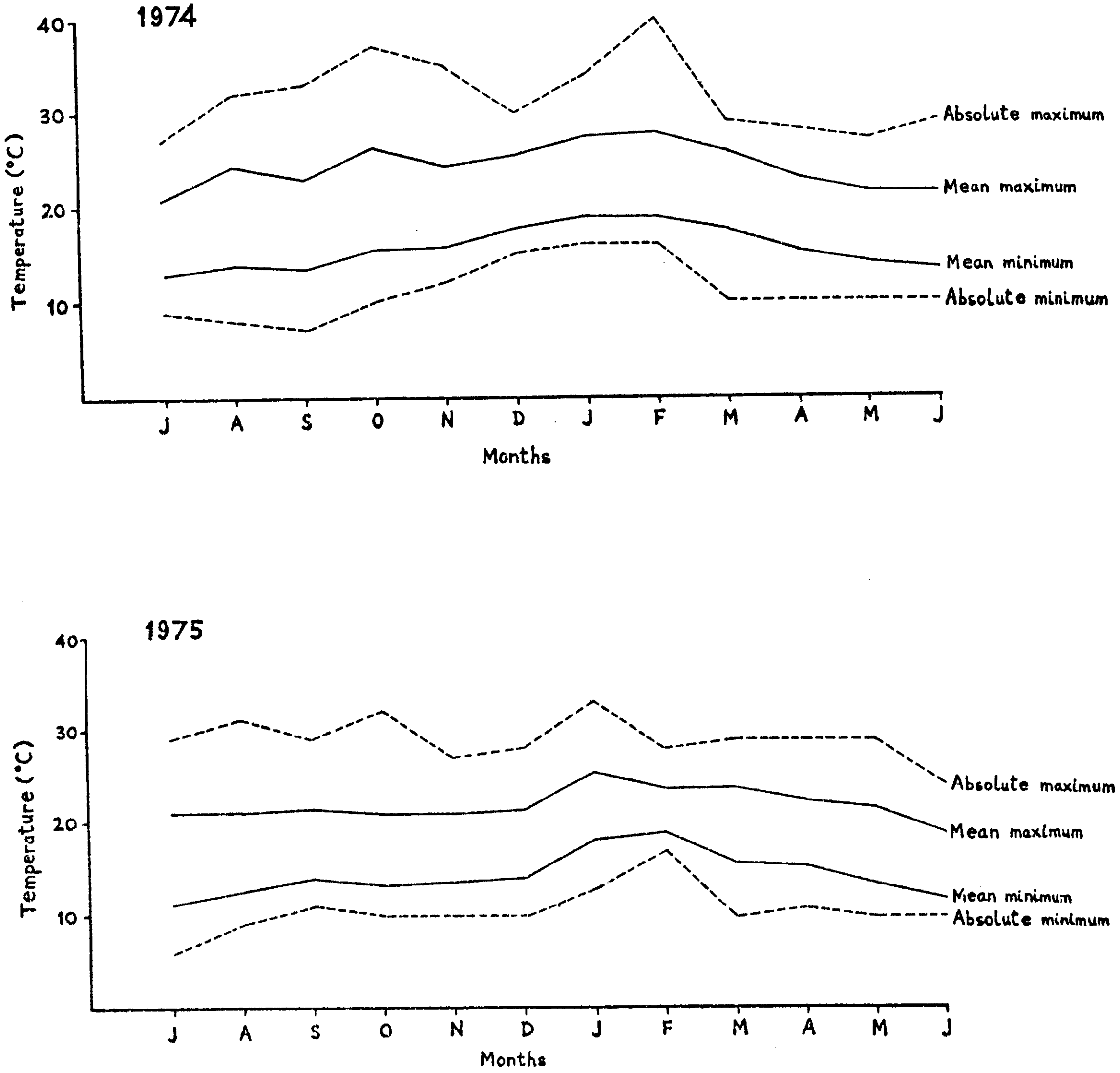

FIG. 5. Air temperatures recorded at Godeni Camp (altitude 457 m a.s.l.), Hluhluwe Game Reserve, during 1974 and 1975 (data from Natal Parks Board records).

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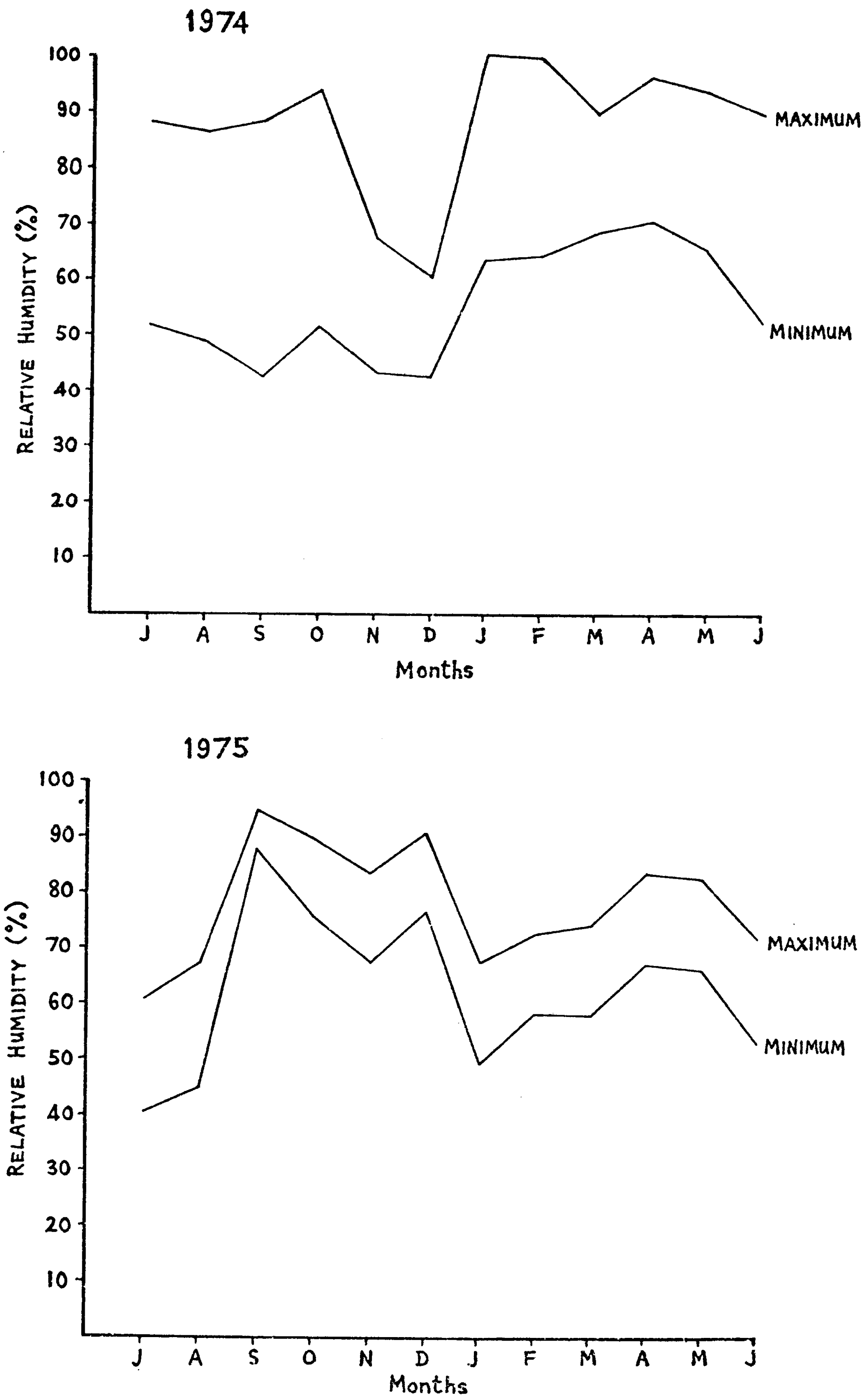

FIG. 6. Relative humidities recorded at Godeni Camp (altitude 457 m a.s.l.), Hluhluwe Game Reserve, during 1974 and 1975 (data from Natal Parks Board records).

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have a high content of carbonate salts (often precipitated as numerous small nodules), but are normally hard and rarely penetrated by plant roots. The riverine soil association comprises unconsolidated alluvia up to at least 5 m deep, deposited most extensively (as fine sand and silt) in the beds and along the banks of the White and Black Umfolozi rivers, and providing moisture to riverine vegetation throughout the year or for a large part of the dry season. A coarser alluvium is found in parts of the beds of streams.

Termitaria, which in the Complex usually occur as low mounds, also have an important influence on soil formation, and Owen-Smith (1973) points out that "a large proportion of the soil surface on ridgecrests may be underlaid by active or abandoned termite workings, resulting in a hard, relatively impervious surface layer."

Many of the soil series occurring in UGR are also found in the Corridor or in HGR, where they can similarly be correlated with topographic situation. In the north of HGR, well-developed, fertile red-brown soils occur on some hill-tops and ridges covered by forest and areas of open grassland.

TOPOGRAPHY AND WATER RESOURCES

The Complex occupies the foothills of the first escarpment rising from the coastal plain (Bourquin, Vincent & Hitchins 1971). The major portion of UGR comprises a wedge-shaped watershed between the White and Black Umfolozi rivers, which leave the reserve at their confluence in the east where the altitude is only about 60m a.s.l. - the lowest point in the Complex. The highest point in UGR is at Zintunzini (579m a.s.l.) on the western boundary, about 26 km from the confluence (Fig. 2). Topography in UGR is predominantly undulating with localised higher hills or hill systems, including Mpila (344 m), the summit of which overlooks the rest camp of this name. The Corridor is mostly hilly with broadly rolling slopes, and Seme Hill (586 m) on the north-western boundary is the highest in the Complex. Similar hilly terrain continues into HGR, becoming particularly rugged in the north, where elevations range from about 90 m in the eastern Hluhluwe River valley to 539 m on Mpanzakazi Hill in the north-west. Numerous drainage lines incise the topography of the Complex and flat areas are largely confined to valley bottoms and alluvial terraces along the rivers and larger streams.

In UGR, surface water is widely available during the wet season, but in the dry season is confined mainly to the Black and White Umfolozi rivers, plus a few springs, pools and pans. The perennial Black Umfolozi River is the most reliable water source in UGR, but has been adversely affected by deteriorating soil erosion conditions in the catchment outside the reserve, so that violent summer floods now contrast markedly with a reduced winter flow. Unlike the White Umfolozi River, the Black Umfolozi river has numerous rocky outcrops and more, deeper pools and muddy substrates. However, the bed of the Black Umfolozi became extensively silted and was considerably widened following very severe, unseasonal floods during July 1963, when this river rose more than 16 m above its bed, and many of the large Ficus sycomorus trees lining its banks were swept away (Vincent 1970, Downing 1972). Subsequently, average flow was considerably shallower and slower than in the past (Vincent op. cit.), and the river became easily fordable by animals for a much longer period of the year, a factor of significance to animal movements between the Corridor and UGR. During the winter of 1970, surface flow ceased for the first time on record (Owen-Smith 1973).

Surface flow by the White Umfolozi River formerly persisted through most winters in the form of a clear, shallow, meandering stream with a wide, sandy bed. Nowadays only scattered pools remain along its course during the dry season, although sub-surface water can usually be found at a depth of about one metre. Warthogs may excavate hollows in the riverbed and so make water available to themselves and other animals. During the wet season, the White Umfolozi normally flows less than one metre deep, but floods rapidly with brown, silt-laden water after heavy rain. At such times, overflow from the White Umfolozi River may fill two small semi-permanent pans at Dadethu and Mgqizweni in the south-east of UGR. Other watercourses in UGR are tributaries of either the Black or White Umfolozi Rivers and only carry flowing water for a few hours, or at most a few days, after heavy rain.

In the Corridor, water is available during the dry season from the perennial Hluhluwe River which crosses the northern section before entering HGR. The Nyalazi River originates in the Corridor but flows only after heavy rain, although some pools generally persist through the dry season in the Nyalazi headwaters, including the Mcumane, Gobhe and Phondo tributary streams. Dry season water is also normally available from pools in the Mpelenyane emnyama and Mpelenyane emhlophe streams in the western corner of the Corridor. However, water appears to be absent or scarce on the higher terrain of the Corridor during the dry season, which may restrict utilisation of these areas by grazing animals. In HGR, the Hluhluwe River and its tributary, the Nzimane Stream, are perennial. The Manzibomvu Stream, also a tributary of the Hluhluwe River, retains water during the dry season in pools scattered along much of its course across the north-east of HGR. During the dry season, much of the channel of the Hluhluwe River comprises a chain of moderately deep, elongated pools, interrupted by rocky bed or sandbanks.

Apart from persistent pools in some seasonal watercourses, e.g. Mphafa, numerous pans (depressions enlarged by animals) scattered through most of the Complex carry water for varying periods into the dry season. Weak perennial springs also occur at several sites, e.g. in the Nyonikazana Stream, a tributary of the Madlozi Stream. At Bekapanzi and Munywaneni observation hides in UGR and HGR respectively, waterholes are artificially maintained during the dry season. Owen-Smith (1973) points out that no part of UGR is more than eight kilometres from one of the two Umfolozi rivers. A similar maximum distance from the nearest dry season water source is also applicable to all points within the Corridor and HGR.

VEGETATION

The Complex lies within the region classified by Acocks (1975) as "tropical lowveld savanna" and "Zululand thornveld," between which there is no clear-cut boundary. The area is floristically rich and Porter (1975) notes that 426 species belonging to 80 families have been recorded in UGR. Many more species could be added to this list if the vegetation communities of the Corridor and HGR were included.

Umfolozi Game Reserve

Downing (1972) has described and mapped the vegetation of UGR, and distinguished nine woody communities, designated by their characteristic tree species:-

(1) Acacia caffra community: occurs as a generally open savanna on shallow, stony soils of hill slopes in upland areas (rarely below 300 m a.s.l.). A. nilotica, A. karroo, A. gerrardii, A. tortilis, Ziziphus mucronata, Dombeya rotundifolia, Sclerocarya caffra, Maytenus heterophylla, Ozoroa paniculosa and Rhus pentheri also occur.

(2) Acacia tortilis community: forms an open savanna usually on ridgecrests with shallow, well-drained soils. Other common trees include A. karroo, A. gerrardii, Ziziphus mucronata and Sclerocarya caffra.

(3) Acacia nigrescens community: characteristic of red-brown clay soils derived from dolerite, very rarely above 145 m a.s.l., and forms an open woodland in which shrubs of the genus Grewia are typical.

(4) Acacia burkei community: grows as an open woodland on sandy soils overlying sandstone, usually in localised areas on ridgecrests. Peltophorum africanum and Strychnos spp. are characteristically present, while other trees also occur.

(5) Combretum apiculatum community: a straggly open woodland associated with sandstone terraces; several other common tree and shrub species also occur, including Spirostachys africana along streambanks.

(6) Acacia nilotica community: forms extensive stands of variable density on deeper soils overlying shales, generally at low and intermediate elevations. Other tree and shrub species commonly occurring include A. tortilis, A. gerrardii, A. senegal, Ziziphus mucronata, Dichrostachys cinerea, Maytenus senegalensis and Euclea schimperi.

(7) *Acacia grandicornuta* community: forms a closed woodland on deep soils of low-lying alluvial terraces; associated trees and shrubs include *Spirostachys africana*, *Pappea capensis*, *A. tortilis*, *Schotia capitata*, *Euclea undulata*, *Maytenus senegalensis* and *Ziziphus mucronata*.

(8) *Spirostachys africana* community: grows as closed woodland flanking watercourses where associated tree species include *Pappea capensis*, *Schotia brachypetala*, *Olea africana*, *Sideroxylon inerme* and *Mimusops africana*; a variety of shrubs occur, of which *Euclea schimperi* and *Maytenus senegalensis* are most common.

(9) *Acacia robusta* community: grows on loose alluvial sands overlying a high water table, and is commonly associated with *Ficus sycomorus*, *Spirostachys africana*, *Schotia brachypetala* and *A. tortilis*, forming riverine woodland; the palm *Phoenix reclinata* is sometimes present.

Thicket vegetation, ranging from small patches to extensive stands, occurs or has developed where fire has been precluded, e.g. on steep, rocky slopes and on termitaria, and particularly in bottomland areas subjected to prolonged, heavy grazing as a consequence of their high soil fertility.

Downing (1972) described nine grass communities in UGR, each distinguished by one or two dominant grasses, and noted some of their physical characteristics (Table 1). The *Themeda-Aristida* community has a patchy ground layer and is characteristic on sandy soils in *Acacia burkei* woodland. The *Trichoneura* community is confined to small areas of sandy soil and common grasses include *Trichoneura grandiglumis*, *Eragrostis* spp., *Aristida congesta*, *Pogonarthria squarrosa* and *Sporobolus pyramidalis*. The *Cynodon* community occurs extensively on loose riverine sands where it forms a lawn-like cover, with *Cynodon dactylon* dominant in open and less shaded parts but succeeded by *Panicum maximum* in more shaded sites where the grasses have been invaded by woody plants; other common grasses include *Urochloa mosambicensis*, *Dactyloctenium giganteum* and *Sporobolus pyramidalis*.

The first six communities listed in Table 1 occur on clay soils and are the most extensive, but represent a retrogressive series characterised by increasing forb cover and decreasing grass canopy cover and height in relation to increasing grazing pressure (Downing 1972, 1974). Open, relatively tall and dense grassland dominated by *Themeda triandra* occurs on the upper slopes and crests of the higher hills and ridges, where periodic fires have limited the number of woody plants. Various trees and shrubs may invade this open grassland, resulting in open woodland usually dominated by either *Acacia caffra*, *A. tortilis* or *Combretum apiculatum*. Associated grasses common in the *Themeda* community include *Cymbopogon* spp., *Digitaria macroglossa*, *Panicum deustum*, *Diheteropogon amplectens*, *Setaria woodii* and *Eustachys paspaloides*. In the

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TABLE 1. Grass communities in Umfolozi Game Reserve and some of their physical characteristics, recorded towards the end of the growing season (March) when the grasses have attained maximum development (from Downing 1972).

Community	Mean grass height (cm)	Mean grass cover (%)	Mean forb cover (%)	Mean grazing utilization (%)*
Themeda	78	59	2	13
Themeda-Panicum	59	39	3	30
Themeda-Urochloa	45	27	7	45
Panicum coloratum	24	16	25	80
Panicum maximum	50	10	30	47
Bothriochloa	60	34	18	32
Themeda-Aristida	40	18	9	35
Trichoneura	84	28	4	18
Cynodon	59	21	11	55

* Crudely estimated from the degree of defoliation.

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Themeda-Panicum community, Themeda triandra is invariably associated with Panicum coloratum, and other common grasses include Cymbopogon spp., Digitaria macroglossa, Panicum deustum, P. maximum, Eustachys paspaloides and Eragrostis capensis. The grass layer under Acacia nigrescens open woodland is often of the Themeda-Urochloa community, extensive areas of which are generally closely cropped; grasses commonly associated with the dominant Themeda triandra and Urochloa mosambicensis are Cymbopogon spp., Panicum coloratum, P. maximum, Digitaria spp. and Eragrostis spp.

The lightly to moderately grazed Themeda, Themeda-Panicum and Themeda-Urochloa communities grow mostly on leached upland soils, often of the Mispah series, and are utilised mainly by zebra and buffalo. However, most of the biomass of grazing ungulates is concentrated year-round on the fertile bottomland soils, where the Panicum coloratum and P. maximum communities are so heavily grazed that they have the sparsest grass cover in UGR. When grazing usage exceeds 50%, the consequent elimination of fire from these pastures (which are mainly associated with the closed woodland communities) encourages the establishment of numerous woody seedlings and so promotes thicket development. Although tufts of palatable grasses such as Panicum maximum and P. deustum may survive under bushes where they are protected from grazing animals, their elimination in the intervening open areas exposes the soil surface and leads to accelerated erosion, or gives rise to a proliferation of forbs and unpalatable grasses such as Bothriochloa insculpta, which typifies the most retrograde grass community stage (Downing 1972, 1974).

Stoloniferous or short tufted grasses predominate in the Panicum coloratum community and include Panicum coloratum, Urochloa mosambicensis, Sporobolus nitens, S. smutsii, Digitaria argyrograpta and Tragus berteronianus. Common grasses of the Panicum maximum community include Panicum maximum (which becomes dominant under protective bushes), P. deustum, Urochloa mosambicensis, Enteropogon monostachyos, Sporobolus smutsii and Tragus berteronianus, and the sparse grass cover is associated with many forbs.

At some point in the retrogressive succession between the Themeda-Urochloa and Panicum coloratum community stages, Themeda triandra is eliminated from the pasture, and Downing (1972, 1974) recommends that for management purposes the veld should not be grazed beyond a stage characterised by a Themeda-Urochloa community. Within the underutilised upland areas and extending to the over-utilised bottomlands, a grazing mosaic is developed to varying degrees, and the short grazed lawns that occur even in areas of predominantly tall grassland are important to warthogs, which generally live in restricted home ranges.

The Corridor

The crowns of several of the larger hills are covered by open *Themeda triandra* - dominated grassland, often intergrading on the lower slopes with wooded grassland containing various densities of woody saplings above the average grass height at the end of the growing season. Large areas of former grassland at intermediate elevations have been invaded by *Dichrostachys cinerea*-*Acacia karroo* thicket and *Acacia karroo* thicket, due to overgrazing and the concomitant limitation of fires, as outlined by Deane (1966).

Small patches of moist, semi-deciduous forest and scrub forest occur on the wetter south aspects of some high hills, e.g. Seme, and also extend along the upper reaches of watercourses in some of the narrow valleys. At lower altitudes, narrow avenues of dense riparian woodland and forest, characterised by either *Spirostachys africana* and *Euclea schimperi* or *Acacia robusta* and *Ficus sycomorus*, occur along the larger watercourses. Other important communities in the Corridor include *Acacia caffra* thicket, *Acacia burkei* woodland and *Acacia nilotica* woodland. The vegetation of the northern Corridor (north of the Mtubatuba-Hlabisa road) was mapped by Whateley in 1975.

Hluhluwe Game Reserve

As mapped by Whateley in 1975, the vegetation of HGR comprises 16 plant communities characterised by physiognomy and dominant species:-

(1) *Celtis africana*-*Harpephyllum caffrum* forest
(2) *Celtis africana*-*Euclea schimperi* forest
(3) *Acacia robusta*-*Ficus sycomorus* riverine forest
(4) *Spirostachys africana*-*Euclea schimperi* riverine forest
(5) *Spirostachys africana* woodland
(6) *Combretum molle* woodland
(7) *Acacia burkei* woodland
(8) *Acacia nilotica* woodland
(9) *Acacia karroo* woodland
(10) *Euclea divinorum* thicket
(11) *Acacia karroo* thicket
(12) *Acacia caffra* thicket
(13) *Acacia davyi* thicket
(14) *Dichrostachys cinerea*-*Acacia karroo* thicket (induced)
(15) *Panicum maximum*-*Cyperus textilis* grassland
(16) *Themeda triandra* grassland

Moist, semi-deciduous forests dominate the higher hills of north-western HGR, particularly on the wetter, south facing slopes, and Whateley (1975) notes that *Euclea schimperi* and *Berchemia zeyheri*, which are characteristic species in forest patches below about 300 m a.s.l., are absent in the higher altitude Celtis africana-Harpephyllum caffrum forest. Grass cover on the forest floor is generally absent or scant.

Open Themeda triandra grassland, where woody plants are rare, has a scattered distribution on the higher hill-tops and ridges, while Panicum maximum-Cyperus textilis grassland occurs mainly as a 100-200 m wide belt along the floodplain of the Manzibomvu Stream and in the Mzini valley, in the north-eastern part of HGR. Fairly extensive patches of rather straggly Acacia karroo woodland occur in north-eastern HGR, whereas Acacia karroo and Dichrostachys cinerea-Acacia karroo thickets, mostly with a moderately tall, tufted grass sward, are extensive and widespread throughout the reserve. Some areas of short Acacia karroo thicket have the appearance of grassland. Acacia davyi thicket has been found in only one restricted locality in the Nzimane valley.

Acacia woodlands similar to those occurring in UGR cover large expanses in the lower-lying south-western region of HGR. At low elevations in the Hluhluwe River basin, extensive tracts of Euclea divinorum thicket occur on sodic soils, often abutting the riverine forest belts. Whateley (1975) found that the Spirostachys africana-Euclea schimperi riverine forest community is floristically very rich, and he identified 74 species in 10 transects.

The species composition of the grass cover in the Acacia nilotica, A. burkei and Spirostachys africana woodland areas, as well as the Themeda triandra grassland, appears similar in both HGR and UGR. Grazing pressure in HGR is also unevenly distributed on an altitudinal basis, but particularly in the northern areas short grass lawns appear more localised than in UGR, and include patches of Dactyloctenium australe in some shaded sites. Grassland on hillslopes of northern HGR mostly comprises a mixture of predominantly coarse grass species, invaded in some localities by Acacia karroo. Hitchins (1976) reports changes in the equilibrium between grasses and woody plants, reflecting the influence of grazing and fire factors. However, fluctuations in vegetation conditions and herbivore populations in the Complex in relation to rainfall cycles remain to be adequately documented and demonstrated.

Hitchins (1976) recorded a marked decline in the black rhino population of HGR between 1961 and 1972, which he associated with habitat changes "brought about by the removal of large numbers of predominantly grazing animals (wildebeest, zebra, warthog, impala and nyala) between 1954 and 1972, involving some 33 115 animals." The improved grass cover arising from the reduced biomass of grazers resulted in fires that reduced the extent and density of Acacia thickets and other woody vegetation on which black rhinos are dependent for food; relatively open wooded grassland, which could support 25% fewer black rhinos than the thicket type vegetation, increased concomitantly.

Upon comparing the vegetation communities in HGR during 1974 with those mapped by Henkel (1937), Downing (1980) found an 8% decrease in the extent of grassland. However, the total area of "grassland" as measured by Downing (op. cit.) includes the Dichrostachys cinerea-Acacia karroo lowland shrub association mapped by Henkel (1937) with the Acacia wooded grassland, Sclerocarya caffra open woodland and Themeda triandra grassland of highland regions, and the floodplain grassland of riverine areas, as mapped by Downing in 1974. Although the extent of the forests which adjoin highland grassland apparently increased by 5% between 1937 and 1974, this was partly due to the presence of a few, not previously mapped, fairly extensive stands of forest as found south of Hlaza and Nkwakwa hills. Downing (op. cit.) detected few, if any, boundary changes in lowland and riverine plant communities (including Combretum molle woodland, Acacia burkei woodland, Spirostachys africana woodland, Euclea divinorum thicket, and riverine forest), which he attributes to edaphic controlling factors that are relatively stable.

LARGE MAMMAL POPULATIONS

Records compiled by Bourquin, Vincent & Hitchins (1971), and observations during the study period, indicate that 19 species of ungulates occur in the Complex (Table 2). Numbers of certain ungulates counted in the Complex during a helicopter census (Whateley & Brooks 1974) are also given in Table 2, although several important species are almost certainly grossly under-counted. Differences in body size, behaviour, etc. affect the visibility of different species during an aerial census, so species are grouped into three categories reflecting the degree of under-counting expected. A few hippopotamuses (Hippopotamus amphibius) occur in the upper reaches of the Hluhluwe Dam in north-eastern HGR, and individuals of this species were formerly also resident in the Umfolozi rivers. Elephants (Loxodonta africana) and eland (Taurotragus oryx) have been documented as occurring in the Complex until late in the previous century (Vincent 1970).

As a consequence of the campaign to combat tsetse flies by game eradication shooting during the 1940's, populations of many large mammals in UGR (excluding the two rhinoceros species) were drastically reduced or even eliminated. No wildebeest or zebra remained, but secretive species such as duiker and bushbuck were still well represented. Tsetse flies were eventually eliminated by aerial spraying with insecticides, and during the 1950's and 1960's there was a slow but steady recolonisation movement of animals from HGR (which had been "comparatively unaffected" by the anti-tsetse fly campaign) across the Corridor into UGR (Vincent 1970, Hitchins & Vincent 1972). Owen-Smith (1973) notes that most of this dispersal of wildebeest, zebra and impala into UGR occurred during the 1960's, with the western section of UGR being colonised last.

Although 7 661 warthogs (the primary source of tsetse blood meals) were recorded shot in UGR during the 7,5 years of the 1940's campaign, evidence from

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TABLE 2. Ungulates present in the Hluhluwe-Corridor-Umfolozi Game Reserve complex during the study period, and estimates of their abundance from the 1974 helicopter counts.

Ungulate species	1974 census data				Degree of reliability*
	HGR	Corridor	UGR	Complex	
Buffalo _Syncerus caffer_	730	809	956	2495	Reliable
Giraffe _Giraffa camelopardalis_	26	10	14	50	
White rhino _Ceratotherium simum_	143	363	836	1342	
Wildebeest _Connochaetes taurinus_	559	764	1364	2687	
Zebra _Equus burchelli_	417	582	657	1656	
Impala _Aepyceros melampus_	2077	1641	1986	5704	Indicator
Kudu _Tragelaphus strepsiceros_	54	264	702	1020	
Reedbuck _Redunca arundinum_	0	9	70	79	
Mountain reedbuck _Redunca fulvorufula_	4	10	71	85	
Waterbuck _Kobus ellipsiprymnus_	13	84	527	624	
Black rhino _Diceros bicornis_	44	39	23	106	Unreliable
Bushbuck _Tragelaphus scriptus_	1	5	5	11	
Nyala _Tragelaphus angasi_	614	340	1030	1984	
Warthog _Phacochoerus aethiopicus_	352	214	941	1507	
Bushpig _Potamochoerus porcus_	0	0	5	5	
Steenbok _Raphicerus campestris_	0	0	24	24	
Klipspringer _Oreotragus oreotragus_	0	0	6	6	
Grey duiker _Sylvicapra grimmia_	4	1	7	12	
Red duiker _Cephalophus natalensis_†	0	0	0	0	

* After Whateley & Brooks (1974) : counts of five species are regarded as accurate, while counts of other species are either unreliable or give only an indication of abundance.

† Occurs mainly in forested areas.

similar game destruction campaigns in Botswana (Graham 1967, Child, Smith & von Richter 1970) and in Zambia (Wilson 1975a) suggests that the warthog population in UGR was unlikely to have been seriously depleted by the intensive hunting to which it was subjected. In this context, Child (1968) notes that the use warthogs make of dense cover and their aptitude for remaining hidden in small patches of scrub are not generally recognised, and probably aid their survival in areas where they are heavily hunted. Regardless of whether the warthog population of UGR had been greatly reduced during the anti-tsetse fly campaign, numbers of warthogs during the 1950's were such that control shooting was started in September 1959, mainly as a measure to alleviate competition for grazing with the white rhinoceros population, which enjoyed a high conservation priority.

Mentis (1970) presented estimates of the large herbivore populations which occurred in UGR prior to the shooting campaigns of 1929-1930 and 1942-1950, and pointed out marked changes in composition. Prior to 1929, zebras were the predominant ungulates, wildebeest numbers were relatively low, and impala and nyala were absent. Downing (1972) tabulated and compared the relative biomasses of grazers, mixed feeders and browsers in UGR and concluded that an almost threefold increase in total ungulate biomass had occurred between 1942 and 1972; this increase was caused chiefly by the grazers, and especially the white rhinoceros. Reedbuck numbers and biomass have declined greatly however, notably in the Corridor, which Deane (1966) attributed to a marked decrease in the extent of open, tall grassland, and concomitant scrub encroachment. In UGR, white rhinos recently comprised over half the total ungulate biomass (Owen-Smith 1973, Porter 1975). Based on an assessment of population size by the recognition of individuals, there were some 328 black rhinos in the Complex during 1972, with the majority (199) in HGR (Hitchins 1976).

Nyala are now widely distributed and abundant in the Complex, but the related bushbuck, which was formerly very numerous, appears to have declined. Of the smaller antelope, klipspringers are rare and steenbok are absent from much of HGR, although widely distributed in UGR. Antbears (Orycteropus afer) are reportedly quite common throughout the Complex (Bourquin et al. 1971) but, probably as a consequence of their nocturnal habits, personal sightings were recorded on only two occasions during the study period. Primates include baboons (Papio ursinus), vervet monkeys (Cercopithecus pygerythrus) and, in forested areas, samango monkeys (Cercopithecus albogularis).

The larger predators of the Complex are lions (Panthera leo), leopards (Panthera pardus), cheetahs (Acinonyx jubatus), spotted hyaenas (Crocuta crocuta), black-backed jackals (Canis mesomelas) and servals (Felis serval). Hyaenas are numerous, and Whateley & Brooks (1978) have estimated a hyaena density of 0,46/km^2 in north-eastern HGR. Leopards, like hyaenas, have always been present,

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but cheetahs and wild dogs (Lycaon pictus) had disappeared during the 1920's and lions by 1938. An immigrant male lion settled in UGR in 1958 (Steele 1970), and following an unofficial reintroduction of a few females in the 1960's, a viable lion population was soon re-established in the Complex. By the end of 1974, the minimum known population of lions in the Complex was 114, mostly in UGR (Anderson 1981), and some dispersion of individuals outside the reserve had become a problem, leading to regular selective culling, particularly of subadult males.

Since 1965, 64 cheetahs have been reintroduced, and although present numbers are unknown, they appear to be maintaining a viable population. Jackals are remarkably scarce in the Complex (unlike MGR where they are common), and were seldom seen or heard during the study period. Few sightings of servals are on record, and they appear to be rare.

MANAGEMENT PRACTICES

Ungulate population increase and associated habitat degradation in certain areas of the Complex has led to the development of a policy of game removal, initially by shooting but subsequently also by live capture (including a large number of white rhinos). The first culling was undertaken in HGR from 1954 onwards, and in UGR from 1959 onwards, and chiefly involved wildebeest and warthogs. Other ungulates which have been subject to control include impala, zebra, waterbuck, nyala and buffalo. Current policy is to designate removal to specific areas, based on the degree of veld deterioration. Mass removal of game has been facilitated by the Oelofse capture method (Densham 1974).

Besides the management of animal impact on the vegetation and soil by live capture and shooting, other management practices in the Complex include the use of firebreaks to control undesired burning, the use of various methods to combat soil erosion, and the burning of selected areas. According to Porter (1975), the main objectives of the currect fire policy are:

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

Since most of the short grass cover in bottomlands does not sustain a fire, rotational burning is largely confined to upland areas at intervals of two to six years, depending on the rate of litter accumulation, and generally takes place soon after the first spring rains.

Although the warthog population in the Complex is only a small component of the regional ecosystem, it represents a valuable renewable resource deserving conservation and enlightened management. The rationale for the present study was to examine warthog reproductive biology, behaviour, population ecology and dynamics to provide a sounder basis for management policy and possibly to identify some future research priorities. Post-mortem material was used mainly to investigate growth and meat production potential, to develop age criteria and to establish the reproductive potential and recruitment pattern of the warthog population. Information on warthog behaviour is important for an appreciation of their environmental requirements and constraints. Efficient management, whether for harvesting or conservation, also requires data on reproductive ecology and population structure so that culling, when necessary, preserves a well-balanced sex and age distribution for future reproduction.

CHAPTER 2

DENTITION AND AGE DETERMINATION

INTRODUCTION

Reliable estimation of age in warthogs is important for interpreting their reproductive biology, growth and population dynamics. Criteria commonly used for mammalian age determination include tooth eruption, replacement and attrition, patterns of dental cementum deposition, and various external morphological characteristics (Morris 1972). Aspects of the dentition and techniques for estimating age have been investigated in varying detail in previous studies of warthogs.

Middleton Shaw (1939) and Guiraud (1948) have described stages in the development and attrition of warthog teeth, especially the third molars, which reflect relative age. In West Africa, Bigourdan (1948) recorded dental formulae of male warthogs and estimated their chronological ages for various stages of attrition of their teeth.

Rough criteria for field age classification, based on body and tusk development, were described by Roth (1965). The pattern of tooth replacement and eruption reported in Zimbabwean warthogs (Child, Sowls & Mitchell 1965) was sufficiently distinctive to allow accurate age estimation up to two years, while the short, well defined breeding season facilitated clear distinctions in the field between three age classes (see also Cumming 1970, 1975a) based on body and tusk size. Child, Sowls & Richardson (1965) have investigated mass of oven-dried eye lenses as an indicator of age. Changes in the development of warts and tusks as a guide to field age classification were illustrated by Cumming (1970), together with a description of distinctive physical characteristics over the annual cycle.

Because warthogs in Nairobi National Park, Kenya have a distinct period of births, Bradley (1972) found that the ratios of tusk length to snout width, measured from a series of photographs, conveniently fell into four categories associated with age classes up to four years. Spinage & Jolly (1974) attempted to predict age beyond four years using an index of growth in the maxillary third molar teeth, but a lack of data from individuals of known age precluded their testing the validity of the relationship.

Besides the value of substantiating the results of studies in other geographic regions with comparative data, difficulties inherent in age estimation of warthogs from their dentition (Spinage & Jolly 1974) have emphasised the desirability of refining and possibly supplementing previously reported methods. In the present study, the availability of material from cropped specimens permitted the use of certain laboratory techniques to investigate age

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determination criteria; in addition,characteristics suitable for age classification in the field were examined.

MATERIAL AND METHODS

SOURCE OF MATERIAL

During cropping in the Hluhluwe-Corridor-Umfolozi Game Reserve complex between June 1973 and June 1975, the skulls of 381 warthogs (183 males, 198 females) were collected to investigate dentition. Several skulls from old warthogs which died from natural causes were also collected and examined. Additional material (30 skulls from cropping plus one found skull of an infant) was collected in Mkuzi Game Reserve, where vegetation and physiographic conditions are analogous to a large portion of the Complex and the climatic regime is similar.

TUSK LENGTH: SNOUT WIDTH RATIOS

Following Bradley (1968, 1972), the proportional relationship of tusk length and snout width with age was investigated for Zululand warthogs. Excluding young individuals where the upper tusks (canines) have not grown beyond the flanges of the lips, and those older individuals with portions of both tusks broken off, length of left and right maxillary canines was measured as the linear distance from the base of the tusk, where it protrudes from the lip, to the tip. Snout width between the tusks was measured as the maximum distance between the lip extremities.

Mean tusk length was calculated as a percentage of snout width, but whereever one tusk tip was broken off, the length of the undamaged tusk was used instead of the mean measurement. Tusk length: snout width ratios were calculated for 362 warthogs (187 males, 175 females) and plotted against the dates of collection to compare age-relative changes.

DENTITION CHARACTERISTICS

Numbers of deciduous and permanent teeth present were recorded on checksheets for all skulls examined, together with a description of approximate stages of eruption and attrition. The mesio-distal length of the crown (erupted portion above the gum line) was measured along the middle of the grinding surface for both upper and lower third molars on both sides.

TOOTH SECTIONS

Introduction

Since the early investigations of Laws (1952, 1953), the method of age estimation of mammals based on annulations or incremental lines in the cementum or dentine of sectioned teeth has been extensively applied and documented (e.g.

Klevezal' & Kleinenberg 1969, Morris 1972, Spinage 1973a, 1976a, b, Steenkamp 1975, Hall-Martin 1976, Smuts, Anderson & Austin 1978, Attwell 1980, Jeffery & Hanks 1981). Among African mammals, age estimation from tooth sections has been used chiefly for herbivores. However, there appear to be no published accounts of the application of this technique to warthogs.

The warthog teeth selected for study were the mandibular first permanent incisor (I_1) and the maxillary third molar (M^3); however, choice may be limited to the latter tooth by the loss with age of most or all of the antecedent teeth, except the canines. Even before the incisors are worn to small remnants or shed completely, the phenomenon of root resorption (which commences at the root apex) could render these teeth unsuitable for age estimation of old warthogs. As Spinage (1973a) has emphasised, resorption proceeds rapidly with senescence and "means that cementum line counts can only give the minimum age an old animal has reached, as an unknown number of lines are likely to have been resorbed."

Unless vestigial, I_1 was extracted from all skulls in addition to the large and complex M^3, whose morphometry has been used as an indicator of age (Spinage & Jolly 1974). In practice, the scarcity of old warthogs from cropping meant that most tooth sectioning involved I_1. Where M^3 was used, rectangular blocks of about 2 cm length and 1 cm thickness were cut from the mid-distal aspect of the tooth. Whole incisors or portions of third molars were then fixed in 10% neutral buffered formalin for at least four weeks.

Undecalcified sections

An experimental selection of formalin-fixed teeth was washed, dried and embedded in blocks of a clear polyester resin, using silicone rubber moulds. Teeth were sectioned using an Isomet low-speed saw with a diamond dusted disc blade of 0,1524 mm thickness, cooled in a water bath. Transverse and longitudinal sections 100 and 150 μm thick were cut, both from the root portions of I_1 and the distal segments of M^3, mounted in DPX, and examined with a projection microscope.

Decalcified sections

Initially, decalcification of warthog teeth was attempted using ethylene diamine tetracetic acid (disodium salt) (EDTA), which was found satisfactory for decalcifying giraffe teeth (Hall-Martin 1976). A solution of 18% EDTA at pH 7,4 was prepared by dissolving the EDTA in 0,1 M phosphate buffer and adjusting the pH with sodium hydroxide. The tooth specimens were placed in EDTA at 60^{o} C, using a volume of the order of 20 times that of the tissue, and the decalcifying fluid was renewed every five days. In the absence of an X-ray apparatus to determine the end-point of decalcification, the palpation method as described by Disbrey & Rack (1970) was used. After 3 - 5 weeks in EDTA, the teeth became soft and pliable and decalcification was considered complete. The specimens were then dehydrated, cleared and embedded in paraffin wax, prior to sectioning on a sledge microtome.

Difficulties in cutting sections as a consequence of incomplete decalcification of the innermost tissue of some tooth specimens led to subsequent abandonment of EDTA in favour of a 1:1 ^{v}/v solution of 50% formic acid and 25% sodium citrate (recommended by Nell <u>pers</u>. <u>comm</u>.). Formalin-fixed incisors, placed in this formic acid-sodium citrate solution at ambient temperature, were completely decalcified after 2 - 3 weeks. The decalcifying fluid was renewed every 2 - 3 days. Incisor teeth were either treated whole or trimmed by removal of the crown. Decalcified specimens were washed for two hours in running tap water prior to dehydration and clearing using the following schedule (Nell <u>pers</u>. <u>comm</u>.):

1.	30% alcohol		2 h
2.	50% alcohol		2 h
3.	70% alcohol		2 h
4.	Butanol I	20 ml n-butyl alcohol 50 ml 95% alcohol 30 ml distilled water	2 h
5.	Butanol II	35 ml n-butyl alcohol 50 ml 95% alcohol 15 ml distilled water	2 h
6.	Butanol III	55 ml n-butyl alcohol 45 ml 95% alcohol	2 h
7.	Butanol IV	75 ml n-butyl alcohol 25 ml 95% alcohol	2 h
8.	Butanol V	(100% n-butyl alcohol)	2 h
9.	Butanol VI	(100% n-butyl alcohol)	2 h
10.	Molten paraffin wax 52-53° C		2 h
11.	Molten paraffin wax 57-60° C		3 h

Specimens were then vacuum embedded in 57 - 60° C molten paraffin wax for 30 min. Several longitudinal sections of 6 and 10 µm thickness were cut through the sagittal plane of each tooth, using a sledge microtome. Longitudinal sections were chosen since "cementum growth is not uniform over the whole tooth root, and transverse sections may miss the zone of maximum increase in thickness" (Spinage 1976a). After mounting on labelled slides using Haupt's adhesive, sections were stained with Ehrlich's haematoxylin and aqueous eosin or Ehrlich's haematoxylin and chromotrope 2R, prior to mounting in DPX. Chromotrope 2R gave comparable results to eosin and was preferred due to the slightly shorter

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staining schedule, as given below:

1. Dewax in xylene 15 min
2. Sections to water
3. Ehrlich's haematoxylin 30 min
4. Blue in running tap water ca 8 min
5. Differentiate in acid alcohol 1 - 2 sec
6. Blue in running tap water ca 5 min
7. Rinse in distilled water 1 sec
8. Dehydrate
9. Chromotrope (saturated solution in absolute alcohol) 5 min
10. Rinse in absolute alcohol 1 sec
11. Xylene I 5 min
12. Xylene II 5 min

Counting of cementum annulations

Sections were first scanned under a binocular microscope at magnifications of x63 and x160 in order to find the best zones for reading of cementum annulations (usually the distal aspect above the root apex of incisors). Dark-staining rest lines that were clearly visible in one plane of a section were often not continuous along the length of the cementum; for example, it may be possible to count the earlier formed lines but not those of more recent origin in one region, while the remaining lines can only be discerned and counted further along the section.

Counts of the maximum number of dark-staining lines, excluding lamellae of very faint and discontinuous appearance, were routinely made under x160 magnification, but x400 magnification was sometimes used to check separation between very closely adjacent lines. The nature of the outermost layer, forking and merging of lines, and areas of discontinuity were noted.

Known-age material

Since warthogs in Zimbabwe have a definite and limited farrowing season, body development, tooth replacement and eruption, and tusk growth permit accurate age estimation up to 24 months, while growth of the third molars provides a reasonably reliable basis for further age estimation up to 36 months (Child, Sowls & Mitchell 1965). Farrowing in Zululand is virtually confined to the months of October, November and December, so that the same criteria can be used to estimate age up to three years, thereby facilitating interpretation of the early patterns of formation of cementum lamellae.

In assigning age to older warthogs by counting rest lines in the cementum of permanent teeth, reference to known-age material is essential to determine the incremental rhythm of cementum deposition. Teeth from seven known-age warthogs up to eight years old (Table 3) were available from the Sengwa Wildlife Research Area, Zimbabwe, where although the seasonal climatic regime is similar, other conditions may differ from Zululand. In addition, the skull of a yearling aged 17½ - 18½ months was obtained from the Kruger National Park.

EYE LENS MASS

To assess the possible value of eye lens mass as an index of age, the eyes of 289 warthogs were removed intact soon after death and stored in 10% formalin, after first incising the sclera to facilitate fixation of the lenses. Undamaged lenses were later removed and dried at 80°C in a forced-draught oven for 12 weeks until a constant mass had been attained. Lenses were removed from the oven in batches of four to minimise post-drying mass increases, and measured to the nearest 0,1 mg.

AGE ESTIMATION IN THE FIELD

A technique for estimating age of free-ranging warthogs is essential for the assessment of population parameters. As a consequence of the restricted birth season in Zululand, warthogs in their first and second years of life can easily be distinguished on the basis of relative body size and development of the tusks and warts. Tusk length may be used to differentiate individuals at the beginning of the 2 - 3 year age interval vis-à-vis the 3 - 4 year class, but subsequently becomes increasingly unreliable, especially in females.

Piglets from sounders for which the month of birth was known and where the mother was individually identifiable were photographed at intervals to record body, tusk and wart development for both sexes up to two years of age (using the size of the adult female as standard). Since resightings of these free-ranging warthogs were unpredictable, the photographic series involved somewhat irregular intervals. Representative measurements for individuals photographed in any month were available from cropped specimens of the same or similar age, which could be estimated to within about two months by backdating to a mean farrowing date (1 November).

The photographs depict those age classes easily recognisable in the field, with the emphasis on relative body size and tusk development, and in view of the seasonality of warthog reproduction in southern Africa, should also be applicable to other populations in this region.

RESULTS

DENTITION

Based on a sample of 29 warthog skulls with deciduous dentition, the dental formula was:

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TABLE 3. Sources of known-age warthog teeth available for investigation of the chronological pattern of cementum layering.

Age	Sex	Material	Locality	Material made available by:
17½ - 18½ months	?	Skull with dentition	Kruger National Park	B. Marshall, Natal Parks Board, S. Africa.
23 months	♂	I_1	Sengwa Wildlife Research Area	D.H.M.Cumming, Dept. of National Parks & Wildlife Management, Zimbabwe.
26 months	♀	I_1		
6 years	♀	M^3		
6 years 6 months	♀	I_1 + M^3		
6 years 6-8 months	♀	I_1		
8 years 2 months	♀	I_1 + M^3		
8 years 4-7 months	♂	I_1 + M^3		

I_1 = mandibular first permanent incisor
M^3 = maxillary third permanent molar

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$$2\left(i\,\frac{1}{2\text{ or }3}\quad c\,\frac{1}{1}\quad pm\,\frac{3}{2}\right) = 20\text{-}22\text{ deciduous teeth.}$$

Deciduous lower incisors most commonly numbered six (48,3% of sample), or four (37,9%), with five teeth recorded in only four specimens (13,8%).

The most common permanent tooth formula was:

$$2\left(I\,\frac{1}{2\text{ or }3}\quad C\,\frac{1}{1}\quad PM\,\frac{2}{1}\quad M\,\frac{3}{3}\right) = 28\text{-}30\text{ permanent teeth.}$$

Occasionally there may be one or three permanent upper premolars in each side of the mouth (Table 4). In two out of 389 cropped specimens, an extra permanent lower premolar (PM_3) was present on one side of the mandible, and was a slender, peg-like tooth with a tapered crown. Total permanent teeth recorded in Zululand warthogs ranged from a minimum of 26 to a maximum of 32. In addition to this variability, loss of incisors, premolars and first and second molars occurs with age.

TOOTH REPLACEMENT, ERUPTION AND WEAR

Both upper and lower deciduous canines had erupted above the gumline in six piglets less than one month old. Examination of a found skull representing a probable age at death of between one and three months showed that the tips of the most anterior cones of the mandibular first molars (M_1) had just started to wear, but eruption of the maxillary first molars (M^1) was less advanced.

TABLE 4. Variations in the numbers of permanent premolars of Zululand warthogs.

		Maxilla				Mandible			
n	% of total	PM^1	PM^2	PM^3	PM^4	PM_1	PM_2	PM_3	PM_4
8	2,1		x	x	x				x
3	0,8		½	x	x				x
360	92,5			x	x				x
2	0,5			x	x			½	x
3	0,8			½	x				x
13	3,3				x				x
389									

x = teeth present on both sides

½ = teeth present on one side only

Replacement of deciduous teeth commences with the canines which are exchanged while M_1 is erupting. The youngest specimen in which eruption of the permanent canines had started was a juvenile female estimated to be 5-6 months of age and with over half of the full crown length of both M_1 and M^1 in wear. The deciduous canines are shed before the age of one year but may still be present alongside the permanent replacements until about 9 - 10 months of age. M_2 and and M^2 commenced eruption and wear between nine and 11 months of age ($n = 12$).

In no instances were the deciduous incisors and premolars replaced during the first year, although the tips of the permanent incisors may start emerging beyond the alveolar margins from about 9-10 months of age. Eruption of I_1 is usually slightly in advance of the other permanent lower incisors, but one or both third deciduous incisors are sometimes never replaced. Of 275 warthogs aged two or more years, i.e. with no permanent teeth unerupted, 156 (56,7%) had six lower incisors, 68 (24,7%) four, and 51 (18,5%) five. In 29 of the latter the extra tooth was on the right side. However, some third deciduous incisors that are not replaced could possibly persist beyond two years of age and be mistaken as permanent teeth, so that the number of permanent lower incisors might have been slightly overestimated. Excluding subadults (2-3 years) from the sample, 97 (55,1%) out of 176 warthogs aged three or more years had six lower incisors, 47 (26,7%) four, and 32 (18,2%) five.

All permanent incisors were fully erupted by about 16 to 20 months of age, with eruption commencing at an approximate average age of 12 months. Replacement of deciduous premolars in the lower jaw tends to slightly precede that in the upper jaw, but pm_3 is not normally replaced (Table 4). The observed age range at commencement of eruption of the permanent premolars was about 12 to 14 months, with PM^4 usually the last to complete eruption. The permanent premolars generally erupt under the deciduous teeth, fragmenting their already worn crowns and leaving chips which tend to persist in the gum, occasionally beyond 24 months of age. In the specimens examined, eruption of permanent premolars was complete by about 20-22 months.

The molars erupt in regular succession from first to third in both maxilla and mandible, with eruption of corresponding teeth tending to commence slightly earlier in the lower jaw. Between about 17 and 20 months of age the third mandibular molar (M_3) starts erupting beyond the alveolar margin, and increase in the length of erupted crown in wear continues into the 3-4 year age class (Fig. 7). The continuous attrition of the premolars and first two molars and the shallowing of their sockets results in a pattern of tooth shedding which, in respect of the molar teeth, resembles the sequence described by Laws (1966) in the African elephant, where "successive teeth grow forwards from the back of the jaw replacing earlier teeth as these wear, move forward, and drop out".

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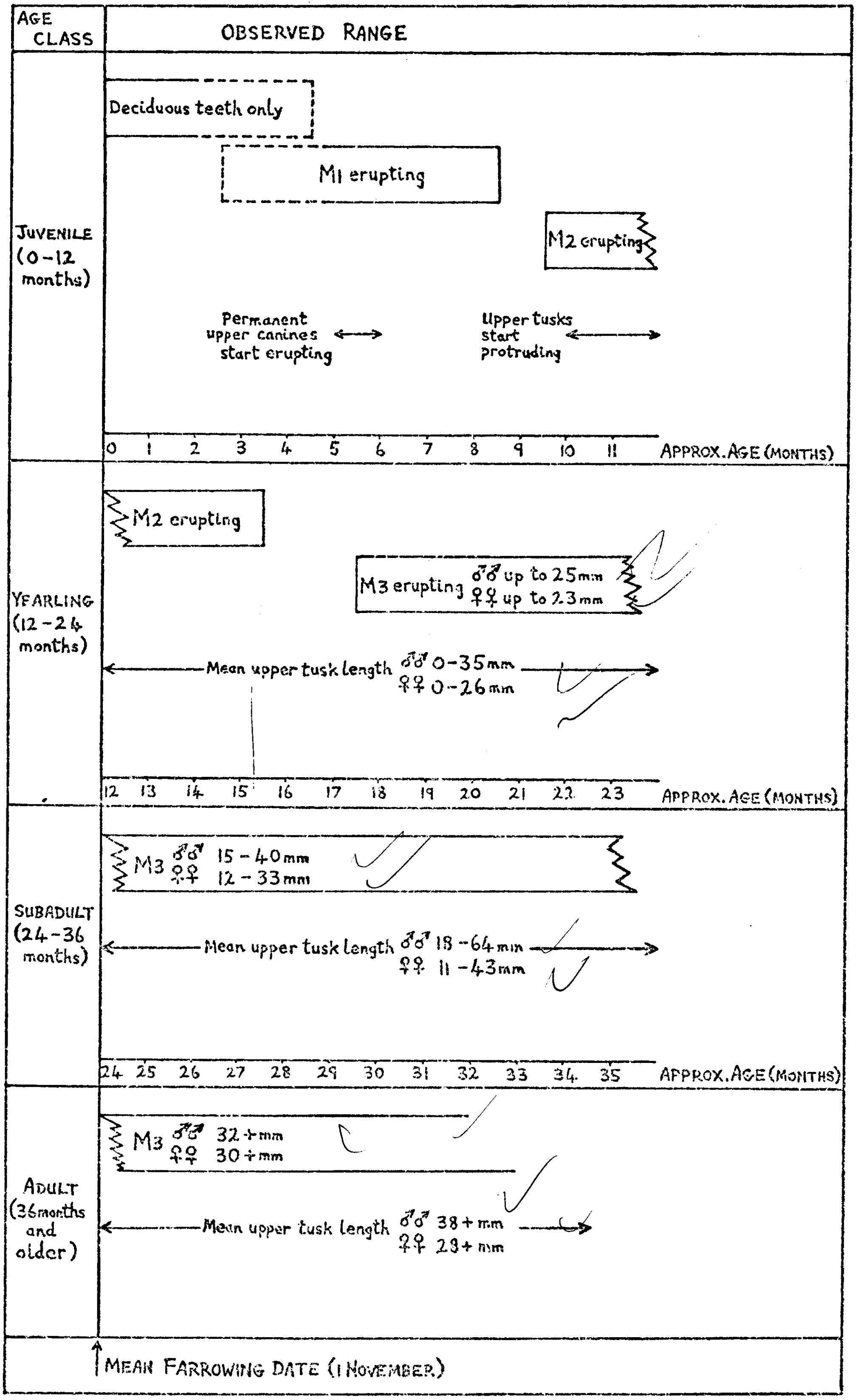

FIG. 7. Age estimation criteria for Zululand warthogs based on replacement and eruption of the dentition and growth of the third molars and upper canines.

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However, the warthog has only three molar teeth in each side of each jaw, compared with six in the elephant.

Besides being the most characteristic of warthog teeth, the third and last molar is one of the most peculiar and complex teeth in the whole class of Mammalia (Middleton Shaw 1939). Compared with the other two molars, it is also a very large tooth since, as Spinage & Jolly (1974) point out, "it bears most of the work load from middle-age or earlier". In Zululand warthogs, the third molars may exceed 65 mm in mesio-distal length at the triturating surface, with a similar maximum vertical height, while the widest part of the crown may attain 16 mm. Where eruption and growth are complete, there is a tendency for the lower molars to slightly exceed the upper molars in mesio-distal crown length, but such difference seldom exceeds 5 mm.

The complex arrangement of dental tissues in warthog third molars is best seen on the triturating surface (Fig. 8, Plate 1a), which presents three rows of enamel-rimmed islands of dentine along most of its length. These islands are the abraded ends of long, slender columns of dentine, encased by thick enamel. The enamel in turn is covered by cementum which packs all the columns together, fills the interspaces between them and invests the exterior of the entire tooth, extending above the gum line almost to the level of the occlusal surface. Being softer, the dentine and cementum wear away faster than the enamel, leaving ridges of enamel which render the occlusal surface rough and eminently suitable for grinding fibrous material.

The dentine-enamel columns are originally open at their bases, where they grow from "semi-persistent" pulps (Middleton Shaw 1939), and in young juveniles with unerupted molars comprise separate cones, not yet fused together by cementum. With advancing age, additional layers of dentine (formed by the odontoblast cells of the pulpal surface) encroach on and progressively occlude the pulp cavity of each column, commencing at the anterior end of the tooth. Roots develop on the bases of the columns concurrently with the enclosure of their pulp cavities.

In third molars where all the columns have erupted and are represented by separate islands on the triturating surface, the number of columns averages 21 or 22, but tends to be variable, and up to 29 have been recorded in a single tooth. Moreover, the columns and their occlusal islands vary in size and shape in different teeth of corresponding age, in different parts of the same tooth, and particularly in teeth of different ages. Eruption progresses sequentially from the mesial towards the distal end of each molar, so that the tips of the most distal columns are last to reach the level of the masticatory surface. Thus the entire lateral profile of the tooth changes as eruption proceeds (Plate 1b), while the form of the occlusal surface varies concomitantly with

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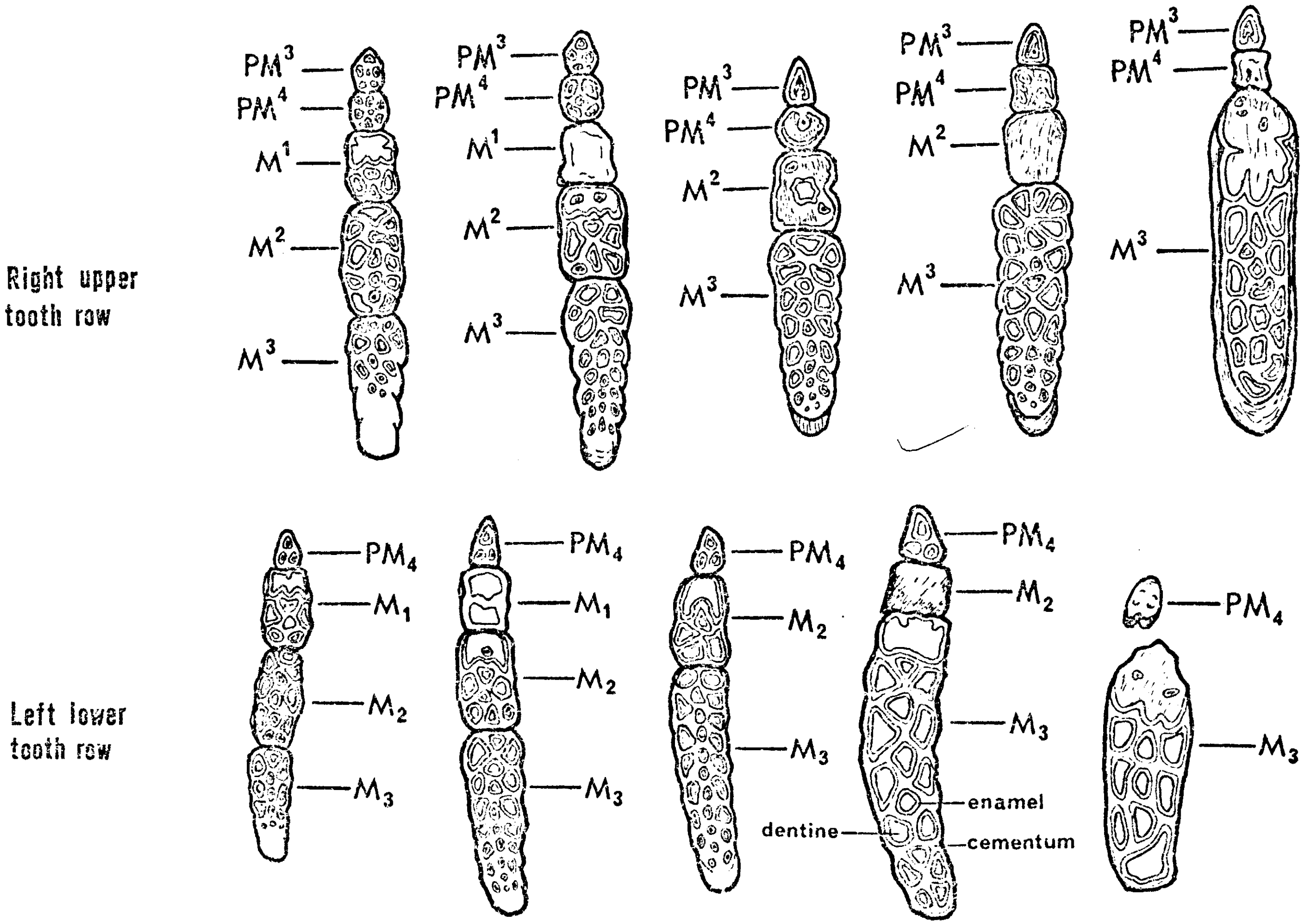

FIG. 8. Molariform teeth rows of the warthog showing the typical sequence of attrition (illustrated in five successive stages from left to right). (Adapted from Guiraud 1948).

the prolonged attrition to which it is subject.

With increasing age, adjoining columns coalesce and lose their separate identities, resulting in a smaller number of columns in the tooth, but with more complex cross-section. Since cementum deposition by the cementoblast cells of the surrounding periodontal membrane continues through most of life (Spinage 1973a), the outer envelope of cementum progressively thickens, and the originally corrugated sides of the tooth became smooth and flat, obscuring the former existence of separate columns.

When attrition of the tips of the columns commences, the resultant dentine-enamel islands on the occlusal surface are small and round. As attrition proceeds and exposes wider portions of each column, the islands increase in size and many assume an oval, triangular or irregular form. Once the tooth has worn down to a level where fusion of adjoining columns is exposed, the occlusal islands display further complexity in form and further increase in size. The anterior group of columns is normally first to coalesce, resulting in one major occlusal island of complex shape, termed the "anterior complex" (Middleton Shaw 1939), which may extend mesio-distally up to half the length of the occlusal surface. Although their pattern alters, enamel rims persist on the occlusal islands even when the crown has worn down close to the roots of the tooth in very old warthogs.

Before eruption of the most posterior columns is completed on the occlusal surface, enclosure of the pulps and development of roots commence with the anterior columns, and with subsequent ageing progresses towards the distal end of the tooth. Forming roots first become apparent usually within a few months of an approximate average age of 36 months. The anterior columns develop a more oblique forwards orientation as root development proceeds, reflecting their earlier cessation of growth relative to continued growth at the back of the tooth, where the pulp cavities remain open longer. As the constricting sockets of the columns develop into roots, while wear of the occlusal surface continues, the height of the columns shrinks concomitantly, and this is most marked in the case of the anterior group of columns. Eventually all the pulps become enclosed, but the anterior roots are normally markedly longer than the remaining roots.

In old warthogs the anterior end of the tooth may be entirely worn away, thus reducing its mesio-distal length. The vertical height between crown and root bases at the anterior ends of the third molars becomes greatly reduced with age, and in some teeth a split was visible where the anterior complex island would shortly separate from the rest of the crown (Plate 1c & d). Examination of four known-age third molars from Zimbabwe (Plate 1e) indicated that enclosure of all the sockets which lodged the complex pulp matrix was

PLATE 1

(a) Left upper tooth row of a 3 - 4 year old warthog sow from Zululand. The tips of the most posterior dentine-enamel columns of the third molar have just started to wear.

(b) Lateral profiles of maxillary third molar teeth of Zululand warthogs showing typical sequence of changes in size and shape with growth, occlusion of the pulp cavities, and attrition. Age classes and approximate chronological ages for the series are (1) juvenile (M^3 unerupted); (2) yearling (M^3 erupting); (3) ca. 24 months (most anterior dentine-enamel columns of M^3 erupted to level of triturating surface); (4) subadult (2 - 3 years); (5) adult (ca. 36 months); (6) 3 - 4 years; (7) ca. 48 months; (8 - 10) ca. 5 - 7 years; (11 - 18) ca. 8 - 10 years; (19 - 24) ca. 10 - 15 years.

(c) Split at anterior end of the right mandibular third molar of a male warthog (estimated to be about 9 - 10 years of age) from Zululand.

(d) Occlusal surfaces of warthog third molars from Zululand showing wear patterns in relation to age : (1) ca. 36 months; (2) ca. 6 - 7 years; (3) ca. 9 - 10 years and with loss of anterior end of tooth imminent.

(e) Maxillary third molars of Zimbabwean warthogs of known age : (1) female aged 6,0 years; (2) female aged 6,5 years; (3) female aged 8,2 years; (4) male aged 8,5 years.

completed at about eight years of age. Judging by the same specimens, splitting off of the anterior complex could commence from about 9 - 10 years of age, unless wear is unusually heavy and assuming comparable rates of wear in Zimbabwe and Zululand. The tremendous variation in shape and size of warthog third molars with growth and attrition is illustrated in Plate 1b, where a series of teeth has been arranged in an approximate sequence of increasing age, starting with the unerupted tooth of a young individual.

In both sexes, the third molars have virtually attained their asymptotic size by four years of age. Examination of sex-specific differences in size of these teeth was therefore restricted to warthogs estimated to be within the 4 - 5 years age class. For a sample of 21 right maxillary molars (M^3), the mean mesio-distal crown length for males ($\bar{x}$ = 46,0 mm, n = 11) was significantly greater ($p < 0,001$) than for females ($\bar{x}$ = 41,9 mm, n = 10), while the maximum labio-lingual crown width was on average 1,3 mm greater in males than in females ($\bar{x}$ = 14,6 mm c.f. 13,3 mm) and this difference was significant ($p < 0,01$).

Successive stages of attrition in the upper and lower tooth rows of the warthog have been illustrated by Guiraud (1948) and were found eminently suitable for describing age-related changes observed in the masticatory teeth of Zululand warthogs (Fig. 8). As posterior columns erupt and lengthen the crowns of the third molars, the anterior ends of these teeth initially exert pressure on the second molars via a restricted zone of contact approximately at the level of the gum line. The continuing forward traverse of the actively growing third molars then compresses both the second and first molars against the fixed premolars at the anterior ends of the tooth rows. Simultaneously, closure of the pulp sockets and wearing down of the crowns of the first and second molars proceeds, and the triturating surfaces are eventually reduced to smooth slabs of dentine and cementum without enamel rims. Sloughing of these worn slabs then ensues, often facilitated by their splitting and fragmentation.

Attrition and shedding of the first molars precedes that of the larger second molars, and is usually completed during the 3 - 4 years age interval, but shrinking remnant chips may persist into the next year class or even beyond. Judging by the degree of closure of the pulp cavities of the corresponding third molars and estimates of age from cementum lines in the mandibular first permanent incisors, the second molars are not normally shed before about 6 - 7 years of age, but there appears to be considerable variation in their maximum longevity. Since wear of the first and second molars is usually slightly more advanced in the mandible than in the maxilla, the loss of these teeth tends to occur slightly earlier in the mandible. Although subject to inaccuracies, counts of incisor cementum annulations suggested about nine to 10 years as the probable age up to which very worn upper second molars or fragments thereof may still be present.

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The shedding of the worn first molars in particular is promoted by forward pressure from the third molars, the crowns of which usually still increase in length during the 3-4 years age interval. Following loss of the first molars, the forward traverse of the third molars possibly continues for a time, perhaps aided by their angular shape and oblique vertical orientation in the alveolar sockets, but the force that they exert on the second molars probably declines. Since mastication in the warthog is achieved by a sideways grinding action of the lower teeth against the upper, the greater amplitude for lateral movement at the front end of the mandible probably expedites attrition of the anterior portions of the tooth rows. Loss of the premolars may largely coincide with disappearance of the second molars or may occur slightly later, with PM^3 usually falling out before PM_4 and PM^4. The upper fourth premolars tend to endure longest, but are usually shed or vestigial by an estimated age of approximately 10 years. The process continues with the wearing down of the anterior ends of M_3 and M^3, which are the only grinding teeth remaining in aged warthogs. At the sites where the premolars and anterior two molars were rooted, the already shallow alveolar sockets close up and, apart from the third molars, the only functional teeth still present are the canines (growth of which continues throughout most of life) and the greatly reduced lower incisors.

The smaller upper incisors (2) are normally lost before the lower incisors (4 - 6), which may be vestigial or worn down practically to the gums by an estimated age of approximately 10 - 13 years. Loss of the incisors is not obviously detrimental to grass prehension, in which the warthog's resilient lips seem to play a major role. The oldest warthog in which the lower first incisors were still present and just large enough for longitudinal sectioning to be practicable was a male estimated to be about 14 years old from a count of dark-staining rest lines in the cementum. Root resorption had evidently not decreased the total number of cementum annulations that could be counted. The anterior crown height of the right upper third molar of this individual, measured as the vertical distance between the triturating surface and the apices of the most anterior roots, was 14 mm. Although only 4 mm separated the crown from the posterior base of these roots, the anterior end of the tooth had not yet broken away, and the mesio-distal crown length was 55 mm. Judging by the vertical dimensions, this tooth and the other third molars seemed capable of enduring about two more years of wear, which would indicate a potential maximum lifespan of about 16 - 17 years for Zululand warthogs. However, age estimation from cementum annulations in incisor teeth is seldom possible in the oldest warthogs, since the incisors are shed or worn to tiny remnants probably before about 13 years in most specimens.

TUSK LENGTH: SNOUT WIDTH RATIOS

Warthog canines grow from persistent pulps within their central cavities. With advancing age these pulp cavities become progressively occluded from the distal ends towards the bases of the tusks by continued formation of dentine upon the surface of the pulps. Following their eruption during the latter half of the first year after birth, the permanent upper canines then develop at more or less the same rate in both sexes up to about 19-20 months of age. Thereafter, differential growth rates and dimorphism in shape of the upper canines between males and females should be considered in age estimation based on continued tusk growth. The tusks grow longer and thicker and are more widely flared in males than in females.

At about 10 months of age the upper canines are usually still level with the flanges of the upper lips, but start protruding from about 12 months. Consequently, juveniles (less than one year old) do not appear in the age class calculations. Due to the fixed parturition period in Zululand, age classes are separated by approximately one year. Regression formulae for tusk length: snout width ratios (y) in relation to age in months (x) were calculated separately for males and females in the 12 - 36 months and 36 - 60 months age groups. The regression lines and their corresponding 95% confidence intervals are shown in Fig. 9. The age estimates from tusk length: snout width ratios were calibrated by reference to tooth replacement, eruption and wear, incisor cementum annulations and physical and reproductive development.

Males exceeded females in their average tusk length: snout width ratios for the yearling, subadult and 3-4 year age classes. Ratios for these age classes comprised reasonably distinct groups, but overlap among older animals was apparently unfavourable to a satisfactory separation of year classes. Maximum ratios of 49 and 73% were recorded for males and females respectively.

TOOTH SECTIONS

Undecalcified sections

Incremental layers were not visible in the cementum or dentine of sections from both I_1 and M^3, even when viewed using anoptical phase contrast.

Decalcified sections

The use of segments of M^3 for sectioning proved unsuitable since the decalcifying fluid dissolved the enamel around each column of dentine, thereby separating the surrounding sheath of cementum which bonds the dentino-enamel columns together. In the decalcified state, this shell of cementum (resembling a honeycomb in cross-section) is rather fragile and tended to collapse or warp during histological processing.

Alternating broad lightly-staining and narrow darkly-staining annulations

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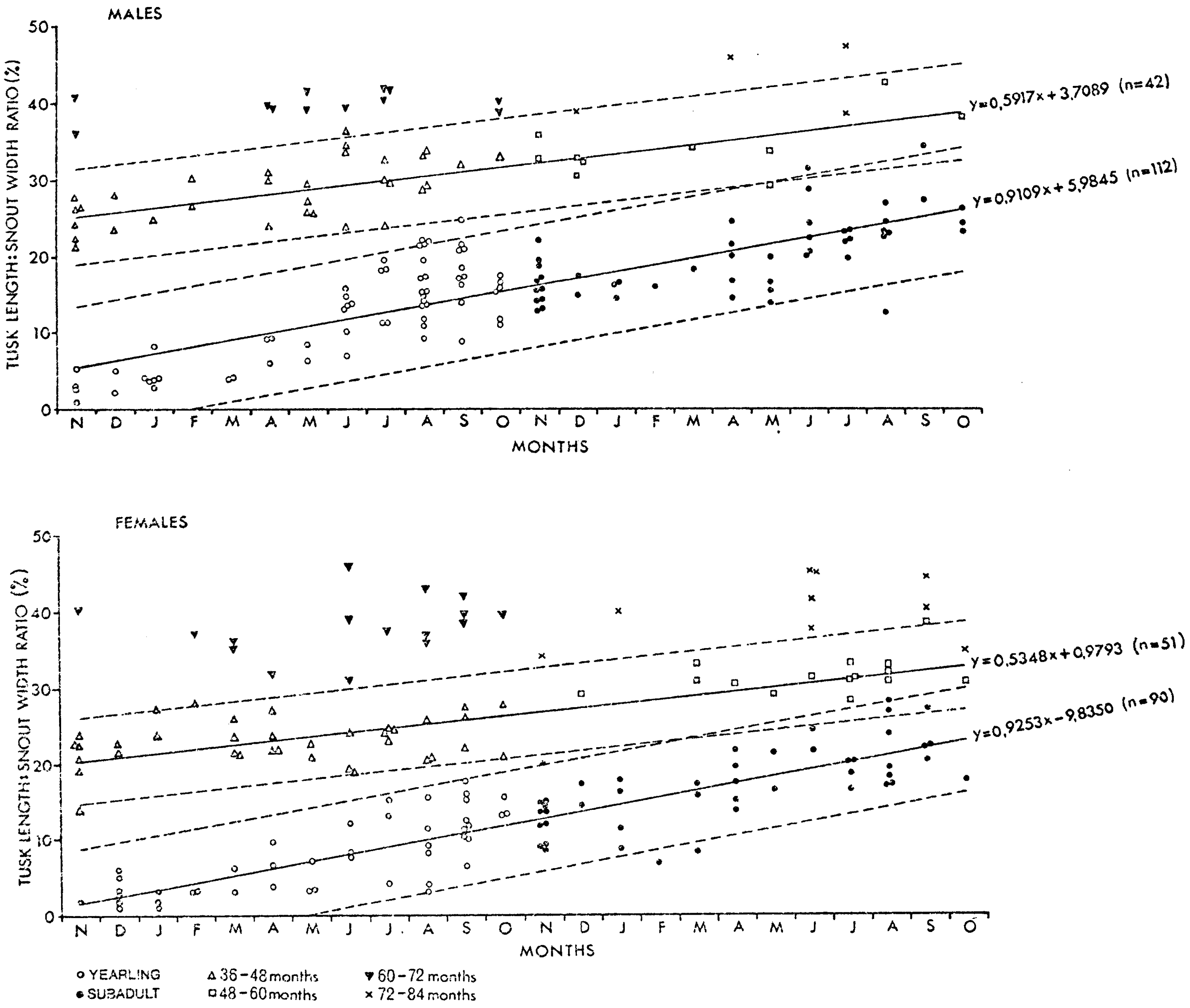

FIG. 9. Regression lines (solid) and their corresponding 95% confidence intervals (broken lines) for the relationship between tusk length: snout width ratios and age for four year-classes of warthogs from Zululand.

were found in the cementum covering the external dentine surface of the root portion of I_1 (Plate 2a). However, approximately 33% of stained sections from 181 mandibular first incisors were unsuitable for age estimation, mostly because of poor delineation of rest lines from the interlamellar bands (Plate 2b). The first cementum deposited adjacent to the dentine forms a lightly-staining band, and examination of tooth sections from yearlings indicated that it is laid down during the second summer and autumn of life, when I_1 is erupting. Although I_1 is established by April (corresponding to an estimated age of 17 months using 1 November as the mean farrowing date), the subsequent lamella, represented by a narrow darkly-staining rest line associated with the winter dry season, was apparently not formed on the outer edge of the cementum until about 19-21 months of age. Thereafter, in the incisors of warthogs up to 24 months old, this rest line was visible outside the first incremental band, close to the periodontal membrane.

In most tooth sections from warthogs within the 2-3 years age class, the basic pattern of a wider layer of pale cementum laid down during the wet season followed by a dark-staining rest line during the dry season was continued. Where differentiation of incremental lamellae in older, known-age specimens was satisfactory (Plate 2a), the number of layers was in close agreement with age, thus confirming the annual rhythm of cementum accretion.

The intensity of staining and delineation of rest lines from the background cementum varied greatly between teeth, between sections from the same tooth, and even within the same section. The spacing between successive rest lines is also variable, with lines often merging where the cementum is thinner. Separation of rest lines was usually best for counting on the distal aspect of the root, above the tip. In older warthogs a large terminal deposition of cementum commonly forms at the base of incisor roots, but rest lines here were obscure and unsuitable for counting. As suggested by Leader-Williams (1979) for reindeer (Rangifer tarandus), the narrow neck of the incisor root socket of warthogs probably acts as a fulcrum about which the base of the root moves as the tooth crown is subjected to the shearing forces of feeding, and this enlarges the lower part of the socket. Where the socket is thus widened, the deposition of layers of cementum much thicker than in areas of restricted socket width is to be expected.

Variation in the width of cementum layers covering different parts of one tooth between the neck of its socket and the base of the root implied that cementum accretion depends to some extent on the space available in the root socket. Areas of thin cementum are usually associated with discontinuity of certain rest lines, which merge with others and reform further along where the cementum is thicker. Ramifications of rest lines (Plate 3a & b) hindered the

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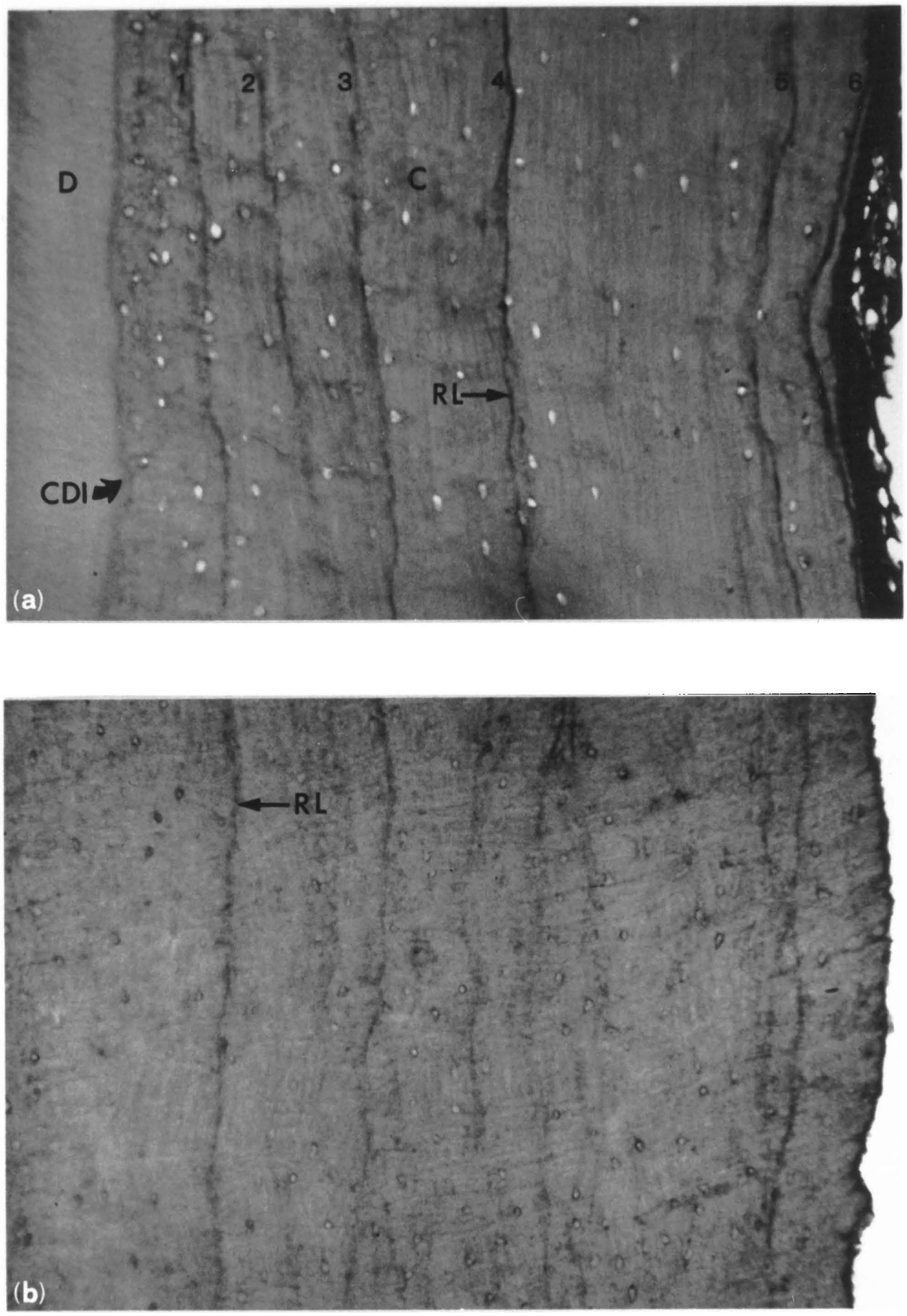

PLATE 2

(a) Decalcified longitudinal section from root of mandibular first permanent incisor of a 6,5-year old female warthog from Zimbabwe showing dentine (D), cemento-dentinal interface (CDI) and cementum (C) with six rest lines (RL) as expected for an annual deposition pattern. 10 µm, haematoxylin & eosin. x 160.

(b) Decalcified longitudinal section from root of mandibular first permanent incisor of an 8,2-year old female warthog from Zimbabwe showing poor definition of rest lines (RL) in the cementum. At least seven rest lines are nevertheless discernible. 10 µm, haematoxylin & eosin. x 160.

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(e)


(f)


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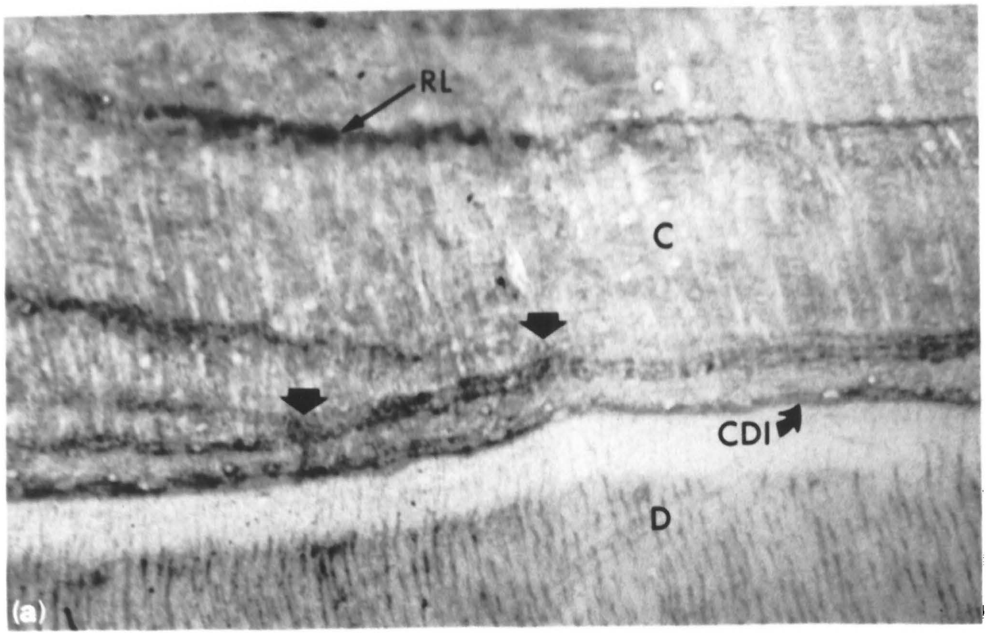
(Photo : R.D. Carr)



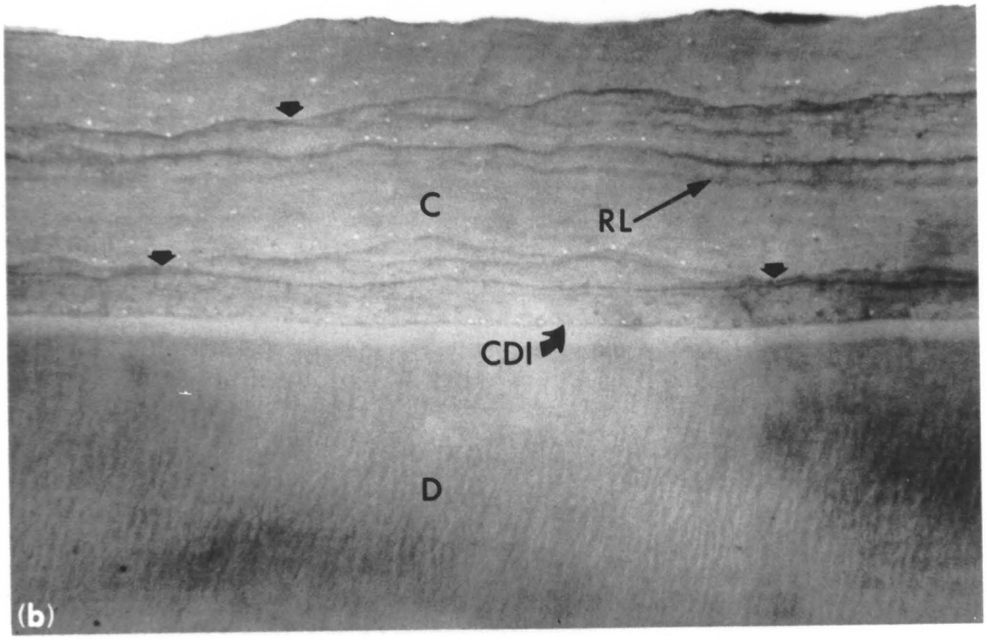


PLATE 3

(a) Decalcified longitudinal section from root of mandibular first permanent incisor of an adult female warthog from Zululand showing convergence of rest lines (RL) in the cementum (C) at points indicated by vertical arrows. D = dentine, CDI = cemento-dentinal interface. 10 µm, Chromotrope 2R. x 160.

(b) Decalcified longitudinal section from root of mandibular first permanent incisor of a 6,5-year old female warthog from Zimbabwe showing ramifications of rest lines (RL) in the cementum (C). Merging of rest lines at points is indicated by vertical arrows. D = dentine, CDI = cemento-dentinal interface. 10 µm, haematoxylin & eosin. x 63.

correct delineation of the boundaries of broad annual layers, which was further complicated by variable staining quality and artefacts of sectioning. Some rest lines became diffuse or faded completely so that a measure of subjective interpretation and counting was inevitable where lines appeared wavy and were in close proximity.

Dividing and merging rest lines were found in both sexes, and incremental layering seemed to become less distinct with increasing age. Occasionally, the cementum of a section showed a slight tear along a rest line, suggesting that these annulations may be weaker than the intervening bands associated with periods of active growth. Where differentiation of incremental layers in incisor teeth of unknown age was satisfactory for counting, the ages suggested by the numbers of rest lines were in broad agreement with the state of attrition of the dentition. No anomalies, such as young animals with few rest lines but very advanced attrition, were noted. However in some sections, particularly from older individuals, poor separation of layers associated with merging of rest lines and low contrast staining, probably resulted in the underestimation of the age of a proportion of specimens by one or two years.

EYE LENS MASS

Mean mass of paired, dried lenses was determined for each warthog, but single lens mass was used whenever one lens had been damaged. A t-test for the difference between paired samples showed no significant difference between dry mass of left and right lenses. Dry lens mass was plotted against age as determined from stage of tooth replacement and eruption for the first three years of life (Fig. 10). The range of lens mass for adult warthogs (at least 36 months old) is also shown.

Combining both sexes, the graph shows a good correlation between lens mass (y) and age (x) up to 36 months, so a linear regression line given by the equation $y = 94{,}7337 + 2{,}8264x$ ($r = 0{,}915$, $p < 0{,}001$) was fitted to the data. Between 24 and 36 months of age, ranges of lens mass overlapped increasingly with those of adults. The decline in the rate of increase in lens mass within the subadult age class indicates that this parameter is of little use for separating specimens beyond 36 months.

AGE ESTIMATION IN THE FIELD

Because warthogs in Zululand have a short breeding season, the age classification described is based on year classes (separated by at least 9-10 months) which are represented in the population throughout the year. Both sexes attain sexual maturity as yearlings, before physical development is complete, while sexual dimorphism in size is apparent by 24 months of age.

Four age classes were recognised (Plate 4):

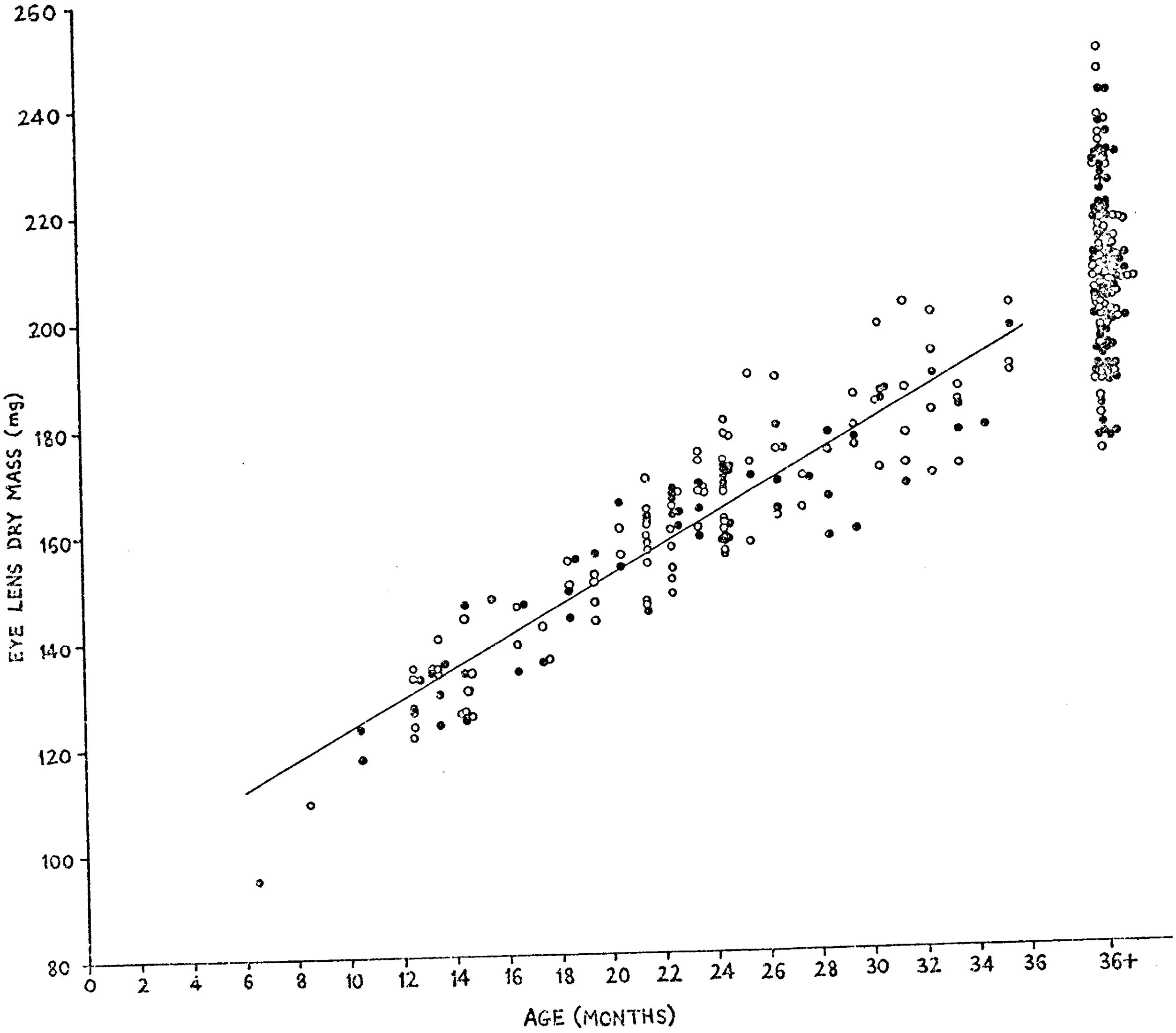


FIG. 10. Relationship of dry eye lens mass to age (as determined from dentition) in juvenile, yearling and subadult warthogs. Males (o), females (●).

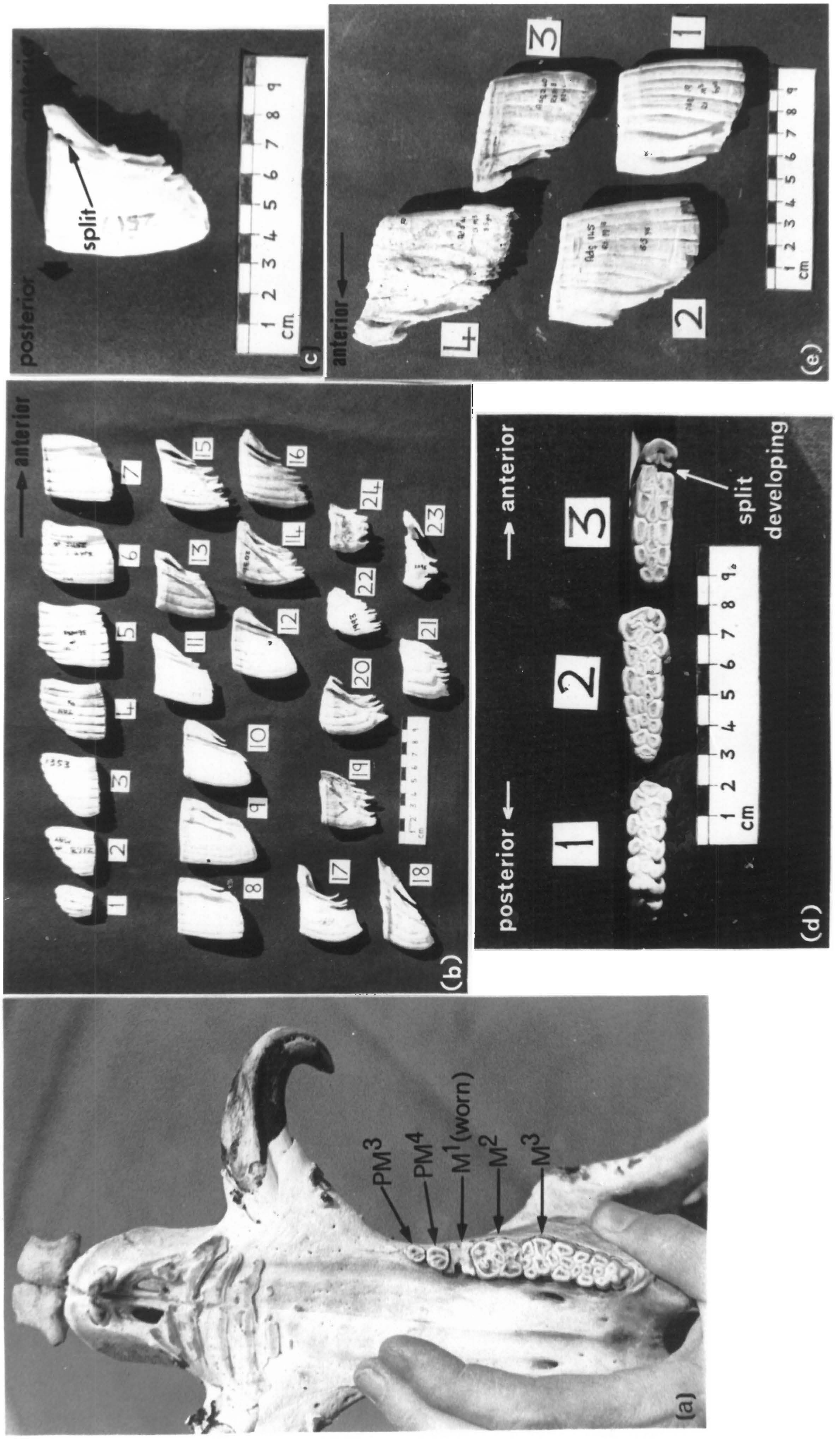

posterior
anterior
split
1 2 3 4 5 6 7 8 9
cm
(c)
anterior
1
2
3
4
1 2 3 4 5 6 7 8 9
cm
(e)
anterior
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24
(b)
posterior
anterior
1
2
3
split developing
1 2 3 4 5 6 7 8 9
cm
(d)
PM3
PM4
M1 (worn)
M2
M3
(a)

PLATE 4

Field sex and age classification of warthogs in Zululand.

(a) Juveniles aged about six to seven weeks with their mother. Warthogs in southern Africa have a short and distinct annual period of parturition and the young born in the most recent season constitute a uniform and easily recognisable group within the population. Note piglet "greeting" mother by nose to nose sniffing.

(b) Juveniles aged about 11 to 12 months with the matriarch of the sounder. The left tusk of the juvenile in the centre of the photograph is just visible at the lip margin, and the sex of this individual can be distinguished as male by the presence of supra-oral warts.

(c) Matriarchal sounder comprising an adult sow with juvenile and yearling progeny (left to right : yearling, adult, juvenile, yearling). Young warthogs (especially females) often rejoin their mother after she has farrowed a new litter and may remain with the group at least until they have attained sexual maturity at about 18 months of age.

(d) Two yearling males and a yearling female (probably littermates) forming a temporary heterosexual association after parting company from a matriarchal sounder. Estimated age about 22 months.

(e) Yearling females estimated to be about 22 months of age and probably pregnant.

(f) Primigravid sow aged about 24 months and close to full term of gestation.

(g) Gravid subadult sow estimated to be about 35 to 36 months of age.

(h) Yearling males aged about 18 to 19 months and sexually mature.

(i) Yearling male aged about 19 to 20 months showing development of the tusks and warts.

(j) Subadult male captured with drive nets and marked with ear tags.

(k) Adult female.

(l) Adult male.

(m) Adult male consorting with an adult female during the mating season. Supra-oral warts are absent in the female warthog and the infra-orbital warts are much smaller than those of adult males. Note pre-orbital areas darkened by glandular secretion, particularly in the boar.

(n) Skull of an old warthog showing long tusks and virtually complete loss of cheek teeth antecedent to the third molars. The left mandibular third molar appears to have shortened through attrition and breaking away of the anterior end. (Found skull from eastern Transvaal in possession of P.C. Viljoen, Transvaal Division of Nature Conservation).

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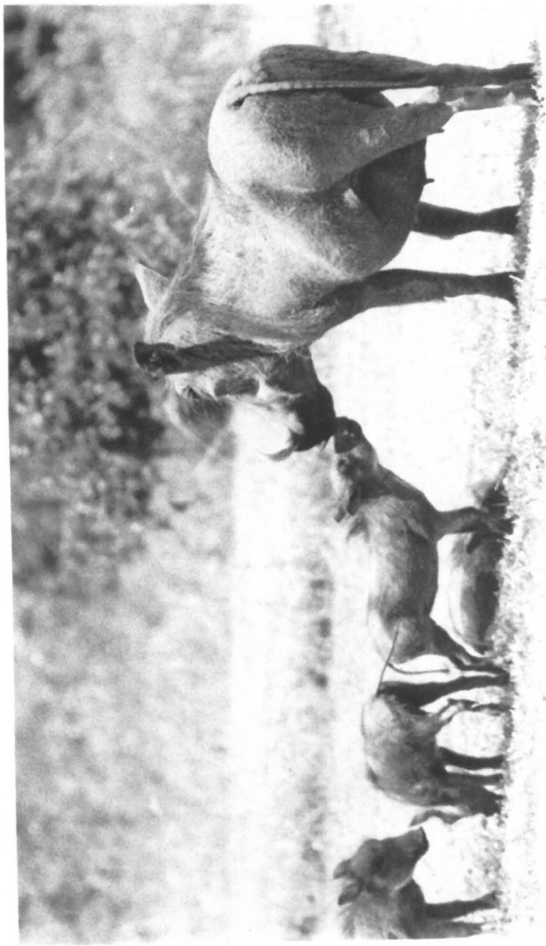

(a)

(b)

(c)

(d)

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1. Juveniles - up to 12 months old
2. Yearlings - 12 to 24 months old
3. Subadults - 24 to 36 months old
4. Adults - older than 36 months.

Piglets of the most recent farrowing season (juveniles) accompany their mother during their first year and are readily distinguished by their small size and generally not visible tusks (Plate 4a, b & c). Neonates are able to stand under their mother's belly and have a linear shoulder height of only 18-20 cm. However, by 10-12 months of age their average shoulder height is above the halfway level between the elbow and shoulders of the standing adult female, but still approximately 9-14 cm below the apex of her shoulders.

Differences in body size between yearlings of both sexes and adult females are less marked and by June are virtually unnoticeable in the field. Indeed, many yearlings are nearly equal to adult females in body size by the end of March, i.e. when about 17 months old. Adult females usually slightly exceed yearlings aged 17-18 months in head plus body length and tend to be heavier in body build, although shoulder heights overlap (Plate 4c). Compared to sub-adult and adult males, yearling males can generally be distinguished throughout the year by their lighter body build and slightly smaller dimensions, particularly total length.

The limitations of body size for age estimation, especially of solitary individuals and groups of one age class, necessitate recourse to additional criteria. The appearance of the head and tusk size and shape are useful for both age and sex classification in the field. As noted by Ewer (1958), females tend to have less widely flared upper tusks than males. Paired infra-orbital warts situated on the zygomatic arches are present in both sexes, but only protrude 1,5 to 2,5 cm in adult females compared with 6 to 12 cm in adult males. Males are further distinguished by a pair of supra-oral warts, which protrude about 3,5 cm in adults (Plate 4k, l & m).

In juveniles and yearlings, the growth of long white hair tufts on the thickened dermal ridges along the ventro-lateral margins of the mandible is more conspicuous than in older warthogs. At the age of 12 months, the tips of the upper tusks have barely started emerging beyond the flanges of the lips, and average 1-3 mm in length for both sexes. By 24 months, tusks of males average about 2-3 cm in length compared with 1,5 - 2,3 cm in females (measuring tusk length across the arc from the base of the upper tusk, where it protrudes from the lip, to the tip). Yearlings may still be seen with their mother even six or more months after she has farrowed again, which then facilitates comparison of three age classes (juvenile, yearling and adult) alongside (Plate 4c).

Tusk length increases more markedly in males than in females after 24 months of age, and by 36 months averages about 4,5 cm in males and 3,0 cm in females. Most 2-3 year old males are distinguishable from those older than 36 months by their tusk development and general physical appearance. Body size is not a valid criterion for recognising subadult from adult females, although the former can generally still be distinguished by their shorter tusks during and for two or three months after the farrowing season. Subsequently, however, females in the 2-3 year age cohort become indistinguishable from older year classes due to overlap in their tusk lengths.

Because recognition of subadult females becomes increasingly unreliable after the farrowing season, only three age classes (juveniles, yearlings and animals older than 24 months) can effectively be distinguished in the field throughout the year.

DISCUSSION AND CONCLUSIONS

DENTITION

The deciduous dentition formula recorded for warthogs in Zululand corresponded with that reported for 80,6% of specimens examined by Child, Sowls & Mitchell (1965) in Zimbabwe, where some variation in the number of deciduous premolars probably reflects their much larger sample size. In both Zululand and Zimbabwe, full permanent dentition usually comprised 14 teeth in the maxilla and 14 or 16 in the mandible, depending on whether four or six lower incisors were present; however, an inherently variable number of premolars may occur, particularly in the upper jaw, in a minority of specimens.

Although Middleton Shaw (1939) found that the number of lower incisors in the warthog is subject to variation, differences in the numbers of permanent incisors and premolars were not noted in other early descriptions. Bigourdan (1948) and Guiraud (1948) both recorded the full permanent dentition as comprising 14 maxillary and 16 mandibular teeth, i.e. four upper premolars and six lower incisors. Notwithstanding d'Huart's (1971) finding of six upper and four lower permanent premolars in a small collection of warthog skulls from the savanna south of Lake Amin in the Virunga National Park, Zaïre, possible inter-population variation in the average numbers of permanent premolars and lower incisors for warthogs in different geographic regions remains to be demonstrated.

Compared with the bushpig and European wild pig, the warthog shows a marked reduction in the numbers of incisors and premolars and hence in the total number of permanent teeth. Similar reduction in the dental complement has occurred in the giant forest hog, for which d'Huart (1978) gives the permanent dental formula as $2\ (\ I\ \frac{1}{3}\ C\ \frac{1}{1}\ PM\ \frac{2}{1}\ M\ \frac{3}{3}\ ) = 30$ teeth. Matschke (1967) recorded the complete permanent dentition of the European wild pig as $2\ (\ I\ \frac{3}{3}\ C\ \frac{1}{1}\ PM\ \frac{4}{4}\ M\ \frac{3}{3}\ ) = 44$ teeth. The permanent dentition of the bushpig has the formula

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$2\ (\ I\,\frac{3}{3}\ C\,\frac{1}{1}\ PM\,\frac{3\text{ or }4}{3\text{ or }4}\ M\,\frac{3}{3}\ )$ = 40-44 teeth; however, the lower first premolars are commonly absent, so that most bushpigs have a total complement of 42 teeth (Sowls & Phelps 1968).

The elongated, multi-cusped, high-crowned (hypsodont) third molars of the warthog are indicative of adaptation to grinding coarse grass and rhizomes. Evolutionary reduction in the number of premolars may well be associated with the gross enlargement of the third molars and contraction of the zone between the third molars and the roots of the canines.

TOOTH REPLACEMENT, ERUPTION AND WEAR

Several studies, notably by Middleton Shaw (1939), Guiraud (1948) and Child, Sowls & Mitchell (1965), have contributed to describing the basic pattern of tooth replacement, eruption and attrition in the warthog. Child *et al*. (*op. cit*.) described eruption and replacement criteria permitting age determination up to 24 months, whereafter 2-3 year old warthogs could generally be distinguished from older warthogs by the relative growth of their third molars (considering males and females separately due to differential growth rates). Similarly in Zululand, the erupted crown lengths of the third molars were useful for differentiating between yearlings, subadults and warthogs older than 36 months, when their molar measurements were compared within any particular month. Notwithstanding some inherent variation in the number of permanent premolars, tooth replacement and eruption were fairly closely linked with chronological age.

Compared with the enlarged third molars, the first two molars and especially the premolars have much lower crowns and are worn down and shed much earlier than the third molars, upon which the warthog then depends for mastication. Wear and loss of the third molars has not been adequately related to age however, and age estimation from incisor cementum annulations was subject to inaccuracies. In Zululand warthogs, loss of the first molars was usually completed during the 3-4 years age interval, which agrees with the findings of Clough (from Spinage & Jolly 1974) in Uganda. However, the persistence of worn fragments of the first molars in some warthogs estimated to be within the 4-5 and even 5-6 year age cohorts indicates that their maximum durability is rather variable. Possible sex differential rates of attrition of the masticatory teeth were not noted in Zululand and are not mentioned in other studies.

Although the condition of the second molars may be used to indicate relative age (Middleton Shaw 1939), incisor cementum annulations suggested considerable variation in the age span over which they may persist, albeit as worn fragments of variable shape. Minimum longevity of upper and lower second molars was estimated as about 6-7 years, with chips of the upper teeth probably persisting up to about 9-10 years in some individuals. While such remnants hardly

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contribute to mastication, their variable durability renders attrition of the second molars somewhat imprecise as a criterion for estimating age. Examination of the skulls from four Zimbabwean warthogs ranging in age from six to eight years indicated that the second molars were still very much in use at six years of age and were still present in one warthog aged eight years (Cumming pers. comm.).

According to criteria formulated by Clough (from Spinage & Jolly 1974) for Ugandan warthogs, M_2 may be a remnant and M^2 is very worn at an estimated age of 3 - 4 years, and in the 4 - 5 years category M^2 is either a small remnant or has been lost. Bigourdan (1948) gives dental formulae of male warthogs in West Africa with estimates of their ages at various stages of sloughing of the cheek teeth antecedent to the third molars, although he does not differentiate between the molars and the premolars. Thus at an estimated age of 10 years, Bigourdan describes the dental formula as $\frac{0-1-2}{2-1-2}$ (16 teeth), but it is uncertain whether the cheek teeth anterior to the third molars are premolars or second molars. Child, Sowls & Mitchell (1965) merely state that the second molars rapidly decrease in length after the third molars attain about 50 mm in crown length, and are subsequently lost, although fragments may persist for a considerable period.

The second molars, which attain 25 mm in crown length and 35 mm in height, are considerably larger than the first molars and so could be expected to endure longer. However, actual longevity of both the first and second molars requires verification from known-age warthogs, possibly by means of tooth impressions taken at intervals from live individuals. Attrition may vary with dietary or even genetic factors so that age ranges corresponding to particular stages of wear in Zululand warthogs might differ in other populations.

In domestic pigs, Mc Cance, Ford & Brown (1961) found that severe and prolonged undernutrition delayed the eruption and development of the permanent teeth, often produced malocclusion in which the mandibular teeth were too far forward for their maxillary opponents, and was associated with crowding, impaction and irregular and extensive wear within the tooth rows. Similar effects that could be attributed to undernutrition were not noted in warthogs during the study period, and malocclusion was only observed where the crowns of particular molar teeth had been fractured, and the opposing teeth were not worn down to the level of the rest of the tooth row. Attwell & Jeffery (1981) found that pronounced differential wear of molariform teeth between mandible and maxilla was common in eland and wildebeest. In the molariform tooth rows of warthogs however, inequalities in wear of opposing teeth were usually minor, which may reflect the proximity of their eruption times in the mandible and maxilla.

With growth and wear, the third molars of warthogs in Zululand showed

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changes in their shape which corresponded to descriptions by Middleton Shaw (1939) and Guiraud (1948). Spinage & Jolly (1974) attempted to predict age using changes in the morphometry of the third molars. From criteria of tooth eruption and wear, they estimated age of warthogs up to five years and found a linear relationship between age and an index of erupted crown length divided by anterior crown height of the maxillary third molars. They assumed that growth in length and decrease in anterior crown height (wear) of the third molars are linearly related beyond age five, but suggested a curvilinear relationship after 10 years due to growth in crown length approaching its asymptote at this age, while wear continued. In Zululand however, asymptotic crown length of warthog third molars was attained by 4 - 5 years of age in both sexes, so Spinage & Jolly's prediction formula appears invalid. This is supported by Cumming (pers. comm.) who considers that Spinage & Jolly's criteria are not applicable to warthogs in the Sengwa area of Zimbabwe, where their prediction graph gave an estimated age of two years for a six year old individual.

Interpretation of age in terms of the morphometry of the third molars could also be impaired because anterior crown height is an inherently imprecise measurement in older warthogs where this dimension has been greatly reduced following occlusion of the pulp cavities, development of roots, and wear. Spinage & Jolly (1974) imply that anterior crown height is measured from the anterior tip of the occlusal surface to the base of the most anterior dentine column(s), but in older specimens it is not clear whether they used the apex of the most anterior roots or the junction of their bases. The anterior extremity of upper third molars is formed by two marginal columns so that two roots normally develop, more or less alongside, from their bases. Variations occur in the length, slant and relative positions of the most anterior roots, while the anterior ends of some teeth incline lingually, thus disturbing the normal relation of the columns. A further drawback is the difficulty of extracting the third molar teeth without damaging their anterior ends.

Rates of wear of the 4-6 mandibular permanent incisors seemed to be quite variable between individuals with the same stage of attrition of the grinding teeth, and might partly reflect variation in shape and size of the pair of upper incisors. Although the arrangement of the incisors with their cutting surfaces concentrated towards the tip of the mouth would facilitate selective grass plucking, their loss with advancing age implies that they are not essential, and old warthogs observed in the field showed no apparent difficulty in grazing either short, finely tufted or tall, long leafed grasses.

TUSK LENGTH: SNOUT WIDTH RATIOS

The regression lines for the Zululand data diverged from those computed by Bradley (1972) for Kenyan warthogs. For both the yearling and subadult age classes, the range in average tusk length: snout width ratios of Zululand warthogs was markedly lower than the comparable range computed by Bradley. Although average tusk growth in warthog populations from Kenya and Zululand could differ, Bradley's sample is based largely on females and his measurements of changes in tusk length and snout width with age are derived from a total of 69 recurrent photographs of 17 identifiable individuals (15 females, two males). In Zululand however, tusk length and snout width were measured directly from shot warthogs, and the sexes were treated separately in the data analysis.

Snout width is considerably less in adult females than in adult males, notwithstanding individual variation such that tusk length: snout width ratios of warthogs with the same tusk measurements may differ by over 8% in both sexes. Bradley (1972) recognises further sources of error inherent in his method of age estimation, viz. (i) from about three years of age, inward curving of warthog tusks increases (particularly in females) until the length, measured across the arc, is no longer an accurate measure of growth; (ii) with increase in age, wear at the tusk tips detracts from annual growth; (iii) if both tusk tips break off early in life, age may later be underestimated if the breaks are not easily discernible.

In view of these limitations and the differences between the Zululand and Kenyan data, the possibility of using volume of the tusk pulp as an index of age seems worth investigating.

TOOTH SECTIONS

Problems of interpretation of the layer structure in dental tissues (e.g. Hall-Martin 1976, Gasaway, Harkness & Rausch 1978, Leader-Williams 1979) are a major source of error in mammalian age estimation using tooth sections. However, as Leader-Williams (op. cit.) points out, few accounts dwell at length on these problems or on the accuracy of the results obtained and "many authors may have given the impression of minimal difficulties, particularly when illustrating their papers with easily interpretable sections containing no problem areas." Indeed, dental layer patterns may even be unsuitable for age determination, as found by Catt (1979) using longitudinal and cross-sections through the cementum of molars, premolars and incisors of Bennett's wallaby, *Macropus rufogriseus fruticus*.

Geographical variation in the pattern of cementum deposition and in the correlation between the number of growth layers and true age may occur within a species, e.g. red deer (Mitchell 1967, Lowe 1967), caribou and reindeer (Mc Ewan 1963, Reimers & Nordby 1968, Miller 1974, Leader-Williams 1979). Although inconsistencies in the pattern of layering in relation to age and season may be attributable to environmental factors, biologists ageing animals have paid little attention to the reasons for the formation of cementum of varying composition (Leader-Williams op. cit.).

Another major difficulty is associated with the staining properties of dental cementum, since clarity of rest lines and colour contrast between rest lines and background cementum are frequently poor. This led Thomas (1977) to investigate the relative merits of a variety of stains and consequently advocate the use of metachromatic stains, particularly toluidine blue, after cemental decalcification. There is also some evidence that certain decalcifying solutions may interfere with the staining properties of cementum. Thus for example, Turner (1977) advised against the use of nitric acid for decalcifying the incisors of North American sheep, since it obliterated otherwise distinct annuli.

In the warthog, the difficulty of identifying rest lines is a source of error in age estimation, and counting errors, even of one line, would be more important in younger than in older animals. Inconsistency in the clarity and number of cementum lines throughout the length of the root emphasised the value of longitudinal sections for maximum counts. While the early pattern of cementum deposition could be interpreted in those individuals aged by tooth replacement and eruption, known-age material proved invaluable in confirming that the same annual rhythm was continued in older warthogs. Although stages of tooth wear and loss are associated with broad age classes, cementum line counts, despite their limitations, permit more precise estimation of the age of adult warthogs, especially beyond about nine or 10 years. However, in applying the cementum technique to large samples, processing could probably be streamlined by sectioning decalcified teeth with a cryostat, thus eliminating wax embedding. Indeed, satisfactory sections were cut in this way from a small number of incisors at -30°C.

Low (1970) has described cemental annulations in permanent first incisors of collared peccaries in Texas. Unless poorly defined, counts of these annulations in transverse sections cut from decalcified teeth gave a quite accurate assessment of age, although accuracy probably decreased in individuals over 10 years old. However, in 34% of peccary teeth, interpretation and counting of annuli varied from difficult to almost impossible. The pattern of formation of annulations was essentially one broad band and one narrow, darker band each year, as for more northern ungulates.

No accounts of the use of tooth sections to determine the age of warthogs and bushpigs have apparently been published, but d'Huart (1980) was able to estimate age of giant forest hogs in equatorial Africa from incremental layering in their lower incisor teeth. Using a new technique involving microradiography, d'Huart found a biannual pattern of rest lines in the dentine of sectioned incisors. Other studies of African mammals living in equatorial regions where the annual rainfall distribution is bimodal have shown the same incremental

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rhythm of two rest lines per year in the dental cementum (Spinage 1967, 1976b, Grimsdell 1973a).

Changes in the structural composition of dental tissue that result in a regular annual pattern of incremental layering are generally attributed to nutritional effects, with possible subsidiary influences of an endocrinological nature, associated with reproduction and lactation. In view of evidence that rest lines in cementum or dentine represent zones of retarded growth and disturbance in the calcification rhythm (Klevezal' & Kleinenberg 1969, Steenkamp 1975), and in African herbivores are apparently formed during dry seasons (Spinage 1967, Simpson & Elder 1969, Rautenbach 1971, Grimsdell 1973a, Spinage 1976a, Hall-Martin 1976), the occurrence of one or two rest lines per year may well be related to unimodal or bimodal nutritional depressions, reflecting the annual rainfall regime. In Zululand, the results of warthog cementum line counts showed one rest line per year, and judging by specimens where a new rest line had apparently just been formed, these lines are laid down during the dry season.

By contrast, studies of animals living in oceanic environments have shown that the formation of alternating layers of different types of cementum is rather irregular, causing inaccuracies in age estimation (Lowe 1967, Leader-Williams 1969). In an introduced herd of reindeer on a subantarctic island, Leader-Williams (op. cit.) found that rest line formation in incisor cementum was frequently aberrant with respect to season, and he suggested that variations in the space available for cementum accretion were responsible for further inconsistencies in the deposition of cementum according to the pattern expected with age and season; separation between rest lines was evidently related to cementum thickness and varied between parts of one tooth, so that there were areas of discontinuity (merging and reforming of certain rest lines) and areas of minimal or even nil-separation. Thus the variable cementum thickness and rest line separation apparent within particular warthog incisors may reflect variations in the dimensions of their alveolar sockets, which could be influenced by root movement due to chewing.

However, apart from Spinage (1976a) and Leader-Williams (1979), the probably important influence of tooth movement on variation in thickness of sequential layers laid down in any one tooth or between parts of one tooth has apparently not been generally recognised in age estimation studies based on the evaluation of tooth sections. In commenting on the differential spacing between rest lines in the molar cementum pad of a known-age black rhinoceros, Diceros bicornis, Spinage (op. cit.) suggested that alveolar and mesial shift of the tooth with increasing age may have been the causal factor initiating a change in the rate of accretion of interlamellar cementum, which did not correlate with a biphasic pattern in average annual rainfall during the animal's life.

Although physiological factors underlying the formation of cementum of varying composition remain inadequately explained (Leader-Williams 1979), most studies indicate that the relationship of cementum layering to age is usually sound in herbivores subject to consistent seasonal differences in nutrition. Nevertheless, incremental layering in warthog and other mammalian teeth should be evaluated with caution, recognising that the deposition of successive layers is subject to irregularities, and allowing for a degree of subjectivity in the interpretation of lamellae. As applied to warthog teeth, the technique could probably be improved considerably by using stains superior to haematoxylin (see Thomas 1977) for delineation of rest lines.

LONGEVITY

A tame female warthog at the Mliwane Wildlife Sanctuary, Swaziland, died at the age of 12 years (Reilly pers. comm.). Of three female warthogs captured when young in the Sudan and kept in the Giza Zoological Gardens, Egypt, two lived for 13,5 years and one for 16,5 years (Flower 1931). Crandall (1974) cites records for two warthogs received at American zoological gardens and surviving for 15,2 and 16,9 years respectively.

Based on age estimates from incremental layering in incisor cementum and the degree of wear of the last (third) molar teeth, the maximum lifespan of warthogs in Zululand is probably about 17 years. This corresponds with longevity records for warthogs in captivity, although it seems likely that maximum ages would be realised less frequently in the wild.

EYE LENS MASS

Although lens mass of Zululand warthogs permitted reasonable separation of the first two year classes and confirmed other age criteria, subsequent overlap in lens mass prevented reliable differentiation of age classes. Similar findings have been reported for warthogs in Zimbabwe, where specimens in the 2-3 year age interval already overlapped considerably with older individuals in their lens mass (Child, Sowls & Richardson 1965). The use of the lens technique to separate the first two year classes cannot be recommended however, since dental criteria provide an easier method. In collared peccaries, Low (1970) found that the regression relationship between eye lens mass and age was unreliable for age prediction beyond 24 months, even though lens mass continued to increase.

While regional differences in eye lens growth patterns of warthogs from Zululand and Zimbabwe were not apparent, it should nevertheless be recognised that lens mass/age relationships may be influenced by stress (Myers & Gilbert 1968) and nutrition (Friend & Severinghaus 1967, Morris 1972).

AGE ESTIMATION IN THE FIELD

Geigy (1955) gives photographs of two-year old male and female warthogs at a European zoo, regarding which Roth (1965) comments that "the tusks seem to be even less developed" than those of similar-aged warthogs in Zimbabwe, where they protruded about 3,0 - 4,5 cm from the lip at 20-21 months. Roth based his observation on two captive warthogs (male and female) for which the measurements apparently refer to tusk length along the outside curve. The known-age warthogs in Geigy's article were captured in Mali and Kenya and in the subsequent photographs their tusk lengths indeed appear more typical of warthogs at an early stage of the yearling age class rather than two years old.

Cumming's (1970) illustrations of the first three year classes in a Zimbabwean warthog population, based particularly on tusk development, correspond with the age categories observed in Zululand, but this does not eliminate the possibility of some geographic variation in average tusk growth and wear. In using body size as an age criterion, the occurrence of runts within some litters should be recognised, and Roth (1965) and Cumming (1970) have noted that growth is sensitive to the plane of nutrition. Both authors found that young warthogs which as a consequence of rearing conditions were virtually as large as adults, could nevertheless still be distinguished by their smaller tusks. Although tusk size apparently remains typical for at least the yearling age class, Cumming (op. cit.) suggests that wart growth may be variable in males, since warts were much larger in tame individuals whose diet had been supplemented than in wild warthogs of comparable age.

Experience in Zululand supported Cumming's (1970, 1975a) finding that subadult females cannot be reliably distinguished throughout the year, so that field classification must be based on three age classes of warthogs - juveniles, yearlings and animals older than 24 months. Very old warthogs, i.e. individuals using their last molars, are usually distinctive by virtue of their long upper tusks (Plate 4n), the tips of which may curve downwards towards the snout, particularly in females. Unless wear at the tusk tips exceeds annual growth, increase in tusk length probably continues for most of a warthog's potential lifespan, judging by old individuals in which occlusion of the pulp cavities was very advanced. Spinage & Jolly (1974) concluded that increase in length of the upper tusks, measured along the outer curve, appeared to approach an asymptote at an estimated age of about 10 years, although increase in mass continued until senescence. However, their analysis makes no allowance for sexual dimorphism in tusk growth and shape.

According to Rowland Ward's records of African game (Best & Best 1977), upper tusks of 38-43 cm in total length (measured along the outside curve as for elephant tusks) are not very uncommon; the world record warthog upper tusk (locality of collection unknown) measures 60,96 cm in total length along the outside curve, compared with 56,20 cm for the second longest recorded specimen (from Uganda). In 1965, Smithers (pers. comm.) measured an upper tusk of a warthog from Goromonzi in the Salisbury district, Zimbabwe, with a total length along the outside curve of 49,85 cm, of which 43,50 cm protruded beyond the gum line.

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CHAPTER 3

BODY COMPOSITION, MEAT PRODUCTION AND GROWTH

INTRODUCTION

Besides the use of live body mass data for the estimation and comparison of population biomass, von la Chevallerie (1970) has stressed its significance in assessing the meat production potential of wild ungulates in Africa - a field that has merited intensive study in recent years (Skinner 1970, 1973, Huntley 1971a, von la Chevallerie, Erasmus, Skinner & van Zyl 1971, von la Chevallerie & van Zyl 1971, Keep 1971, 1972, Irby 1975, Hall-Martin, von la Chevallerie & Skinner 1977). However, unless live body mass and gain in live body mass are related to body composition, they may well be inadequate or misleading indicators of the meat production potential of animals and of the primary productivity of the vegetation (Ledger 1965).

A sample of warthogs from West Africa has been measured by Bigourdan (1948), who also recorded the gain in mass of two young warthogs from one to 12 months of age, while Roth (1965) measured captive warthogs in Zimbabwe from one to 21 months of age. In addition, postnatal growth of male and female warthogs, based on the body dimensions of 110 specimens from the Nagupande area of Zimbabwe, was described by Child, Sowls & Mitchell (1965), who also recorded body mass of 36 warthogs. Hirst (1975) used published data on warthog body mass to compute theoretical von Bertalanffy growth curves for body mass of male and female warthogs up to 36 months of age.

Smith & Ledger (1965) recorded total carcass fat and full, fat-free digestive tract mass as percentages of body mass for a sample of 40 warthogs from East Africa. In a paper on the meat production attributes of wildlife, Ledger, Sachs & Smith (1967) presented information on body and carcass composition for 20 mature warthogs (see also Ledger 1968). Sachs (1967) recorded body mass and dimensions of 16 adult male and two adult female warthogs from Tanzania. Clough & Hassam (1970) determined mean live mass and mean stomach fill of 168 warthogs (71 adult males, eight yearling males and 89 adult females) from Uganda. Other East African data comprise Boshe's (1981) measurements of mean live mass of 102 Tanzanian warthogs (50 males and 52 females) which he assigned to seven age classes on the basis of the tooth eruption and wear criteria described by Spinage & Jolly (1974).

Management measures to reduce grazing pressure in areas of the Complex have included the control of warthog numbers by live capture and shooting. Cropping during the present study permitted the collection of data on warthog body composition. While cropping of game populations may involve a drain of nutrients from the ecosystem, meat and other products are a potential source of revenue that could contribute towards conservation. During game control operations from September 1959 to December 1964, a period of just over five years, 9 347 warthogs with an estimated gross mass of 590,8 metric tons and an estimated dressed carcass mass of 295,7 metric tons were removed from UGR (Bigalke 1966).

Although Hitchins (1968) recorded body mass for 102 warthogs from HGR, there is no published information on growth rates of warthogs from Zululand. Data on growth, based on measurements of individuals at different ages in the population, were collected for both pre- and postnatal warthogs. Allometric growth (change of proportions with increase in size) was investigated from body measurements of postnatal warthogs.

Apart from some values for perinephric and other fat deposits measured during autopsies of 40 warthogs from East Africa (Smith 1970), there appears to be no published information on estimation of physical condition of warthogs. Whether based on free ranging individuals or carcasses, evaluation of physical condition may be of value in assessing mortality rates among sex and age classes within a population, and for interpreting growth rates and reproductive parameters according to seasonal and environmental variations in nutritional levels of individuals and populations. Mitchell & Lincoln (1973) found evidence that body condition was an important "secondary factor" influencing the time of conception in red deer in Scotland, and could also account for year to year fluctuations in median conception dates.

Bone marrow fat content has been used as a measure of body condition in African ungulates (Sinclair & Duncan 1972, Hanks, Cumming, Orpen, Parry & Warren 1976, Sinclair 1977, Brooks, Hanks & Ludbrook 1977, Brooks 1978) and elephants (Malpas 1977). The possible occurrence of major declines in body condition of warthogs in the Complex was investigated by analysis of samples of their bone marrow, collected throughout the year.

MATERIAL AND METHODS

BODY AND CARCASS MEASUREMENTS

Although most warthogs were shot during the morning, cropping operations sometimes continued after mid-afternoon. Individuals were shot through the heart, head or neck, usually with a ,308 or ,303 calibre rifle. The warthogs were usually transported to a central site for measurement and dissection, but this was sometimes conducted in the field (Plate 5).

The body mass of each whole warthog was measured using a Salter spring balance of 100 kg capacity. Body mass as recorded in this study represents the closest approximation possible to the live mass (=liveweight) of the individual in the field at the time of collection, and therefore includes the mass of the reproductive tract and its contents in females. Bleeding by severing carotid arteries and jugular veins following shooting and before mass

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PLATE 5. Skinning and dissection of a warthog carcass in the field (Umfolozi Game Reserve, March 1974).

measuring was avoided. However, loss of blood and body fluids as a consequence of shooting inevitably occurred, and the amount lost could have been influenced by the location of the bullet wound and the time elapsing between shooting and mass measuring. No correction for this source of error was possible and several hours sometimes elapsed between shooting and recording of body mass.

The following standard body measurements, as described by Ansell (1965), were taken from 264 warthogs (129 males, 135 females) shot between June 1973 and June 1975 in the Complex:

1. Head and body length (L) - measured along the contours of the body from the tip of the snout to the junction of the tail with the body.
2. Shoulder height (H) - the linear measurement from the highest point of the withers to the base of the hoof, with the front leg held at right angles to the body as nearly as possible in the natural position, and with the hoof in a standing position, i.e. its lower surface held parallel to the anterior/posterior line of the body. The highest point of the withers was established by placing a board tangentially to the withers and perpendicular to the line of the leg.
3. Chest girth (G) - the circumference of the chest measured directly behind the front legs.
4. Hind foot length - the linear measurement from the point of the hock to the tip of the hoof.

Body mass and standard measurements were also recorded for 19 warthogs (11 males, 8 females) collected in MGR during the dry season of 1973.

Ages were derived as described in Chapter 2. Due to the limitations of cementum layer counts for age estimation, the discussion of growth and carcass parameters is based on only four age classes, viz. juvenile, yearling, 2-3 year old, and older than three years. Most growth is complete by the age of 36 months. Since warthogs in Zululand have a short, clearly defined farrowing season, the ages of warthogs within the first three year classes can be deduced to within about two months by backdating to a mean farrowing date (1 November). A combination of criteria (tusk length, stage of tooth eruption, reproductive and bodily development) was used to separate these age classes. Yearlings can be distinguished by the stage of eruption and morphometry of the third molar teeth, and 2-3 year old warthogs can usually be distinguished on the same basis. Cementum layer counts, used with caution, provided a further indicator for separating 2-3 year old warthogs from older individuals.

Scatter diagrams depicting postnatal growth were plotted for body mass against the other body measurements, and regression analysis was used to investigate criteria for predicting body mass. Growth curves for male and female warthogs were plotted by calculating mean body dimensions for each age class.

The body of each warthog, suspended head down, was dissected into three main groups of components - external offal, internal offal, and the dressed carcass (Ledger 1963, 1968), and the mass of each was recorded. The dissection technique was as follows:

1. The unskinned head, complete with tusks and tongue, was removed by severing it from the neck at the atlas joint and continuing the cut along the posterior line of the jaw.
2. The unskinned feet were removed by severing them from the legs at the carpal and tarsal joints.
3. The carcass was skinned and the tail (included with the hide) was severed at the junction of the sacral and coccygeal vertebrae.
4. The skinned carcass was opened ventrally along the anterior/posterior line of the body. After sawing through the centre of the sternum to open the thoracic cage, the cut was continued posteriorly through the abdominal wall to the pelvis, where the pubic symphysis was split medially to open the pelvic channel.
5. The diaphragm was trimmed off as close to the ribs as possible and the rectum was loosened from its attachments to the body. Leaving the kidneys plus any perinephric fat in the carcass, the body was then eviscerated (including removal of the genitalia and udder).

External offal comprises the unskinned head, feet and tail, plus the hide. Although not always measured separately, mass of the unskinned head was recorded for 169 warthogs. Internal offal comprises the abdominal viscera and contents of the thoracic cage (including diaphragm, full bladder, and alimentary tract plus digesta), omentum fat, udder, reproductive tract (including external genitalia and contents of gravid uteruses), and recoverable blood from dressing the carcass. After severing the stomach from the oesophagus and duodenum at the cardiac and pyloric sphincters, the mass of the wet stomach contents was usually measured. The dressed carcass is the eviscerated body less the external offal and diaphragm, but retaining the kidneys plus any perinephric fat. Dressing percentages (=carcass yields) were calculated on the live mass and the warm carcass mass.

Measurements of carcass length, buttock length and buttock circumference were recorded for 149 warthogs. The carcass was first split into two sides by sawing down the centre of the vertebral column. Length of carcass was measured from the anterior edge of the middle of the first rib to the mid-point of the pubic symphysis, which also provides the proximal reference point for the measurement of buttock length.

BONE MARROW FAT AS AN INDEX OF CONDITION

The relationship between percentage dry mass and percentage fat content of warthog bone marrow was investigated as described for other African ungulates by Sinclair & Duncan (1972), Hanks, Cumming, Orpen, Parry & Warren (1976), and Brooks, Hanks & Ludbrook (1977). Between 2-10 g of marrow was taken from the combined metacarpal and metatarsal bones of each warthog and mass measured to the nearest 0,1 g. Only the marrow from the central section of each bone was used, after separating and discarding the haemopoietic tissue at the ends. Since the fat content of the bone marrow is of limited use as a measure of condition in younger animals (Hanks _et al_., _op. cit_.), marrow from warthogs under two years of age was not used in this study.

Marrow samples from 203 warthogs were placed in beakers and oven-dried at 100° C for 10 days, which allowed attainment of relatively constant mass, i.e. further decrease in mass of individual samples concomitant with a longer drying period did not exceed a few centigrams on succeeding days. The dry mass was expressed as a percentage of the fresh mass. A selection of the dried samples with percentage dry mass values ranging from low to high were then transferred to a Soxhlet apparatus and fat was extracted with petroleum ether (b.p. 30-60°C) for eight hours. After drying overnight at 60°C, the fat extracted from each sample was mass measured and expressed as a percentage of the fresh mass of bone marrow.

Fat content of bone marrow samples from 42 warthogs was analysed and the regression equation relating percentage fat to percentage dry mass was calculated. Since this relationship had a very high positive correlation ($r = 0{,}999$), further fat extraction was not undertaken as fat content could be predicted from the percentage dry mass.

MUSCLE FIBRE DIAMETER

Muscle fibre thickness is an important determinant of meat quality as it determines the coarseness of grain and texture of the meat (von la Chevallerie (1972). Meat samples of about 8,0 cm^3 were taken from the m. longissimus dorsi of five warthogs at the third lumbar vertebra, and fixed in 10% formalin. Muscle fibre diameter was measured from subsamples of these meat cubes according to the method described by Joubert (1956) and was expressed as the mean diameter of 25 fibres.

RESULTS

BODY MASS

Although blood and evaporation loss after shooting are sources of error, the data on body mass are a close approximation to the live mass of the warthog. Several other factors which influence individual body mass were investigated:

Sex

In most African ungulates mature males are heavier than mature females (von la Chevallerie 1970). This sexual dimorphism is marked in the warthog and the heaviest males may exceed the mass of the heaviest females by up to 50% (Table 5).

Age

The mean body mass, in relation to the standard deviation and range, for four different age groups of warthogs is shown in Table 5. Differences in mean body mass of warthogs in the yearling, subadult and adult age groups were significant for both sexes. Thus examination of the effects of season on body mass was confined to warthogs at least three years old, by which age most growth in body mass is complete.

Season

Females were classified according to pregnancy and it was found that pregnant females were significantly heavier than non-pregnant females in both yearling ($P < 0{,}01$) and subadult ($P < 0{,}05$) age classes. However, there was no significant difference in body mass between pregnant and non-pregnant adult females.

The seasonal changes in body mass of male and female warthogs at least three years of age are shown in Fig. 11. Mean body mass of both sexes was lowest during September, notwithstanding the advanced stage of pregnancy of all females examined at this time. Comparison of seasonal groupings (Table 6) showed highest body mass of both males and females during the period March to

TABLE 5. Body mass (kg) of warthogs of different age groups from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973-June 1975.

Age class*	n	Mean	S.D.†	Range
(a) Males				
Juvenile**	4	6,1	9,6	1,0- 20,5
Yearling	39	42,5	10,1	21,2- 58,3
Subadult	33	63,9	9,8	45,8- 80,4
Adult	56	79,6	10,0	59,3-103,9
All males	132	62,5	20,9	1,0-103,9
(b) Females				
Juvenile**	6	8,6	8,1	1,0- 18,8
Yearling	27	36,6	8,5	21,5- 50,7
Subadult	31	47,8	6,3	39,4- 66,6
Adult	74	56,5	5,4	44,6- 69,1
All females	138	48,6	13,1	1,0- 69,1

* Using a mean farrowing date (1 November) to indicate the start of the annual population cycle, when all individuals in a particular year class are considered to pass into the next age class. Juvenile = birth-12 months; yearling = 12-24 months; subadult = 24-36 months; adult = more than 36 months.

† S.D. = standard deviation.

** Including three live neonates.

TABLE 6. Body mass (kg) of adult warthogs in different seasons, Hluhluwe-Corridor-Umfolozi Game Reserve complex, July 1973-June 1975.

Season	n	Mean	S.D.	Range
Males				
July-October	14	76,6	8,9	59,3- 87,0
November-February	27	77,8	10,8	60,2- 98,2
March-June	15	85,5	6,9	74,6-103,9
Females (including reproductive tract)				
July-October	26	55,7	4,7	46,0- 62,0
November-February	22	54,5	4,2	44,6- 63,1
March-June	26	59,0	6,2	46,0- 69,1

June.

Among adult males, body mass was lowest during July to October, the period of poorest veld conditions, but was not significantly different from body mass during November to February. However, the March to June group was significantly heavier than the November to February group, 85,5 kg c.f. 77,8 kg ($P < 0{,}02$). In the case of females the March to June group was significantly heavier than the November to February group, 59,0 kg c.f. 54,5 kg ($P < 0{,}01$) but there was no significant difference between the July to October and November to February groups. During September and October pregnant females were in the last third of gestation. Since body mass includes mass of the gravid uterus, the comparatively low values observed during July to October, when only one of the 26 females examined was not pregnant, probably reflect the lowered plane of nutrition during the dry season. The 22 adult females examined during November to February included only five pregnant animals, of which the last was collected on 11 November.

The mass of the gravid reproductive tract was recorded separately (Table 7) for only three adult females, all in advanced pregnancy (the mean mass of the most developed foetuses was about 100 g less than the estimated mean birth mass). Although this sample is small and foetal growth was incomplete, the data indicate that the gravid uterus may comprise over 7% of live mass of the female. Thus the mean body mass of females during July to October would have been slightly lower if the extra mass of foetuses and amniotic fluid had been subtracted.

TABLE 7. Mass of reproductive tract plus contents as a component of body mass of female warthogs in advanced pregnancy, Hluhluwe-Corridor-Umfolozi Game Reserve complex. (All mass values in kg).

Age class	Date	Body mass	Mass of gravid reproductive tract*	Gravid reproductive tract as % of body mass	No. of foetuses	Total foetal mass	Mass of wet stomach contents
Yearling	74-10-25	48,6	3,7	7,6	3	2,1	0,7
Subadult	74-11-02	41,7	1,8	4,3	2	1,0	0,1
Adult	74-11-02	60,0	3,8	6,3	4	2,1	0,6
Adult	74-11-09	49,6	3,6	7,3	3	2,1	0,8
Adult	74-11-11	58,8	3,5	6,0	3	2,0	1,8

*Including full bladder and vagina.

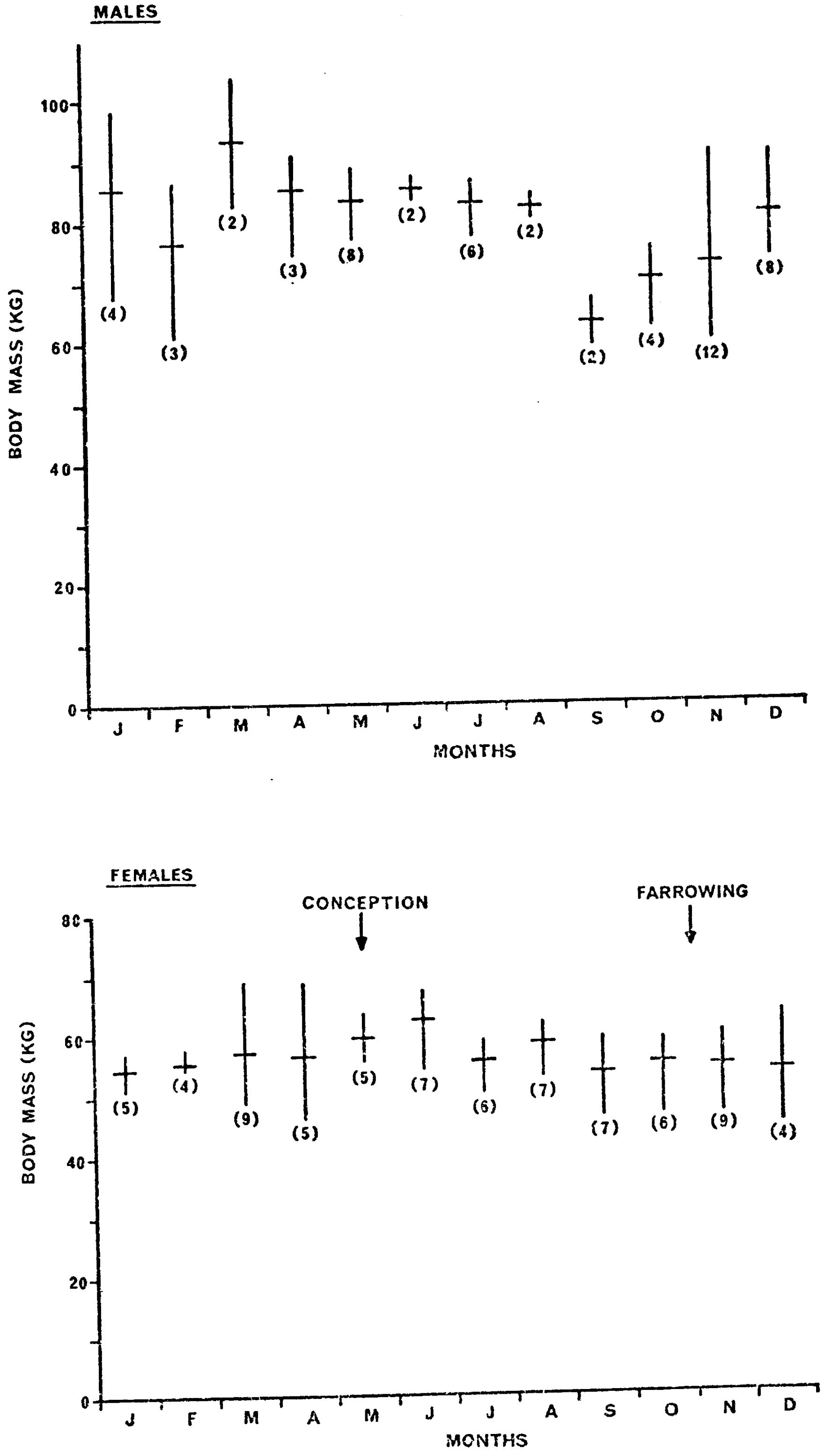

FIG. 11. Seasonal changes in body mass of adult warthogs (at least three years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex (males: July 1973 - May 1975; females: July 1973 - June 1975; range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

Stomach fill

Stomach fill (wet mass) as a percentage of body mass (Table 8) ranged from 0,4 to 7,7% in adult males (n = 42) compared with 0,3 to 9,1% in adult females (n = 57). The heaviest individual stomach fills for adult males and females were 5,7 kg and 5,8 kg respectively. Thus it appears that stomach fill has a greater influence on body mass of females than of males.

Although abdominal space could be expected to decrease with advancing pregnancy so that stomach fill might also decrease in consequence, no correlation between gestation time and stomach fill was apparent (Fig. 12). Indeed, the mean stomach fill as a percentage of body mass in pregnant adult females was significantly higher than in non-pregnant adult females ($P < 0{,}05$). Pregnant adult females had more food in their stomachs than non-pregnant adult females and the difference was almost statistically significant at the 5% level ($t = 1{,}97$; d.f. = 55), but there was no significant difference in mean body mass. However, variations in stomach fill with time of day (Fig. 13) could account for the observed difference between pregnant and non-pregnant females and, when pregnancy is advanced, could mask any compression effect of the gravid tract on abdominal space available for stomach contents. Temporal variation in stomach fill was inadequately quantified, but the possibility remains that a higher stomach fill among pregnant females could be a response to lower quality grazing during the dry season in relation to the nutritional demands of females during the last third of pregnancy. A comparison of mean stomach fill as a percentage of body mass for adult males showed no significant difference between the dry season (April to September) and the wet season (October to March).

BODY COMPOSITION

Although the dressed carcass composition is of primary importance for assessing meat production, "body composition data are useful in studies of the amount of meat, viscera and other body parts consumed by predators, scavengers or decomposers; and as a means of assessing live mass of an animal by prediction methods" (Hall-Martin, von la Chevallerie & Skinner 1977). Three main groups of body components as a percentage of body mass for warthogs of different age groups are given in Table 9, and carcass measurements are given in Table 10. During dissection some loss of mass due to evaporation, etc. inevitably occurred, but did not exceed 1% of the body mass.

In the adult age class, males had a significantly higher mean carcass dressing percentage than females, 55,1 c.f. 51,8 ($P < 0{,}001$), despite the relatively greater mass of the head in males. The unskinned head as a percentage of body mass for adult males (n = 37; $\bar{x}$ = 13,2% ; range = 11,5 - 16,0%) was significantly greater ($P < 0{,}001$) than for adult females (n = 47; $\bar{x}$ = 11,9% ;

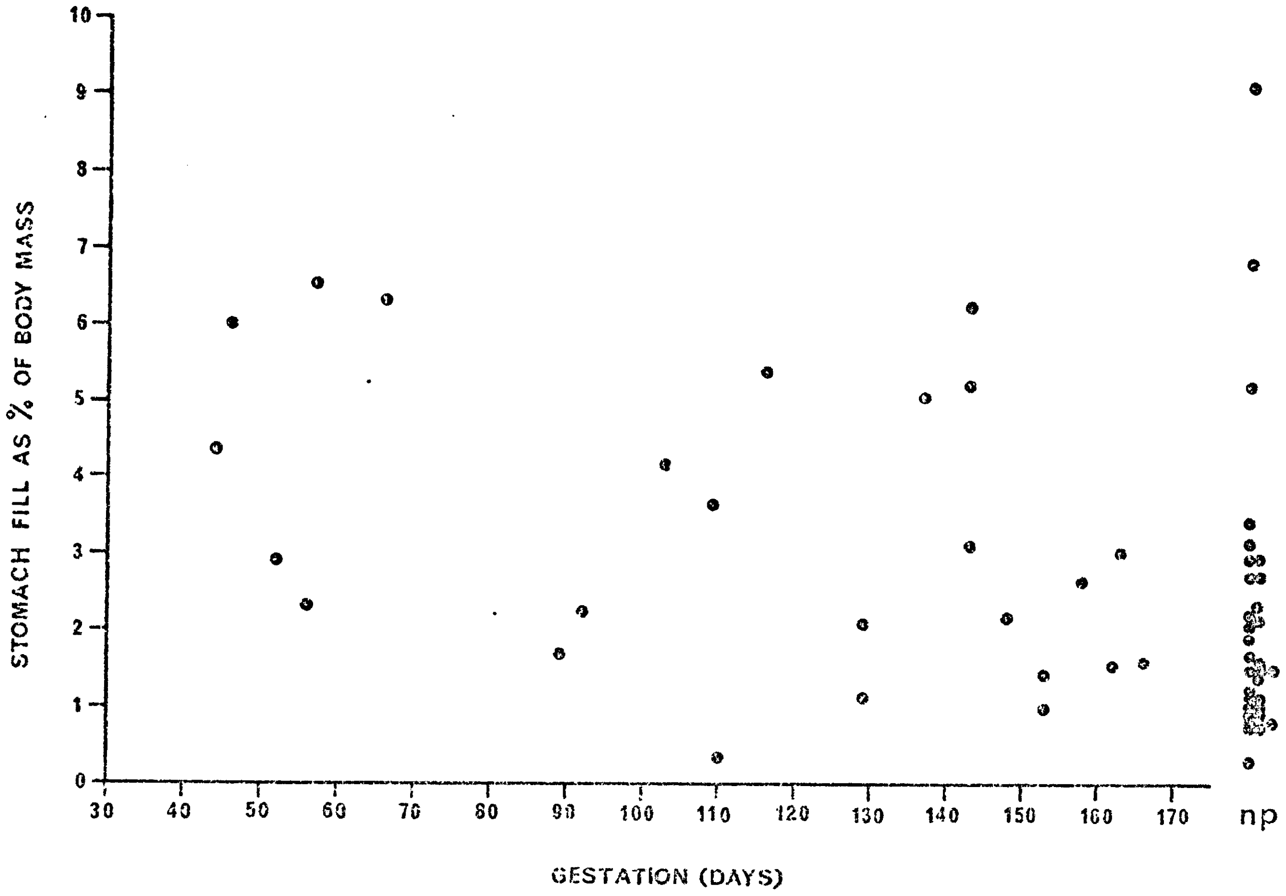

FIG. 12. Stomach fill of adult female warthogs as a percentage of body mass at gestation time. np = non-pregnant.

range = 10,4 - 13,5%). External offal as a percentage of body mass was significantly greater in males than in females ($P < 0,001$). However, internal offal as a percentage of body mass was significantly greater in females ($P < 0,001$).

Carcass dressing percentages of males were also significantly higher ($P < 0,01$) than for females in the subadult age class, but in the case of yearlings the mean carcass dressing percentage was significantly higher in females ($P < 0,05$). Comparison of external offal as a percentage of body mass between males and females showed no significant differences for either yearlings or subadults. The percentage contribution to body mass of internal offal was not significantly different between yearling males and females, but among subadults was significantly higher in females ($P < 0,01$).

When carcass yields of pregnant and non-pregnant adult females were

TABLE 8. Wet mass (kg) of stomach contents of warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, for the period December 1973 to May 1975.

Sex & age class*	n	Mean body mass	S.D.	Range	Mean wet mass of stomach contents	S.D.	Range	Mean stomach fill as % of body mass	S.D.	Range
Yrlg.♂♂	31	40,5	9,7	21,2 - 57,2	1,0	0,6	0,2 - 2,8	2,4	1,2	0,5 - 5,8
Subad.♂♂	23	66,1	9,2	47,0 - 80,4	1,4	1,0	0,2 - 4,8	2,1	1,4	0,3 - 6,4
Ad.♂♂	42	80,9	9,5	59,3 - 103,4	1,8	1,3	0,4 - 5,7	2,3	1,6	0,4 - 7,7
Juv.♀♀	2	16,3	-	13,8 - 18,8	0,4	-	0,3 - 0,5	2,4	-	2,2 - 2,7
Pregnant yrlg.♀♀	9	43,3	4,0	39,4 - 50,7	0,8	0,6	0,4 - 1,9	1,9	1,1	0,9 - 3,8
Non-pregnant yrlg.♀♀	14	35,2	7,5	23,0 - 47,0	0,6	0,3	0,2 - 1,1	1,8	1,0	0,7 - 3,6
All yrlg.♀♀	23	38,4	7,5	23,0 - 50,7	0,7	0,4	0,2 - 1,9	1,8	1,0	0,7 - 3,8
Pregnant subad.♀♀	6	52,6	9,2	41,7 - 66,6	1,4	1,0	0,1 - 2,6	2,7	2,1	0,2 - 5,3
Non-pregnant subad.♀♀	15	47,8	5,2	39,4 - 60,4	1,3	0,7	0,4 - 3,0	2,7	1,5	1,0 - 6,4
All subad.♀♀	21	49,1	6,7	39,4 - 66,6	1,3	0,8	0,1 - 3,0	2,7	1,6	0,2 - 6,4
Pregnant ad.♀♀	25	56,8	4,5	47,1 - 64,2	1,9	1,1	0,2 - 3,8	3,3	1,9	0,3 - 6,5
Non-pregnant ad.♀♀	32	56,8	5,9	44,6 - 69,1	1,3	1,2	0,2 - 5,8	2,2	1,9	0,3 - 9,1
All ad.♀♀	57	56,8	5,3	44,6 - 69,1	1,5	1,2	0,2 - 5,8	2,7	1,9	0,3 - 9,1

*juv. = juvenile (birth - 12 months)
yrlg. = yearling (12 - 24 months)
subad. = subadult (2 - 3 years)
ad. = adult (≥3 years)

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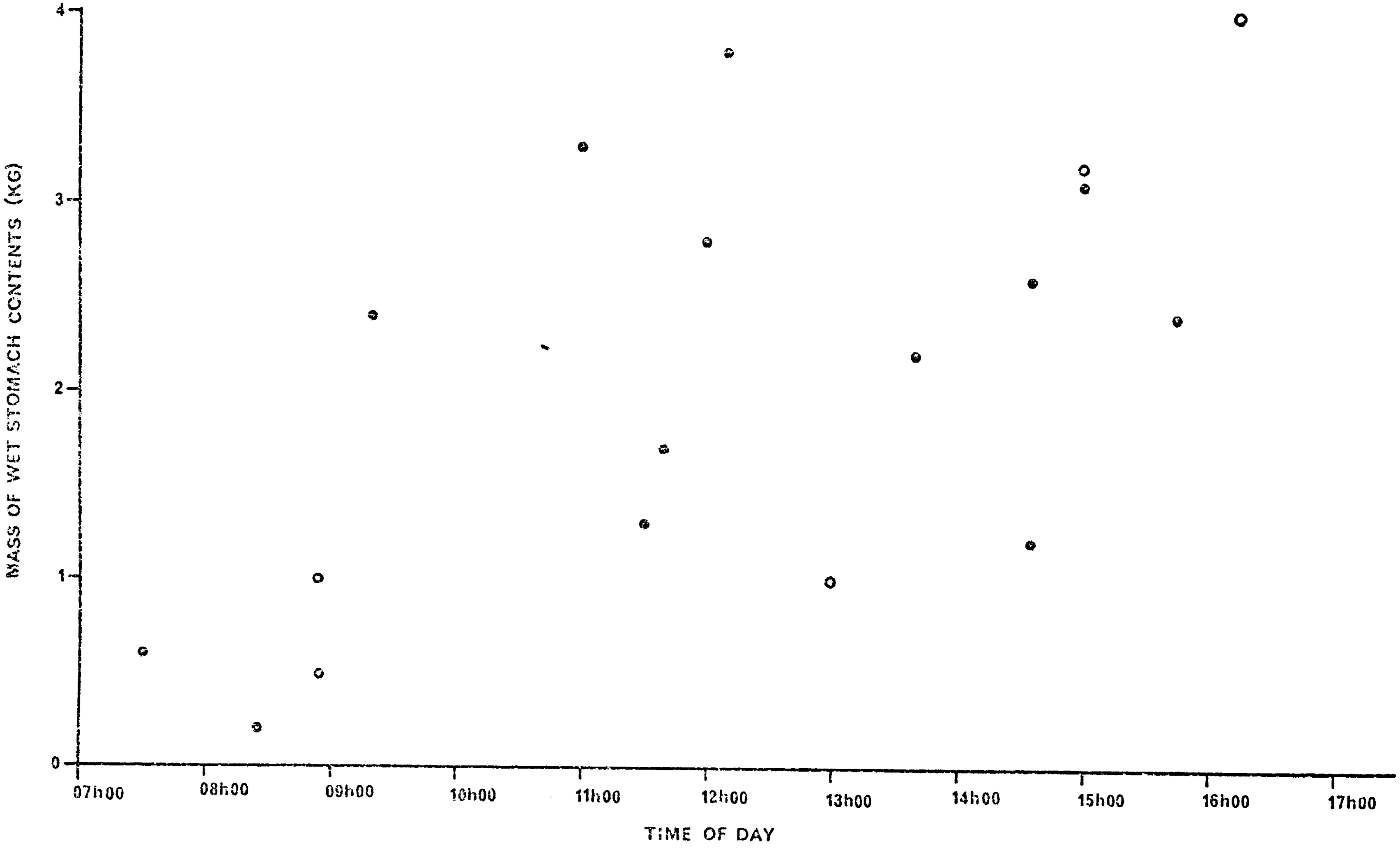

FIG. 13. Stomach fill of female warthogs at least two years of age in relation to time of day. ⊕ = pregnant, o = non-pregnant.

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TABLE 9. Body composition of warthogs of different age groups from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, August 1973 - May 1975.

	MALES					FEMALES			
	n	Mean	S.D.	Range		n	Mean	S.D.	Range
					Juvenile				
					Body mass (kg)	2	16,9	-	15,0-18,8
					Unskinned head (kg)	2	2,2	-	2,0-2,4
					Dressed carcass (kg)	2	8,8	-	8,0-9,6
					As % of body mass:				
					Dressed carcass	2	52,2	-	51,1-53,3
					External offal	2	19,3	-	18,6-20,0
					Internal offal	2	28,5	-	26,7-30,3
Yearling					Yearling‡				
Body mass (kg)	35	42,3	10,5	21,2-58,3	Body mass (kg)	23	35,3	8,3	21,5-48,6
Unskinned head (kg)	23	4,8	1,3	2,6- 7,4	Unskinned head (kg)	17	4,1	1,1	2,6- 5,6
Dressed carcass (kg)	35	22,5	5,7	11,2-31,6	Dressed carcass (kg)	23	19,1	4,4	11,4-26,4
As % of body mass:					As % of body mass:				
Dressed carcass	35	53,2	2,0	46,8-57,1	Dressed carcass.	23	54,4	1,8	50,7-57,1
External offal	35	19,7	1,3	16,7-22,7	External offal	23	19,2	1,0	17,6-21,4
Internal offal	35	26,8	2,1	23,0-32,5	Internal offal	23	26,1	2,0	22,6-30,4
Subadult					Subadult‡				
Body mass (kg)	26	64,7	10,1	47,0-80,4	Body mass (kg)	22	48,0	6,5	39,4-66,6
Unskinned head (kg)	20	7,7	1,4	5,6- 9,7	Unskinned head (kg)	17	5,7	0,9	4,8- 7,3
					Udder* (kg)	2	0,34	-	0,30-0,37
Dressed carcass (kg)	26	35,4	5,5	25,5-46,3	Dressed carcass (kg)	22	25,5	4,0	20,2-36,2
As % of body mass:					As % of body mass:				
Dressed carcass	26	54,9	1,5	52,2-59,0	Dressed carcass	22	53,1	2,5	48,5-58,8
External offal	26	19,8	0,8	18,2-22,2	External offal	22	19,8	1,7	17,9-25,4
Internal offal	26	25,1	1,6	21,9-28,0	Internal offal	22	26,9	2,6	20,5-33,1
Adult					Adult (non-pregnant)				
Body mass (kg)	45	80,7	9,4	62,6-103,9	Body mass (kg)	34	56,3	5,9	44,6-69,1
Unskinned head (kg)	37	10,6	1,3	8,2-13,1	Unskinned head (kg)	25	6,8	0,6	5,7-7,7
					Udder* (kg)	9	0,52	0,22	0,34-0,96
Dressed carcass (kg)	45	44,5	5,5	31,2-59,0	Dressed carcass (kg)	34	29,8	3,6	23,7-39,2
As % of body mass:					As % of body mass:				
Dressed carcass	45	55,1	2,5	49,6-59,7	Dressed carcass	34	52,9	2,7	47,2-58,4
External offal	45	20,9	1,4	18,1-25,6	External offal	34	19,9	1,2	16,9-22,4
Internal offal	45	23,7	2,4	16,8-29,6	Internal offal	34	26,9	2,4	22,5-32,4
					Adult (pregnant)				
					Body mass (kg)	26	56,6	4,8	46,4-64,2
					Unskinned head (kg)	22	6,7	0,8	5,6-8,4
					Dressed carcass (kg)	26	28,6	3,6	21,1-33,7
					As % of body mass:				
					Dressed carcass	26	50,4	3,3	42,4-56,3
					External offal	26	19,4	1,0	17,5-21,2
					Internal offal	26	29,9	3,3	23,2-36,2

‡ Including pregnant females

*Lactating, post-parturient females.

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TABLE 10. Carcass measurements (cm) of warthogs of different age groups from the Hluhluwe – Corridor – Umfolozi Game Reserve complex, August 1973 – May 1975.

	MALES				FEMALES			
	n	Mean	S.D.	Range	n	Mean	S.D.	Range
Juvenile								
Carcass length					2	46,5	-	46,4–46,6
Buttock length					2	30,3	-	29,0–31,5
Buttock circumference					2	35,4	-	32,8–38,0
Yearling								
Carcass length	25	60,6	5,1	50,6–67,5	14	57,2	4,4	50,5–63,7
Buttock length	25	37,5	2,1	32,5–40,8	14	35,7	2,6	31,5–39,4
Buttock circumference	25	46,8	4,5	37,5–54,0	14	45,1	3,5	39,8–51,3
Subadult								
Carcass length	18	68,2	3,8	62,0–74,0	11	63,4	3,0	59,2–69,6
Buttock length	18	41,9	1,9	37,0–45,3	11	38,7	1,8	35,2–41,5
Buttock circumference	18	54,8	3,9	49,6–60,8	11	49,3	2,9	44,8–54,8
Adult								
Carcass length	33	73,7	2,9	68,0–79,3	42	67,2	2,3	62,5–71,1
Buttock length	33	43,8	2,0	39,7–49,5	42	38,9	1,5	37,0–42,7
Buttock circumference	33	57,9	3,1	51,4–64,1	42	51,3	2,8	44,0–57,5

compared, it was found that the former had significantly lower carcass dressing percentages ($P < 0,01$), reflecting the larger component of internal offal among females in the later stages of pregnancy. Internal offal as a percentage of body mass was significantly higher in pregnant compared to non-pregnant adult females ($P < 0,001$), but there was no significant difference in percentage of external offal. The gravid reproductive tract (including full bladder and vagina) of three adult females in advanced pregnancy (Table 7) comprised from 18,2 to 24,7% of the mass of internal offal, of which 10,4 to 14,4% constituted foetal mass alone.

Regression equations for the prediction of body mass from carcass measurements, together with correlation coefficients (r), are given in Table 11. The highest correlation coefficients were found for the relationship between carcass length and body mass in both sexes. Although still highly significant, the same relationship gave a distinctly lower correlation when adults (the largest age class component of the sample) were treated separately.

Since body mass is affected by variations in stomach fill and stage of pregnancy, dressed carcass mass could be expected to provide a better indication of seasonal trends in body condition. Seasonal variations in dressed carcass mass of adult warthogs are shown in Fig. 14. Mean dressed carcass mass of both sexes was lowest during September, October and November. However, the subsequent increase in mean dressed carcass mass of males, reflecting the improved grazing after the commencement of the wet season (about October), appeared retarded in females. Mean dressed carcass mass of females remained low during November and December, probably as a consequence of the demands of nursing young. The peaks in mean dressed carcass mass of males and females occurred during March and May respectively. These differences were also apparent when seasonal groupings were compared (Table 12), although mean dressed carcass mass of both sexes was highest during the period March to June. Among males, the March to June group was significantly heavier than the November to February group, 47,9 kg c.f. 43,8 kg ($P < 0,05$), which in turn was significantly heavier than the July to October group, 43,8 kg c.f. 39,0 kg ($P < 0,05$). In the case of females there was no significant difference between the July to October and November to February groups but the March to June group was significantly heavier than the November to February group, 31,2 kg c.f. 28,0 kg ($P < 0,01$).

BONE MARROW FAT AS AN INDEX OF CONDITION

The relationship between percentage fat content and percentage dry mass of warthog bone marrow, shown in Fig. 15, had a very high positive correlation ($r = 0,999$). The prediction of percentage fat content (y) from percentage dry mass (x) is given by the regression equation: $y = 1,0065x - 6,1384$. The slope of the regression line is sufficiently close to unity to allow a more general formula $y = x - a$ where a is a constant representing the non-fat residue in the marrow (Sinclair & Duncan 1972). For the purpose of condition evaluation based on marrow fat estimates, the following approximation was therefore used: % marrow fat = % dry mass - 6.

Percentage dry mass values were used subsequently to estimate the fat content of bone marrow from a further 161 warthogs at least two years of age. The variation in percentage fat content is shown in Fig. 16. On the basis of visual appearance, most marrow samples could be classified as white and waxy, i.e. high fat content (see Els 1973). Indeed, 83% of females and 74% of males had bone marrow with a fat content of at least 70%.

Analysis of seasonal trends in bone marrow fat content (Table 13) showed lowest values during the period November to February. However, the observed pattern is confounded by age (lower marrow fat values could be expected for old individuals), and is somewhat out of phase with the pattern in body mass and

TABLE 11. Regression equations of carcass length, buttock length and buttock circumference on body mass of warthogs from the Hluhluwe - Corridor - Umfolozi Game Reserve complex, August 1973 - May 1975.

	n	Regression equation†	r value	Significance
(i) Carcass length/body mass				
Adult males	33	-	0,699	* * *
All males[1]	76	$y=64,0+2,8(x-68,1)$	0,949	* * *
Adult females	42	-	0,560	* * *
All females[2]	69	$y=49,7+2,0(x-64,0)$	0,931	* * *
(ii) Buttock length/body mass				
Adult males	33	-	0,269	N.S.
All males	76	$y=64,0+5,2(x-41,3)$	0,858	* * *
Adult females	42	-	0,376	*
All females	69	$y=49,7+3,8(x-37,9)$	0,787	* * *
(iii) Buttock circumference/body mass				
Adult males	33	-	0,772	* * *
All males	76	$y=64,0+3,1(x-53,5)$	0,945	* * *
Adult females	42	-	0,722	* * *
All females	69	$y=49,7+2,5(x-49,3)$	0,907	* * *

[1] Comprising 33 adults, 18 subadults and 25 yearlings.

[2] Comprising 42 adults, 11 subadults, 14 yearlings and 2 juveniles.

† $y=\bar{y}+b(x-\bar{x})$, where y = body mass in kg, x= carcass or buttock measurement in cm.

$***$ $P<0,001$; $*$ $P<0,02$; N.S.=non-significant.

TABLE 12. Dressed carcass mass (kg) of adult warthogs in different seasons, Hluhluwe - Corridor - Umfolozi Game Reserve complex, August 1973 - May 1975.

Season	n	Mean	S.D.	Range
Males				
July - October	11	39,0	6,7	24,6 - 45,5
November - February	22	43,8	5,7	34,3 - 55,4
March - June	14	47,9	3,9	42,8 - 59,0
Females				
July - October	21	28,5	3,5	21,1 - 33,7
November - February	20	28,0	2,3	24,2 - 33,0
March - June	22	31,2	3,7	23,7 - 39,2

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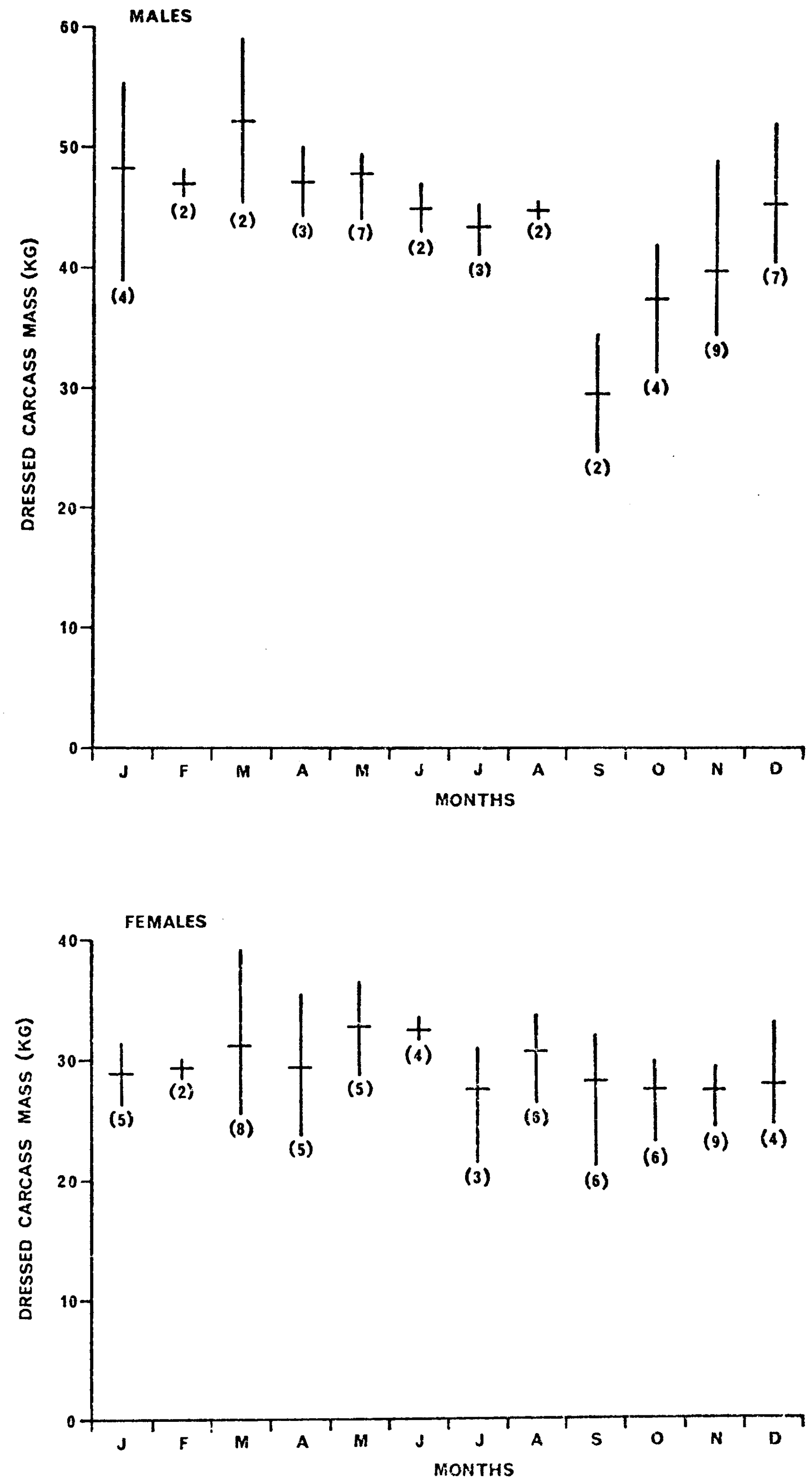

FIG. 14. Seasonal changes in dressed carcass mass of adult warthogs (at least three years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex (males: August 1973 - May 1975; females: September 1973 - May 1975; range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

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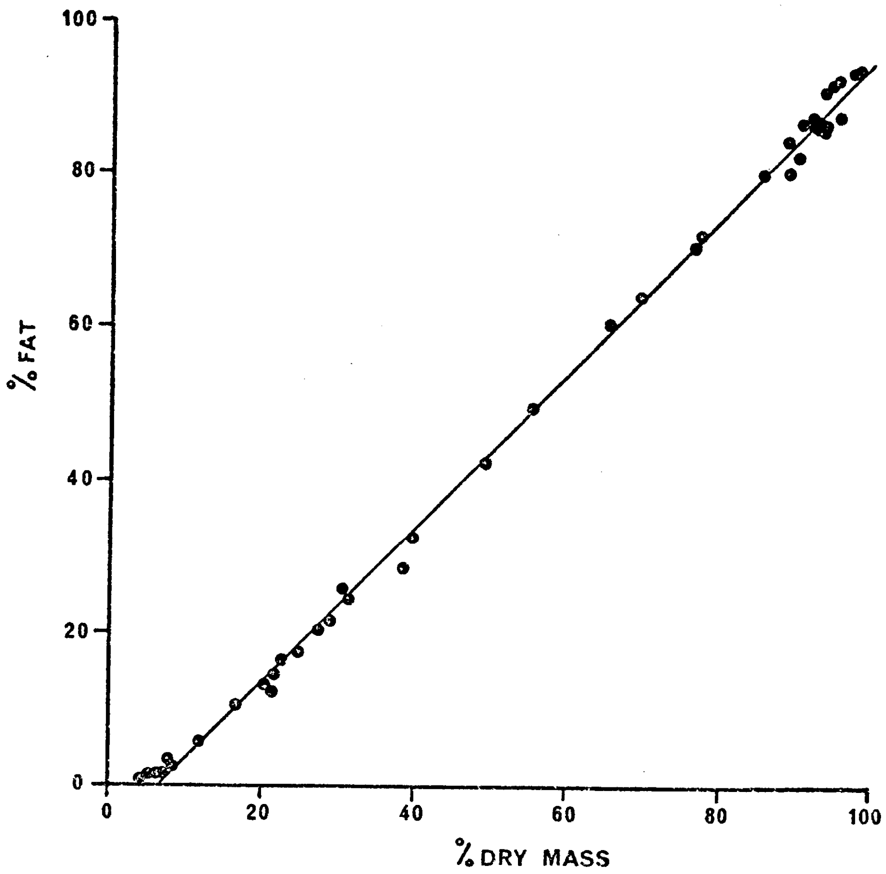

FIG. 15. The relationship between percentage fat content and percentage dry mass of warthog bone marrow (n = 42).

TABLE 13. Percentage bone marrow fat content of warthogs (at least two years of age) in different seasons, Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - June 1975.

Season	n	Mean	S.D.	Range
Males				
July - October	25	65,62	31,56	0,83 - 92,11
November - February	39	63,01	27,25	10,27 - 90,58
March - June	34	85,35	4,86	70,78 - 95,48
Females				
July - October	32	83,76	10,58	44,54 - 93,24
November - February	33	63,37	28,86	1,28 - 90,02
March - June	38	82,59	9,65	31,68 - 89,38

dressed carcass mass (see Tables 6 & 12). Thus mean bone marrow fat content of females was unexpectedly high for the period July to October, when most females are pregnant. Analysis of the relationship between marrow fat reserves (divided into two classes) and body mass was limited to warthogs at least three years of age (Table 14). Adult warthogs with marrow fat reserves above 70% were significantly heavier than those with less than 70% fat in their bone marrow (males : $P<0,05$; females: $P<0,01$).

TABLE 14. Body mass (kg) of adult warthogs (at least three years of age) in relation to two classes of bone marrow fat content, Hluhluwe-Corridor-Umfolozi Game Reserve complex, July 1973 - June 1975.

	< 70% marrow fat				>70% marrow fat			
	n	Mean	S.D.	Range	n	Mean	S.D.	Range
Males	15	74,8	11,3	59,3 - 91,5	37	81,6	9,2	61,0 - 103,9
Females	12	53,0	4,0	44,6 - 58,0	54	57,6	4,9	46,0 - 69,1

MUSCLE FIBRE DIAMETER

Mean muscle fibre diameters of three yearlings, one subadult and one adult warthog are presented in Table 15. The overall mean fibre diameter was 66,6 µm and the difference between the yearlings and older animals was marked.

TABLE 15. Muscle fibre diameter (µm) from m. longissimus dorsi of five warthogs from Zululand (1 µm = 0,001 mm).

Sex and age	Locality	Date of collection	Total body mass (kg)	Muscle fibre diameter	
				Range	Mean
Yearling ♀*	MGR	73-09-06	40,0	40-78	54,7
Yearling ♂	UGR	74-06-01	46,6	40-90	62,9
Yearling ♂	UGR	74-05-25	49,5	48-86	62,8
Subadult ♂	UGR	73-09-24	74,0	48-106	73,5
Adult ♂	UGR	73-08-26	80,5	58-120	79,1

*Pregnant

POSTNATAL GROWTH

When mean body dimensions for each age class were calculated (Table 16),

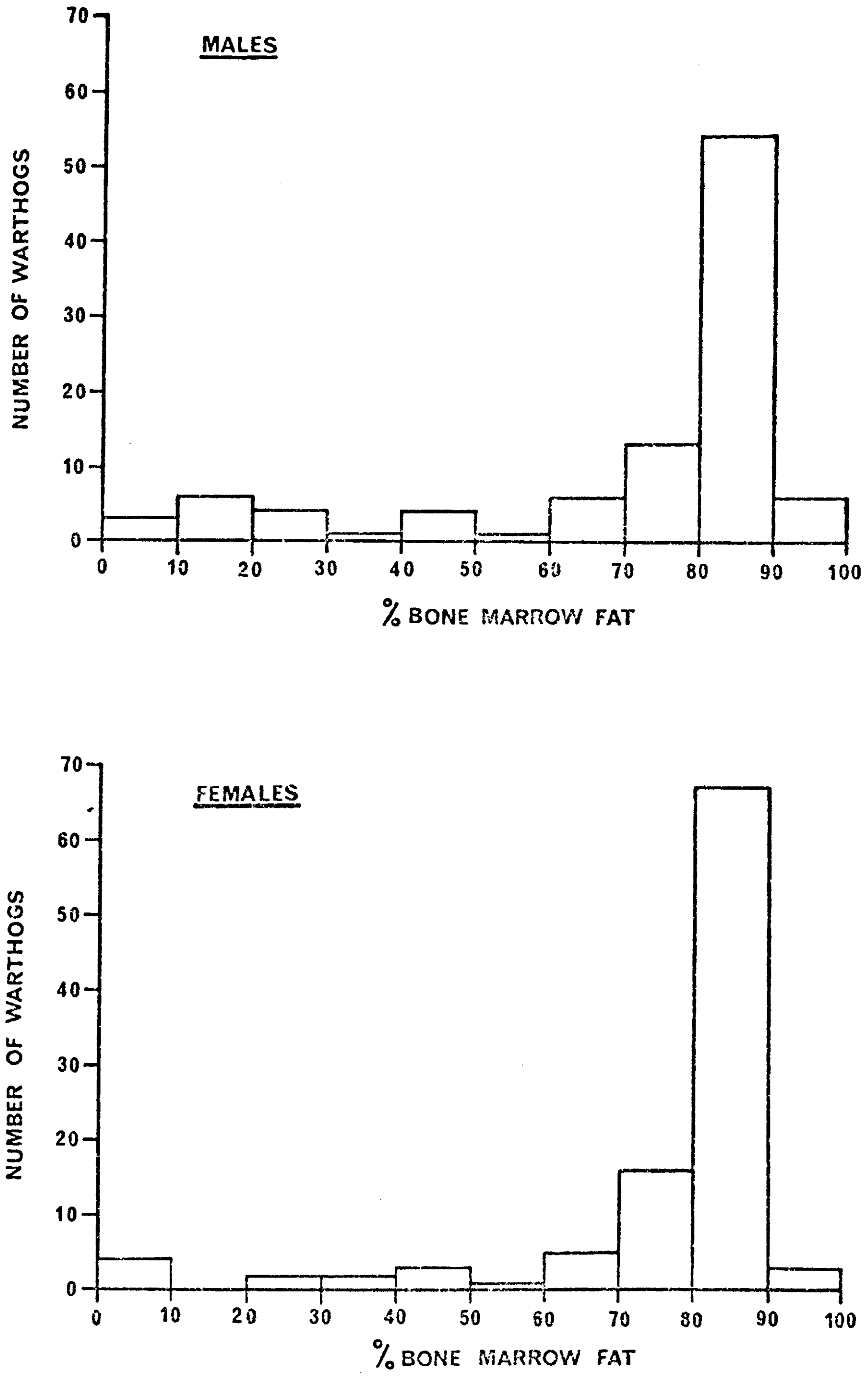

FIG. 16. Histograms showing the variation in percentage bone marrow fat content of 201 warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - June 1975.

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clear sex-specific differences in growth rate were evident. By extrapolating back to a mean farrowing date (1 November), the ages of warthogs up to 36 months were estimated and used to plot growth curves (Figs. 17, 18 & 19). Growth in head and body length, shoulder height, chest girth and body mass is most rapid during the first 16 - 17 months. Although the sexes are about the same size at birth, sexual dimorphism appears during the yearling stage and becomes pronounced in the subadult age class. In adults, head and body length, head length, shoulder height, and chest girth of males exceeded the corresponding mean dimensions of females by 11,9, 12,5, 14,0, and 16,1% respectively. Data for the juvenile age class were insufficient to validate separation of the sexes. However, sex-specific growth differences prior to the age of 12 months are probably slight and easily obscured by individual variation in size, and were not noticeable in the field.

By the age of 12 months, male and female warthogs attained respectively 68 and 73% of the mean head and body lengths of adults. Growth in head and body length was 92% complete in females at the age of 24 months, but 24- month-old males were some 13% smaller than adult males. Mean shoulder heights of males at 12 and 24 months of age were respectively 72 and 90% of the corresponding dimension for adult males. At 12 months females averaged 82% and at 24 months 95% of the shoulder height of adult females. Indeed, the lower range of shoulder heights and, to a lesser extent, head and body lengths, displayed by adult animals may be attained by two years of age in both sexes. With the exception of hind foot length which reaches an asymptote at the early age of approximately 16 months in both sexes, all the other body measurements approach their asymptotic values earlier in females.

Notwithstanding considerable individual variation in age-specific body dimensions, seasonal effects are noticeable in the growth patterns (Figs. 17, 18 & 19). Yearlings grow rapidly between 12 and 16 - 17 months of age, corresponding with the wet season, but the growth rate slows during the subsequent dry season.

Body mass and other size parameters were also recorded for 19 warthogs collected in MGR during the dry season of 1973 (Table 17). Although the sample is small, the size parameters of the Mkuzi warthogs tended to be lower than corresponding dry season values for comparable warthogs from the Complex, which is possibly indicative of poorer physical condition in the Mkuzi population.

ALLOMETRIC GROWTH

Following preliminary examination of the relationship between body mass and dimensions by plotting scatter diagrams, curvilinear regression equations for each relationship were calculated for males and females separately (Table 18).

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TABLE 16. Body dimensions (cm) of warthogs of different age groups from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - June 1975.

	MALES				FEMALES			
	n	Mean	S.D.	Range	n	Mean	S.D.	Range
CHEST GIRTH								
Juvenile	4	32,2	19,7	21,0 - 61,5	6	37,5	15,3	21,3 - 53,6
Yearling	39	75,3	8,0	58,6 - 89,0	27	70,6	6,7	57,3 - 81,0
Subadult	33	88,3	5,7	74,2 - 99,7	31	78,6	4,5	71,0 - 88,1
Adult	56	95,8	5,6	82,9 - 106,2	74	82,5	4,2	72,0 - 91,6
SHOULDER HEIGHT								
Juvenile	4	25,6	13,9	18,0 - 46,4	6	30,5	12,3	18,0 - 44,8
Yearling	39	57,4	4,8	48,1 - 67,5	27	53,9	3,5	47,0 - 60,7
Subadult	33	64,3	3,0	57,2 - 71,4	31	57,8	2,7	53,6 - 65,6
Adult	56	68,2	2,6	61,2 - 72,0	74	59,8	2,3	54,3 - 65,7
HEAD AND BODY LENGTH								
Juvenile	4	47,3	26,2	32,0 - 86,3	6	57,6	24,6	32,8 - 84,0
Yearling	39	107,5	8,6	88,2 - 121,0	27	101,8	8,7	85,1 -113,5
Subadult	33	122,8	6,6	111,0 - 132,0	31	111,9	3,9	103,8 -121,0
Adult	56	132,3	5,0	116,5 - 144,0	74	118,2	3,8	109,0 -126,8
HEAD LENGTH								
Juvenile	4	16,5	7,1	12,7 - 27,1	6	20,0	6,9	12,8 - 27,8
Yearling	39	35,8	3,1	29,8 - 40,2	27	34,1	2,8	28,2 - 37,8
Subadult	33	40,9	2,2	36,3 - 44,5	31	37,4	1,3	34,2 - 40,0
Adult	56	44,1	1,4	40,0 - 46,8	74	39,2	1,4	36,2 - 43,6
HIND FOOT LENGTH								
Juvenile	4	12,1	6,8	8,1 - 22,2	6	14,9	6,0	8,4 - 21,3
Yearling	39	25,1	1,1	22,7 - 26,9	27	24,0	1,1	22,2 - 25,7
Subadult	33	26,3	0,5	25,1 - 27,5	31	24,5	0,5	23,6 - 25,3
Adult	56	26,4	0,8	24,2 - 28,0	74	24,7	0,7	22,5 - 26,2

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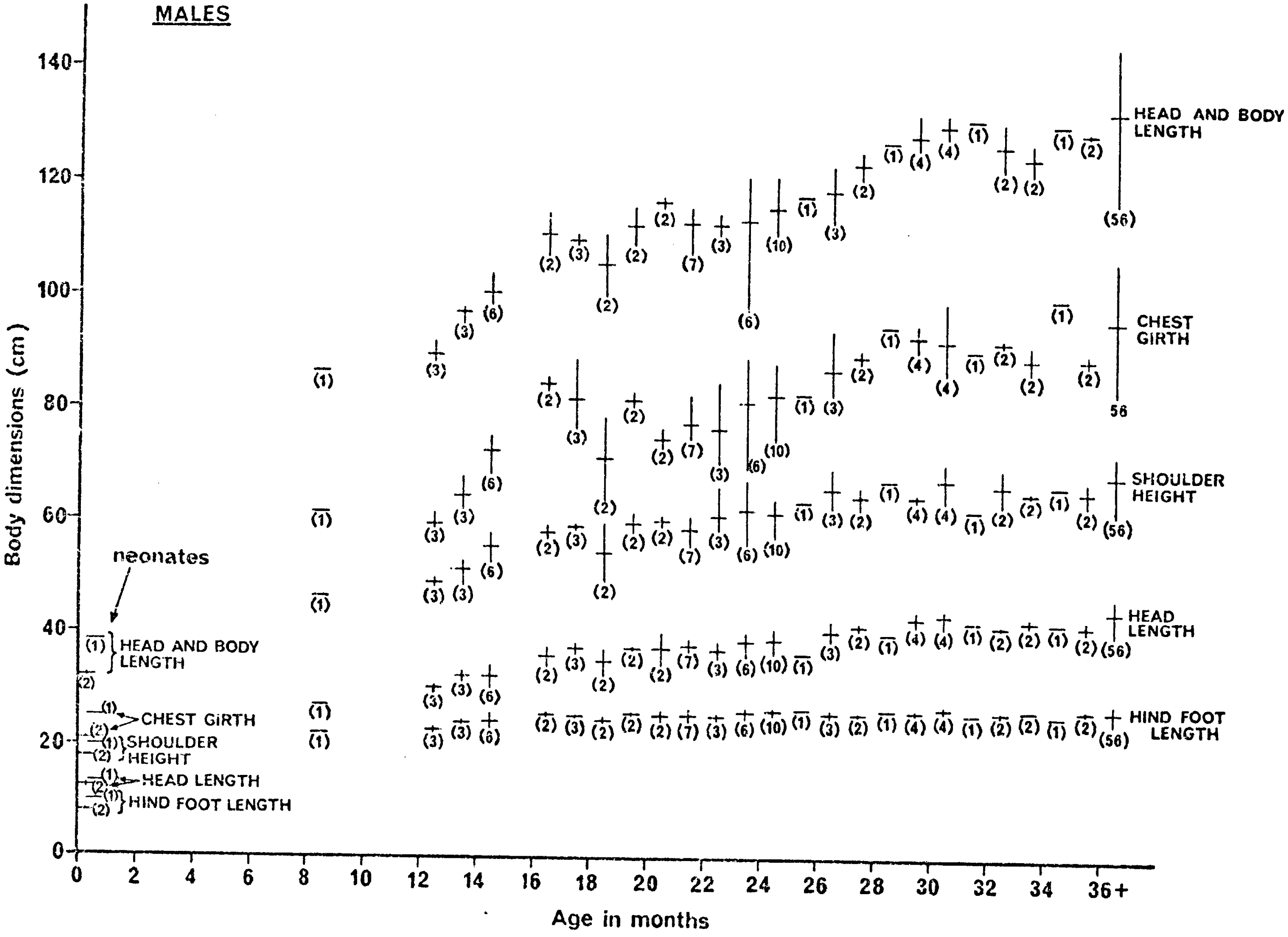

FIG. 17. Body dimensions (cm) at age for male warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - June 1975 (range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

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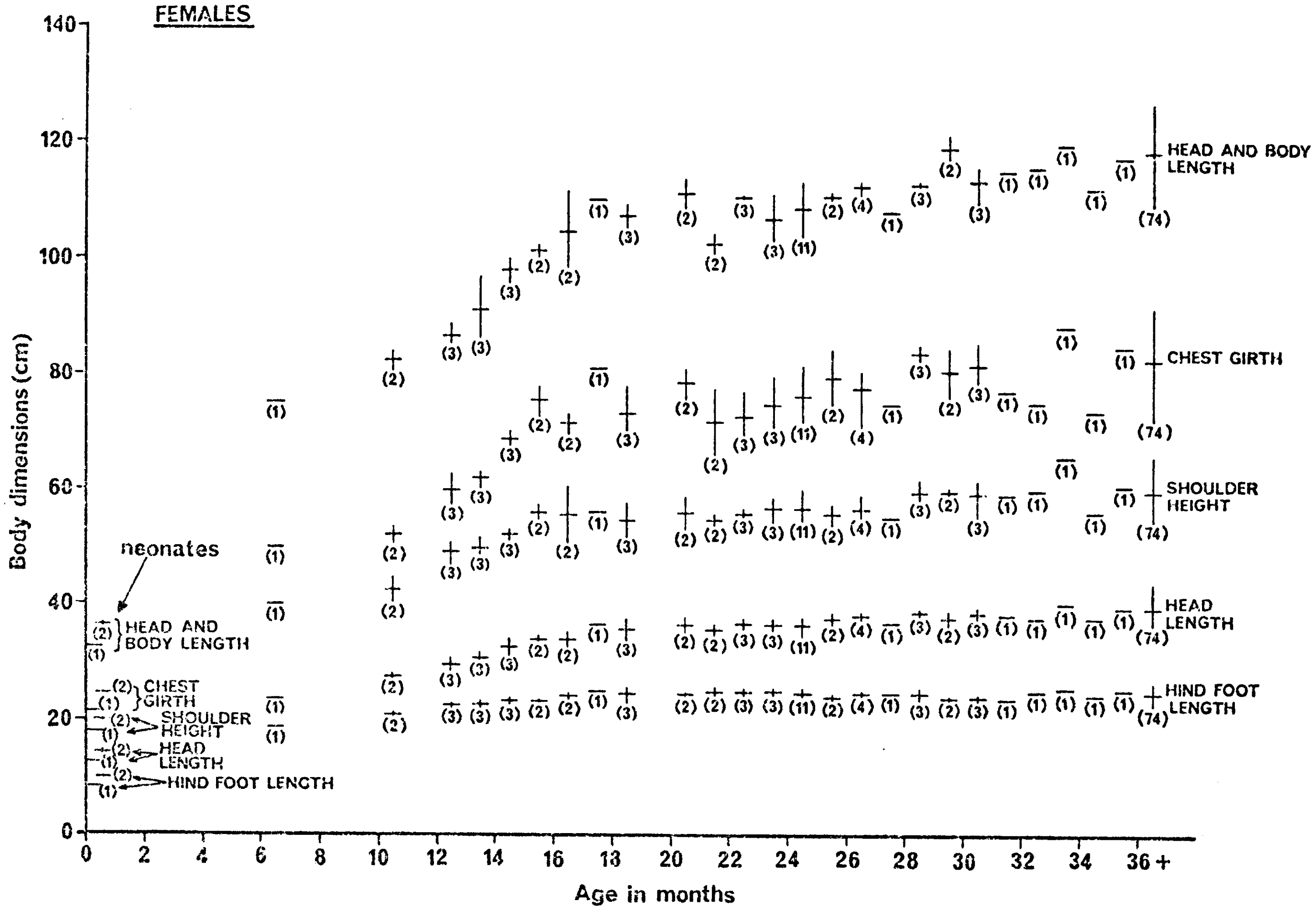

FIG. 18. Body dimensions (cm) at age for female warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, July 1973 - June 1975 (range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

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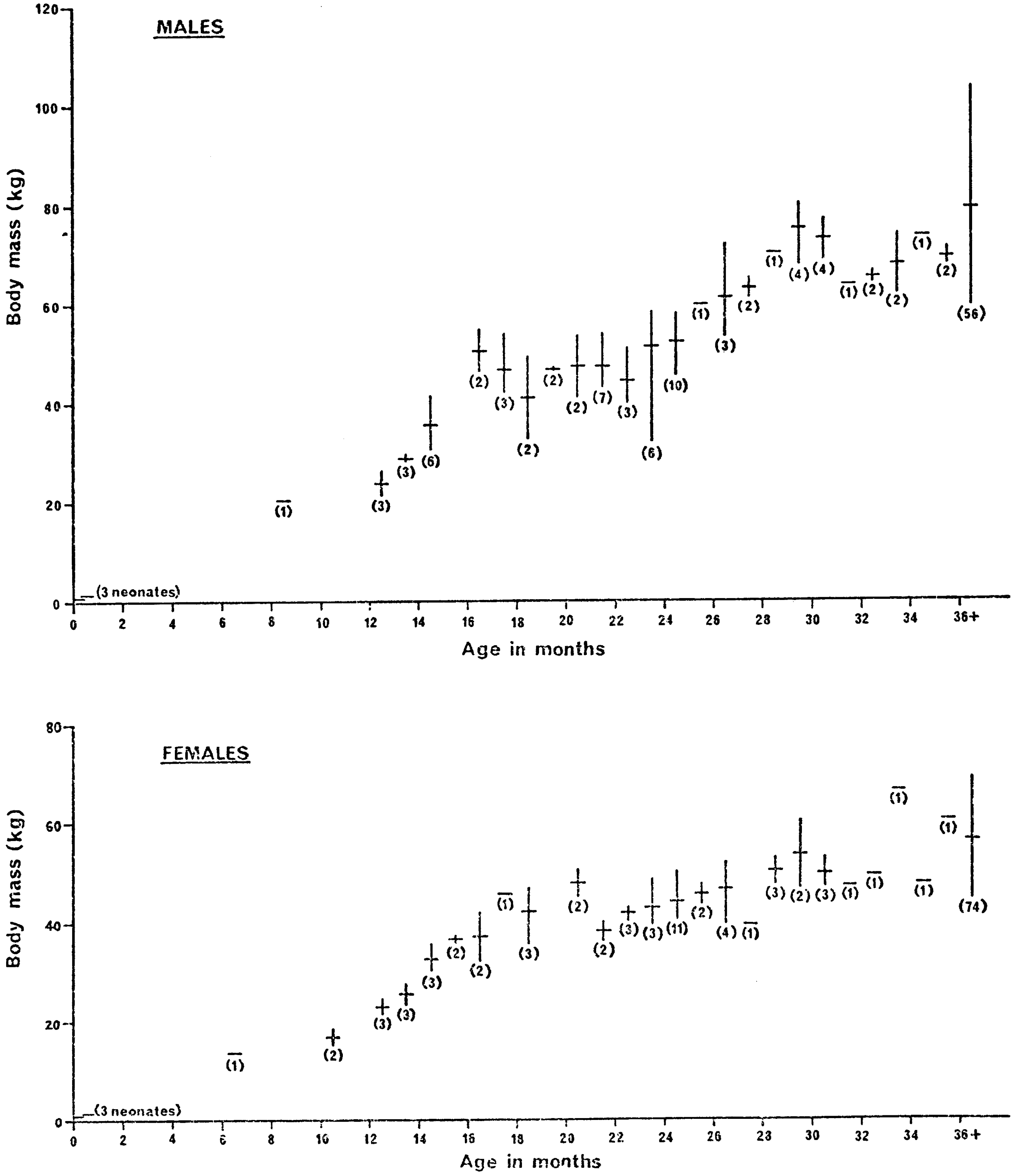

FIG. 19. Body mass (kg) at age for warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex (males: June 1973 - June 1975; females: July 1973 - June 1975; range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

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TABLE 17. Body mass (kg) and dimensions (cm) of warthogs from Mkuzi Game Reserve, July 1973 - September 1973.

Age class	n	Body mass		Chest girth		Shoulder height		Head and body length		Head length		Hind foot length	
		Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
(a) Males													
Juvenile	1	19,5	-	56,1	-	48,3	-	88,6	-	26,0	-	21,9	-
Yearling	8	41,1	32,5-51,0	78,3	69,0-86,9	59,5	55,3-63,6	108,8	104,5-113,9	35,7	33,1-39,2	25,3	24,0-26,2
Subadult	1	66,0	-	95,1	-	68,0	-	128,8	-	40,3	-	25,8	-
Adult	1	61,0	-	90,4	-	67,0	-	126,3	-	40,1	-	24,0	-
(b) Females													
Juvenile	1	12,3	-	49,0	-	43,2	-	80,0	-	24,5	-	19,2	-
Yearling*	2	38,5	37,0-40,0	73,4	70,5-76,2	54,6	54,4-54,7	106,6	104,5-108,7	33,9	33,4-34,4	24,1	23,6-24,6
Subadult*	1	37,5	-	74,0	-	60,0	-	111,1	-	34,1	-	23,6	-
Adult*	4	47,7	42,3-55,0	81,3	79,2-85,0	60,2	58,3-62,2	117,9	112,4-123,0	36,4	34,8-38,0	23,2	22,4-24,1

*The yearling, subadult and adult females were all pregnant.

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TABLE 18 . Relations between body mass in kg (M), chest girth in cm (G), shoulder height in cm (H) and head and body length in cm (L) of warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex.

n	Sex	Relationship*	r
132	males	$M = 0{,}0002545\ G^{2{,}7738}$	0,989
138	females	$M = 0{,}0002083\ G^{2{,}8322}$	0,984
132	males	$M = 0{,}00009513\ H^{3{,}2203}$	0,981
138	females	$M = 0{,}00008914\ H^{3{,}2558}$	0,978
132	males	$M = 0{,}00002363\ L^{3{,}0757}$	0,992
138	females	$M = 0{,}00002731\ L^{3{,}0462}$	0,990
132	males	$M = 4{,}242 + 61{,}542\ LG^{2}$	0,981
138	females	$M = 3{,}475 + 64{,}812\ LG^{2}$	0,961
132	males	$\text{Log } M = 4{,}421 \text{ Log } G - 6{,}794$	0,926
138	females	$\text{Log } M = 2{,}820 \text{ Log } G - 3{,}659$	0,984
132	males	$\text{Log } M = 5{,}229 \text{ Log } H - 7{,}648$	0,936
138	females	$\text{Log } M = 3{,}241 \text{ Log } H - 4{,}024$	0,977
132	males	$\text{Log } M = 4{,}967 \text{ Log } L - 8{,}575$	0,941
138	females	$\text{Log } M = 3{,}033 \text{ Log } L - 4{,}537$	0,990

All r values are highly significant ($P < 0{,}001$)

* Length x girth ^{2} in m ^{3}

All the regressions had very high correlation coefficients, indicating that good predictions of body mass could be made from measurements of head and body length, chest girth, shoulder height and body volume.

Logarithmic transformations also gave very good estimations of body mass from body dimensions which, unlike the mass estimation equations for the untransformed data, were consistently better in the case of females (Table 18). Differences in predictive efficiency between the various relationships are small. The regression equations for the mass-length relationship had the highest correlation coefficients for both sexes (0,992 for males, 0,990 for females).

DISCUSSION AND CONCLUSIONS

BODY MASS AND COMPOSITION

Comparison of the mass of warthogs in different parts of their geographical range has limitations. For example, published information on live mass of

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females may not include the uterus and its contents, which may comprise over 7% of body mass (Table 7). Some reports of live body mass in female warthogs fail even to mention whether the animals were pregnant or not. In the present study inclusion of the reproductive tract and its contents does not allow for variation in stage of gestation.

Temporal variation in visceral contents due to the feeding and drinking habits of a particular species is also an important factor that influences live mass (Mc Culloch & Talbot 1965). Standardisation of the time of day when body mass is measured was not possible in the present study and, except for the data of Smith & Ledger (1965) (see also Ledger, Sachs & Smith 1967, Ledger 1968), could apparently not be taken into account in studies on warthogs in other regions.

Smith & Ledger (1965) investigated variability in live mass due to digestive tract fill for eight species of wild ungulates in East Africa. They found that the mass of the full, fat-free digestive tract as a percentage of live mass could vary from as little as 8,2% in lesser kudu Tragelaphus imberbis to 29,4% in the hippopotamus, and from 14,6 to 21,1% for a sample of 40 warthogs, ranging in age from two months to adult and in body mass from 13,0 to 99,6 kg. However, their data cannot be directly compared with the present results, where the mass of the wet contents of the stomach alone was recorded (Table 8). Stomach contents as a percentage of body mass in Zululand warthogs ranged from 0,2 to 9,1% and the range for adult females was greater than for adult males. Maximum and mean stomach fill of adult males and females from Zululand considerably exceeded corresponding values for warthogs from Uganda, recorded by Clough & Hassam (1970).

Depending on the circumstances and slaughter techniques, blood loss may be a further source of bias in the measurement of body mass. Although the mass of whole warthogs was measured directly in this study, no allowance for loss of blood and body fluids between shooting and mass measuring was possible. Evaporative loss during dissection could also have affected the results on mass of internal offal particularly, and lower dressing percentages are characteristic of carcasses which have been cooled. Skinner (1970) states that game carcasses lose approximately 3% of their mass on cooling, while Huntley (1971a) found decreases of 1,4 and 1,8% in carcass yield of blesbok and kudu respectively, after cooling the carcasses for at least eight hours.

Season and physical condition may also cause differences in reported values for live mass, and as Robinette (1963) and Wilson (1968) emphasise, compilations of measurements from trophy specimens are not representative of average dimensions. The range of body mass recorded in the literature for "adult" warthogs may partly reflect an age effect, depending on the proportions of young, prime and old adults sampled. In some studies, 2 - 3 year old warthogs may have been classed as adult due to lack of uniform ageing criteria. Because of the variables that influence live mass data, examination of comparative records for possible geographical variation in the size of warthogs should be cautious. In the following comparison of mean body mass of warthogs (Table 19), the data for the present study refer to warthogs at least three years old. Boshe's (1981) data on mean body mass of warthogs from the Selous Game Reserve, Tanzania, have likewise been segregated to exclude warthogs aged less than three years.

For a series of mass measurements of adult mammals from Zambia, Robinette (1963) omitted what were believed to be masses of immature warthogs (less than 45,4 kg for females and 63,5 kg for males). Robinette's arbitrary lower limits agree well with the respective minimum body masses of 44,6 kg and 59,3 kg recorded for adult female and adult male warthogs in the Complex (Table 19). Further data for two sub-samples of warthogs from Zambia were recorded by Wilson (1968). The mass measurements from the Luangwa Valley were for exceptionally large warthogs shot as trophy specimens. Since the sample from the adjoining plateau area involved warthogs shot non-selectively on tsetse control, Wilson rightly regards their mass measurements as more representative of average adult specimens (basing adulthood on full permanent dentition).

In recording live mass and dimensions of warthogs and other wild ungulates from the Serengeti area in Tanzania, Sachs (1967) deducted the mass of the gravid uterus in pregnant animals; however, reproductive status is not specified for any of the female ungulates in his compilation, and the same applies to the data of Meinertzhagen (1938) and Boshe (1981) for body mass of adult female warthogs from Kenya and Tanzania respectively. Nevertheless, most of the adult sows in Boshe's sample would have been pregnant since they were collected during the dry season when Boshe (op. cit.) recorded a pregnancy rate of 87% for sexually mature sows. Together with data on body and carcass composition of East African warthogs, Ledger (1968) gives the mean live mass of 10 adults of both sexes, but his minimum value for mass of females appears erroneous. Although Ledger states that live mass of females excludes the mass of the full uterus (gravid or otherwise), the reproductive status of the individuals sampled is not mentioned.

The mass measurements reported by Child, Sowls & Mitchell (1965) for 16 adult warthogs shot during tsetse control operations in the Nagupande area, Zimbabwe, are for specimens at least three years old. Their data for females represent whole body mass of the animal as collected, but reproductive status is not mentioned.

Referring to his compilation of body mass values for 102 adult warthogs shot during game control operations in HGR, Hitchins (1968) states that adults were separated from immature animals on the basis of their dentition, and mass of

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TABLE 19. Body mass (kg) of adult warthogs in various regions.

Locality	Description of sample	n	Mean	Range	Source
Zambia	Adult ♂♂	16	82,1	63,5 - 99,8	Robinette (1963)
	Adult ♀♀ (non-pregnant)	9	56,7	45,4 - 71,2	
	Adult ♀♀ (pregnant)	6	67,1	48,5 - 81,6	
Zambia (plateau area, Chipata district)[1]	Adult ♂♂	68	74,8	59,9 - 98,9	Wilson (1968)
	Adult ♀♀ (non-pregnant)	74	62,6	57,6 - 76,2	
Zambia (Luangwa Valley)[2]	Adult ♂♂	7	82,1	76,7 - 101,6	
	Adult ♀♀ (non-pregnant)	4	68,9	62,1 - 77,6	
Kenya	Adult ♂♂	18	-	70,3 - 106,1	Meinertzhagen (1938)
	Adult ♀♀ (reproductive status unspecified)	6	-	55,8 - 67,6	
Tanzania (Serengeti area)[3]	Adult ♂♂	16	86,6	54,0 - 106,7	Sachs (1967)
	Adult ♀♀ (reproductive status unspecified)	2	52,9	52,3 - 53,4	
Tanzania (eastern Selous Game Reserve)	Adult ♂♂	18	65,3	-	Boshe (1981)
	Adult ♀♀ (reproductive status unspecified)	16	51,6	-	
East Africa[4]	Adult ♂♂	10	87,8	71,9 - 99,6	Ledger (1968)
	Adult ♀♀ (reproductive status unspecified)	10	60,2	62,2 - 70,7	
Uganda (Rwenzori National Park)	Adult ♂♂	71	84,7	-	Clough & Hassam (1970)
	Adult ♀♀ (non-pregnant)	47	58,3	-	
	Adult ♀♀ (pregnant)	42	64,8	-	
Zimbabwe (Nagupande area)[5]	Adult ♂♂	6	75,1	58,1 - 97,5	Child, Sowls & Mitchell (1965)
	Adult ♀♀ (reproductive status unspecified)	10	53,6	40,4 - 73,9	
Zululand (HGR)[6]	Adult ♂♂	36	76,6	51,7 - 103,9	Hitchins (1968)
	Adult ♀♀ (reproductive status unspecified)	66	51,9	39,9 - 68,9	
Zululand (Complex)	Adult ♂♂	56	79,6	59,3 - 103,9	Present study
	Adult ♀♀ (non-pregnant)	42	56,6	44,6 - 69,1	
	Adult ♀♀ (pregnant)	32	56,3	46,0 - 64,2	
Zululand (MGR)	Adult ♂♂	1	61,0	-	Present study
	Adult ♀♀ (pregnant)	4	47,7	42,3 - 55,0	

[1&5] tsetse control shooting

[2] trophy specimens

[3&4] excluding mass of gravid uterus in pregnant animals

[6] excluding mass of conceptus in pregnant animals.

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females was "exclusive of the conceptus". Apart from slightly lower minimum and average values, the mass measurements reported by Hitchins (op. cit.) correspond closely with the body mass data collected for adult warthogs from the Complex during the present study (Table 19).

Compared to Zululand, the higher average live mass values recorded for adult warthogs of both sexes in the largest East African sample (n = 160), which was collected over a 7 - year period in Rwenzori National Park, Uganda (Clough & Hassam 1970), could indicate superior average physical condition in that population. Although seasonal stringencies in nutrition would be much greater in Zululand than in Rwenzori, where more equable, equatorial conditions prevail, such interpopulation comparison may nevertheless be biased by differences in sample composition, as emphasised by Brooks (1978). The average live mass values recorded by Boshe (1981) for adult warthogs from the Selous Game Reserve, Tanzania are considerably lower than for the Rwenzori warthog population, and at least part of this difference could be attributable to the collection of all the Tanzanian specimens during the dry season. In contrast to the bimodal distribution of annual rainfall in Rwenzori National Park (Grimsdell 1973), the Selous Game Reserve experiences a single rainy season each year (Boshe op. cit.).

Generally, the mean masses and range in mass of Zululand warthogs are fairly similar to values reported from Zimbabwe, Zambia and East Africa, notwithstanding higher maximum mass values of females from these latter areas. The heaviest body mass values reported are 81,6 kg for a pregnant adult female from Zambia (Robinette 1963) and 106,7 kg for an adult male from Kenya (Sachs 1967). In West Africa, the heaviest adult male warthog measured by Bigourdan (1948) scaled 101 kg and the heaviest female 80 kg. Of seven warthogs (including immature animals) measured by Smithers (1971) in Botswana, the heaviest male attained 88,5 kg in body mass compared with 56,2 kg for a non-gravid female.

While geographical variation in average size of a species may well occur in response to differences in nutrition (Sachs 1967, Robinson 1979), this is not readily apparent for warthogs from the available data. Seasonal fluctuation in body mass is a feature of African ungulates confounding comparisons (von la Chevallerie 1970), and was evident for the warthog population in the Complex (Fig. 11). Moreover, restricted sampling period and small sample size in respect of some of the published data on warthog body mass render comparisons difficult and can result in misleading conclusions. Several recent studies have provided data substantiating the effect of season on live mass of wild ungulates in southern Africa (Huntley 1971b, von la Chevallerie, Erasmus, Skinner & van Zyl 1971, Irby 1975, Hanks, Cumming, Orpen, Parry & Warren 1976, Hall-Martin, von la Chevallerie & Skinner 1977).

Despite differences in procedure of dressing carcasses and other variables (van Zyl, von la Chevallerie & Skinner 1969), the carcass dressing percentages of warthogs (Table 9) closely approximate the lower range of values (ca. 55%) for most African ungulates summarised by von la Chevallerie (1970), and compare favourably with average values for domestic livestock. Zebu beef-steers give carcass yields of the order of 50 - 60% but some 15 - 35% of the carcass comprises separable fat (Ledger 1968). However, Ledger points out that similar carcass yields in game animals were attained with less than 5% carcass fat and he found "no evidence that these animals compensated the low carcass fat by increased deposits of internal fat (pericardial, omental and mesenteric)".

For a sample of 20 adult warthogs (10 males, 10 females) from East Africa, the mean mass of carcass fat comprised 1,8% of the dressed carcass mass in both sexes, with values ranging from 1,3 - 2,8% in males and 1,1 - 3,2% in females (Ledger 1968). The amount of separable fat on dressed warthog carcasses from Zululand was similarly very small. Mean dressed carcass masses (including kidneys and perinephric fat) of the warthogs measured by Ledger (op. cit.) were 48,2 kg (range 35,6 - 57,6 kg) for males and 33,5 kg (range 25,8 - 39,7 kg) for females; the corresponding carcass yields ranged from 49,4 - 57,4% (mean 54,7%) in males compared with 51,9 - 58,2% (mean 55,7%) in females. The mean carcass yield of adult male warthogs from the Complex (Table 9) was 55,1% while adult females (pregnant and non-pregnant) averaged 51,8%. However, dressed carcasses of adult warthogs from the Complex were on average 4 - 5 kg lighter than those measured by Ledger.

Of 17 wild ungulate species investigated by Ledger, Sachs & Smith (1967) (see also Ledger 1968), warthogs had the highest mean values for carcass muscular tissue (lean meat) as a percentage of dressed carcass mass - 82,9% in adult males (n = 10, range = 78,8 - 84,6%) and 83,9% in adult females (n = 10, range = 82,6 - 86,0%). Due to the high percentage of carcass muscular tissue, the warthog can be considered as a useful animal for meat production.

Since carcass measurements may be useful as indices of live mass where facilities for measuring body mass in the field are lacking or where animals have already been eviscerated, the relationships of body mass in the warthog as a function of buttock length, buttock circumference and carcass length were investigated. The highest correlation coefficients (males: r = 0,949; females: r = 0,931) were found for the relationship between body mass and carcass length (Table 11). However, this relationship was markedly less satisfactory when adults (the largest age class component of the sample) were grouped separately. Based on a sample of 40 warthogs from East Africa, Smith & Ledger (1965) have reported very high correlation coefficients (both sexes and all ages grouped) for the relationships between body mass and mass of both the hindleg and foreleg (r values of 0,998 and 0,979 respectively), despite differences in digestive tract fill and a wide range in body mass.

BONE MARROW FAT AS AN INDEX OF CONDITION

Ledger (1968) considers that the low total fat content of game animals compared to domestic stock indicates a difference in metabolic processes and illustrates the inappropriateness of describing roundness in form as "fat" when assessing the condition of game animals. Geigy (1955) found that not even the largest of 25 warthogs examined in Tanzania had a layer of sub-dermal fat, although all appeared in excellent physical condition, and he suggested that the ability to accumulate sub-cutaneous fat deposits is absent in the warthog. Similarly, Smith (1970) found no measurable sub-cutaneous fat on 40 warthogs from East Africa, although all were collected during "seasonally optimum environmental conditions." However, Harris (pers. comm.) reported 5 - 8 mm of sub-dermal fat distributed over most of the body of a yearling female warthog that had been living within maize lands in the Naboomspruit district, Transvaal. Sub-dermal fat was virtually absent on all warthogs examined in both the Complex and MGR, and with few exceptions, perinephric and channel fat was negligible. For this reason, bone marrow fat and not kidney fat was used as an index of condition. However, Smith (1970) used the kidney fat index described by Riney (1955) to assess physical condition of warthogs in East Africa, and found values ranging from 1,2 to 26,1%. In the Complex, the only warthogs with fair amounts of channel and kidney fat were a pregnant subadult female examined on 74-08-09 and several males and females (mainly subadult or adult) examined during March 1975. The uncommon occurrence of measurable amounts of kidney fat in the warthogs from the Complex therefore suggests a lower level of condition than for the population sampled by Smith (1970), although selective cropping in overgrazed areas might have influenced this trend.

The observations of Ransom (1965) and Brooks, Hanks & Ludbrook (1977) indicate that the bone marrow fat reserves are the last to be mobilised when an animal is already subject to undernutrition, thus qualifying their use as a measure of seasonal variation in condition. Evidence from four ungulate species (Brooks et al., op. cit.) showed a positive sequence of marrow fat mobilisation in the limb bones that was initiated in the humerus and femur; indeed, they recorded differences of up to 83% in the fat content in the humerus and femur of individual impala which nevertheless had a very similar high fat content in the metacarpus and metatarsus. A condition assessment restricted to a collection of terminal bones may therefore give very misleading results, although the occurrence of differential fat mobilisation in the limb bones of warthogs has not been investigated. Nevertheless, the high fat values of most warthog marrow samples (Fig. 16) suggest that the majority of warthogs were probably not within the lower ranges of condition associated with advanced nutritional stress. However, the generally minimal amounts of perinephric fat in the 264 warthogs examined in the Complex could indicate that their physical condition was only marginally above the range where mobilisation of bone marrow fat commences. In buffalo, eland and impala, Brooks _et al_. (_op_. _cit_.) found that perinephric fat is mobilised before bone marrow fat, and the fat content of bone marrow only declines once the kidney fat index falls below about 40%. A very similar relationship has been reported in female white-tailed deer (Ransom 1965).

The relationship between the kidney fat index and bone marrow fat content in the warthog nevertheless remains speculative and the lower range of perinephric fat reserves associated with mobilisation of bone marrow fat has not been documented. On the basis of visual criteria relating to prominence of pelvic bones, ribs and tail rostrum (Riney 1960), most warthogs observed in the field appeared in good condition, even during the dry season, although there were exceptions (Plate 6). However, roundness of form as an indication of good physical condition can be misleading, and Huntley (1971b) recorded changes of up to 980% and 570% in the mass of kidney fat in mature blesbok and kudu respectively within seven months, but this fluctuation was not reflected in their external appearance. Male impala may differ substantially in their deposited fat reserves, as measured by the kidney fat index and bone marrow fat content, and yet have identical body mass and chest girth measurements (Hanks, Cumming, Orpen, Parry & Warren 1976). Total body fat reserves in warthogs are extremely low (0,3 - 1,5% of live mass) although found to be significantly correlated ($P<0,01$) with kidney fat (Smith 1970). Thus a major decrease in total fat reserves, as indicated by kidney fat, would be accompanied by only a very small decrease in live mass. Indeed, Huntley (1971b) associates the suddenness of population collapses known in many game species (see for example Wilson 1970, Ferrar & Kerr 1971, Keep 1973) with "the insidious loss in condition to state of near starvation before this becomes manifest in the animal's general appearance."

The data on mean bone marrow fat content of warthogs at least two years old (Table 13) suggest an annual cycle in condition, notwithstanding wide individual variation with low values frequently associated with old animals. Body mass and dressed carcass mass of warthogs at least three years old (Figs. 11 & 14) also indicate a seasonal pattern of variation in condition, with low values during July to October; however, in females the minima for these parameters do not coincide with that for mean bone marrow fat content, which was unexpectedly high for the period July to October and reached a minimum between November and February (Table 13). Most females are pregnant between July and October when their mean bone marrow fat content was highest, but their mean body mass and dressed carcass mass were not correspondingly high, implying that deterioration in body condition commences before marrow fat reserves are mobilised. A similar

PLATE 6. (a) Adult warthog sow in poor condition, photographed shortly after emerging from a hole in which she and four juveniles had spent the night. Three freshly aborted foetuses were found inside the hole. (UGR, 74-08-27).

(b) Juvenile female warthog in very poor condition, from the same sounder in which the matriarch had aborted her new litter. (UGR, 74-08-27).

trend in relative condition was reported for elephants in Wankie National Park, where pregnant females had a higher average kidney fat index than non-pregnant females (Williamson 1975).

Although mean dressed carcass mass of male warthogs increased rapidly during the period November to February (Fig. 14), the corresponding increase was distinctly slower in females, probably as a consequence of the demands of nursing young. Since mean bone marrow fat content of males was also lowest between November and February, it appeared that replenishment of marrow fat reserves during the wet season lagged behind the improvement in body mass and especially dressed carcass mass. The heaviest individual adult male and female warthogs recorded (103,9 and 69,1 kg respectively) were both measured late in the wet season (March).

Monthly records of natural game deaths in HGR from 1967 to 1972 show 83% of warthog deaths between May and September, "when veld conditions are at their worst" (Brooks 1973). Although the sample size was small, the trend suggests that highest mortality coincides with the dry season minima in body mass and dressed carcass mass associated with lowered physical condition.

Recent results published by Brooks (1978) for impala rams emphasise that differences in bone marrow fat in relation to age, reproduction and social status should be considered in the sampling strategy, if seasonal trends in condition are to be clearly demonstrated. Subject to this proviso, Brooks suggests that the bone marrow fat index could be used as a valid estimate of the physiological adjustment of a population to its environment. However, it appears that the adequacy of bone marrow fat as an index of condition in wild ungulates may require critical re-evaluation, judging by the data of Monro & Skinner (1979).

Monro & Skinner (1979) defined condition by a formula reflecting body composition in terms of both fat and non-fat constituents; using this as a standard, they evaluated bone marrow fat as an index of condition for a sample of nine adult male impala but found no correlation. Although body protein has been suggested as a possibly important source of reserve energy in wild ungulates (Smith 1970, Monro & Skinner op. cit.), elucidation of their catabolic reactions under nutritional stress awaits further research.

MUSCLE FIBRE DIAMETER AND MEAT QUALITY

The very limited data on muscle fibre diameters of warthogs (Table 15) can be compared with those of von la Chevallerie (1972) for adult males of seven wild ungulate species, viz, springbok (45,5 µm), red hartebeest (52,6 µm), blesbok (53,8 µm), black wildebeest (53,9 µm), impala (56,9 µm), eland (66,3 µm), gemsbok (69,0 µm). Despite inadequate sample size, the observed trend of fibre diameter increasing with body mass (viz. males against females, old against young) is in agreement with the findings of Joubert (1971), von la Chevallerie (1972) and Hall-Martin, von la Chevallerie & Skinner (1977).

Since meat of finer grain is indicated in younger warthogs, they would be more acceptable from a consumer viewpoint. The strong musky odour that characterises the meat of adult male warthogs would also favour the use of younger individuals in any marketing programme involving warthog meat. In domestic pigs, the unpleasant "sex odour" of boar flesh or fat is caused by an androstenone, formed under testicular control (Patterson 1968a,b,c; see also Sink 1967).

Warthog meat is characteristically light coloured, but measurement of tenderness, moisture content and flavour as parameters of meat quality (von la Chevallerie 1972) was not possible. However, Crawford (1968) found that the amino-acid profiles of meat protein from warthogs and domestic pigs are virtually identical, but the mean fat content of meat from warthogs (n = 3) was only 1,8% compared with 20 - 60% fat in domestic pork and bacon. Thus from a nutritional viewpoint the high proportion of fat in domestic pork constitutes a significant dilution of the protein content.

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POSTNATAL GROWTH

Jeffery (1979) found that certain post-mortem body measurements of eland varied considerably from the corresponding live measurements; in measuring height at withers in particular, important discrepancies were associated with the difficulty of arbitrarily aligning the forelimb in a position that reproduces the live standing state. Similar biases exist in the data on warthog body dimensions, although care was taken not to straighten the forelimb unnaturally at the elbow joint when measuring shoulder height from the prostrate carcass.

Despite the inclusion of mass and measurements of six live neonates in the sample of juvenile warthogs (normally exempt from cropping), the data are inadequate to depict growth during the first year. However, Roth (1965) measured growth of five captive warthogs in Zimbabwe between one and 21 months of age, and found that gain in mass "was not steady in the course of body development." Briefly, his results showed that growth in shoulder height and head and body length was rapid during the initial suckling period, whereas live mass increased very slowly; when the animals were weaned at about 7 - 10 weeks of age, development "stagnated" but thereafter the growth rate increased steadily and increase in mass exceeded linear growth. Although development subsequent to weaning was influenced by the artificial diet, the growth rate of one animal that was weaned to natural grasses was retarded during the first dry season but increased again during the second wet season after birth.

Mass and measurements of 66 yearling and 64 subadult warthogs obtained during cropping in the Complex were analysed to quantify growth between one and three years of age (Figs. 17, 18 & 19). Growth in live mass is clearly influenced by season, notwithstanding pregnancy effects in females. Although the foetal mass (excluding amniotic fluid, etc.) carried by a female in advanced pregnancy may exceed two kilograms, the comparatively low values for body mass of pregnant adult females during July to October (Table 6) suggest that this addition to live mass is offset to a considerable extent by poorer body condition due to the lowered plane of nutrition concomitant with the dry season. Mean body mass of pregnant and non-pregnant adult females in the Complex was not significantly different, whereas in Rwenzori National Park, Uganda, mean mass of pregnant adult females (n = 42) exceeded that of non-pregnant adult females (n = 47) by 6,5 kg (Clough & Hassam 1970). In both Rwenzori (Clough & Hassam op. cit.) and the Complex, mean stomach fill was higher in pregnant adult females than in non-pregnant adult females. The finding that average live mass of adult females in the Complex was not increased as a consequence of pregnancy, despite indications that pregnancy may be associated with an increased food intake, emphasises the magnitude of the depressive effect of the dry season on body mass and condition of warthogs in Zululand.

In the field, separation of the sexes in the juvenile age class was not feasible on the basis of size, which agrees with Roth's (1965) conclusion that true sexual dimorphism in size does not appear before the age of one year. Between about 18 and 24 months of age, the retarding effect of the second dry season on warthog growth curves is particularly noticeable for the parameters of head and body length, chest girth and body mass in both sexes. During the third wet season there are renewed but less marked increases in these growth rates until about 30 months of age, whereafter further depressions in the growth curves coincide with the third dry season. However, by this stage growth is almost complete, especially in females.

Yearlings are generally more slender and shorter in the body than older warthogs, although occasional runts in the subadult age class might be mistaken for yearlings. Juveniles are easily distinguished from yearlings by their much smaller size. However, as in domestic pigs, Roth (1965) found that growth in warthogs is very sensitive to the plane of nutrition. Roth described the remarkable growth of a captive female which was reared on a greatly supplemented diet and attained a mass of 68 kg after one year, and ultimately reached 95 kg. This individual had reached yearling size already at six months and the physical proportions of an average adult before one year, at which age she was only distinguishable from free-ranging adults by her small tusks.

Roth (1965) has emphasised the significance of parasite infestation in retarding development in juvenile pigs. Two out of six obviously emaciated warthogs examined during cropping in the Complex carried heavy infestations of gut nematodes. Very thin juveniles, noticeably smaller than their littermates of the same age, were occasionally observed during the dry season. In these cases, the possible occurrence of acute parasitism could have intensified retardation of physical development.

ALLOMETRIC GROWTH

Good correlations between body mass and volume have been reported for black rhino (Freeman & King 1969), impala (Howells & Hanks 1975) and giraffe (Hall-Martin 1977). In the warthog also, the regression relationship between body mass and volume showed a high correlation coefficient. Of various functions used to describe allometry of size in the warthog (Table 18), the relation between body mass and head and body length gave the highest correlation coefficients for both sexes. However, the other relations also provide valid regressions of high predictive efficiency, especially since the data were collected during all seasons from a variety of age and mass classes. Since the data were derived from a single population of warthogs, local application of the regression equations could be expected to give the most accurate estimates of body mass.

Although warthogs are incompatible with intensive stock rearing or agriculture (Kingdon 1979), they are potentially valuable for meat production in savanna regions, especially by virtue of their high fecundity and resistance to African swine fever, which is fatal to domestic pigs. Known hosts of African swine fever virus include wild pigs, particularly warthogs, and the tick *Ornithodoros moubata*, which probably plays a major role in transmitting the infection to domestic pigs (Plowright, Parker & Pierce 1969). However, other animals which regularly or occasionally use burrows infested by these ticks could also serve as possible sources of the virus.

Crawford (1968) questioned the wisdom of introducing domestic pigs in areas where this necessitates costly disease protection measures when warthogs, which can carry African swine fever virus without apparent concern, could be used instead for meat production. On the other hand, as Kingdon (1979) indicates, warthogs may suffer from other diseases, the most serious being rinderpest, from which large numbers have died in the past. The damage that warthogs may cause to crops and their digging of gaps under fences pose additional management problems if warthogs are to be utilised for meat production. Thus warthogs would compete best with domestic stock, in terms of productivity, under extensive grazing conditions.

Compared to domestic pigs and livestock, warthogs offer a high proportion of lean meat and their carcass yields are favourable. The commercial value of warthog tusks and hides for by-products should not be underestimated, and additional revenue could be derived from recreational and trophy hunting. Warthogs also constitute a popular tourist attraction.

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CHAPTER 4

REPRODUCTION IN THE MALE WARTHOG

INTRODUCTION

Numerous papers mention the occurrence of breeding seasons in warthog populations living in regions where the climate is markedly seasonal. On the equator however, warthogs breed throughout the year, as in western Uganda (Clough 1969) and further west in Virunga National Park, Zaïre, where there are nevertheless two peaks of farrowing corresponding with the start of the two wet seasons (d'Huart *pers. comm.*)

Apart from an investigation of epididymal smears and testis mass of warthogs in Zimbabwe (Child, Roth & Kerr 1968), the only comparative data on testicular activity in relation to age and season were recorded by Clough (1969), who also described the anatomy of the reproductive tract in both sexes. The histology of the accessory glands has apparently not been examined, although Parkes (1966) has described that of the testis.

MATERIAL AND METHODS

Reproductive tracts were collected from 155 male warthogs shot in the Complex between June 1973 and June 1975, and from 16 males shot in MGR between July and September 1973. Each testis and the paired epididymes were mass measured to the nearest 0,1 g when fresh. Slices of tissue were taken from the mid-portion of one testis of each animal, fixed in Bouin's fluid for two days and then stored in 70% alcohol for subsequent histological examination. The specimens were cleared in xylol, embedded in paraffin wax, sectioned at 6 µm, and stained with Delafield's haematoxylin using aqueous eosin as counterstain. The stained sections of testes were examined microscopically for spermatogenesis and where autolysis did not prevent it, mean seminiferous tubule diameters were calculated from 25 circular tubules measured in cross-section with a Zeiss micrometer eyepiece.

RESULTS

ANATOMY

The ovoid testes of the warthog are carried with their long axis approximately vertical and the *cauda epididymes* dorsally, in a scrotum which is situated below the anus between the thighs. The descent of the testes into the scrotal sac has occurred before birth. Passing forward through the inguinal canal with the spermatic cords, the *vasa deferentia* of opposite sides converge at the bladder, where they loop over the ureters and become closely attached to the dorsal surface of the bladder. The *vasa deferentia* then extend posteriorly along the neck of the bladder and ventral to the conspicuous paired seminal vesicles, but are not characterised by distinct ampullae at the urethral end. The elaborately sacculated seminal vesicles discharge their secretions into the urethra immediately anterior to a small lobed prostate gland, which is attached to the dorsal wall of the urethra at the site where the vasa deferentia enter the proximal end of the urethral canal. Except for an external lobe, the prostate gland is contained within the muscular wall of the urethra. Conspicuous ovoid bulbo-urethral glands are attached to the dorso-lateral aspect of the pelvic urethra, just anterior to the crura of the penile urethra.

The distal part of the penis is spirally twisted and a large preputial gland that emits a strong smell is located at the glans penis.

MASS CHANGE IN THE REPRODUCTIVE TRACT

Of 171 male warthog reproductive tracts examined, only three instances of gross genital abnormalities were recorded. One yearling and one adult male had no right testis in the scrotum, but the left testis was normal. Unilateral testicular hypoplasia was found in one adult male where the left testis was infertile and markedly smaller than the right (3,5 g v. 30,0 g); however, spermatogenic activity in the right testis was normal. In 79,8% of all warthogs (n = 168, comprising 3 juveniles, 55 yearlings, 43 subadults and 67 adults), the left testis was heavier than the right, but this difference was not significant.

Growth in mass of the paired testes in relation to body mass (Fig. 20) shows a fairly uniform increase until a body mass of about 45 kg is attained, whereafter there is a wide range in testes mass. Growth in mass of the paired testes with age is illustrated in Fig. 21. Testicular development below 12 months of age is inadequately represented due to the small sample size of only three juveniles. Although there is a tendency for mass of paired testes and epididymes to increase with age up to about three years (Table 20), examination of the scatter in Fig. 21 shows wide variation in testes mass among animals in each of the yearling, subadult and adult age classes. Peaks in testes mass occur at about 18 months of age and again at about 30 months, although testicular growth is still incomplete.

SEMINIFEROUS TUBULE DIAMETERS

The data on seminiferous tubule diameter in relation to age are plotted in Fig. 22. Minimum values recorded for mean tubule diameters of adults were already attained by some yearlings at 16 and 17 months of age. While mean tubule diameters of yearlings are less than those of subadults, the maximum values for subadults and adults largely coincide (Table 20 & Fig. 22). The pattern of wide variation in tubule diameter within the yearling and subadult age classes,

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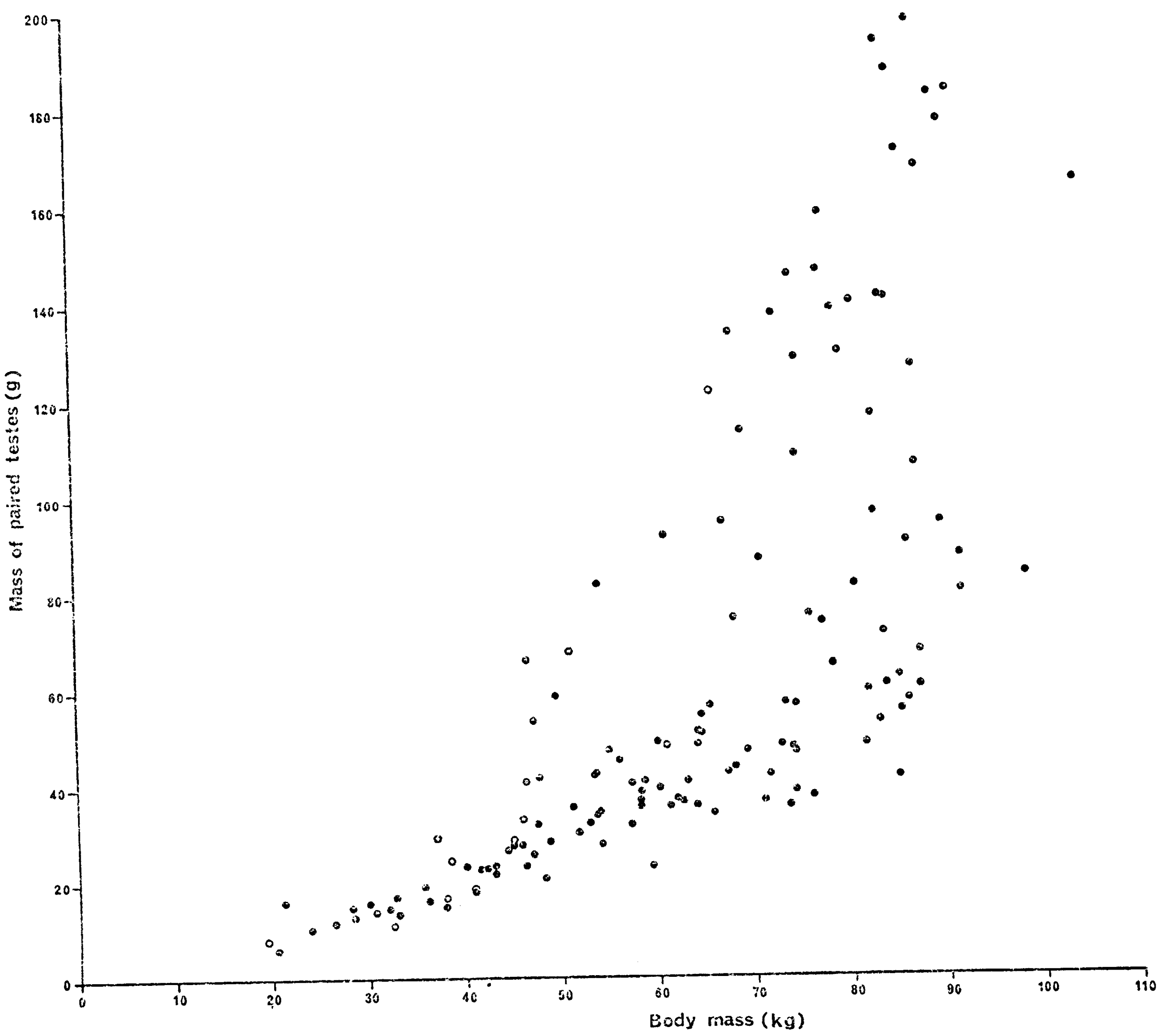

(● = Complex)

FIG. 20. The relationship between testes mass and body mass of warthogs from Zululand (o = MGR)

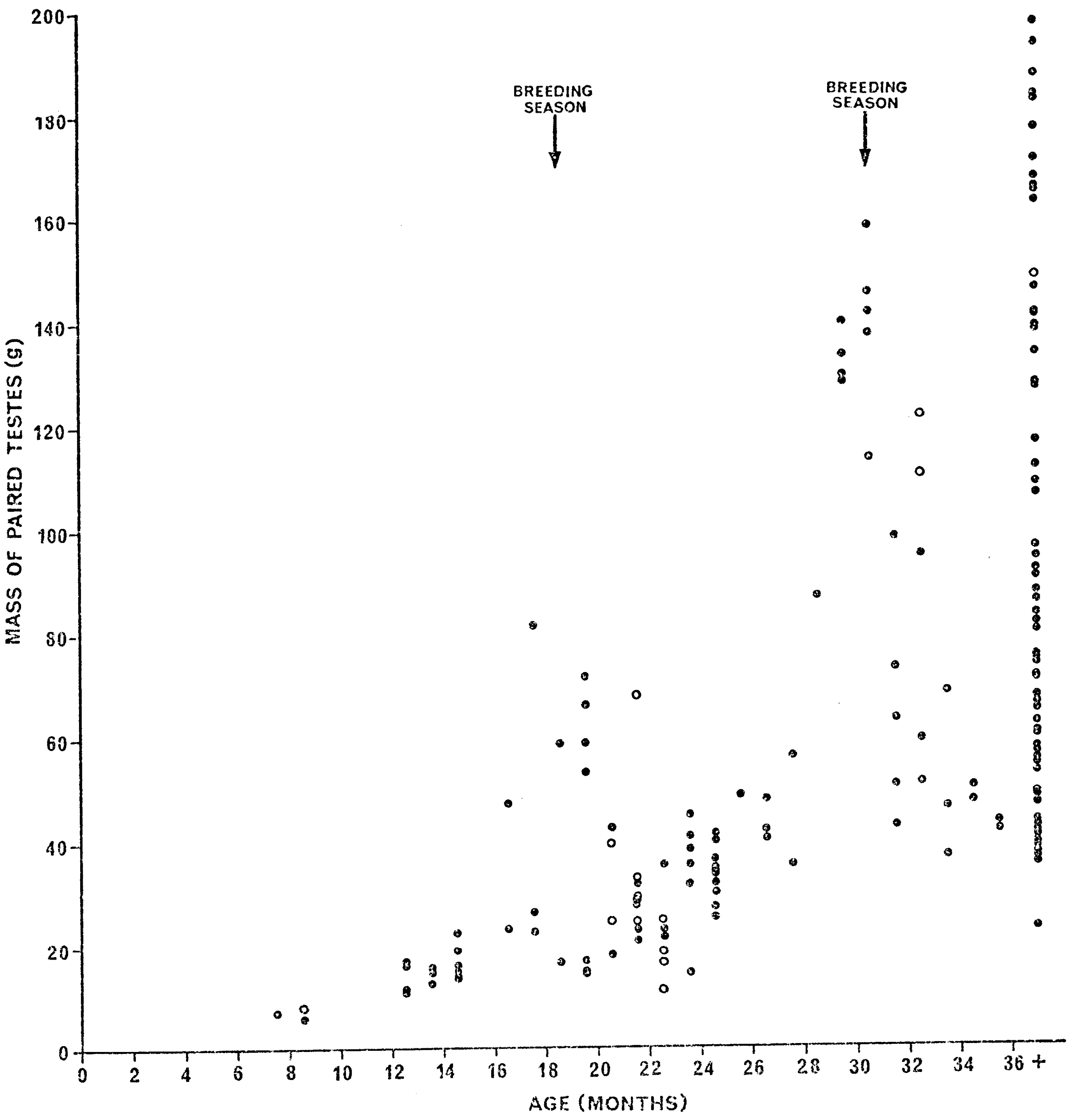

FIG. 21. Growth in mass of warthog testes with age (n = 168; ◑ = Complex; o = MGR).

TABLE 20. Growth in mass (g) of the testes and epididymes and growth in seminiferous tubule diameter (µm) with age for warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex.

	Paired testes mass				Paired epididymes mass				Mean seminiferous tubule diameter			
Age class	n	Mean	S.D.	Range	n	Mean	S.D.	Range	n	Mean	S.D.	Range
Juvenile	3*	7,1	1,0	6,1 - 8,1	3	0,9	0,2	0,6 - 1,0	3	61,6	8,7	56,6 - 71,6
Yearling	44	29,1	17,6	10,5 - 81,6	44	4,1	2,9	1,2 - 12,5	44	100,7	34,3	46,8 - 182,1
Subadult	41	67,5	40,8	25,6 - 158,2	41	10,1	5,5	2,8 - 21,2	37	142,5	41,5	90,6 - 219,8
Adult	65	92,7	49,6	23,1 - 197,3	65	13,6	6,0	4,6 - 26,4	51	158,0	38,8	89,6 - 240,2

* Including one juvenile from MGR.

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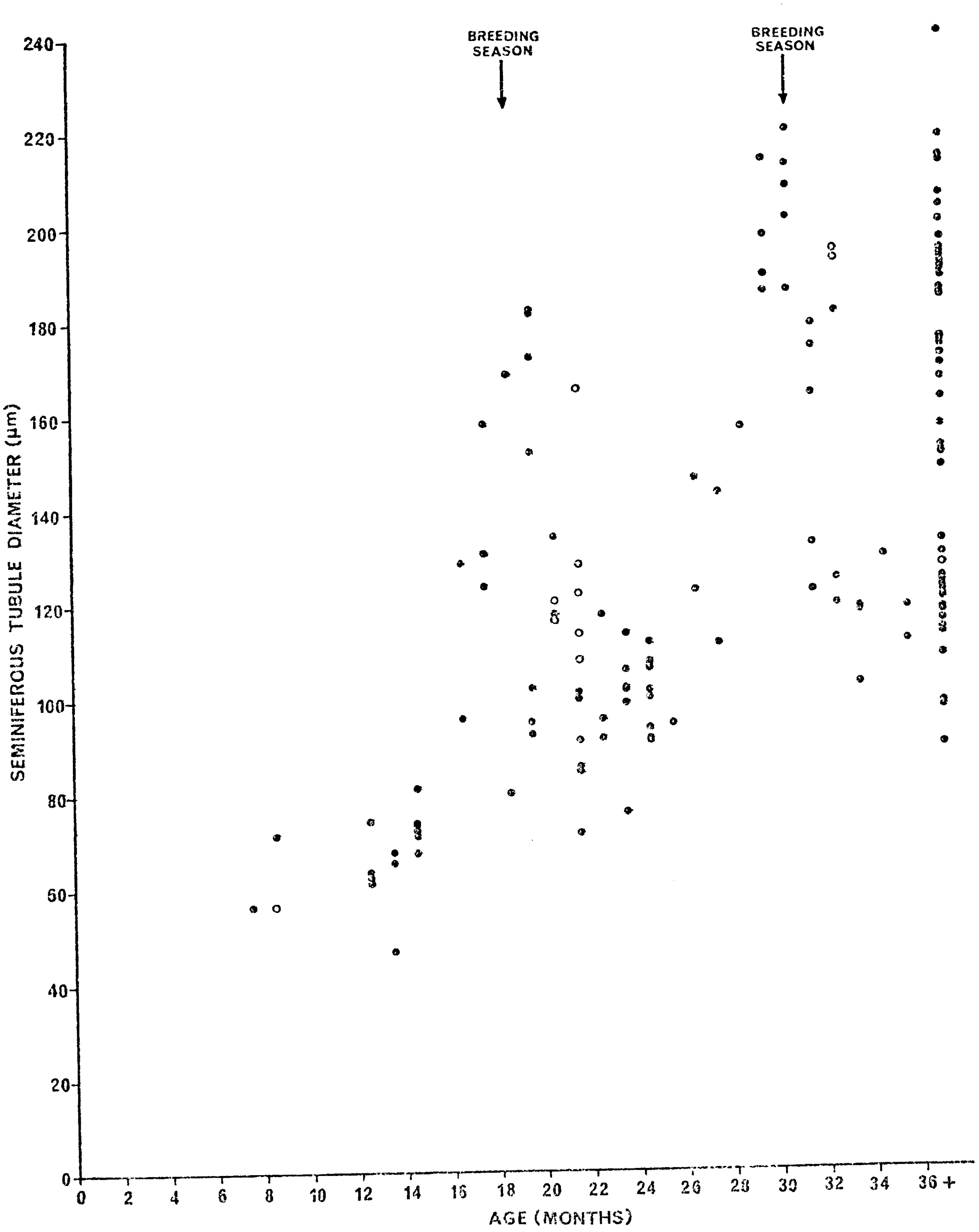

FIG. 22. Variation in mean seminiferous tubule diameter of warthogs with age (n = 146; ● = Complex; o = MGR).

with peaks at about 18 and 30 months of age, is essentially similar to that of testes mass. The wide scatter indicates a lack of precise definition of an asymptotic diameter.

SPERMATOGENESIS AND ATTAINMENT OF SEXUAL MATURITY

Various stages of spermatogenesis, involving spermatogonia, primary spermatocytes, spermatids and spermatozoa (Plate 7), were evident in the Zululand material, but quantitative analysis of intratesticular components and cell associations during the spermatogenic cycle was not undertaken. However, each testis section was classified according to the presence or absence of elongating spermatids and/or spermatozoa (Table 21).

TABLE 21. Percentage of warthogs with spermatozoa or at least spermatids undergoing elongation in the seminiferous tubules, Hluhluwe-Corridor-Umfolozi Game Reserve complex (n = 139).

	YEARLINGS		SUBADULTS AND ADULTS	
Month	n	% with spermatozoa/ elongating spermatids	n	% with spermatozoa/ elongating spermatids
Jan.	6	0,0	5	60,0
Feb.	0	-	5	80,0
Mar.	2	0,0	3	100,0
Apr.	3	100,0	7	100,0
May	2	100,0	15	100,0
Jun.	7	57,1	15	100,0
Jul.	2	50,0	8	100,0
Aug.	6	16,7	4	50,0
Sep.	3	0,0	3	33,3
Oct.	6	0,0	4	0,0
Nov.	4	0,0	17	5,9
Dec.	3	0,0	9	22,2

Spermatozoa and elongating spermatids were first observed in the seminiferous tubules of yearling warthogs from the Complex during April, corresponding with an estimated age of about 17 - 18 months (taking 1 November as the mean farrowing date). Mass of paired testes of the three yearlings examined during April ranged from 22,9 to 81,6 g. Epididymal semen from one of these warthogs, a 54,1 kg animal collected in UGR on 75-04-15, contained spermatozoa in numbers estimated at 1,24 x 10^9 and 1,34 x 10^9 per ml in the left and right epididymes respectively (Dott *pers. comm.*). The masses of paired testes and epididymes of this animal were 81,6 and 9,4 g respectively. Round spermatids were already present in the tubules of two yearlings (paired testes masses of 23,2 and 47,4 g) collected

PLATE 7

(a) Section of testis from a 12-month old immature warthog showing grouping of seminiferous tubules and abundant intertubular tissue. 6 µm, haematoxylin & eosin. x 63.

(b) Section of testis from a mature yearling warthog aged about 19 months showing large seminiferous tubules with numerous primary spermatocytes (spe) and bundle formation of spermatids (sp). Type B spermatogonia (B) are located along the basement membrane. 6 µm, haematoxylin & eosin. x 160.

(c) Section of testis from a yearling warthog aged about 18 months upon attainment of sexual maturity, showing both round and elongated spermatids (sp). Type B spermatogonia (B) are located along the basement membrane. 6 µm, haematoxylin & eosin. x 400.

(d) Warthog spermatozoa. x 1 800.

(e) Yearling male sniffing the enlarged vulva of a yearling female which was probably in late oestrus. (UGR, 75-06-05).

(f) Adult male with swollen and protruding testes during the mating season (HGR, 74-04-19).

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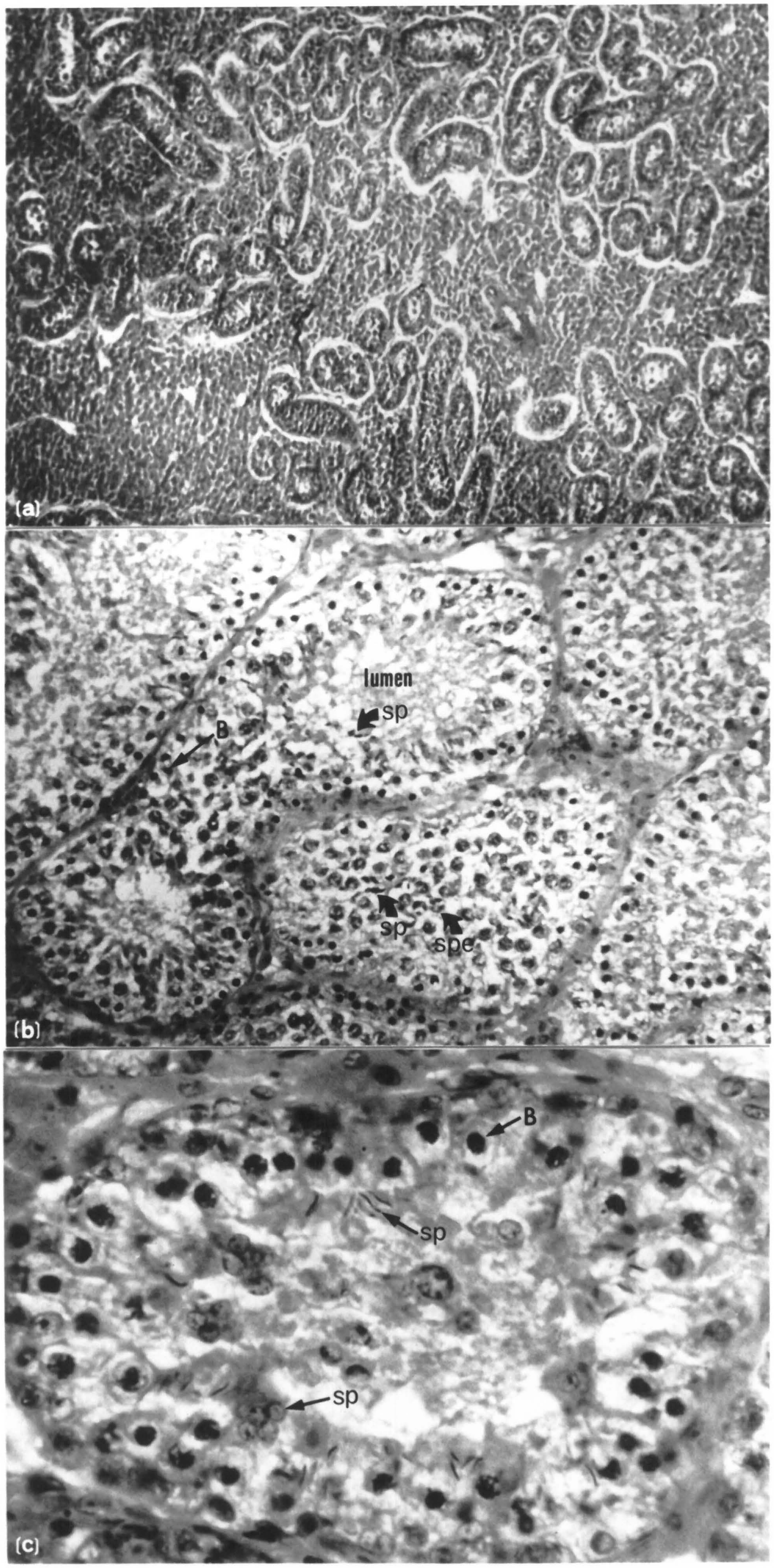

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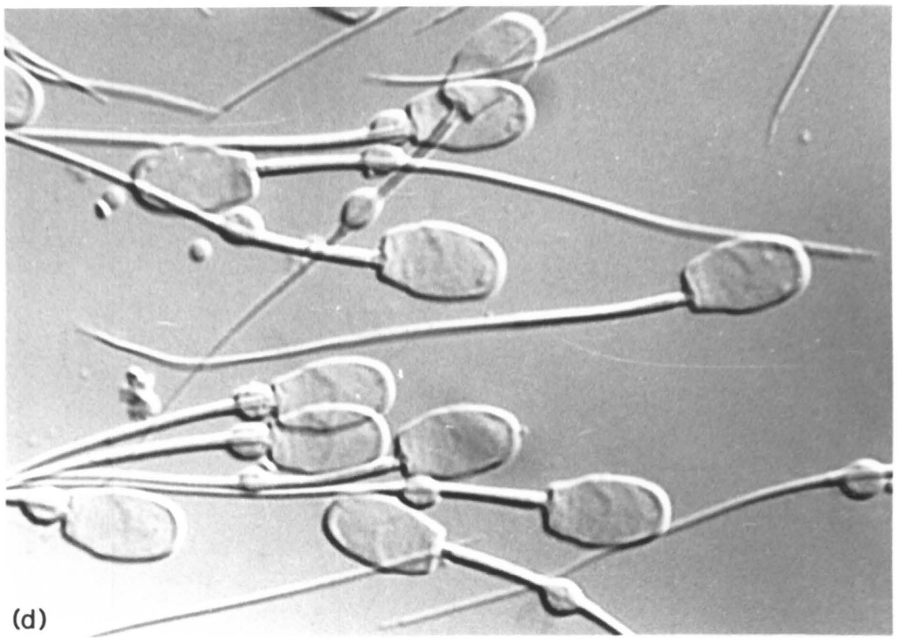
(d)

(Photo : Dr. H.Dott)


(e)


(f)

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during March, i.e. from an estimated age of about 16 months onwards.

Histological examination of the testes of three juveniles, ranging in age from about seven to nine months, showed that they were still immature. The proliferation of spermatozoa in the testes of yearlings during April and May (Table 21) coincides with the mating season (see SEASONAL REPRODUCTIVE CYCLE). Since active spermatogenesis with production of spermatozoa was absent in juveniles, the occurrence of spermatozoa in the seminiferous tubules and epididymes of some yearlings indicates that male warthogs attain sexual maturity at about 18 months of age in Zululand. Field observations of sexual behaviour by yearling males during the breeding season (Plate 7e) support this conclusion. Testicular sections of all subadult (2 - 3 years old) warthogs showed spermatogenesis.

The minimum mass of paired testes (without epididymes) measured for an adult warthog was only 23,1 g, but this was an old animal in poor physical condition (body mass only 59,3 kg) with a heavy infestation of intestinal nematodes, and was collected on 74-09-07 in UGR. The next highest values for paired testes mass recorded in the adult age class were 35,3 and 35,6 g. By comparison, the minimum mass of paired testes for a subadult warthog was 25,6 g.

If a paired testes mass of 25 g is taken as a reasonable lower limit for sexually mature animals, then 57,1% of the 14 yearlings collected in the Complex during the period March to June (inclusive) exceeded this value. However, the paired testes of 13 yearlings for the period November to February were all less than 25 g in mass. On this basis the 50% proportion of mature males is attained within the age range of 16 to 20 months. Of 17 yearlings measured between July and October, corresponding with an estimated age range of 20 to 24 months, 64,7% had testes heavier than 25 g (45,5% of 11 yearlings shot in MGR during July, August and September had testes exceeding 25 g in mass). That the proportion of yearlings with paired testes heavier than 25 g was not higher during the period July to October reflects the pattern of maxima and minima associated with seasonal effects, i.e. mean testes mass declines after June.

Notwithstanding a seasonal decline in spermatogenic activity (Table 21), the tubules of males in the older age classes (probably exceeding 10 years) showed no indication that fertility decreases in old age.

SEASONAL REPRODUCTIVE CYCLE

Masses of paired testes and epididymes and mean seminiferous tubule diameters of warthogs estimated to be at least two years old showed a clear seasonal pattern (Figs. 23 & 24) with maximal values during March, April and May, when mating occurs. Mean testes mass increased four-fold from the minimum

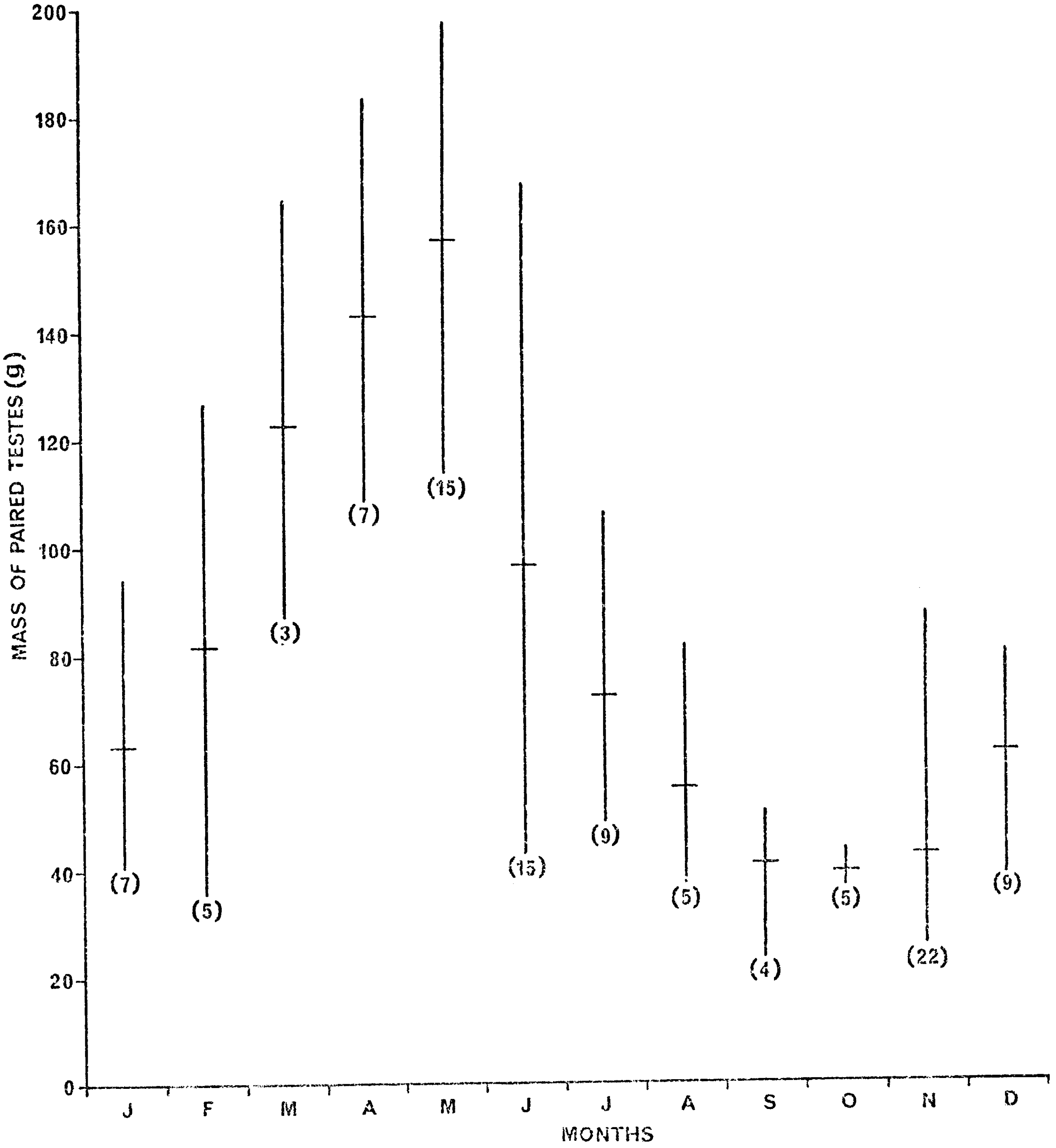

FIG. 23. Seasonal change in combined testes mass of warthogs (at least two years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - May 1975 (range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

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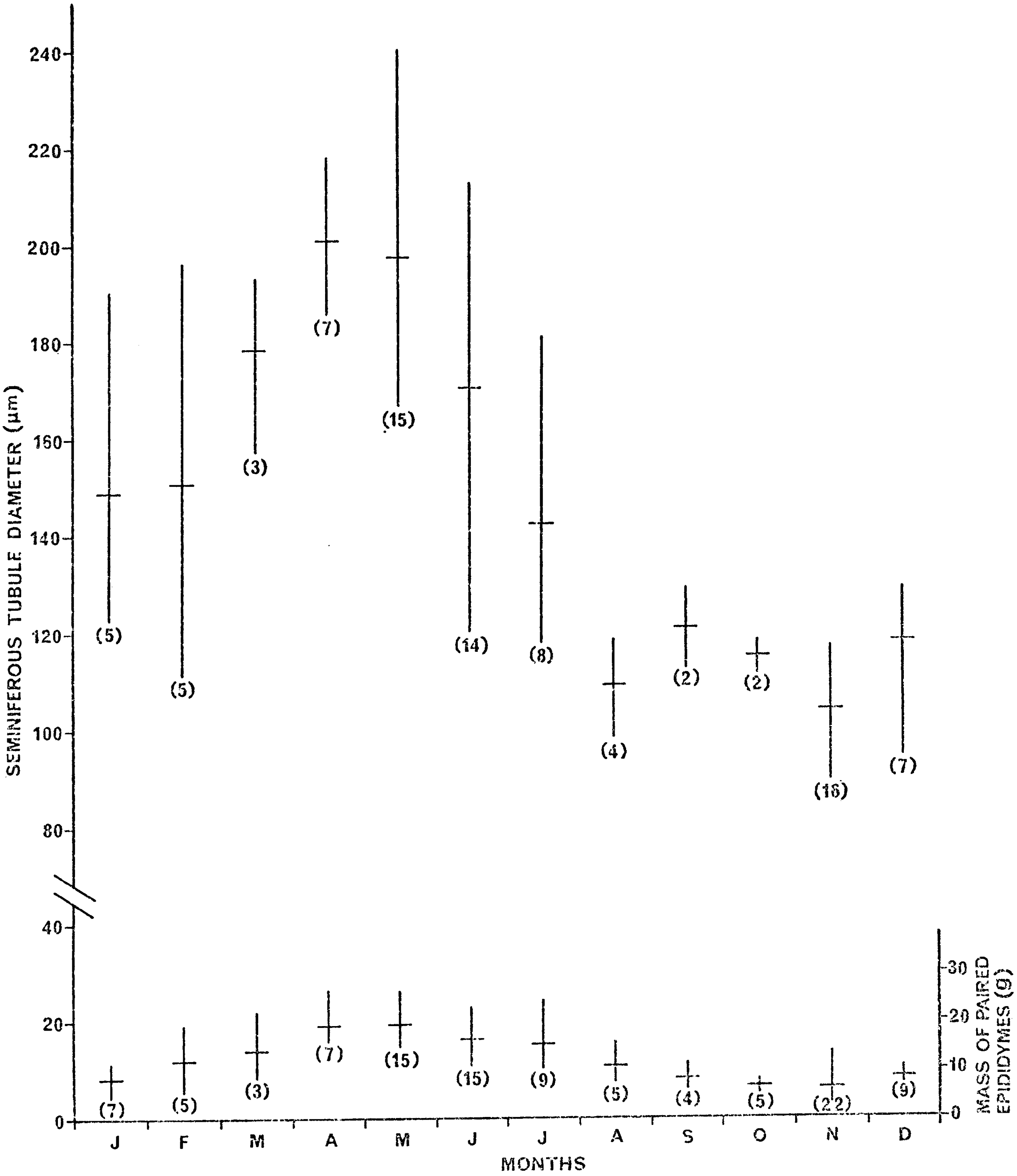

FIG. 24. Seasonal change in seminiferous tubule diameter and combined epididymes mass of warthogs (at least two years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973 - May 1975 (range - vertical line; mean - crossbar; monthly sample size is shown in brackets).

value in October (spring) to the maximum value in May, near the peak of the breeding season, and there was a similar although less pronounced seasonal variation in seminiferous tubule diameter. In the field, the testes of adult males appear large and conspicuous from about early February to late June (Plate 7f), but are markedly smaller outside this period. Seasonal variation in epididymes mass closely followed that of the testes. Even among yearling males, tubule diameters and testes mass peaked during April, May and June (corresponding to an age range of about 17 - 20 months), although their mean testes mass was still below that of adults. The presence of spermatozoa in the seminiferous tubules (Table 21) indicated that yearling males are fertile at this time.

The relationship between paired testes mass (y) and seminiferous tubule diameter (x), illustrated in Fig. 25, is given by the regression equation $y = 0{,}00249\ x^{2{,}05213}$ and has a good correlation coefficient ($r = 0{,}9156$) that is highly significant ($p < 0{,}001$). However, the scatter for mature animals is such that testes mass can decline markedly with little or no concomitant change in tubule diameter.

DISCUSSION AND CONCLUSIONS

Fundamental features of the male warthog reproductive tract noted during this study corresponded with the description of Clough (1969), who comments on the close similarity of the prostate gland and penis in the warthog and the domestic boar. However, the warthog penis is shorter and also differs in that the erectile tissue, which is arranged in a 'C' shape along the dorsal surface, "reaches to within 1 mm of the tip" (Clough op. cit.). The warthog preputial gland could have significance in a social context by depositing a scent mark on the female during mating; other unknown functions might also be involved.

The consistent pattern of maxima and minima in testes mass, epididymes mass and seminiferous tubule diameter, recorded over a two year period in adult and subadult warthogs, indicates a seasonal sexual cycle as occurs in many southern African species. These criteria and others such as testicular testosterone concentration and the presence of testicular and/or epididymal spermatozoa have been used as indicators of sexual function in elephant (Hanks 1972, 1973), African antelope (Skinner, van Zyl & Oates 1974), hippopotamus (Skinner, Scorer & Millar 1975), zebra (Smuts 1976a) and giraffe (Hall-Martin, Skinner & van Dyk 1975, Hall-Martin, Skinner & Hopkins 1978). Monthly trends in testes mass and relative abundance of spermatozoa indicated a regular annual cycle of reproductive activity among warthogs in Zimbabwe (Child, Roth & Kerr 1968), very similar to that found in Zululand warthogs. In contrast to the marked seasonal changes in male warthog reproductive activity in southern Africa, Clough (1969) found no indication of a regular annual cycle among warthogs at the equator, and all adult males that he examined over a seven month period had abundant spermatozoa in their epididymes. The relationship between paired testes mass and mean seminiferous tubule diameter in mature warthogs indicated that testes mass can vary widely over a narrow range of tubule diameters, thus supporting findings in impala that seasonal decline in testes mass "is not necessarily due primarily to a change in the diameter of the seminiferous tubules" (Hanks, Cumming, Orpen, Parry & Warren 1976).

Upon examination of the testes of the warthog and giant forest hog, Parkes (1966) drew attention to the unusual abundance of intertubular secretory tissue, distributed in large confluent blocks so that the seminiferous tubules appear restricted to isolated clumps (Plate 7a). Apart from these features, the basic cellular composition of the seminiferous epithelium and interstitium corresponds closely to published descriptions for other mammals (Johnson & Buss 1967, Ortavant, Courot & Hochereau 1969, Hall-Martin, Skinner & Hopkins 1978).

Attainment of the minimum mass of combined testes and epididymes observed in adults has been used as a criterion of sexual maturity in some studies, e.g. for hippopotamus (Laws & Clough 1966), warthogs (Clough 1969) and buffalo (Grimsdell 1973). The presence of spermatogenesis and especially spermatozoa in the testes sections was used to separate mature warthogs from prepubertal animals in this study. Analysis of paired testes mass of mature warthogs suggested that a minimum mass of 25 g could be used as an indicator of sexual maturity. By this criterion, estimated age at maturity was 16 to 20 months. However, Clough (op. cit.) used 50 g as the combined mass of testes and epididymes at puberty and found 50% occurrence of mature warthogs at about 18 to 19 months of age. Allowing for the epididymes probably comprising 5 to 10 g, a minimum mass at puberty of about 40 g for paired testes alone would be indicated for Clough's data, which is still considerably higher than that found in Zululand warthogs. Clough recorded only one animal with a combined testes and epididymes mass of less than 50 g that showed the presence of epididymal spermatozoa.

In the Zululand material, spermatozoa were already present in the seminiferous tubules of one yearling (aged about 17 - 18 months) with a paired testes mass of only 22,9 g; the paired epididymes mass was 2,3 g but the occurrence of epididymal spermatozoa was not determined. Spermatozoa were found in the epididymes of another yearling aged about 17 - 18 months and were also present in the seminiferous tubules; however, the masses of paired testes and paired epididymes of this individual were 81,6 g and 9,4 g respectively. There will nevertheless be a slight difference between the mean age at appearance of testicular compared with epididymal spermatozoa. In Uganda, the maximum mass

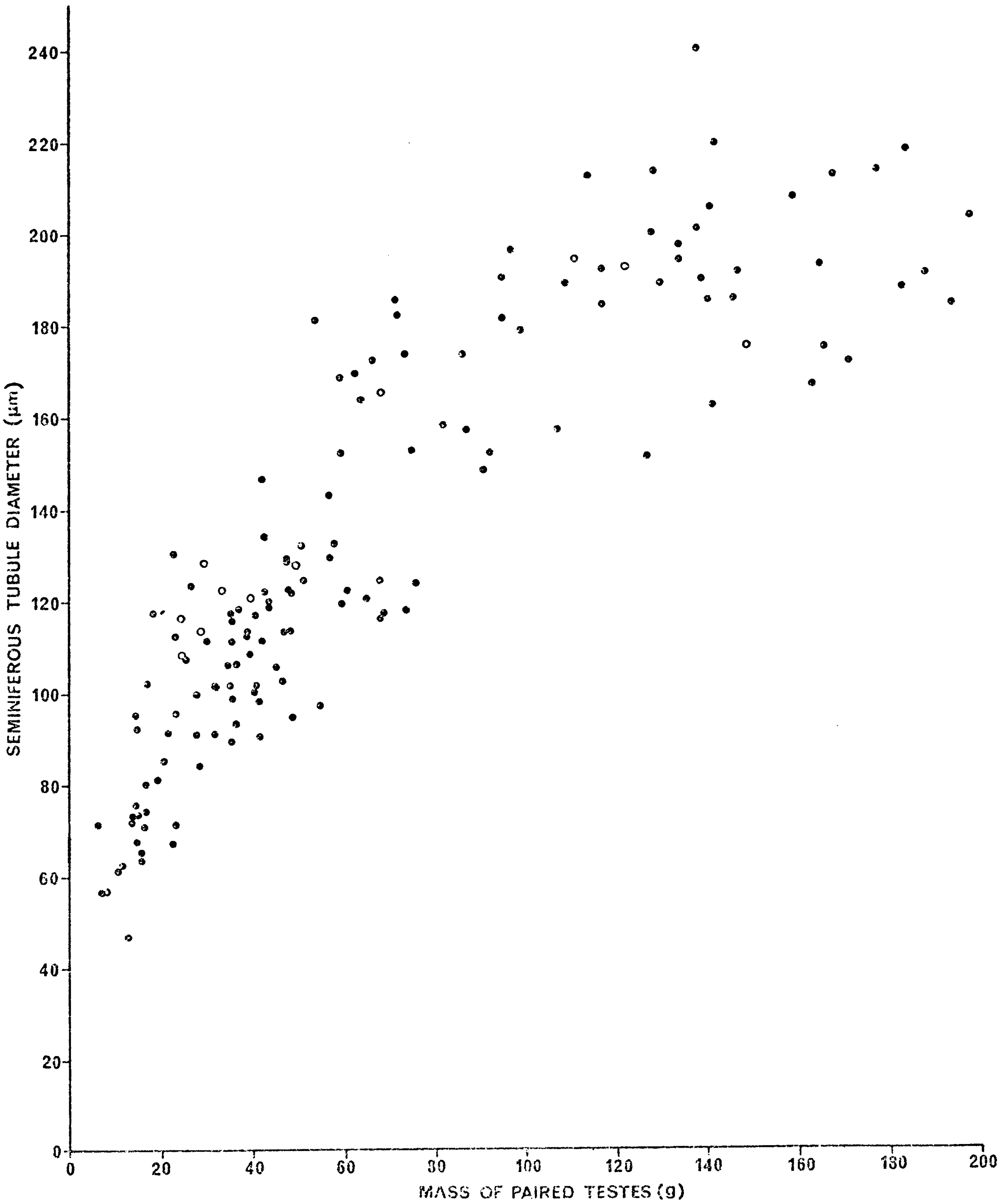

FIG. 25. Scatter diagram of mean seminiferous tubule diameter plotted against combined testes mass for 134 warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex (● = Complex; o = MGR).

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of combined testes and epididymes recorded by Clough (1969) for a single warthog was about 260 g, compared with a maximum of 223,5 g in Zululand warthogs. Skinner et al. (1975) found that testicular size of mature hippopotami in Kruger Park was smaller than in Ugandan hippos examined by Laws & Clough (1966). If average testicular size in mature Zululand warthogs is indeed smaller than in Ugandan warthogs, then average testicular size at puberty could also differ.

On the criterion of presence of spermatozoa in the seminiferous tubules, the minimum age of 17 - 18 months at attainment of sexual maturity in Zululand warthogs corresponds with observations by Cumming (1975a) that male warthogs in Zimbabwe mature at about 18 - 20 months of age. Although Child, Roth & Kerr (1968) considered, on evidence from epididymal smears, that male warthogs in Zimbabwe reached sexual maturity at approximately 26 months of age, they did not examine testes from males between 18 and 26 months old. Some pre-copulatory behaviour was observed in yearling males during the mating season in Zululand, and although not culminating in mounting, its occurrence at this time was probably a manifestation of the attainment of sexual maturity. During May in Wankie National Park, Zimbabwe, Simpson (1964) also observed pre-copulatory behaviour by a yearling male, which rested his chin on the rump of a yearling female in oestrus; however, the female showed no indications of readiness to copulate, although she subsequently accepted mounting by an adult male.

Following the breeding season there was some disruption of spermatogenesis, and spermatozoa were absent from testicular sections of at least some adult and subadult males between August and February (Table 21). Some five months after the peak (May) in the sexual cycle, the proportion of males with spermatozoa or elongating spermatids in the seminiferous tubules had decreased to zero, although spermatogenesis never retrogressed entirely. While reservoirs of epididymal spermatozoa might persist so that some males might still be capable of reproducing for some time after the breeding season, the decline in spermatogenic activity during 6 - 7 months of the year suggests that the fertility of most males is minimal by October.

Notwithstanding the seasonal decline in testicular function after the breeding season, the tubules of the oldest warthogs examined (estimated over 10 years of age) showed no cessation of spermatogenesis. Clough (1969) also found no evidence that fertility in the male warthog declined with age, although in one old male relatively few of the tubules were fully active and the remainder were "in a state of apparent inactivity;" however, many spermatozoa in the epididymes indicated that this animal was probably fertile. Estimates of epididymal sperm abundance were obtained for one yearling, one adult and two subadult male warthogs collected on 75-04-15 in UGR, and ranged from 1,23 x 10^9 to 9,17 x 10^9 sperm per ml for a single epididymis (H. Dott pers. comm.).

CHAPTER 5

REPRODUCTION IN THE FEMALE WARTHOG

INTRODUCTION

Published records of the timing of parturition in the warthog are available for many regions within their geographic range. Spinage (1973b) has reviewed peak months of farrowing from 13 different latitudes and converted these peaks to conception dates. Clough (1969) used the regression relationship between the cube root of foetal mass and foetal age (Huggett & Widdas 1951) to estimate the time of conception and birth for 16 warthog litters from Uganda. Child, Roth & Kerr (1968) delineated the farrowing period of warthogs in Zimbabwe from records of pregnant or lactating sows, and used mean monthly foetal masses to plot a foetal growth curve. Boshe (1981) established the reproductive cycle of warthogs in Tanzania from records of pregnancy and lactation. However, the only studies where features of reproduction in the female warthog such as age at sexual maturity, ovulation, implantation and litter size have been investigated in some detail, based on examination of post-mortem material, are those of Child _et al_., Clough and Boshe (_op_. _cit_.).

The purpose of the present study was to investigate reproduction in the warthog sow in Zululand and relate the results to findings elsewhere. Foetal growth is also described and methods of estimating foetal age in the field are given.

MATERIAL AND METHODS

During cropping operations in the Complex, the reproductive tracts of 141 female warthogs were collected between June 1973 and June 1975. The age composition (see Chapter 2) of this sample was 78 adults (at least three years old), 31 subadults, 29 yearlings and three juveniles. Additional reproductive tracts from one juvenile, two yearlings, two subadults and six adults were collected in MGR during July, August and September 1973.

The ovaries were removed as soon as the warthogs were eviscerated, fixed for two days in Bouin's fluid, and stored in 70% alcohol. Preliminary counts of the number of corpora lutea in each ovary were recorded from the fresh specimens. Individual ovaries were later mass measured, sliced into sections about 1 to 2 mm thick, and examined macroscopically for the presence of corpora lutea, corpora albicantia (pigmented luteal scars), and follicles of particular size classes. Only those follicles larger than 2 mm in mean diameter, measured in two dimensions at right angles, were counted. The numbers of corpora albicantia and corpora lutea were also recorded and mean diameters of the latter were obtained by measuring the greatest and least diameters at right angles with

Vernier calipers. Ovaries from a sample of prepubertal and mature sows at different stages of the ovarian cycle were routinely dehydrated, embedded in paraffin wax, sectioned at 5 μm and stained with Delafield's haematoxylin and eosin for subsequent microscopic examination.

During 1973 and 1974, 199 embryos and foetuses were collected from 61 litters, ranging in size from one to five. Except for nine litters comprising 32 foetuses from MGR, the material was collected in the Complex, mainly in UGR. Foetal sex, position and distribution in both uterine horns were noted. The mass of each foetus was measured soon after collection and crown/forehead-rump lengths were measured where practicable as described by Ansell (1965) and van Zyl & Skinner (1970). Biggs (pers. comm.) provided comparative data on foetal masses and crown-rump lengths for a sample of 30 warthog foetuses, comprising 10 litters ranging in size from one to four, from the Boro River floodplains, Botswana.

Mean ages of prenatal warthog litters were calculated by substituting the values for mean foetal mass of each litter in the foetal growth equation of Huggett & Widdas (1951), viz. $W^{1/3} = a\ (t - t_0)$ where $W^{1/3}$ is the cube root of foetus mass in grams; a is the specific foetal growth velocity; t is foetal age in days; t_0 is a numerical estimate derived from the expression $t_0 = 0{,}2 \times t_g$ for animals with a gestation time (t_g) from 100 - 400 days. The gestation period of warthogs is about 173 days (Brown 1936), so $t_0 = 34{,}6$ days. Using a mean birth mass of 837,5 g (Clough 1969), a was calculated as 0,068, which is fairly low compared with published values for other medium to large ungulates.

The projected months of conception and birth for each litter, calculated from the mean foetal mass, were used to delimit the mating and farrowing seasons. Field observations, especially of recently born piglets, provided confirmatory evidence of seasonal periodicity in farrowing. Mass measurements of six live piglets from two recently farrowed litters in UGR were used to corroborate published information on mean birth mass of the warthog.

RESULTS

ANATOMY

The morphology of the reproductive tract is illustrated in Plate 8, as well as the size difference between the tracts of an immature and a pregnant sow. The ovaries are partly enclosed by a wide ovarian bursa and the two uterine horns are long and convoluted, exceeding the body length in mature females when laid out straight. Intra-uterine space is apparently sufficient to accommodate a maximum of four foetuses to term in each horn. On the inner walls of the cervix are spiral, fibrous ridges (Plate 8b) projecting into the narrow lumen so that they form a spiral tube corresponding with the spirally twisting

PLATE 8

(a) Reproductive tract of a non-pregnant subadult warthog sow with parts labelled as follows: left ovary (A), right ovary (B), left oviduct (C), left uterine horn (D), bladder (E), vagina (F), vulva (G). Ripe follicles were present in the ovaries. (UGR, 74-05-10).

(b) Cervix of a non-pregnant subadult warthog sow showing spiral grooves formed by fibrous ridges on the inner walls. (UGR, 74-05-10).

(c) Udder of an adult warthog sow during lactation showing the four teats. (UGR, 74-03-04).

(d) Translucent gelatinous copulatory plug inside the cervix of an adult warthog sow probably in or near oestrus. (UGR, 74-05-23).

(e) Reproductive tract of a juvenile female warthog aged about six to seven months. (HGR, 74-05-27).

(f) Reproductive tract of a gravid adult warthog sow showing left and right ovaries (A & B), cervix (C), uterine cornua (D & E) and location of a foetus (F) from a litter estimated to be about 109 days post-conception. (UGR, 74-08-21).

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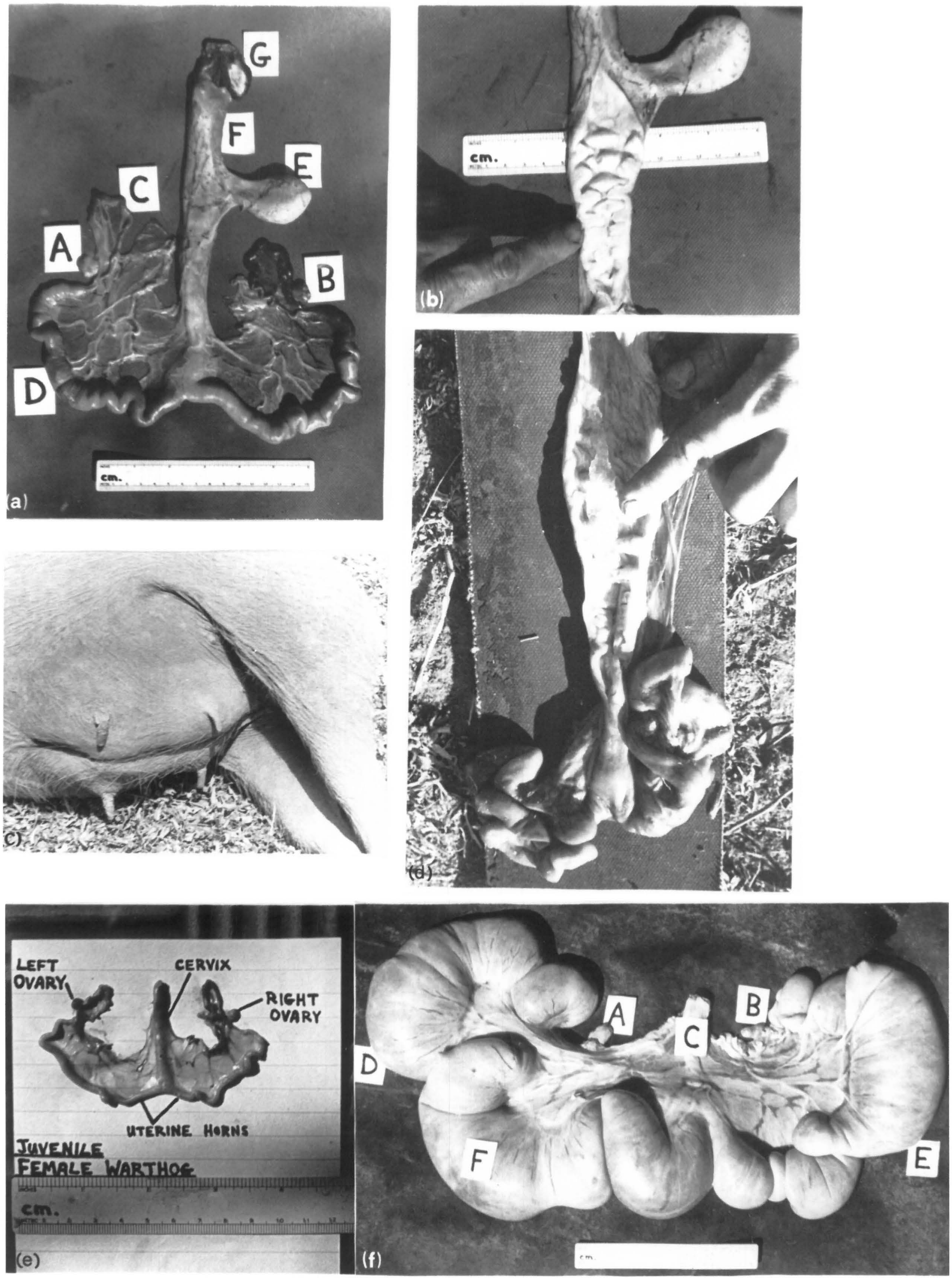

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(corkscrew) tip of the penis. This arrangement probably facilitates ejaculation of semen virtually directly into the uterus and reduces back-flow of semen through the vagina.

During copulation a translucent, gelatinous vaginal plug is deposited (Plate 8d). Substantial copulatory plugs were found in the cervical ends of the vaginas of two adult female warthogs autopsied during the mating season in Zululand. Both sows were accompanied by single adult males with large tusks and bulging testes, and one sow was reportedly mounted shortly before she was shot; although not visibly pregnant, her ovaries contained developing corpora lutea. In the other case, the sow was probably in or near oestrus as indicated by her somewhat swollen vulva from which mucus was being exuded, slightly oedematous uterine epithelium, and the presence of newly erupted follicles in her ovaries; moreover, the accompanying boar was displaying sexual interest and was observed to chase after her briefly. The clear, viscous, almost rubbery secretion from the large bulbo-urethral glands of the warthog boar seems to be the primary source of material for the vaginal plug.

The warthog sow has only four mammary glands, one pair abdominal and the other pair inguinal (Plate 8c). The number of productive teats on a sow or in an association of two or more sows is usually equal to the number of piglets in the family group.

ATTAINMENT OF SEXUAL MATURITY

Knowledge of the age at onset of sexual maturity and the age at first conception in the female warthog is important for assessing the recruitment potential of the population. Females were classified as sexually mature if their ovaries contained at least one corpus luteum or corpus albicans. On this basis, 22 of the 152 females examined from both the Complex and MGR were immature, including all juveniles (n = 4) and 58,1% of yearlings (n = 31.) However, all subadult (2 - 3 years) (n = 33) and adult females (n = 84) were in the mature category.

Although the earliest records of visible embryos in the uteruses of yearling females occurred during July, corresponding with an estimated age of 20 - 21 months, the youngest mature female with corpora lutea of ovulation in her ovaries was estimated to be about 18 months old. The slightly oedematous uterine epithelium of this individual, collected on 74-05-23 in UGR, suggested that oestrus had occurred recently or that implantation might be imminent; no corpora albicantia that could be indicative of earlier ovulation cycles were present in her ovaries. Mean post-conception ages of prenatal litters (see SEASONAL REPRODUCTIVE CYCLE) from 12 yearling females were subtracted from the dates of collection and gave a mean age at first conception of 18 - 19 months. Another two primigravid females,which had just entered the subadult age class when collected (i.e. shortly after 1 November), were estimated to have conceived on 1 June and 4 June respectively, when about or slightly exceeding 19 months of age. Nearly all yearling females in the Zululand sample conceived at or soon after maturity, with the exception of two females which were still immature at an estimated age of 19 - 20 months; the small follicles in their ovaries were not indicative of approaching ovulation and they were collected on 73-06-27, just after the mating season.

SEASONAL REPRODUCTIVE CYCLE

Foetal growth and conception dates

The cube root of mean foetus mass for each litter is plotted against post-conception age in Fig. 26, and mean crown-rump length, mass and age of the foetuses are illustrated in Fig. 27. The mass and crown-rump length measurements of 30 warthog foetuses collected in Botswana (Biggs, pers. comm.) were also plotted on the graphs of foetal growth for the Zululand specimens and fitted well. Increase in foetal mass with age follows an exponential curve, with the increase being in an exponential phase during the last third of pregnancy. The relationship between crown-rump length and mean litter age is linear, and for the Zululand sample is given by the regression equation $x = 37{,}784 + 5{,}386y$ (where x = age in days and y = crown-rump length in cm). Since the correlation coefficient is 0,998 and is highly significant ($P < 0{,}001$), this equation can be used with confidence for predicting foetal age.

From the masses of 154 warthog foetuses collected in the Complex during 1974, it was calculated that most conceptions occurred in May that year (Table 22); peak farrowing in November is thus indicated, which agrees with field observations during the study period. A similar seasonal pattern in the predicted dates of conception and farrowing is evident for the Botswana sample (Table 23); however, Biggs (pers. comm.) considered that parturition by both warthogs and impala in his Botswana study area (the Boro River floodplains in the locality of Chief's Island) was later than average during 1973. Indeed, the latest conception date (73-06-26) for the Botswana sample was some 2 - 3 weeks after the latest dates (73-06-06 and 74-06-12) calculated for Zululand warthogs. The earliest conceptions in Zululand were calculated as 73-04-23, for an adult female from HGR, and 74-04-17, for a subadult female from UGR. Corresponding earliest conception dates for the Botswana sample are 73-05-09 and 74-05-25.

The monthly proportions of yearling, subadult and adult females conceiving are given in Table 24. No marked differences in conception times between age classes are apparent, but sample size for yearlings and subadults is relatively small. Combining the data for 1973 and 1974, a breeding season of about eight weeks' duration is indicated for warthogs in Zululand; however, elements of courtship behaviour displayed by males towards females may be observed, at least sporadically, during February and March already, and some year to year variation

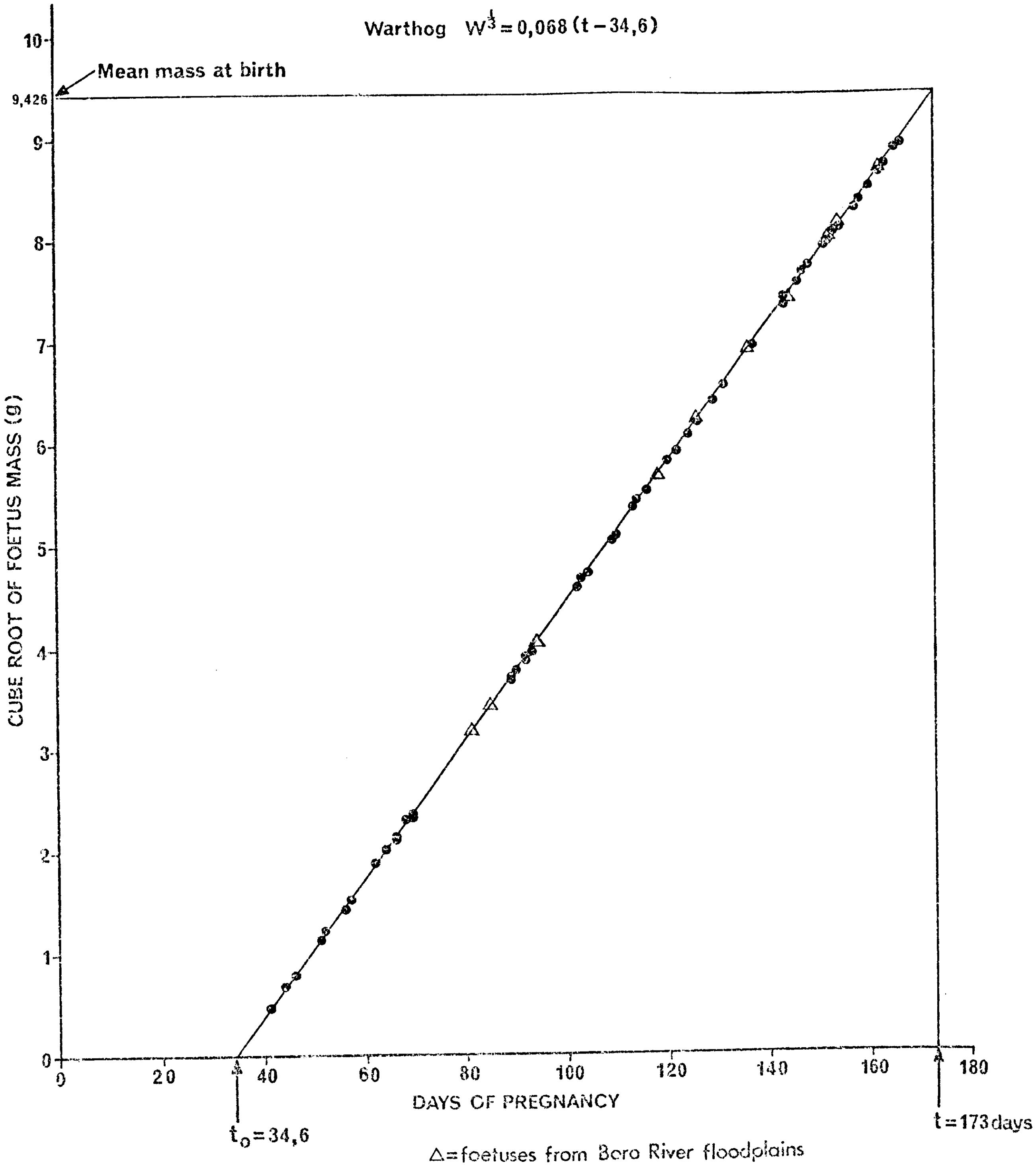

FIG. 26. Plot of cube root of mean foetus mass against conception age for Zululand warthogs (n = 61 litters). Measurements of 10 prenatal warthog litters from Botswana (Biggs pers. comm.) are included for comparison.

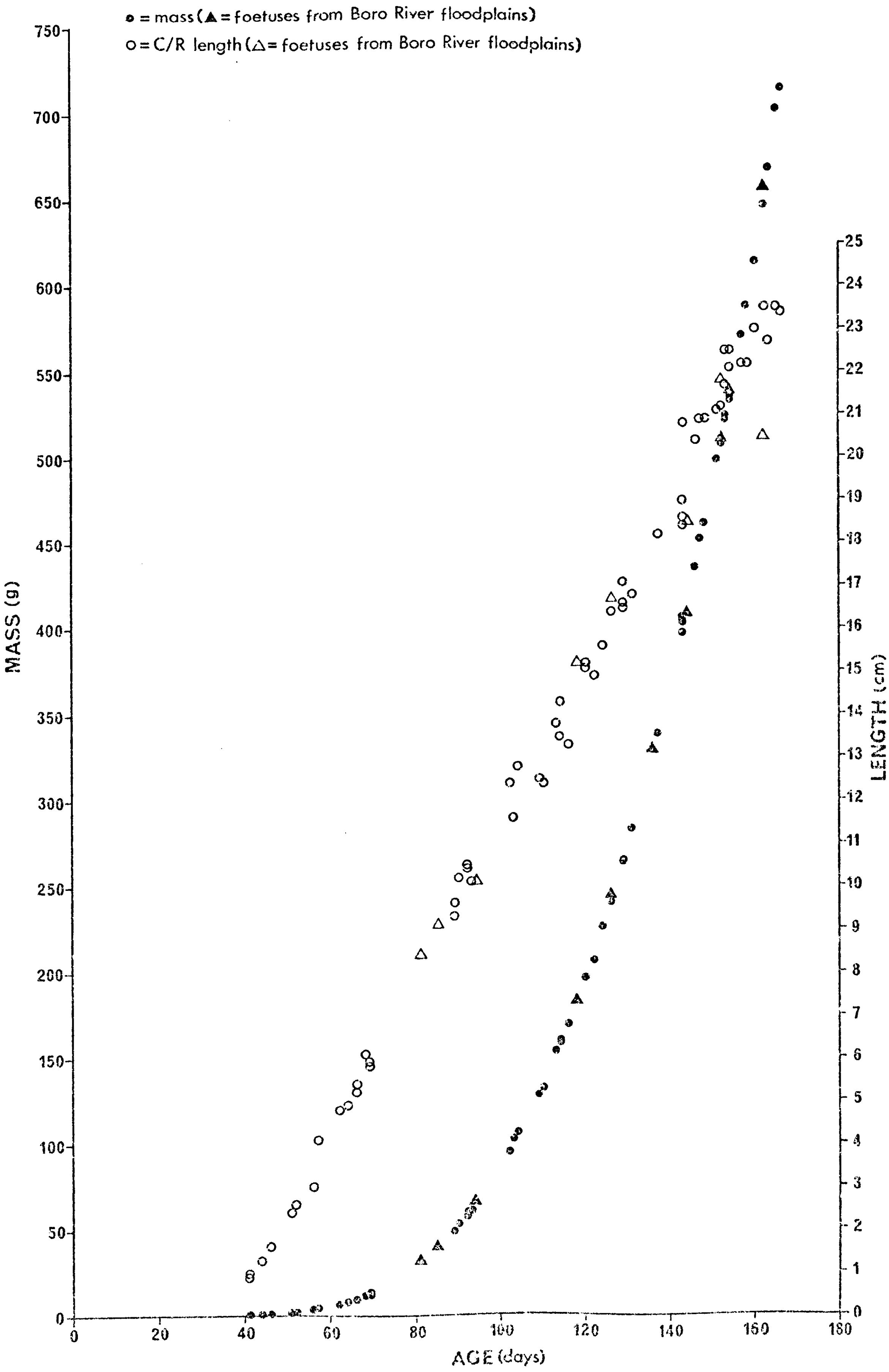

FIG. 27. The mean mass and crown-rump length (C/R) at age for warthog foetuses from Zululand (n = 61 litters). Measurements of 10 prenatal warthog litters from Botswana (Biggs pers. comm.) are included for comparison.

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TABLE 22. Mean foetal measurements and estimates of conception dates for 61 warthog litters from Zululand. (Post-conception age is given by $t = \frac{W^{1/3}}{a} + t_0$ where a = 0,068 and t_0 = 34,6 days).

Age class of sow	Date of collection	No. of embryos or foetuses	Mean mass (g) of embryos or foetuses	$W^{1/3}$	Mean crown-rump length (cm) of embryos or foetuses	Post-conception age (days)	Conception date
	1973						1973
Subadult	18 Jun.	3	0,1	0,464	0,9	41	8 May
Subadult*	4 Jul.	5	0,1	0,464	1,0	41	24 May
Adult*	8 Aug.	3	13,1	2,357	5,8	69	31 May
Adult*	8 Aug.	3	9,5	2,118	5,4	66	3 Jun.
Subadult*	8 Aug.	4	9,6	2,125	5,2	66	3 Jun.
Adult*	8 Aug.	4	8,1	2,008	4,9	64	5 Jun.
Adult*	6 Sep.	4	106,8	4,745	12,8	104	25 May
Adult*	6 Sep.	3	95,4	4,569	12,4	102	27 May
Yearling*	6 Sep.	4	61,8	3,954	10,1	93	5 Jun.
Yearling*	6 Sep.	2	58,1	3,873	10,4	92	6 Jun.
Adult	13 Sep.	3	402,6	7,384	20,8	143	23 Apr.
Adult	21 Sep.	3	206,9	5,915	14,9	122	22 May
Adult	25 Sep.	4	159,2	5,420	13,5	114	3 Jun.
	1974						1974
Adult	12 Jun.	4	0,5	0,794	1,6	46	27 Apr.
Adult	12 Jun.	3	0,3	0,669	1,3	44	29 Apr.
Adult	8 Jul.	3	3,6	1,533	4,1	57	12 May
Adult	8 Jul.	4	2,9	1,426	3,0	56	13 May
Adult	8 Jul.	3	1,8	1,216	2,6	52	17 May
Adult	6 Jul.	5	1,5	1,145	2,4	51	18 May
Yearling	22 Jul.	3	12,5	2,321	5,9	69	14 May
Yearling	22 Jul.	3	12,2	2,302	6,1	68	15 May
Adult	22 Jul.	3	9,4	2,110	5,4	66	17 May
Subadult	22 Jul.	4	6,7	1,885	4,8	62	21 May
Adult	8 Aug.	1	60,2	3,919	10,5	92	8 May
Yearling	8 Aug.	3	53,8	3,775	10,2	90	10 May
Adult	8 Aug.	4	49,5	3,672	9,3	89	11 May
Adult	8 Aug.	4	49,5	3,672	9,6	89	11 May
Subadult	9 Aug.	5	158,1	5,407	14,3	114	17 Apr.
Adult	21 Aug.	3	169,5	5,534	13,3	116	27 Apr.

Continued:-

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TABLE 22, continued

Age class of sow	Date of collection	No. of embryos or foetuses	Mean mass (g) of embryos or foetuses	W $^{1/3}$	Mean crown-rump length (cm) of embryos or foetuses	Post-conception age (days)	Conception date
	1974						1974
Adult	21 Aug.	4	128,3	5,044	12,5	109	4 May
Adult	21 Aug.	4	102,7	4,683	11,6	103	10 May
Adult	22 Aug.	3	132,2	5,094	12,4	110	4 May
Yearling	28 Aug	2	153,6	5,355	13,8	113	7 May
Yearling	7 Sep.	3	263,6	6,412	17,1	129	1 May
Yearling	7 Sep.	3	225.7	6,089	15,6	124	6 May
Yearling	7 Sep.	3	195,8	5,807	15,1	120	10 May
Subadult	7 Sep.	3	196,4	5,813	15,2	120	10 May
Adult	22 Sep.	4	240,0	6,214	16,4	126	19 May
Adult	23 Sep.	3	396,4	7,346	19,0	143	3 May
Adult	23 Sep.	4	338,5	6,969	18,2	137	9 May
Adult	23 Sep.	2	263,6	6,412	16,6	129	17 May
Adult	24 Sep.	4	282,5	6,562	16,8	131	16 May
Adult	24 Sep.	3	263,1	6,408	16,5	129	18 May
Adult	7 Oct.	2	403,6	7,390	18,6	143	17 May
Yearling	8 Oct.	3	435,9	7,582	20,4	146	15 May
Adult	8 Oct.	4	405,5	7,402	18,4	143	18 May
Yearling	25 Oct.	3	701,9	8,887	23,5	165	13 May
Adult	25 Oct.	3	461,9	7,730	20,9	148	30 May
Adult	28 Oct.	3	647,3	8,650	23,5	162	19 May
Subadult	28 Oct.	4	614,2	8,500	23,0	160	21 May
Yearling	28 Oct.	2	533,3	8,109	22,5	154	27 May
Adult	28 Oct.	3	535,0	8,118	22,1	154	27 May
Adult	28 Oct.	4	522,0	8,052	22,5	153	28 May
Adult	28 Oct.	3	452,2	7,676	20,9	147	3 Jun.
Adult	2 Nov.	4	523,9	8,002	21,7	153	2 Jun.
Subadult	2 Nov.	2	497,9	7,926	21,1	151	4 Jun.
Subadult	5 Nov.	2	571,1	8,297	22,2	157	1 Jun.
Adult	9 Nov.	3	713,4	8,935	23,4	166	27 May
Adult	9 Nov.	2	588,2	8,379	22,2	158	4 Jun.
Adult	11 Nov.	3	667,8	8,741	22,7	163	1 Jun.
Adult	11 Nov.	4	508,3	7,981	21,2	152	12 Jun.

* Mkuzi Game Reserve

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TABLE 23. Estimates of conception dates for 10 warthog litters from the Boro River floodplains, Botswana, based on foetal measurements provided by Biggs (pers. comm.)

Body mass of sow (kg)	Date of collection	No. of embryos or foetuses	Mean mass(g) of embryos or foetuses	$W^{1/3}$	Mean crown-rump length (cm) of embryos or foetuses	Post-conception age (days)	Conception date
	1973						1973
48,0	20 Aug.	2	31,9	3,172	8,4	81	31 May
40,0	28 Sep.	3	66,1	4,043	10,1	94	26 Jun.
70,0	8 Oct.	4	510,6	7,993	21,8	152	9 May
49,0	12 Oct.	3	408,1	7,417	18,5	144	21 May
43,5	9 Nov.	1	657,0	8,693	20,5	162	31 May
57,0	9 Nov.	4	539,2	8,139	21,2	154	8 Jun.
	1974						1974
55,5	18 Jun.	3	40,1	3,423	9,1	85	25 Mar.
49,0	10 Aug.	4	243,9	6,248	16,7	126	6 Apr.
53,0	19 Aug.	3	182,5	5,672	15,2	118	23 Apr.
	1975						1975
42,0	11 Sep.	3	328,6	6,901	-	136	28 Apr.

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in the peaks of mating activity is to be expected.

TABLE 24. Monthly percentage of conceptions for three age classes of warthogs, calculated from foetal mass data collected in Zululand during 1973 and 1974.

	YEARLING		SUBADULT		ADULT		TOTAL FEMALES CONCEIVING	% OF ALL FEMALES CONCEIVING
	n	%	n	%	n	%		
APRIL	0	0,0	1	11,1	4	10,0	5	8,2
MAY	10	83,3	5	55,6	28	70,0	43	70,5
JUNE	2	16,7	3	33,3	8	20,0	13	21,3

Farrowing in Zululand normally extends from about mid-October to early December, thus corresponding with the start of the wet season. During both the 1973 and 1974 farrowing seasons, the first sightings of piglets in the Complex were recorded on 28 October, in HGR (the earliest reports of piglets in UGR were on 73-12-05 and 74-10-30). For the first week or two after birth, piglets are not likely to be seen since they remain in or near the hole where they were born. Thus very few sightings of piglets were recorded during November, and the bulk of sightings occurred from December onwards. Unpublished Natal Parks Board records for the Complex mention some dates of first sightings of recently born warthogs: 58-10-04, 59-11-30, 61-11-15, 62-11-05, 63-09-12, 65-11-23. Only four observations of mounting (59-05-29, 60-05-12, 60-05-16 and 62-05-05) are on record; however, Anderson and Whateley (*pers. comms.*) witnessed mounting on 74-04-15 and 75-05-11 respectively, in HGR. Two separate instances of single adult males seen mounting sows were reported on 75-06-05, during cropping in UGR. A copulatory plug and developing corpora lutea were found in one of these sows but not in the other. Farrowing in UGR during 1963 was apparently rather early since no foetuses were found in shot females after mid-October, and as early as 27 August the spoor of infants had been seen around the entrance of a hole (P.J. Daniel, Natal Parks Board records).

PREGNANCY

Implantation and placentation

Transuterine migration of blastocysts, as indicated by the number of corpora lutea of pregnancy in each ovary relative to the number of foetuses in the corresponding uterine horns, was recorded in 35 out of 61 pregnancies (57,4%). Single blastocysts were involved in 29 transmigrations, compared with only six instances where two blastocysts migrated. In most cases (23 against 12)

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migration was from the left to the right uterine horn. The distribution of implantations between the two horns of the uterus was roughly even, although the left horn was slightly favoured; out of 199 foetuses, 102 (51,3%) implanted in the left horn. When implantation is near the caudal extremity of a uterine horn, that end of the chorionic vesicle contiguous with the common uterus may extend up to some 30 cm into the opposite uterine horn.

A maximum of four embryos in a single uterine horn was found in only one female, and the unequal numbers of corpora lutea in her ovaries indicated that one of these embryos had migrated from the opposite side, where a fifth embryo still remained. During later foetal development however, no cases of more than three foetuses per horn were recorded. Thus survival to term of more than three foetuses in one horn is probably unusual. In 32 out of 34 warthog sows where transuterine migration had occurred and the numbers of ova contributed by each ovary were unequal, transmigration of blastocysts was from the side of the more prolific ovary. Only one instance of migration was recorded where equal numbers of corpora lutea of pregnancy were present in the left and right ovaries.

The only warthog reproductive tract collected with three near term foetuses in one uterine horn was from an adult female shot on 74-11-11. All three foetuses were in the anterior presentation position relative to the cervix, and when the uterine horn was straightened out after dissecting off the supporting ligaments, the spacing between the rump of the most caudally situated foetus and the forehead of the next foetus was measured as only some 13 cm. However, the forehead of the third foetus (nearest the oviduct) was spaced about 33 cm from the rump of the foetus in the middle position. Measuring spacing between implantation sites as the distances between the approximate mid-points on the body of each foetus (while still within the unruptured chorionic vesicle), it was found that the first foetus was 17 cm from the median septum of the common uterus, and 34 cm from the second foetus, which in turn was spaced 52 cm from the third. Mean forehead-rump length of the three foetuses was 20,7 cm (range 18,5 - 23,7 cm). A fourth foetus with a forehead-rump length of 22,8 cm was present in the other uterine horn, located about 23 cm from the junction of the two horns. Taking 30 cm as the approximate minimum spacing required between implantation sites in the same uterine horn towards the end of gestation, each horn of the warthog uterus should be long enough to accommodate up to four foetuses.

The placenta of the warthog is diffuse and of the epitheliochorial type. The chorionic vesicle is fusiform with a plicated epithelial surface lying in close contact with the uterine mucosa. Dilation of the chorionic vesicle by growth of the allantois never extends to the extremities, so that the uterine cornua remain undilated where the undeveloped terminal portions of neighbouring chorionic vesicles lie close together.

Involution of the uterus following parturition is rapid and oedema of the uterine endometrium had disappeared by an estimated three to four weeks post-partum. Disappearance of vascularisation at implantation sites was also largely complete about a month after farrowing.

Birth mass and relationships between sex, number and size of foetuses

The largest individual foetus collected, a female of 753,2 g body mass with a forehead-rump length of 23,8 cm and hind foot length of 8,2 cm, was from a litter of triplets (two females, one male) from a yearling sow shot on 74-10-25 in UGR. Estimated post-conception age was 165 days, and the advanced development is also apparent in the smaller male littermate (Plate 9a). In another litter of triplets (two males, one female) (166 days), the heaviest individual foetus was a male of 719,0 g with a forehead-rump length of 23,1 cm and hind foot length of 7,7 cm.

Considerable discrepancy of size and development may occur among foetuses of the same litter. The most marked difference during late gestation was found among four foetuses, estimated 152 days post-conception, from an adult sow shot on 74-11-11 in UGR. The uterus of this sow carried three foetuses (two males, one female) of 708,2, 368,2 and 330,7 g body mass in the right horn and a single (female) foetus of 626,0 g in the left horn; two corpora lutea were present in each ovary indicating that one blastocyst must have migrated from the left to the right side. Forehead-rump and hind foot lengths ranged from 18,5 - 23,7 cm and 5,8 - 7,7 cm respectively. The largest foetus in this case was a male, but the size range indicates that development of some piglets may be retarded at birth relative to that of other littermates.

In addition to the morphometric data from near term foetuses, measurements of six live piglets (Table 25) from two litters found inside burrows provided confirmatory evidence of the approximate size of neonatal warthogs. The piglets of the first litter were judged to be about three weeks old, since they were able to stand and move about. However, the piglets of the second litter were probably not more than a week old, and were unsteady on their legs. The largest piglet in the younger litter was a female whereas the single male in the older litter was larger than his two female siblings. Some substantiation of the age estimates for these two litters was derived by comparison of the mean mass of littermates (Table 25) with the mass of 1,7 kg for warthogs at one month of age, reported by Bigourdan (1948).

Of four litters involving male and female twin foetuses, the males were slightly heavier. However, the sample size is too small for statistical comparison. Although different stages of gestation are involved, the maximum mass difference measured between male twins was less than between male and female twins. In seven out of eight litters of quadruplets where the distribution of

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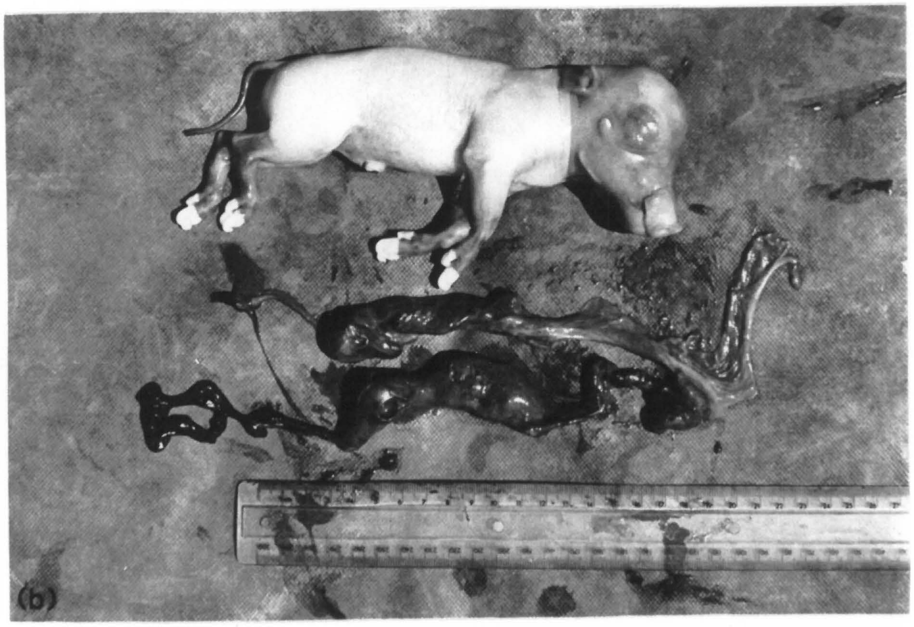

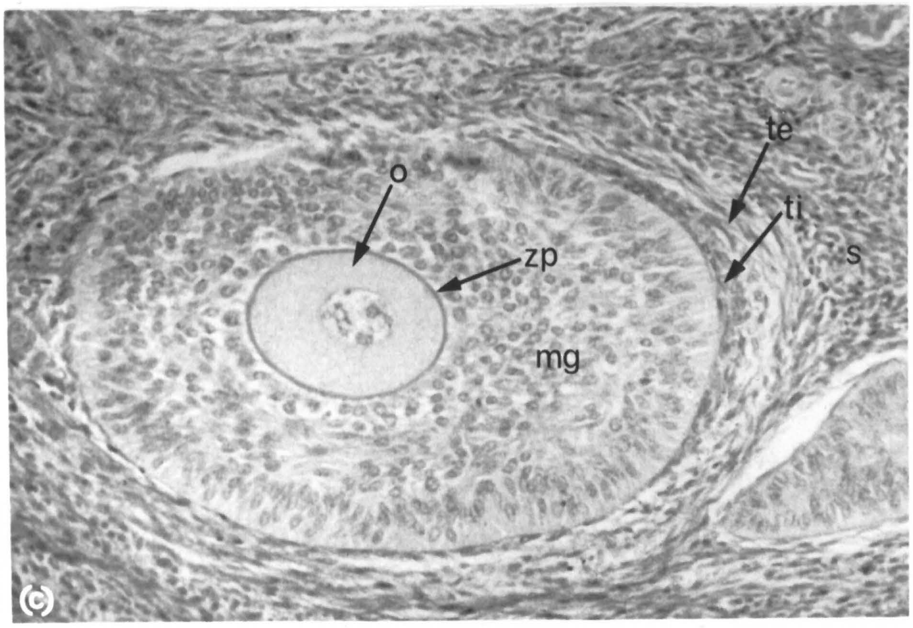

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PLATE 9

(a) Near-term male warthog foetus (mass 682,2 g; forehead-rump length 23,3 cm) from a yearling sow estimated to be about 165 days pregnant. (UGR, 74-10-25).

(b) Two atrophied foetuses and a normal male littermate (mass 281,5 g; forehead-rump length 17,1 cm) from an adult warthog sow estimated to be about 129 days pregnant. (UGR, 74-09-24).

(c) Section of ovary from a pregnant adult warthog sow showing a secondary follicle (o = oocyte, zp = zona pellucida, mg = membrana granulosa, ti = theca interna, te = theca externa, s = stroma). 5 μm, haematoxylin & eosin. x 160.

TABLE 25. Body dimensions (cm) and mass (g) of recently born warthogs from two litters found inside burrows during the 1974 farrowing season in Umfolozi Game Reserve.

Date	Sex	Body mass	Head & body length*	Tail length	Chest girth	Shoulder height†	Hind foot length(c.u.)	Ear length
18 Nov.	♂	1694,7	38,6	11,3	25,0	20,0	10,0	4,4
	♀	1639,4	36,7	11,1	24,8	20,0	10,0	4,4
	♀	1620,9	36,3	11,0	24,7	20,0	10,0	4,4
6 Dec.	♀	1022,7	32,8	9,0	21,3	18,0	8,4	4,0
	♂	984,5	32,2	8,7	21,1	18,0	8,2	4,0
	♂	976,4	32,0	8,5	21,0	18,0	8,1	4,0

* over curves

† linear

foetuses between the left and right uterine horns was equal and where each litter comprised equal numbers of males and females, the male foetuses slightly exceeded their female siblings in body mass, but the difference was not statistically significant. A tendency towards slight sexual dimorphism of size in warthog foetuses was still discernible in the total sample of heterosexual litters (n = 40), where the heaviest foetus was a male in 27 instances. However, unequal distribution of foetuses between the two uterine horns may influence the size of individual foetuses.

Of 18 litters with an estimated post-conception age of at least 120 days and where a single foetus was present in one uterine horn and two or more foetuses in the other, the single foetus exceeded the mean body mass of the foetuses on the contralateral side, and the difference was nearly significant at the 5% level (t = 2,099 ; d.f. = 17). Only two of these litters involved three foetuses in one uterine horn, and in both cases their average mass was markedly less than the mass of the single foetus in the opposite horn; indeed, this difference was as much as 157 g in the litter closest to term (152 days post-conception).

Where two or more foetuses of at least 120 days post-conception age occupied a single uterine horn, the heaviest foetus occurred nearest the cervical end in 23 out of 33 instances. Ideally, a valid comparison of size differences between singletons, twins, triplets, quadruplets and quintuplets requires a larger sample of same age foetuses, particularly during the last third of gestation, than was obtained during the present study. The best comparison can be made among the 143 days post-conception foetuses. Of the four litters in this group, two had three foetuses, one had two foetuses, and one had four foetuses. However, the mean body mass of the foetuses in the quadruplet litter slightly exceeded that in the smaller litters.

REPRODUCTIVE POTENTIAL

Prenatal sex ratio and litter size

A total of 199 foetuses was collected from 61 sows (including the yearling age class), giving an average of 3,26 foetuses per female (range = 1 - 5). However, evidence was found suggesting recent parturition of one foetus by a gravid female collected in UGR on 74-11-09, during the period of peak farrowing. Three corpora lutea of pregnancy were present in the ovaries of this female, but only two foetuses were found in her uterus. Development of both these foetuses was advanced, and although their body masses of 646,3 g and 530,0 g were less than the mean birth mass of 837,5 g recorded by Clough (1969), and used in this study, they were nevertheless within the lower range of birth mass reported by Bigourdan (1948). A distinct vascularised zone extending some 45 cm in the endometrium of one uterine horn indicated the probably recent presence of the chorionic vesicle of the missing foetus. The addition of one extra foetus to the sample would have given a mean prenatal litter size of 3,28. Excluding the nine litters comprising 32 foetuses (16 females, 11 males, 5 unsexed) from MGR, prenatal litter size for the warthog population of the Complex averaged 3,21 foetuses per female.

The most frequent litter size was three (n = 29), followed by quadruplets (n = 20), twins (n = 8), quintuplets (n = 3), and only one singleton litter (evidently deriving from an original litter of four). Post-conception age of the most advanced of the quintuplet litters was estimated as 114 days, corresponding with an average foetus mass of 158,1 g.

Of 172 foetuses which could be sexed, 82 were females and 90 males. This ratio (1:1,1) did not depart significantly from unity at the 5% level. Number of viable foetuses per litter and body mass of the mother (Fig. 28) were significantly correlated ($P < 0,01$), but the correlation coefficient was poor ($r = 0,351$). Analysis of prenatal litter sizes indicated that fewer young are produced at the first pregnancy than at subsequent pregnancies. The mean prenatal litter size of 14 primigravid females was 2,71 foetuses per female (S.D. = 0,61; range = 2 - 4) compared with 3,43 foetuses per female (S.D. = 0,80; range = 1 - 5) for older females (n = 47).

Prenatal mortality

For the 61 sows with macroscopically visible embryos, the corresponding totals of corpora lutea recorded in the left and right ovaries were 129 and 90

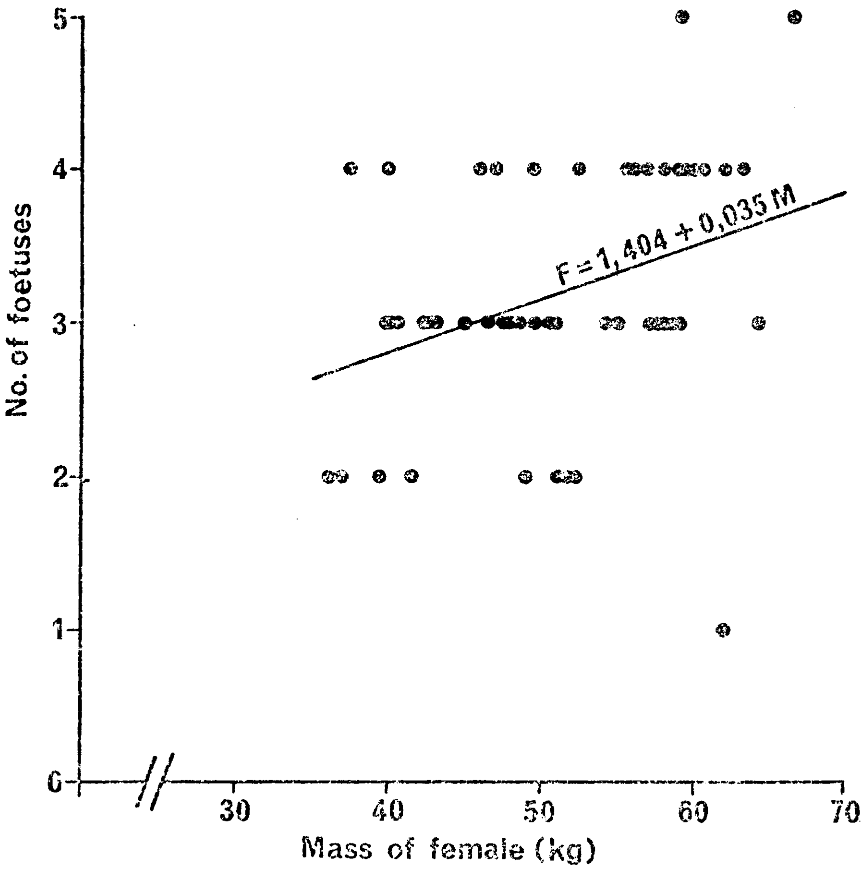

FIG. 28. Relationship between number of viable foetuses (F) and body mass of female (M) for 55 warthog litters from Zululand.

respectively; giving an ovulation rate of 3,59 ova per female. Embryonic loss (the difference between the 219 ovulations and the corresponding total of 199 viable foetuses conceived) is 9,13%. When the MGR material is separated from the total sample, a prenatal mortality of 9,24% is indicated for warthogs in the Complex (184 ovulations and 167 foetuses from 52 pregnancies), compared with a prenatal mortality of 8,57% for the MGR sample (35 ovulations and 32 foetuses from 9 pregnancies).

Increased vascularisation typical of implantation sites was noted in the empty left uterine horns of two otherwise gravid adult females. The mean mass measurements of the viable foetuses in their right uterine horns corresponded with estimated post-conception ages for the two litters of 92 and 129 days. Corpora lutea counts indicated intra-uterine mortality, either through resorption or abortion, of three foetuses in the 92 days pregnant female and one foetus in the 129 days pregnant female. Only one pregnancy involving clear evidence of foetal resorption was recorded (Plate 9b), also in an adult female, whose right uterine horn contained one atrophied and one normal foetus, while one atrophied and two normal foetuses were present in the left horn. There were no corpora lutea in the right ovary but the left ovary was crowded by six.

No other evidence of foetal resorption or abortion was noticed in the reproductive tracts examined, so most prenatal mortality, reflected by the excess of corpora lutea over foetuses, presumably comprises loss of ova through

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non-fertilisation or failure to implant and develop. Of 14 pregnancies where intra-uterine loss had occurred, this involved single ova, blastocysts or foetuses in 11 females, two in another female, and a maximum of three in the case of only two females.

Reproductive success

Out of 77 sexually mature females over the age of 20 months, examined between 1 July and 31 December (a period when the occurrence of conception is easily determined), 58 were pregnant and another 15 were both lactating and had regressing corpora lutea in their ovaries, indicating that they had recently farrowed. The remaining four females in the non-pregnant, non-lactating category included an adult female, shot in MGR on 73-07-04, which had five well developed corpora lutea in her ovaries. Nine other mature females examined during July (including one other from MGR) were estimated from 41 to 69 days pregnant, so the absence of visible embryos in the single instance recorded that month could be a consequence of a relatively later oestrus than in most females (but nevertheless within the limits of possible conception); assuming fertilisation had occurred, there is no way of determining whether implantation (indicative of successful conception) had failed, so this female was excluded from the calculation of reproductive success.

A non-lactating subadult female, shot on 74-11-23, had three apparently recent corpora albicantia in her left ovary only, suggesting that fertilised ovulation and implantation had occurred, followed by reproductive failure at a later stage or mortality of the litter at or soon after birth. The ovaries of a non-lactating adult female shot on 74-12-19 contained regressing corpora lutea, while residual vascularisation in her uterine cornua also indicated that she had been pregnant. However, in both these cases it was not possible to determine whether mortality had followed birth or whether pregnancy had failed before term due to factors such as abortion and resorption.

The only definite case of infertility (in the sense that no conception occurred) involved a very thin adult female, shot on 74-08-12, in UGR. No corpora lutea were present in her ovaries, but 13 corpora albicantia were counted and the larger follicles (up to 1,9 mm in mean diameter) were atretic; her uterine cornua appeared shrunken.

Thus, on the basis of one case of infertility and two possible cases of reproductive failure after conception, out of 76 females examined, a reproductive success rate ranging between 96,1 and 98,7% is indicated. This sample included 24 females of between 20 and 26 months of age, all of which had conceived for the first time during the mating season in their second year of life, coinciding with attainment of sexual maturity. However, two yearling females collected on 73-06-27, just after the mating season, had failed to ovulate and were still sexually immature. If the 10 sexually mature females examined in MGR during 1973 are excluded from the total Zululand sample, estimated reproductive success for the warthog population in the Complex alone was 95,5 - 98,5% (n = 67 females).

The reproductive performance of the population in the Complex, estimated from the mean prenatal litter size of 3,21 foetuses per female and a minimum reproductive success rate of 95,5%, was about 307 young per 100 mature females per year. Since population fertility (the proportion of mature females conceiving) was very high during the study period, while prenatal mortality was low, the estimated reproductive performance was close to the theoretical maximum reproductive potential (354 young per 100 mature females if all ova were fertilised and produced viable embryos). However, the proportion of mature females which breed, and average litter size, could be expected to vary with conditions from year to year.

Few very old females (probably exceeding 10 years of age as judged by cementum line counts and the morphometry of the third molar teeth) were examined, but none showed signs of reproductive senescence.

OVARIAN STRUCTURE AND DYNAMICS

During oestrus and pregnancy the shape and size of the ovary varies according to the size and number of developing follicles and corpora lutea. The warthog ovary has a smooth surface except where protrusions are formed by corpora lutea or large vesicular follicles. In 61 pregnancies involving 219 corpora lutea, 58,9% of the latter were distributed in the left ovary, indicating that the left ovary is slightly more active than the right. Of the 61 pairs of ovaries from pregnant females, the left ovary had a greater mass than the right in 43 instances (70,5%), and this deviation from the expectation that the ovaries are of equal mass was highly significant ($\chi^2 = 26,44$; $p < 0,001$).

The follicles

Ripe follicles are clear and semi-transparent and protrude from the surface of the ovary. The microscopic structure of a section through a normal secondary follicle is shown in Plate 9c. As in other mammals, a transparent, non-cellular zona pellucida encases the warthog oocyte and separates it from the surrounding follicular epithelium (membrana granulosa). In the vesicular stage, the oocyte, still ensheathed by several layers of granulosa cells, forms a hillock (the cumulus oophorus) projecting from the membrana granulosa into the antrum. A thecal layer is present immediately adjacent to the granulosa of the follicle, and both the glandular theca interna and the fibrous theca externa could be distinguished.

Follicular atresia affects both the oocyte and the granulosa cells; lifting and folding on the intact membrana granulosa may occur and granulosa cells commonly become detached and drift into the antrum.

When numbers of follicles exceeding 2 mm in mean diameter were plotted against age (Fig. 29a), age-specific differences were slight compared with seasonal effects. For females that were not visibly pregnant, average numbers of >2 mm follicles per pair of ovaries in the yearling (n = 19), subadult (n = 24) and adult (n = 44) age classes were not significantly different. Within the yearling age class, the largest numbers of >2 mm follicles were recorded in females aged between 16 and 19 months, coinciding with their attainment of sexual maturity during the mating season. The subadult and adult females with the largest numbers of >2 mm follicles were collected on 5 and 12 June respectively, at the end of the mating season; newly-formed corpora lutea were present in both, although neither was visibly pregnant. Maximum numbers of large follicles in all females over one year of age occurred between March and June (Fig. 29b). The largest follicle measured (7,5 mm in mean diameter) was from the left ovary of an adult female shot on 75-06-04. This follicle (plus another of 4 mm in the same ovary) was atretic; three newly-formed corpora lutea averaging 7,4 mm in mean diameter were present in the right ovary. The largest non-atretic follicle measured, from a subadult female shot on 74-05-10, was 5,6 mm and would probably have ruptured that month. Thus ovulation probably occurs in follicles exceeding at least 6 mm in mean diameter.

The ovaries of two of the four juveniles examined, including the youngest which was estimated about 6 - 7 months old, contained no macroscopically visible follicles. Largest follicles in the other two juveniles, estimated about 9 - 10 months and 10 - 11 months old, measured 0,6 mm and 0,5 mm respectively, and several of the smaller follicles were atretic. If these follicle sizes are representative of the juvenile age class, notwithstanding the small sample size, then follicular growth shortly before 12 months of age must be rapid (Fig. 29c). However, no marked differences in mean diameters of largest follicles were apparent between the yearling and subadult age classes, but there was a definite decline in size associated with pregnancy. Among females that were not visibly pregnant, largest follicles averaged 2,5 ± 0,5 mm for 17 yearlings, 2,3 ± 1,0 mm for 24 subadults, and 2,4 ± 1,2 mm for 44 adults, and these differences were not significant. Combining the yearling, subadult and adult age classes, largest follicles averaged 2,4 ± 1,0 mm for non-pregnant females (n = 85) compared with 1,9 ± 0,7 mm for pregnant females (n = 61), and this difference was significant ($P < 0,001$).

Among females of two years of age and over, more follicles exceeding 2 mm in mean diameter were found in non-pregnant females than in pregnant females (mean of 2,6 ± 3,1 c.f. 1,2 ± 1,9), and this difference was

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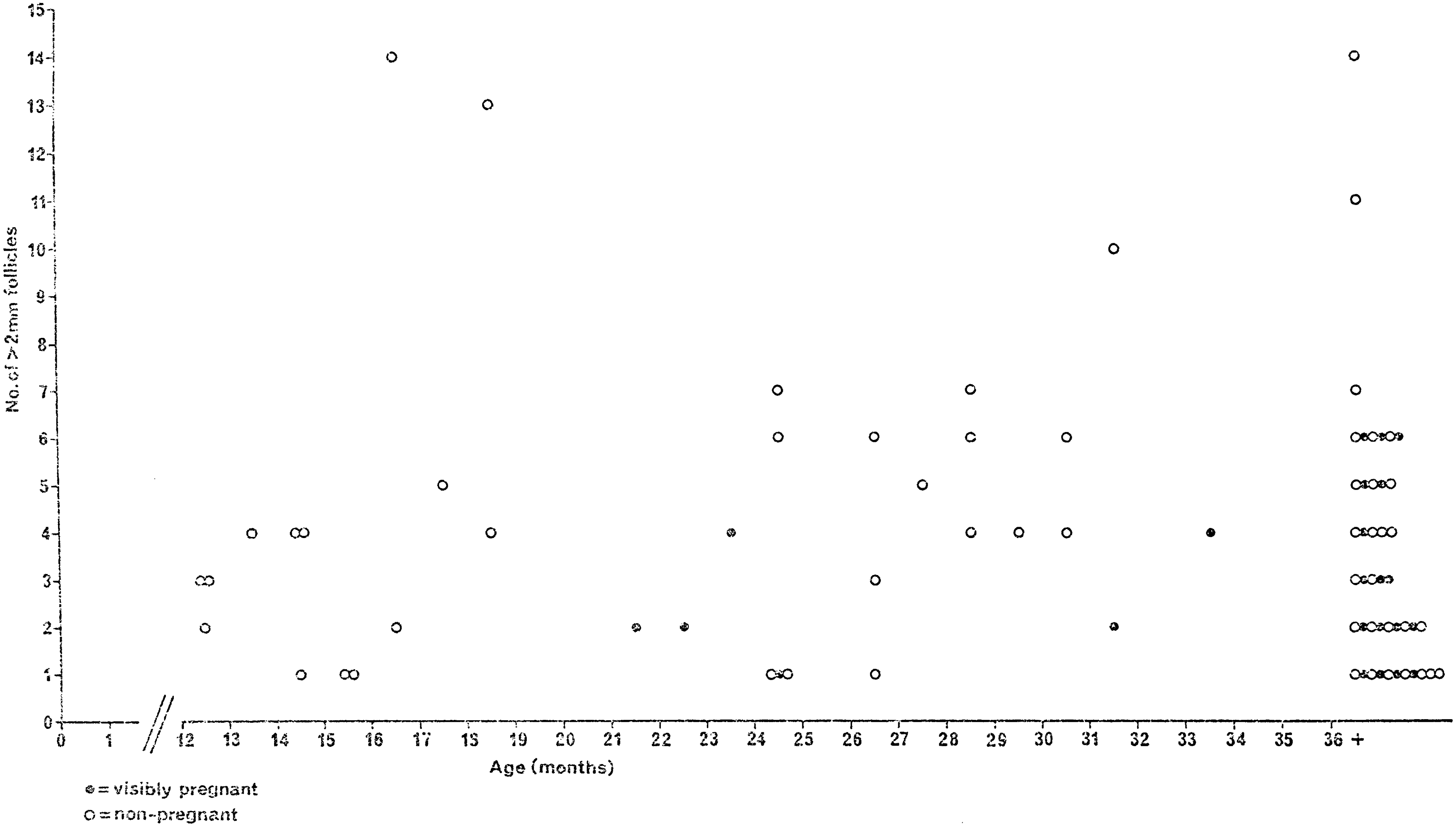

FIG. 29a. Number of >2 mm follicles in relation to age of pregnant and non-pregnant warthogs from Zululand.

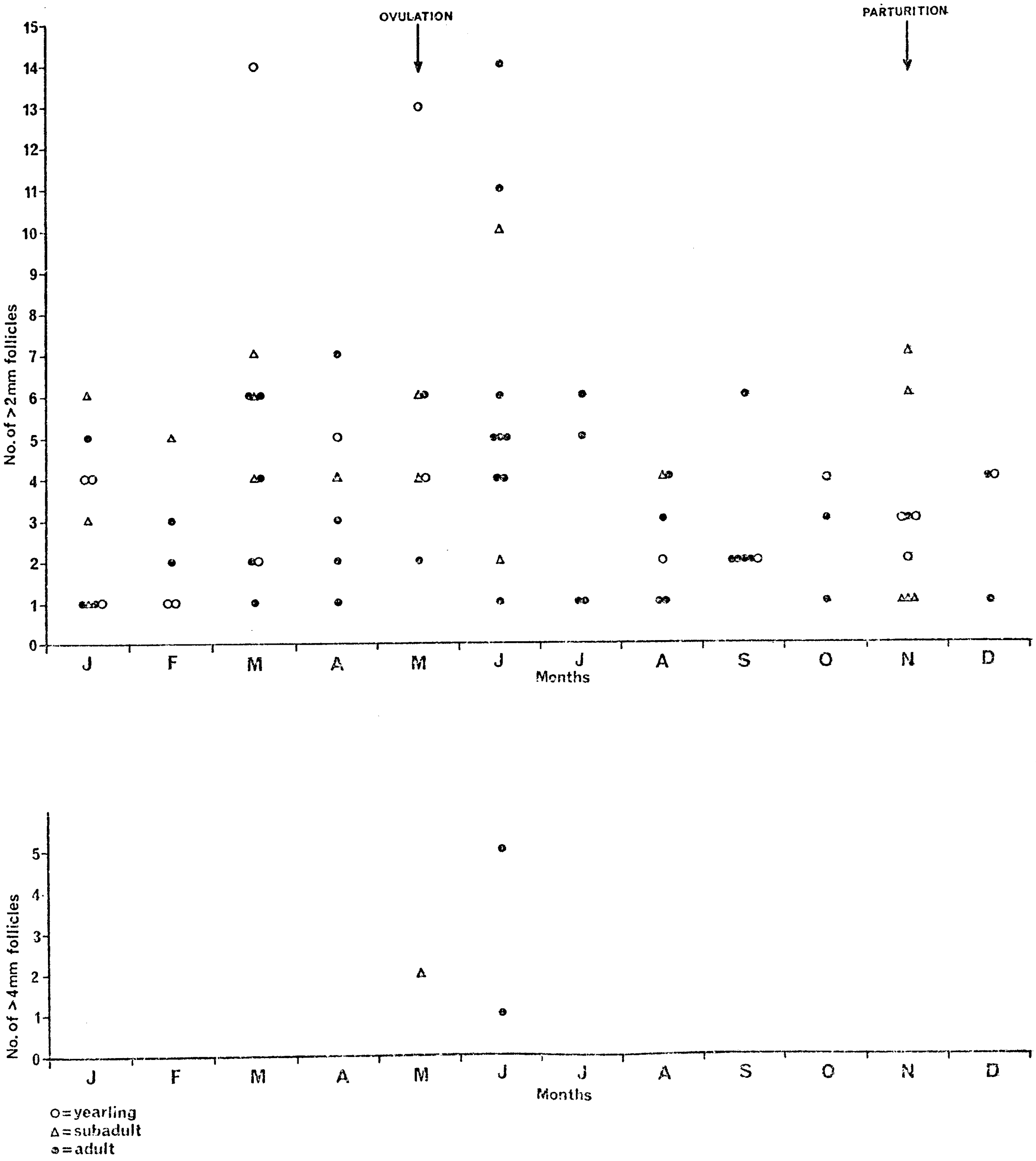

FIG. 29b. Seasonal variation in number of follicles in paired ovaries of warthogs from Zululand.

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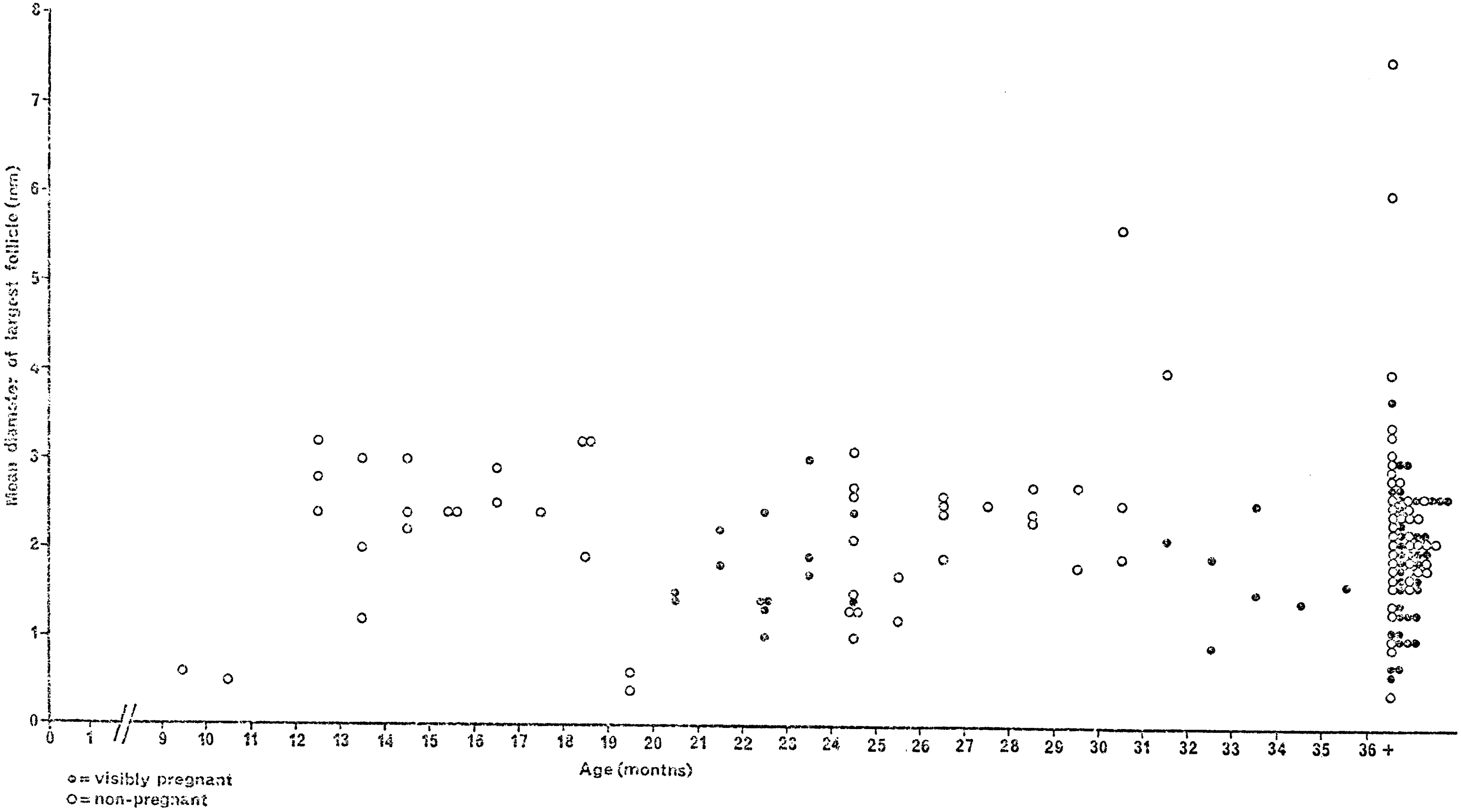

FIG. 29c. Mean diameter of largest follicle in relation to age of pregnant and non-pregnant warthogs from Zululand.

significant (P < 0,01); however, the sample of non-pregnant females (n = 68) included ten with newly-formed corpora lutea but no visible embryos, and one with corpora haemorrhagica. Follicles > 2 mm declined in number after the initial third of gestation (Fig. 29d). Excluding the yearling age class, the mean number of > 2 mm follicles per pair of ovaries for 35 females gravid for between 70 and 170 days was significantly less (P < 0,01) than for 14 females gravid for between 40 and 70 days (mean of 0,7 ± 1,4 c.f. 2,4 ± 2,4). However, when the mean number of > 2 mm follicles per pair of ovaries for females with a gestation age between 105 and 170 days (n = 29) was compared with females gravid for between 40 and 105 days (n = 20), no significant difference was found (0,9 ± 1,4 and 1,7 ± 2,3 follicles respectively, P < 0,05).

With advancing gestation the mean diameter of the largest follicle did not decrease noticeably, but there was considerable scatter (Fig. 29e). For 29 subadult and adult females gravid for between 105 and 170 days, mean diameter of the largest follicle averaged 1,8 mm (S.D. = 0,8), compared with 2,0 mm (S.D. = 0,6) for 20 subadult and adult females gravid for between 40 and 105 days, and this difference was not significant.

The corpora lutea

As the cells lining the ruptured follicle hypertrophy and become luteinised, a rather orange coloured corpus luteum is formed. Development of the corpora lutea following ovulation is rapid and they probably attain their maximum size within about two weeks (Fig. 33, p. 147). By the time visible implantation occurs, the corpus luteum has become a lighter (yellow) colour, which endures throughout gestation.

Excluding three corpora haemorrhagica of 2,4 - 3,1 mm in diameter from a single female, 42 corpora lutea of the ovarian cycle (n = 11 females) averaged 6,8 ± 1,0 mm in mean diameter compared with 7,7 ± 0,8 mm for 219 corpora lutea of pregnancy (n = 61 females), and this difference was significant (P < 0,001). Corpora lutea of pregnancy may measure up to 9,6 mm in mean diameter. The smallest corpus luteum of pregnancy measured 5,4 mm and was one of six, averaging only 6,1 mm, in a single ovary; however, two of the five foetuses in the uterus of this sow were being resorbed. The recorded size range of corpora lutea of the ovarian cycle was 4,4 - 8,2 mm.

An accessory corpus luteum was recorded in only one instance, an adult sow carrying three foetuses and with three normal corpora lutea of pregnancy in her ovaries, and probably originated either from the same ovulation cycle as the other corpora lutea, or by luteinisation of an unovulated follicle. This single accessory corpus luteum measured 3,6 mm in mean diameter and was located with two corpora lutea of 7,5 and 7,6 mm in the left ovary, while a third corpus luteum measuring 7,0 mm was present in the right ovary. Mean

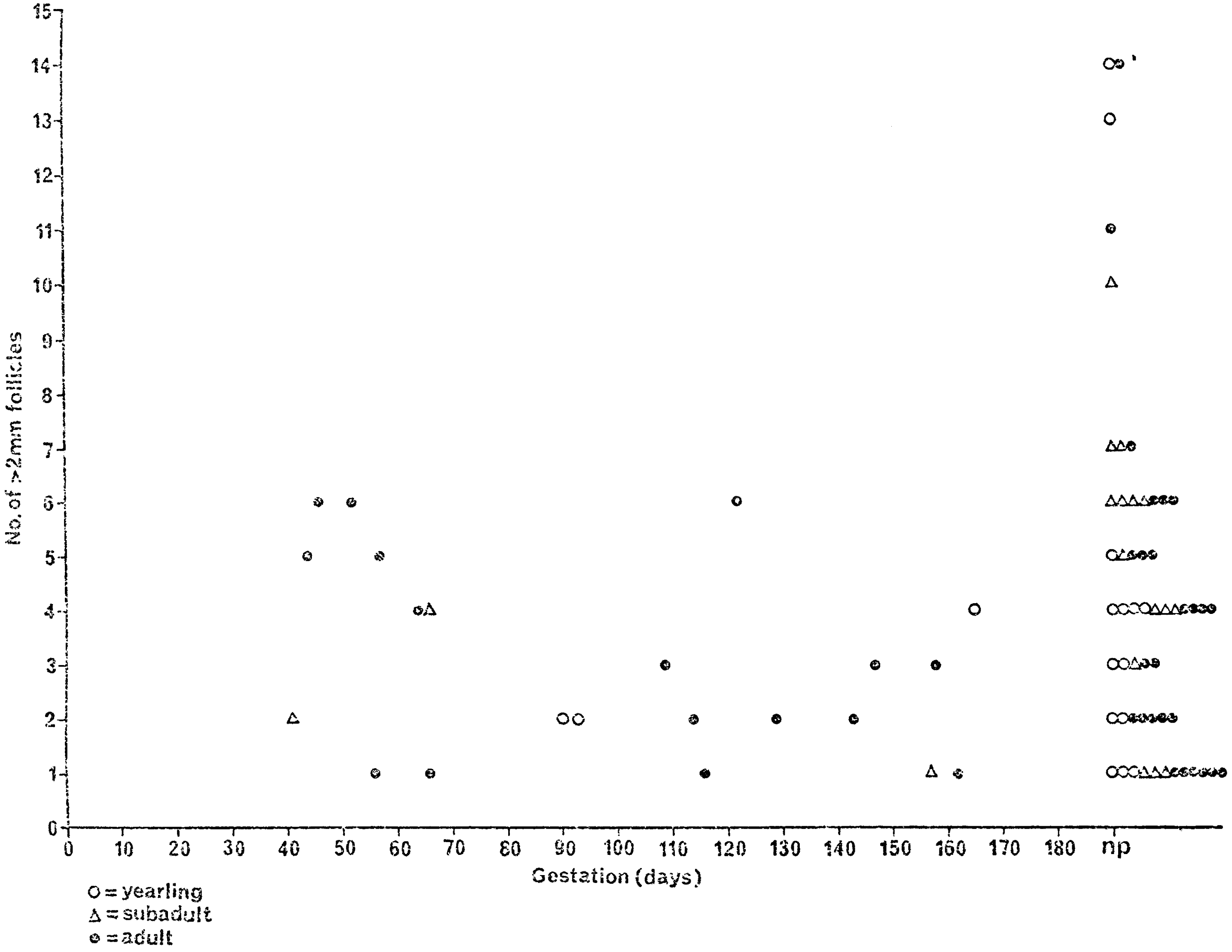

FIG. 29d. Number of >2 mm follicles in relation to stage of gestation in visibly pregnant warthogs from Zululand. Follicle numbers in the paired ovaries of non-pregnant (np) females are also indicated.

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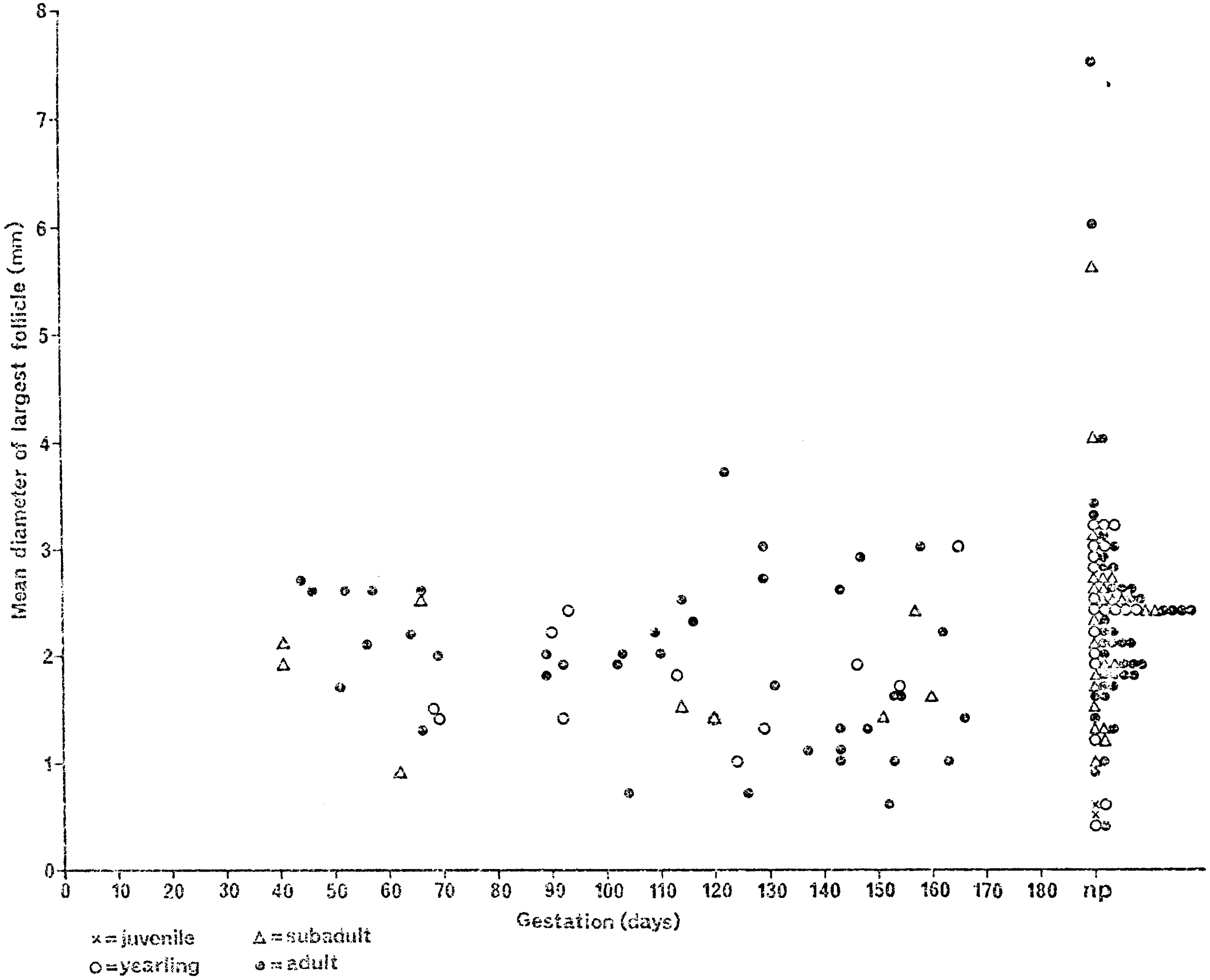

FIG. 29e. Mean diameter of largest follicle in relation to stage of gestation in visibly pregnant warthogs from Zululand. Largest follicle diameters of non-pregnant (np) females are also indicated.

post-conception age of the foetuses on the date of collection (74-08-21) was estimated as 116 days.

Although the corpora lutea remain of large size throughout gestation, there was some correlation between size and stage of gestation (Fig. 30, Table 26). Two linear regression equations for average diameter of corpora lutea from 40 - 100 days and 100 - 170 days were calculated. The equation of the line (1) showing decreasing corpora lutea diameters from 40 - 100 days is $y = 9{,}272 - 0{,}024\,x$ ($r = 0{,}650$; $p < 0{,}01$) where y is mean diameter of corpora lutea per pair of ovaries and x is gestation time. The ascending phase of corpora lutea development from 100 - 170 days is described by a line (2) where $y = 6{,}093 + 0{,}012\,x$ ($r = 0{,}352$; $p < 0{,}05$). The regression lines intersect at about 88 days of gestation. Diameter of the largest corpus luteum per pair of ovaries (Table 26) showed a very similar pattern, decreasing between 40 days and mid-term, and then increasing towards term.

In all cases where left and right ovaries were of unequal mass, the heavier ovary contained the greater number of corpora lutea, and the relationship between total ovarian mass and number of corpora lutea was positive (Fig. 31). Fewer corpora lutea were present in yearling (primigravid) females than in subadults, but no differences were apparent between subadult and older animals.

Corpora albicantia and regressing corpora lutea

Corpora lutea degenerate rapidly after parturition. The largest regressing corpus was 8,3 mm in mean diameter, from a 24 - 25 months old female shot on 74-11-08, probably only a few days after parturition, since her uterine endometrium was still markedly vascularised and oedematous. The margins of this corpus albicans (and another measuring 7,8 mm in the opposite ovary) were still clearly defined and regression in size had not yet commenced. However, another 24 - 25 months old (primiparous) female shot on the same date, but judged at least a week post partum, had three corpora albicantia measuring 3,7, 4,2 and 4,5 mm in mean diameter.

By about one month after parturition, corpora albicantia average some 2,5 mm in diameter and have darkened in colour from a light yellow in very early post partum females, to light brown, which subsequently darkens considerably. Older corpora albicantia are usually 0,1 - 2,0 mm in diameter and may be irregularly shaped with rather diffuse margins; some occur as thin crescent-shaped lines on the rims of large follicles and corpora lutea of pregnancy.

The corpora albicantia usually persist for over a year. The first corpora albicantia were found in the ovaries of primiparous females aged 24 - 25 months, i.e. just after farrowing (Fig. 32), and had regressed to an average diameter

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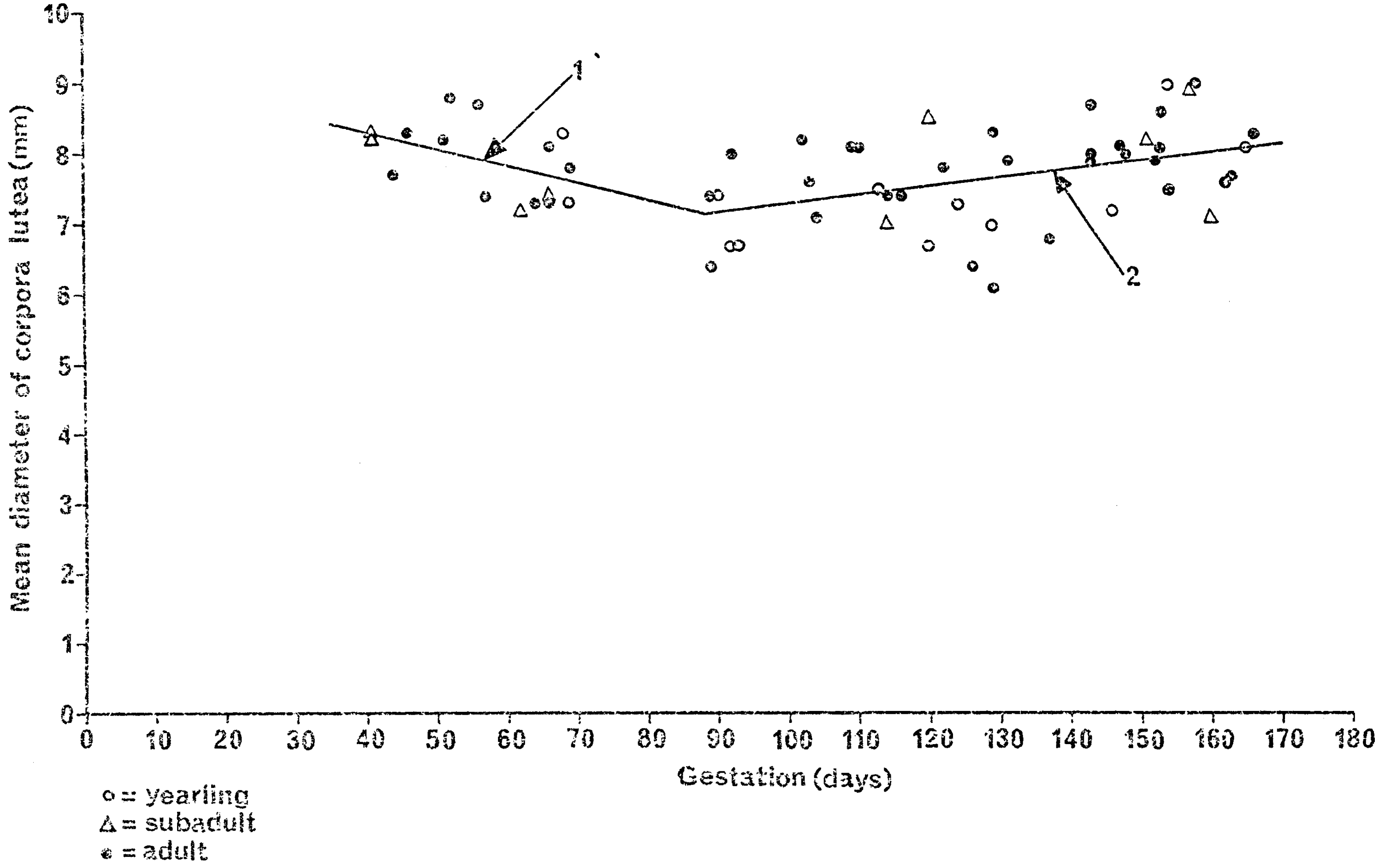

FIG. 30. Mean diameter of corpora lutea in relation to stage of gestation in visibly pregnant warthogs from Zululand.

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TABLE 26. Dimensions of corpora lutea of pregnancy in warthogs from Zululand.

Stage of gestation (days)	No. of females	Mean diameter of corpora lutea (mm)	S.D.	Range	Significant size differences	Mean diameter of largest corpus luteum (mm)	S.D.	Range	Significant size differences
40 - 80	16	7,9	0,5	7,2 - 8,8		8,4	0,7	7,5 - 9,4	
80 - 140	25	7,4	0,7	6,1 - 8,5	<40 - 80:p<0,01	7,8	0,7	6,7 - 9,2	<40 - 80:p<0,01
140 - 170	20	8,1	0,5	7,1 - 9,0	>80 -140:p<0,001	8,5	0,6	7,4 - 9,6	>80 -140:p<0,01

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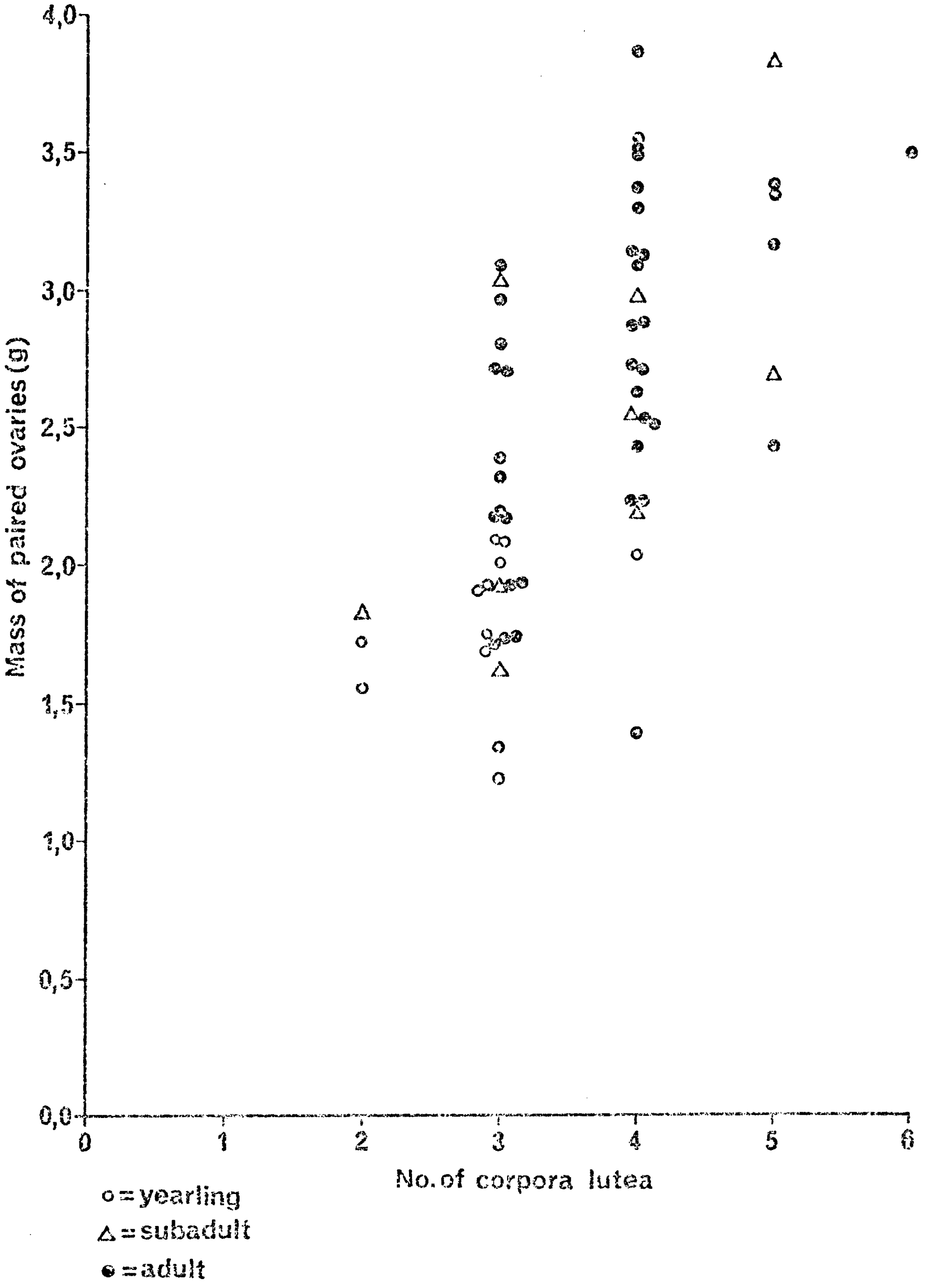

FIG. 31. Number of corpora lutea in relation to mass of paired ovaries of visibly pregnant warthogs from Zululand (n = 61).

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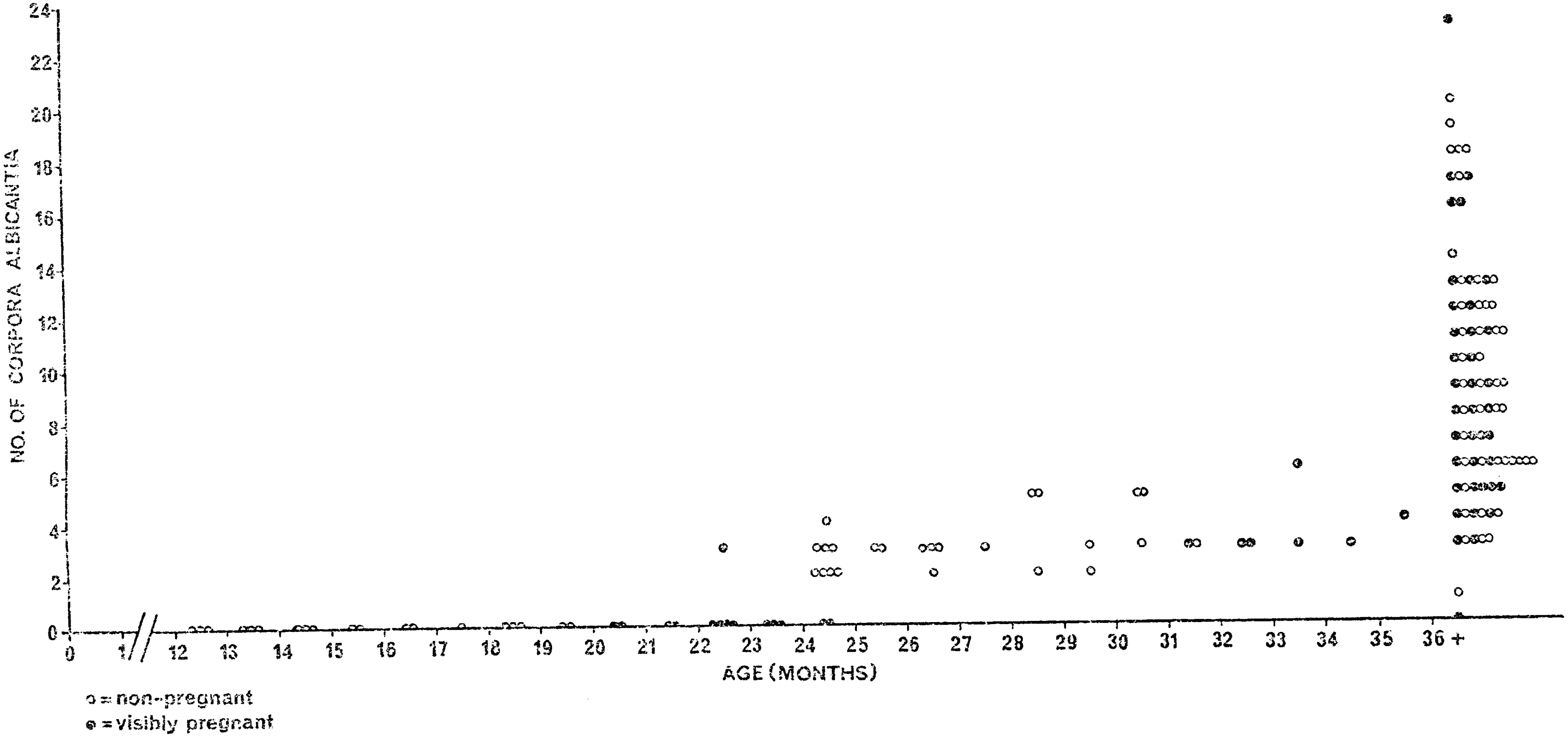

FIG. 32. Number of corpora albicantia in relation to age of pregnant and non-pregnant warthogs from Zululand.

of roughly 1 mm in females aged about 36 months. Among older (adult) females, two more or less distinct size classes of corpora albicantia could frequently be distinguished in the same ovary or pair of ovaries for over half of the 12-month period between successive farrowing seasons. Most of the larger corpora albicantia (with a minimum diameter of about 0,8 mm) are probably the pigmented scars of degenerated corpora lutea of the immediate past pregnancy, while many of the smaller corpora albicantia are probably a year older. However, in some cases compression and splitting of corpora albicantia due to growth of large vesicular follicles and corpora lutea of pregnancy apparently blurs the size distinction between corpora albicantia of two successive reproductive years, since sizes intergrade. Invasion of regressing corpora lutea by follicles was sometimes noted within a month or two after parturition.

Corpora albicantia were not recorded in the yearling age class, except in one pregnant female aged about 22 - 23 months. Three corpora lutea, but no corpora albicantia, were present in her left ovary only, and the three corpora albicantia in her right ovary were tiny specks, possibly derived from corpora lutea of the cycle (unfertilised ovulations); if so, corpora lutea of the cycle may degenerate much more rapidly than corpora lutea of pregnancy, since these structures were nearly indiscernible only 92 days after the estimated conception date.

The maximum number of corpora albicantia found per pair of ovaries was 23, compared with a maximum of 14 in a single ovary, both cases involving adult females. Corpora albicantia counts from 115 females gave 507 in the left ovary compared with 365 in the right ovary, and this deviation from the expectation of equal numbers of corpora albicantia in each ovary was highly significant ($\chi^2 = 23{,}12$; $p < 0{,}001$). The mean number of corpora albicantia per pair of ovaries in 31 subadult (primiparous) females was 3,19 ± 1,05, which was not significantly more than the mean number of corpora lutea of pregnancy (2,86 ± 0,53) in 14 primigravid females of the previous year class. The mean number of corpora lutea of pregnancy in visibly pregnant adult females (n = 40) was 3,78 ± 0,73 (not significantly different from subadult females), but adult females (n = 84) had significantly more corpora albicantia than subadult females (9,17 ± 4,72 c.f. 3,19 ± 1,05; $p < 0{,}001$). Such a large difference suggests that corpora albicantia of pregnancy may persist through at least two mating seasons, and that some corpora albicantia may be derived from sources other than regressing corpora lutea of pregnancy. Assuming that the warthog in Zululand is seasonally polyoestrous, i.e. experiencing more than one oestrous period during each mating season, some corpora albicantia may be the remains of corpora lutea of the cycle, but this source seemed unimportant due to the dearth of regressing corpora lutea of ovulation accompanying functional corpora lutea of early pregnancy.

Seasonal ovarian activity

Analysis of the ovaries of 117 females aged two or more years shows a distinct seasonal pattern of reproductive activity, as evidenced by the monthly incidence of recent ovulations and large follicles (>4 mm) (Table 27). Of 68 non-pregnant subadult and adult females, 53 were classified as anoestrous (including 33 that were lactating), the rest having either recent corpora lutea of ovulation and/or follicles exceeding 4 mm in mean diameter. Of the 53, two were shot on 10 May, one on 27 June, and one on 12 August, whereas the remainder were collected between November and April (non-breeding season). Follicular growth in the ovaries of the two females shot during May was possibly still proceeding towards ovulation, but both of the females shot during June and August respectively had failed to conceive; however, four of the 19 corpora albicantia in the ovaries of the female shot on 27 June slightly exceeded the others in average size, and could therefore have originated from corpora lutea of ovulation or luteinisation of atretic follicles during the mating season in the preceding months of April and May.

Fig. 33 shows the mean diameters of the largest follicle (open symbols) throughout the annual cycle and the mean diameters of the corpora lutea of pregnancy (solid symbols) throughout gestation. Follicular activity, as evidenced by the size of the largest follicle, is cyclical with maximum size occurring during May and early June, when ovulation occurs. There follows a relatively long period during which the diameter of the largest follicle averages about 2 mm or less, until January, when 2 mm is exceeded and this larger size is maintained until the growth surge in May. During 1974, the first visible embryos from warthog cropping in UGR were recorded on 12 June, whereas enlarging corpora lutea were first observed on 18 May. In 1975, the first enlarging corpora lutea were noted on 30 May.

Notwithstanding a small decrease in average size of corpora lutea towards mid-term (Fig. 30), their large size and the absence of microscopic signs of degeneration throughout gestation presumably indicate that they remain active as endocrine glands (secreting progesterone which is necessary for the maintenance of pregnancy) until shortly before parturition. The possibility that the placenta may contribute to the maintenance of plasma progesterone levels during gestation was not investigated.

Ovulation does not occur during pregnancy or lactation and no active corpora lutea were present in any lactating females. Within the age group exceeding 24 months, the largest follicles in the ovaries of two non-lactating sows that had apparently lost their litters within about two months after birth considerably exceeded the average size for lactating, post partum females collected during the same period. This may indicate that females losing their litters

TABLE 27. Monthly incidence of large follicles, recent ovulations, and corpora lutea of pregnancy in the ovaries of warthogs two years old or more from Zululand.

Month	No. of females examined	No. with >2mm follicles	%	No. with >4mm follicles	%	No. with recent ovulations or c.l. of oestrus	%	No. with c.l. of pregnancy	%
J	9	6	66,7	0	0,0	0	0,0	0	0,0
F	5	3	60,0	0	0,0	0	0,0	0	0,0
M	12	8	66,7	0	0,0	0	0,0	0	0,0
A	7	5	71,4	0	0,0	0	0,0	0	0,0
M	8	5	62,5	1	12,5	5	62,5	0	0,0
J	11	11	100,0	2	18,2	5	45,5	3	27,3
J	8	4	50,0	0	0,0	1	12,5	7	87,5
A	13	5	38,5	0	0,0	0	0,0	12	92,3
S	12	5	41,7	0	0,0	0	0,0	12	100,0
O	8	2	25,0	0	0,0	0	0,0	8	100,0
N	18	6	33,3	0	0,0	0	0,0	7	38,9
D	6	2	33,3	0	0,0	0	0,0	0	0,0
Total	117	62	53,0	3	2,6	11	9,4	49	41,9

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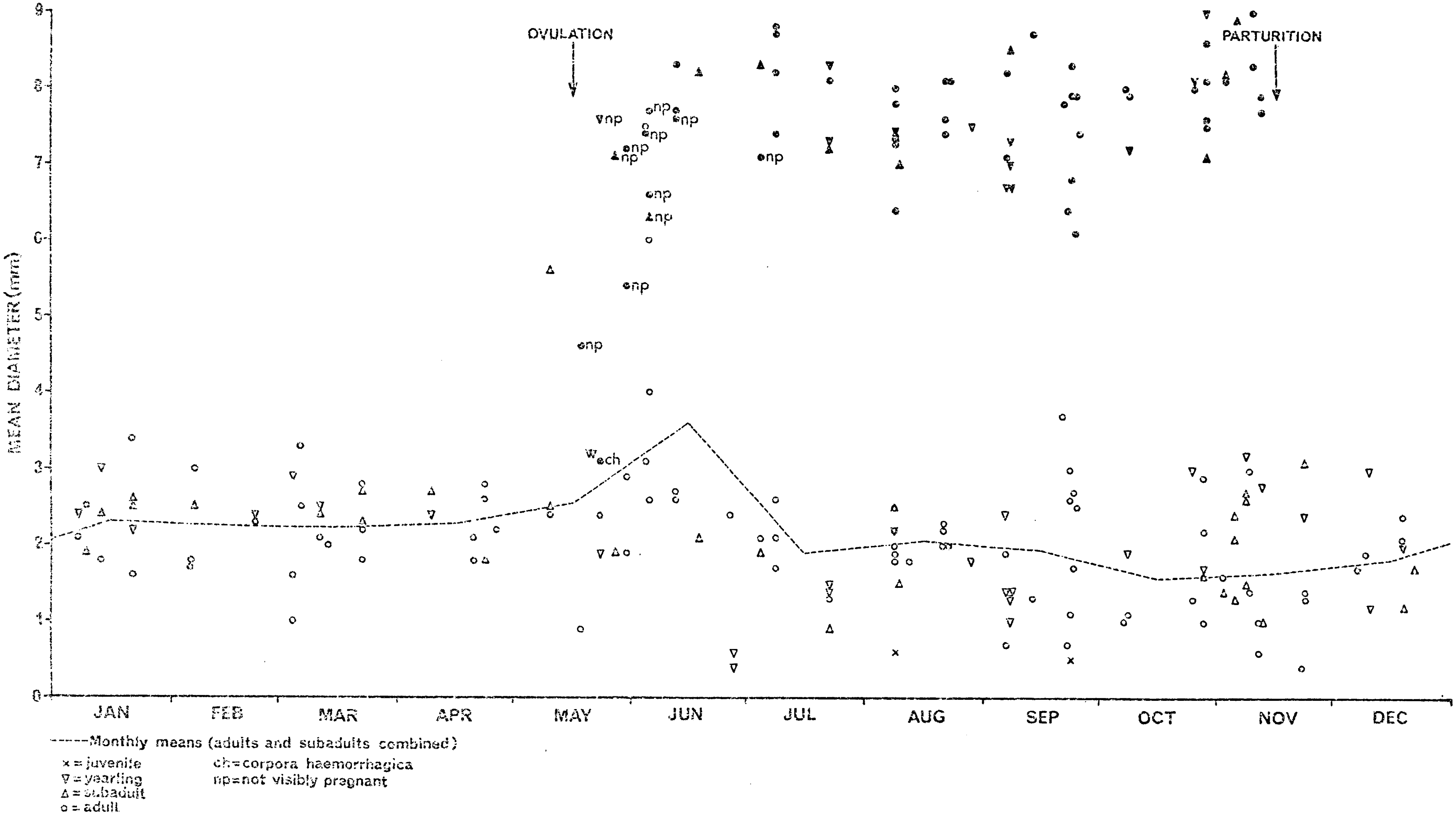

FIG. 33. Ovarian cycles of activity in warthogs from Zululand showing the mean diameter of the largest follicle (∇Δo) and of the corpora lutea of oestrus and pregnancy (▼▲●) in relation to calendar time.

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soon after birth come into oestrus slightly earlier in the mating season than females experiencing a normal duration of lactation.

Monthly variation in total ovarian mass is shown in Fig. 34, which indicates a large increase following ovulation, due mostly to the development of corpora lutea. The rapidity of regression of the corpora lutea after parturition is reflected in the rapid decline in ovarian mass. However, the pigmented scars of degenerated corpora lutea of pregnancy (corpora albicantia) commonly persist beyond the next pregnancy, becoming smaller and paler as they become older.

LACTATION

Duration

Very small amounts of a rather viscous secretion could be expressed from the teats of some pregnant females as early as 20 days pre-partum, concomitant with a visible increase in size of their udders. In the resting state, the warthog mammary gland is flat except where the four teats protrude. Although only 11 mammary glands were measured (Table 9, p. 72), maximum mass of the lactating gland probably exceeds one kilogram.

The duration of lactation was estimated by observing the approximate stage of involution of the mammary glands of sows accompanied by young of the recent farrowing season (including four identifiable sows), and by examination of shot animals. Generally, the udders of sows with surviving piglets were still secreting milk during March in both 1974 and 1975, but in conformation protruded noticeably less around the active teats than during the preceding three months. Udder regression was advanced or complete by mid-April, although recently active teats were often still relatively elongated. The last date when a little milk could be expressed from the udder of a shot female was 23 April, which coincided with the last observation of suckling (involving a different female). During May all sows accompanied by juveniles, either observed in the field or shot during cropping, had completely regressed udders, indicating April as the terminal month of lactation. Allowing for some individual variation, lactation in the warthog thus continues for about five months.

The seasonal synchronisation of oestrus and mating activity was such that conceptions during the study period were concentrated between mid-April and early June, with a peak during May. Thus the post partum reconception interval in the warthog in Zululand is only slightly longer than the full lactation period. Involution of the udder as a consequence of loss of the litter during the first few months after farrowing appeared rapid and lactation probably ceased within two weeks of the removal of the suckling stimulus. Although ovulation was not recorded before the normal breeding season, follicular development in females where lactation ceases early after parturition could tend

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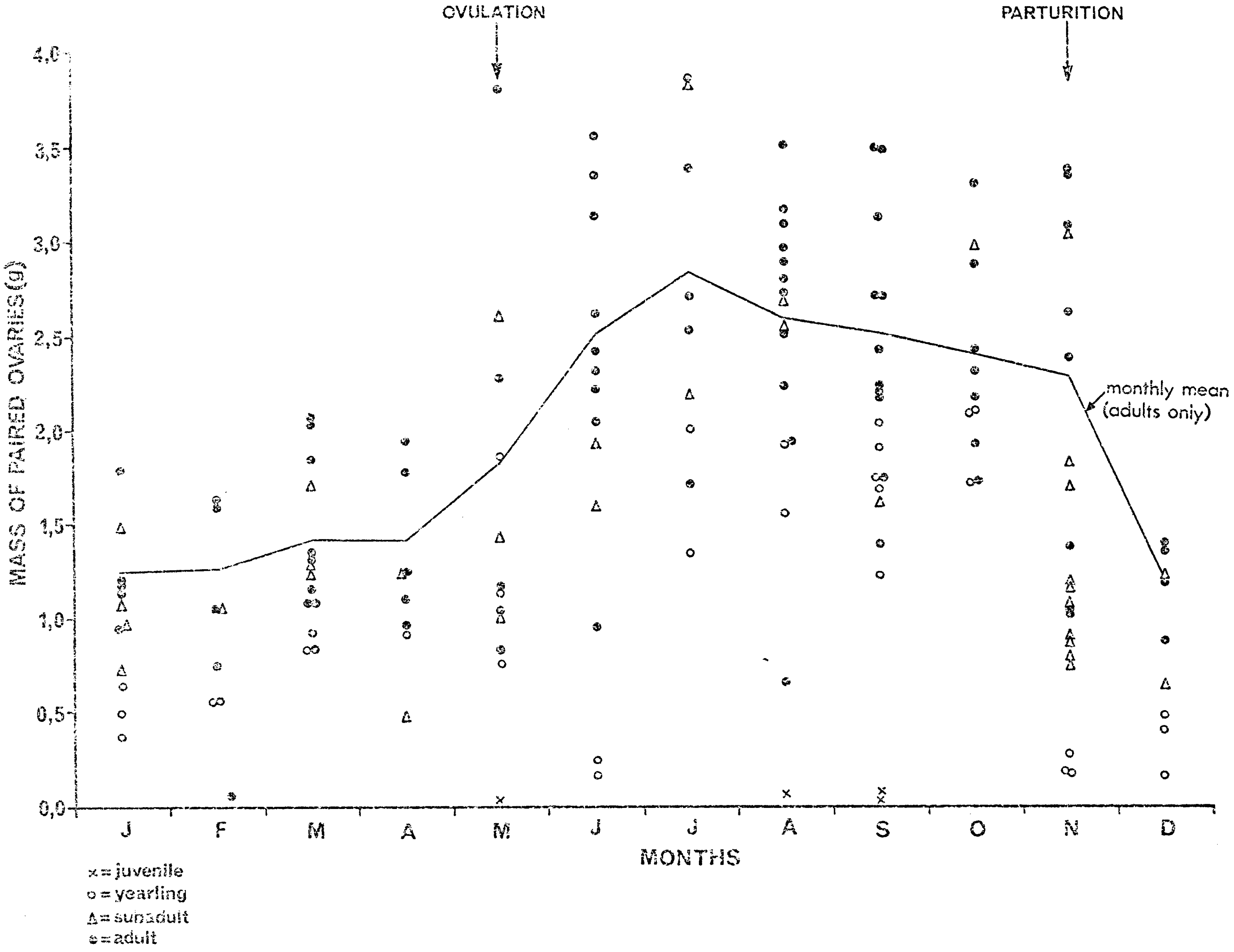

FIG. 34. Seasonal variation in mass of paired ovaries of warthogs from Zululand (n = 150).

to be slightly advanced compared with females where lactation extends the full period.

Among females of two or more years of age examined during March, shortly before the mating season, the diameter of the largest follicle averaged 2,6 mm (range 2,0 - 3,3 mm) for five sows where involution of the udder was complete, compared with 2,2 mm (range 1,8 - 2,8 mm) for five sows that were still lactating. Although the sample size is small and the difference in follicle size was not significant, sows where lactation continues towards the potential maximum duration possibly tend to ovulate slightly later during the breeding season than sows with a shorter lactation period.

Milk composition

Although the udders of some lactating females appeared full of milk, only very small samples could be expressed by digital manipulation during post mortem examination. This paucity of milk ejection disallowed complete analysis of warthog milk composition. Only total solids were analysed (Labuschagne _pers_. _comm_.), giving values ranging between 14,9 and 18,3% (mean = 16,1%) for three females of at least two years of age and judged about one to three weeks post partum. Total solids comprised 26,3% in a small sample of pre-lactation secretion from an adult sow estimated 20 days pre-partum.

DISCUSSION AND CONCLUSIONS

ANATOMY

The internal and part of the external anatomy of a female warthog were described by Owen (1851), and a more detailed account of the reproductive tract is given by Clough (1969). The description of the main features of female warthog reproductive anatomy as given in this study corresponds with the findings of Owen and Clough (_op_. _cit_.). However, photographic illustrations have been used to supplement the diagrammatic representation of the reproductive tract given by Clough.

Like the warthog, the domestic pig has a penis with a spiral tip which engages strongly-ribbed, muscular folds in the cervical portion of the female tract, while the taut and oedematous condition of the cervix during oestrus provides the appropriate stimulus for ejaculation (Hunter 1975a). Similar transverse, fibrous ridges have been described in the upper part of the vagina of the hippopotamus, but the adaptive function was not explained (Laws & Clough 1966).

A translucent, gelatinous vaginal plug similar to that found in the warthog is deposited during copulation in both the domestic pig (Burger 1952, Mann 1964) and collared peccary _Dicotyles tajacu_ (Sowls 1966). The length of time that the plug persists in the vagina of the warthog following copulation is not known, although Sowls (op. cit.) found a 25,8 g plug filling nearly half of the vagina of a collared peccary 76 minutes after copulation, and the plug from another female had a mass of 30,8 g. Gelatinous plugs measuring up to 16 cm long and 2,5 cm in diameter and firmly held by the rugae of the cervix may be found in domestic sows within 15 minutes of coitus (Burger 1952).

In the domestic boar, mixing of the secretions of the bulbo-urethrals and seminal vesicles during ejaculation results in rapid coagulation to form a gelatinous mass with a high content of a sialomucoprotein derived from the bulbo-urethral glands. The gelatinous portion of the seminal plasma may comprise half of the entire ejaculate; ejaculation is protracted and the last fraction of the semen is richest in gel (Mann 1964). As suggested for the domestic pig (Burger 1952, Melrose 1963, Mann 1964, Hunter 1975b) and peccary (Sowls 1966), a probable function of the plug in the warthog is to form a compact barrier in the cervix and vagina, minimising leakage of the liquid fraction of the ejaculate back through the vagina, and thereby assisting passage of spermatozoa into the uterus. The mean volume of semen in a normal ejaculate of the domestic boar is in the region of 250 ml with a sperm concentration of 1 - 2 x 10^8 per ml (Polge 1956); however, the bulk of spermatozoa are in the first 50 ml of fluid ejaculated (Melrose 1963), and only a very small proportion of the massive number of spermatozoa deposited at mating can be recovered from the oviducts (Hunter 1975a).

Hartung & Dewsbury (1978) found no copulatory plugs in four species of muroid rodents with a locking pattern of copulation, whereas seven non-locking species always deposited plugs. While admitting that the absence of plugs may not be characteristic of all locking species, they considered that the failure of the locking species to deposit plugs appeared to correlate with reduction in the size or number of the male accessory sex glands. By contrast, the bulbo-urethral glands and seminal vesicles are well developed in the warthog, and the internal morphology of the cervix may have adaptive value in the mating strategy by supplementing the role of the vaginal plug. Besides minimising loss of spermatozoa, the plug could conceivably reduce the chances of subsequent insemination by other males.

Although Bradley (1968) recorded one instance "where two piglets maintained two teats on each of the two sows they were suckling from," his finding that the number of active teats normally decreases in proportion to mortality in a sow's family was in agreement with observations of Zululand warthogs.

ATTAINMENT OF SEXUAL MATURITY

Although poor nutrition can delay the onset of sexual maturity in mammals (Sadleir 1969, Sayer & Rakha 1974), studies in several geographic regions show that wild female warthogs mature as yearlings. In West Africa, Bigourdan (1948) estimated sexual maturity at 17 to 20 months of age, while in Nairobi National Park, Kenya, field observations by Bradley (1968) also indicated maturity in the second year. Boshe (1981) examined shot warthogs in the Selous Game Reserve, Tanzania, and estimated that females reach sexual maturity and breed at about 20 months of age. In Wankie National Park, Zimbabwe, Simpson (1964) noted signs of oestrus (dark stains down the hindquarters and an enlarged vulva) in a yearling female, which accepted mounting by an adult male. At the time (May), this female would probably have been about 18 - 19 months old, since warthogs in Wankie Park have a very well defined farrowing season, normally commencing in October or November (Wilson 1975b). In the Nagupande area of Zimbabwe, Child _et al_. (1968) recorded the earliest ovarian activity and pregnancies from yearlings, with first mating at about 19 months of age. On the criterion of presence of one or more corpora lutea or corpora albicantia, female warthogs in Uganda matured at a mean age of about 17 to 18 months, with a probable range of not more than two to three months on either side of the mean (Clough 1969). These data thus agree well with the findings in Zululand where most warthogs first conceive at about 18 to 19 months of age.

In black-tailed deer (_Odocoileus hemionus columbianus_), over 50% of female fawns reared in captivity on a diet conducive to maximal growth attained early puberty and conceived (Mueller & Sadleir 1975). Similarly, accelerated growth due to a constant, high plane of nutrition is probably associated with early puberty in some captive warthogs. While Frädrich (_pers. comm._) established the age at sexual maturity of a captive-born female at the Berlin Zoo as 19 months, two reports have indicated that much earlier maturation is possible. A female warthog born at the Frankfurt Zoo on 59-01-07 farrowed for the first time on 60-05-20, i.e. at an age of 16,5 months (Faust 1961). Assuming that her gestation had continued the full period, she would therefore have matured and conceived at about 10,7 months of age. Frädrich (1965) cites a case of a female born at the Münster Zoo which first farrowed at 18 months, indicating conception at approximately 12 months.

Roth (1965) recorded the first signs of heat in a captive female warthog at seven to eight months of age, when this individual was over twice the average body mass of free-ranging juveniles of the same age, due to her greatly supplemented diet; first mating at 17 to 19 months of age was unsuccessful, although coinciding with symptoms of oestrus. Clough (1969) recorded the first signs of heat, together with a pro-oestrous vaginal smear, in a captive female at about 15 months of age; although mounting occurred subsequently on various occasions, complete intromission was not observed and Clough suggests that the first few oestrous cycles are not accompanied by ovulation. This could explain an observation in HGR during May 1976, when a male warthog of at least two years in age briefly mounted a juvenile female aged about six to seven months, after following her for several minutes (Whateley *pers. comm.*). However, the possible significance of this behaviour as an indication that signs of oestrus might occur in some free-ranging females during their first year remains to be established.

THE OESTROUS CYCLE

The length of the oestrous cycle is 21 days in the domestic pig (Signoret 1967) and 21 to 23 days in the European wild pig (Henry 1968a). However, Mauget (1972) reported the existence of well-defined reproduction periods which distinguished the wild species from the domestic.

Oestrus in the domestic pig normally lasts 40 - 80 hours (Signoret 1967), while Henry (1968a) recorded an oestrous period of one to three days in the European wild pig. Sowls (1966) found that the average duration of oestrus in the collared peccary varied between 3,5 and 4,8 days. In the domestic pig, the vulva begins to enlarge 2 - 8 days before the onset of oestrus, which is also characterised by the appearance of a mucous discharge and the internal labial mucosa becoming red (Signoret, Baldwin, Fraser & Hafez 1975). A discharge of mucus from a swollen vulva was apparent in some warthog sows judged to be in or near oestrus (see also Simpson 1964, Roth 1965). However, Sowls (*op. cit.*) found that external manifestations of heat were unreliable indicators of oestrus in the collared peccary, and were only occasionally apparent in captive females.

No information about the oestrous cycle of the warthog sow during the mating season was obtained in Zululand, but Clough (1969) recorded behavioural oestrus on two occasions, each of at least 48 hours' duration, at an interval of six weeks, in a captive yearling female in Uganda. Subsequently, Clough & Hassam (1970) established that the oestrous period can last 72 hours. Cumming (1975a) notes that a tame free-ranging yearling sow in Zimbabwe first showed signs of oestrus four days before she was seen mating.

SEASONAL REPRODUCTIVE CYCLE

Foetal growth and conception dates

Growth in length and mass of warthog foetuses (Fig. 27) followed the expected straight line and exponential curve respectively. Similar growth curves of foetal domestic pigs and collared peccaries have been described by Ullrey, Sprague, Becker & Miller (1965) and Low (1970). Since within-litter variations in crown-rump length and body mass of foetal warthogs were considerable, better estimates of litter age might be expected by using the mean measurements of all individuals in a litter rather than the measurements of each individual (see also Ullrey *et al.*, *op. cit.*).

Conception dates, determined by subtracting the gestation age from the date of collection of 61 females (Table 22), showed a restricted seasonal period of mating in the Zululand warthog population, with a peak during May. Consequently, as Bourquin, Vincent & Hitchins (1971) have stated, litters of young warthogs may be seen from late October in the Complex, "although farrowing in the burrows probably occurs somewhat earlier." During 1963, when farrowing in UGR was earlier than usual, exceptional floods in July of that year had caused heavy mortality in the warthog population (Natal Parks Boards records), but whether this could have influenced the early parturition is not known. ?

The occurrence of breeding seasons in warthog populations in southern Africa is well documented, e.g. South West Africa (Wilhelm 1933), South Africa (Stevenson-Hamilton 1947, Pienaar 1963, Fairall 1968), Botswana (Smithers 1971, Sheppe & Haas 1976), Zimbabwe (Child *et al*. 1968, Cumming 1970,1975a). Reported times of peak mating and farrowing correspond closely, although some individual variation is to be expected. Thus, in the Nylsvley Nature Reserve, Transvaal, the first litter of the 1978 season was sighted as early as 15 August (Booth *pers. comm.*). Such instances of unusually early farrowing might involve sows whose previous lactation period was very short.

[illegible] farrowing period

In South West Africa, Wilhelm (1933) gives the mating season as May and June, which would indicate farrowing between October and December. A near-term sow was shot on 76-12-16 in the area between Outjo, Kamanjab and Khorixas and two of the four piglets delivered by Caesarian section, survived (Jordaan *pers. comm.*). Farrowing in the Okahandja and Tsumeb districts is reported from November to December (Gaerdes *pers. comm.*).

Stevenson-Hamilton (1947) gives October as the month in which most of the young are born in the Transvaal, and Fairall (1968) states that warthogs in the Kruger National Park have a definite farrowing season in November and December. Along the lower Chobe River, Botswana, breeding is highly seasonal and young began to appear in large numbers late in October (Sheppe & Haas 1976).

Kruger

Records for Zimbabwe include the Nagupande area in the northwest, where Child *et al*. (1968) delimited farrowing between September and December with most births in October and early November; however, they point out that the season may vary locally. Wilson (1975b) states that warthogs in Wankie National Park have a well defined farrowing season, normally in November, although the earliest sightings of piglets were recorded in October. In the Sengwa area, Cumming (1970, 1975a) confirmed a seasonal breeding peak by the increase in juvenile : adult ratio during November - December each year.

Judging by the size of two piglets caught on 24-11-30, and relative development of eight litters of foetuses collected during the preceding three months, Hubbard (1929) concluded that warthogs in the Zambezi River region of western

NB ↓ early farrowing

Moçambique farrow during October/November, although variations do occur.

In Zambia, on the plateau areas west of the Luangwa Valley and north of the middle Zambezi Valley, peak farrowing occurs in July and August, with early litters in June and late ones in October, whereas farrowing in the Luangwa Valley is later, from late September to December (Ansell 1960). Child et al. (1968) cite the first report of infants of the 1964 season on 14 August in the Luangwa Valley, plus records of five females with small sucklings and another lactating female during the first week in September. The variation in timing of farrowing between these two localities perhaps reflects phenological differences in the grazing related to the availability of green floodplain grasses (and rhizomes) during the late dry season months; burning of the grass cover could also complicate the issue.

adaptive breeding

In the Kafue National Park, Zambia, Mitchell (1963) reported a very distinct peak of farrowing during July, when 76,1% of 71 recorded litters were born; the amplitude of the farrowing season was "in the order of six weeks." Mitchell considers that the Kafue Park warthogs have adapted their breeding season to coincide with the period at which the roots of certain grass species, particularly Loudetia superba and Hyparrhenia spp., contain maximum food value, thus providing favourable conditions for rearing the young. He mentions that the local warthogs concentrate their feeding on the roots of these grasses during the dry season months July to October; Loudetia superba stores food reserves in a very large rhizome and, as an adaptation to fire, does not utilise these reserves to grow new foliage until mid-October, just before the start of the rainy season.

Southern Africa.

Notwithstanding some variation in the timing of parturition apparently in response to local habitat conditions, the evidence shows that warthogs in southern and south-central Africa tend to farrow at the most favourable time of the year for survival of the young. Thus the prevailing time of farrowing in this region slightly precedes or coincides with the beginning of the wet season, when fresh grass shoots become available (also to the benefit of females in early lactation). Since the duration of pregnancy is approximately six months, and parturition occurs during a fixed optimal season, the onset of the mating season in autumn is probably determined by decreasing day length. While photoperiod may be the proximate factor initiating mating activity in the unimodal summer rainfall regions of southern Africa, marked seasonal differences in nutrition could well be the ultimate factors reinforcing the photoperiod cue to ensure that births occur at an optimal time (Sadleir 1969, Spinage (1973b).

et
ting

unimodal

Kruuk (1972) has suggested that the synchrony of mating in some species has evolved to mitigate predation via the concentration of births within a limited period. The degree to which this may apply in the warthog is not known, but

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the rate of predation would be influenced, inter alia, by the nature of warthog social units and their use of burrows, so that the situation is not directly comparable to that reported, for example, in East African wildebeest (Estes 1976).

[illegible] near equator

In seasonally breeding mammals, the synchrony of reproduction may be affected by rainfall and the resultant levels of nutrition as found, for example, in the elephant in Zambia (Hanks 1969). Leuthold & Leuthold (1975) have indicated that seasonal reproduction is more marked in grazers than in browsers, suggesting a relationship with seasonal changes in food quality. However, even in grazers, a tendency towards continual breeding could be expected at the equator since environmental stimuli favouring reproductive seasonality are absent or much less pronounced. Reproductive rhythms of warthog populations close to the equator could therefore be related to factors such as rainfall and nutrition, in the absence of any significant changes in day length.

[illegible]modal

In both the Nairobi and Tsavo East National Parks, Kenya, where bimodal rainfall regimes prevail, warthogs have a restricted, unimodal reproductive season; farrowing occurs during October and November, slightly preceding the November/December rainy season (Bradley 1968, Leuthold & Leuthold 1975). The mating season thus coincides with the March - May wet season. Of the two dry seasons, that coinciding with pregnancy (June to October) in the local warthog populations causes more severe nutritional stress to herbivores than the January to March season (Leuthold & Leuthold op. cit.). The synchrony of warthog reproduction in these two localities therefore appears to favour survival of the young. Since seasonal variation in day length at Nairobi Park does not exceed three minutes while the range of mean monthly temperature fluctuations is only 3^{0}C (Hall-Martin, Skinner & van Dyk 1975), the timing of the conception and farrowing peaks is probably related to the seasonal maxima of rainfall via the nutritional status of the grazing.

On the equator, Clough (1969) concluded that warthogs in Rwenzori National Park, western Uganda, breed all the year round. This was based on the equal distribution between wet and dry seasons of eight observed cases of oestrus, and of predicted farrowing times for 16 prenatal warthog litters. However, Clough concedes that a larger sample may well show birth peaks in the wet seasons, as found in hippopotamus (Laws & Clough 1966), waterbuck (Spinage 1969) and buffalo (Grimsdell 1973b) in the same area. In the Rwenzori Park, there are two wet seasons each year, March to May and September to November, separated by dry seasons (Grimsdell op. cit.).

Further west, but still on the equator, d'Huart (pers. comm.) states that warthogs in the Virunga National Park mate and farrow throughout the year, but with two peaks in the frequency of farrowing during September and January, corresponding with the beginning of the two wet seasons; his description of two short mating "seasons" in April and August is possibly misleading if the true

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meaning that he intended to convey is of practically year-round mating with peak activity at these times. At Lulimbi, just east of Lake Amin (formerly Edward) in the central region of the Virunga Park, mean monthly rainfall over a three year period shows a bimodal pattern with two minima in July and December (d'Huart 1978). Based on monthly sightings of piglets probably less than one month old, d'Huart (1978) recorded two pronounced birth peaks during July - August and January - February in the Virunga Park population of giant forest hogs; piglets were observed in all other months except June and December. The timing of these birth peaks is such that the piglets of both warthogs and giant forest hogs benefit at weaning from the tender new growth of annual grasses with a nutritive value (protein content) superior to that of perennial grasses (d'Huart 1978, d'Huart pers. comm.).

In the Rwenzori National Park warthogs, Clough (1969) found no indications of post partum oestrus, and nor did ovulation occur during lactation, which agrees with the findings in Zululand. Therefore, in view of their almost six months' gestation, mature warthog sows would produce only one litter per year. Thus Clough (from Mentis 1972) suggests that a particular group of sows farrows at one wet season, while different sows comprising a second group farrow at the next wet season. According to Clough (from Mentis op. cit.), females may shift between the two groups when they fail to conceive or lose litters between seasons; "scattered births and the impression of non-seasonality arise through late mating, failure to conceive at first mating, or abortion in early pregnancy followed by successful remating."

While the absence of post partum oestrous cycles justifies Clough's assertion that the same sow would not farrow twice per year, the "impression of non-seasonality" could well be quite firmly based if some conceptions indeed occur during any month in warthog populations at the equator. Probable year-round breeding, but with two lambing peaks roughly coinciding with the two rainy seasons, has been reported in a population of impala living at the equator near Lake Elmenteita, Kenya (Kayanja 1969). On the Akira Ranch (0^{0} 55' to 1^{0} 05' S), about 50 km north-west of Nairobi, Field & Blankenship (1973) found that Coke's hartebeest, Thomson's and Grant's gazelles may breed during any month of the year, probably reflecting the equable habitat conditions during most months and the rainfall and photoperiod patterns. Anderson (1979) attributed the basically year-round, although bimodal, pattern of conceptions in a South African population of nyala to their equable habitat phenology, such that seasonal differences in nutrition provided insufficient feedback stimuli to reinforce photoperiod cues and favour seasonal reproduction; moreover, the peaks were masked by the occurrence of post partum oestrous cycles and an approximately seven month gestation period.

Conception and farrowing times in warthog populations elsewhere in Africa are inadequately documented, but include the following records, which provide some basis for comparison:-

Guinea : Prunier (1946) states that farrowing occurs during February and March.

Senegal : Guiraud (1948) reported gravid sows in all periods of the year except August, September and October, when none were hunted, and considered that most farrowing occurred towards the start of the rainy season (June - July).

Mali : Geigy (1955) cites a report of a litter born early in June near Ansongo, on the banks of the Niger River.

Tanzania : On the basis of a litter of recently born sucklings located at a burrow on 14 September, and foetal development in seven reproductive tracts examined during July, August and September, Geigy (1955) concluded that farrowing in the Ulanga district commenced early in September and probably continued into November, i.e. slightly preceding the shorter of the two rainy seasons in that region. In the eastern Selous Game Reserve, which has a single rainy season from late November to early May, Rodgers (1977) records "the farrowing period starting in September, through to November." This was confirmed by Boshe (1981) who recorded a birth peak in October.

Rwanda : In the Akagera National Park, Monfort (1974) records farrowing from mid-September to mid-November, with a peak in October, thus coinciding with new grass growth after the dry season.

While these records indicate reproductive seasonality in warthog populations away from the equator, a more comprehensive geographical documentation should highlight the extent of correlation between breeding and climatic patterns, and might show interesting deviations in response to local habitat conditions.

PREGNANCY

Implantation and placentation

The placenta of the warthog is similar to that described in the domestic pig (Patten 1948), and the chorion can be peeled away from the uterine mucosa, i.e. relatively tenuous attachment rather than fusion with the deeper uterine tissue as in other types of placentae. Implantation in the domestic sow is a gradual process, from the appearance of small areas of attachment between the trophoblast and the uterine epithelium by about 13 days post-conception, until completion during the following week (Mc Laren 1972). The time at which implantation begins in the warthog was not ascertained since no blastocysts less than 41 days old were collected.

Transuterine migration of ova is a usual phenomenon in the domestic sow,

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and there is a tendency for the number of embryos on each side to be equalised (Asdell 1964). As Patten (1948) states, "if all the ova originating on one side remained in the corresponding horn of the uterus there would be crowding of embryos on one side and unutilized space on the other." Smith & Sowls (1975) reported an equal distribution of foetuses in the left and right uterine horns of collared peccaries, although a few ova migrated before implantation. Apart from a trend towards slightly more implantations on the left side, a roughly even distribution of implantations between uterine horns was found in warthogs, not only in Zululand, but also in Zimbabwe (Child et al. 1968) and in Uganda (Clough 1969); migration of fertilised ova was recorded in all three localities, and Clough (op. cit.) found a 52% incidence, compared with 57,4% in Zululand.

Foetal and uterine dimensions in the warthog indicate that a maximum of four foetuses could be accommodated to term in each horn and, indeed, isolated occurrences of seven or eight piglets in a single litter have been reported (Frädrich 1966, Child et. al. 1968). The maximum capacity of the domestic pig uterus is 14 foetuses (Dziuk 1968).

more 4 offspring?

Duration

Brown (1936) recorded gestation periods of 171 and 175 days for two captive warthogs. This has been corroborated by Frädrich (pers. comm.) who observed a 172 - 174 day gestation period for a warthog sow at the Berlin Zoological Gardens. Dates of mating and farrowing of two tame free ranging warthog sows in Zimbabwe indicated gestation periods of 160 and 167 or 168 days respectively (Cumming 1975a). However, Cumming notes that the sow with the estimated 160 day gestation period first showed signs of oestrus four days before she was seen mating and so may have conceived slightly earlier. If the shorter of Cumming's (1975a) estimates is excluded, recorded gestation periods in the warthog range from 167 to 175 days. This exceeds the ± 151 days recorded in the giant forest hog (d'Huart 1978) and the four months reported in the bush-pig (Asdell 1964). Henry (1968) recorded an average gestation period of 115,2 ± 2,3 days in the European wild pig, ancestor of the domestic pig, while Sowls (1966) established a gestation period of 142 to 149 days in the collared peccary.

Birth mass and relationships between sex, number and size of foetuses

According to Bigourdan (1948), individual warthog birth masses are inversely related to litter size, varying between 480 - 620 g in litters of three or four and 800 - 850 g in twins. However, Frädrich (1966) recorded a mass of 910 g for one piglet from a litter of five born at Frankfurt Zoo. In Uganda, mean body mass of five foetuses obtained from two females at full term was 837,5 g and the heaviest was 870 g, from a litter of triplets (Clough 1969).

litter of 5

In Zululand, the heaviest foetus recorded was 753,2 g, from a litter of triplets carried by a sow estimated 6 - 10 days pre-partum. Disparity in mass between near term foetuses in the same litter may exceed 370 g. Foetal mass data collected by Child *et al*. (1968) in Zimbabwe showed considerable variation between members of a litter, and no inverse correlation was evident between litter size and mass of individual foetuses. However, a larger sample of near term foetuses of the same age might show a tendency for foetuses from small litters to be heavier than in large litters, as suggested by Smith & Sowls (1975) for the collared peccary. Including one additional record of 530 g for a male at Frankfurt Zoo (Frädrich *pers*. *comm*.), the evidence indicates that warthogs vary considerably in birth mass. In domestic pig farming it is well recognised that there may be a wide range of individual birth masses within any one particular litter (Blaxter 1961).

Especially during the latter stages of gestation, there was a tendency for male warthog foetuses to be slightly heavier than their female siblings, but the difference was not significant. Similarly, Child *et al*. (1968) found no significant mass difference between the sexes in the same litter in a sample of 80 foetuses from Zimbabwe. Henry (1968b) reported no apparent within-litter differences in crown-rump measurements between the sexes in European wild pig foetuses ranging from 20 to 110 days in post-conception age. Smith & Sowls (1975) found a slight but non-significant difference in mass of male and female peccary neonates, and concluded that there was no sexual dimorphism of size in peccary foetuses.

REPRODUCTIVE POTENTIAL

Prenatal sex ratio and litter size

Records of prenatal sex ratios and average numbers of young *in utero* for warthogs from various regions (Table 28) indicate an average litter size of three and a sex ratio close to parity at birth. Clough (1969) cites a mean of 3,4 foetuses per female in a sample of 26 pregnant females from Uganda; however, since his total of foetuses recorded was 78 (see pp. 328 and 333 of his article), one of these figures appears to be erroneous. Bigourdan (1948) recorded that two to five young are born per litter in West Africa, but the usual litter size was three to four. In Zambia, Ansell (1960) reported two to seven young per birth, and usually three to four. A sample of 21 pregnant sows from the Selous Game Reserve, Tanzania, carried litters ranging in size from one to four with a mean of 2,6 foetuses per sow (Boshe 1981).

— many more 4 foetuses

Litters seldom exceed five piglets per sow. Frädrich (1966) reported a litter of seven born at Frankfurt Zoo, of which one piglet died and two were hand-reared separately after it became apparent that competition for teats was jeopardising their survival. Of 97 prenatal warthog litters collected over a

(Competition for teats

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TABLE 28. Prenatal sex ratios and average litter sizes recorded in warthog populations.

Locality	No. of pregnancies	No. of viable foetuses	Mean litter size	Min. litter size	Max. litter size	No. of foetuses sexed	% of ♀ foetuses	Source
Senegal	16	50	3,13	1	5	-	-	Guiraud (1948)
Tanzania	7	24	3,43	2	4	24	58,33	Geigy (1955)
Zimbabwe	97	291	3,00	1	⑧	78	44,87	Child, Roth & Kerr (1968)
Uganda	26	78	3,40	1	-	62	51,61	Clough (1969)
Botswana	10	30	3,00	1	4	30	43,33	Biggs (*pers. comm.*)
Zululand	61*	199	3,26	1	5	172	47,67	Present study

*Comprising 52 pregnant sows from the Complex and nine from MGR.

NB! max 4 piglets

four year period in Zimbabwe, only one litter of six and one of eight foetuses were recorded (Child *et al*. 1968).

Frädrich (1965) recorded 31 female and 17 male warthogs from 15 births in zoological gardens. During cropping in the Complex between 1961 and 1963, 367 warthog foetuses in litters of one to five were recorded in a sample of 119 pregnancies, giving an average of 3,08 foetuses per female; the most frequent litter size was three, closely followed by four, and the foetal sex ratio was 136 males to 231 females, or 62,94% female (P.G. Stewart, Natal Parks Board records). Since most vertebrates have a sex ratio very close to 1 : 1 at birth (Caughley 1977), this significantly disparate ($p < 0,001$) sex ratio of 1,7 females per male contrasts markedly with the classifications shown in Table 28. A recent collection of 58 warthog foetuses from Tanzania, comprising 30 females and 28 males, also indicated a sex ratio close to parity at birth (Boshe 1981).

The disparity was particularly marked in the Tshenteka area of UGR, where females comprised 68,24% of the 148 foetuses from 42 pregnant sows shot during 1963. By comparison only 52,14% of 117 foetuses from 39 pregnant sows shot in HGR during 1963 were female. Early in July 1963, drastic unseasonal floods caused high mortality of warthogs in low-lying areas of the Complex (Natal Parks Board records). The Tshenteka area adjoins the White Umfolozi River and mortality through drowning would have coincided with early pregnancy in the warthog population. Since the floods followed the mating season, the unusually high proportion of female foetuses found during subsequent control shooting here from 15 September onwards probably cannot be construed as a population response compensating for mortality in July. However, this does not rule out the possibility that differential male mortality *in utero* had occurred, perhaps reflecting poor maternal condition - an association suggested by Trivers & Willard (1973). Farrowing in the Tshenteka area during 1963 was apparently rather early, with the first sighting of piglets on 12 September and a dearth of foetuses in shot females after mid-October (P.J. Daniel, Natal Parks Board records).

prenatal sex ratio

In view of evidence suggesting that shifts in prenatal sex ratios may have adaptive significance (Trivers & Willard 1973), a predominance of female foetuses could set the stage for rapid population growth following a period of adverse conditions. Natal Parks Board records mention that warthogs in the Complex were generally in very poor physical condition during the dry season of 1958, to the extent that large numbers were dying. As part of a game removal programme to alleviate habitat degradation, warthog control shooting commenced in HGR during 1957, when 39 were shot, and was continued every year to the present time, also including UGR from 1959 onwards.

From 1957 to 1965 inclusive, a total of 18 775 warthogs was removed from the Complex by shooting (live capture was added to shooting as a means of removal from 1966 onwards). Despite this intensive removal, a large proportion of warthogs in very poor condition was again reported during the dry season of 1964, notwithstanding considerable assistance in population reduction by the July 1963 floods.

Unfortunately, prenatal sex ratios were only recorded for a limited proportion of pregnancies during warthog control shooting in the Complex, so a possible association of poor nutrition and/or intensive removal with shifts in the sex ratio in the direction of more female offspring cannot be demonstrated. Data on sex ratios of wild wolf pups (Mech 1975) apparently conflict with Trivers & Willard's (1973) hypothesis that female parents in poor condition should produce more female offspring. A significant excess of male pups was produced in a saturated, high-density wolf population, whereas packs from populations of much lower density had equal sex ratios of pups or a disproportionate number of female pups. Mech suggests disproportionate viability, success, or numbers of the sperm cells that determine either sex as the most reasonable explanation for the disproportionate sex ratios. In white-tailed deer, Woolf & Harder (1979) reported evidence that "poor nutrition and low ovulation frequency have been associated with both unusually high and low proportions of male offspring," and concluded that the data do not fully support Trivers & Willard's hypothesis. Thus it appears that the possible adaptive significance of sex ratio shifts vis-à-vis long-term population dynamics remains unproven, pending further documentation for a variety of species.

Comparative data on prenatal sex ratios and litter sizes in the other African wild pigs are limited. Reported litter sizes in bushpig range from one to eight, with three to four the most common, and seldom exceed six - the number of mammae (Ansell 1960, Sowls & Phelps 1968, Skinner, Breytenbach & Maberly 1976). In the giant forest hog population in the Virunga National Park, Zaïre, d'Huart (1978) observed four to six young per litter and a sex ratio of unity among small juveniles.

Hagen & Kephart (1980) recorded averages of 9,8 and 6,2 foetuses per litter in primiparous Yorkshire and feral gilts respectively, and concluded that the smaller litter size in the feral line resulted from a lower ovulatory rate. Mauget (1972) reported an average of 4,62 foetuses per female in the European wild pig in the Chizé Forest, France. Litter size in the collared peccary is smaller and Smith & Sowls (1975) recorded an average of 1,96 foetuses per female.

Combining the data of Sowls (1966) and Smith & Sowls (1975) gives a prenatal sex ratio for the collared peccary of 60,7% females (n = 183), which is significantly different from unity ($p < 0,01$). While Asdell (1964) and Nalbandov (1976) reported figures of 50,4% and 47,2% females respectively for the sex ratio of domestic pigs at birth, a foetal sex ratio of 38% females (n = 50) was recorded for feral pigs in South Carolina (Sweeney, Sweeney & Provost 1979).

Indications of smaller litters in primigravid warthog sows in Uganda (Clough 1969) and in Tanzania (Boshe 1981) were supported by the findings in Zululand, where sows in their first pregnancy carried an average of 2,71 foetuses compared with 3,43 foetuses in older females.

Prenatal mortality

On the basis of the discrepancy between 65 ovulations and a corresponding total of 54 foetuses, Child _et al_. (1968) recorded a 16,92% prenatal mortality of warthogs in Zimbabwe, but there was no evidence of foetal resorption or abortion. Clough (1969) recorded 95 ovulations and 78 foetuses in 26 pregnant warthog sows in Uganda, giving a 17,89% loss of ova and embryos; in the absence of any indications of foetal resorption, he presumed that most of this loss was through non-fertilisation or failure to implant.

By contrast, the 9,13% prenatal mortality recorded in Zululand warthogs is much lower, and included indications of either foetal resorption or abortion in two pregnancies and definite evidence of resorption in another. An instance was also recorded where a sow in poor condition aborted a litter inside a burrow. During September 1964 in the course of cropping operations in UGR, abortion was reported in several sows in very poor condition; severe drought conditions prevailed at the time and the poor carcasses of many of the warthogs shot were judged unfit for human consumption (Natal Parks Board records). The mechanism of abortion in the warthog is probably the same as in the domestic pig, involving disruption of luteal function, a sharp fall in progesterone secretion, and the premature triggering of physiological mechanisms resembling those which occur at parturition (Wrathall 1975). Unlike the removal of conceptuses from the uterus by gradual autolysis and reabsorption _in situ_, abortion is a muscular process by which they are forcibly expelled (Wrathall _op_. _cit_.).

A relatively high incidence of foetal resorption in springbok (_Antidorcas marsupialis_), attributed to the disturbance of shooting during the early stages of pregnancy, was reported by Els (_pers_. _comm_.). Child _et al_. (1968) observed the maximum reproductive potential in a Zimbabwean warthog population during the first year of a four year period of tsetse control hunting, "before the population was disturbed by prolonged hunting;" under the "dry marginal" conditions in their study area, sows were in poor physical condition during the second half of pregnancy, reflecting limited dry season grazing and water.

Thus it appears that both habitat conditions and circumstances pertaining to removal may contribute to explaining variations in prenatal mortality rates

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of warthog populations. Unfortunately no data on prenatal mortality in relation to population density are available. The low incidence of abortion and foetal resorption under the moderate conditions prevailing during the present study suggests that loss of ova through non-fertilisation or failure to implant and develop were the predominant forms of prenatal mortality. Results from natural mating in the domestic pig show that complete failure of fertilisation of ova occurs in only 5% of sows served twice during oestrus, although the proportion of ovulated ova which are fertilised is 100% in most sows (Polge 1978). However, embryonic losses may amount to 30 - 40% of the fertilised ova (Perry 1960), so that the average litter size is considerably below the ovulation rate. Also, if insemination is delayed for longer than eight hours after ovulation, fertility declines very sharply due to diminished efficiency of sperm transport and an increase in the proportion of animals where none of the ova is fertilised (Hunter 1967). Typically, most prenatal mortality has occurred by the 25th day of pregnancy and arises mainly through degeneration of fertilised ova associated with failure of implantation (Perry *op. cit.*, Perry & Rowlands 1962). A prenatal mortality of 31,4% can be inferred from data on reproductive biology of feral pigs (Sweeney *et al.* 1979). Smith & Sowls (1975) recorded 68 corpora lutea of pregnancy and 45 viable foetuses in 23 female collared peccaries, indicating a fertilisation rate (the proportion of ova fertilised and producing viable foetuses) of 66,18%; prenatal mortality was therefore 33,82% (including a 9,64% intrauterine mortality of foetuses in females pregnant 40 days or longer).

As Child *et al.* (1968) point out, the high prenatal losses in domestic pigs occur despite a usually high plane of nutrition, whereas pregnancies in the warthog coincide with the dry season in southern Africa, when natural grazing conditions deteriorate. In the domestic pig, loss from stillbirths averages about 6% and is greater in litters with prolonged farrowings, affecting particularly the second half of the litter to be farrowed; many of the piglets involved smother while still in the uterus after having attempted to breathe (Asdell 1964). Nalbandov (1976) noted that average litter size of domestic pigs ranged from 6,6 to 11,2 depending on breed, so the incidence of stillbirths is likely to be much less in warthogs, with their much smaller average litter size.

Reproductive success

NB!!

Apart from the frequency of production of offspring, the two indicators for measuring reproductive efficiency in the domestic pig are farrowing rate (the proportion of sows farrowing) and litter size (the number of live young born) (Polge 1978). On good farms in Britain, an average farrowing rate of

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85% with a litter size of 11,0 has been reported using natural mating (Polge op. cit.). While the average litter size of 3,26 for warthogs in Zululand during 1973 and 1974 is much smaller, the minimum reproductive success rate of 96,1% is superior to that of domestic pigs. Child et al. (1968) reported a maximum farrowing rate of 72% for the Nagupande warthog population in Zimbabwe, and found that average prenatal litter sizes may vary with conditions from year to year, and there was also some variation between different areas; during their four year study period, the annual average litter size declined from 3,8 to 2,5 foetuses per female. Of a sample of 58 mature warthog females in Uganda, 15,5% were classed as anoestrous, i.e. neither pregnant, lactating, nor with a recent corpus luteum of ovulation (Clough 1969). In the Selous Game Reserve, Tanzania, Boshe (1981) recorded a farrowing rate of 87% for mature warthog sows (n = 39), and a mean prenatal litter size of 2,6 foetuses per sow.

Although it could be expected that high removal intensity may stimulate population turnover and reproductive success (Graham 1967, Child, Smith & von Richter 1970), undernutrition associated with high population density may cause considerably lower natality. Natal Parks Board records for the Complex indicate that very poor physical condition was widespread among warthogs, particularly in game removal areas, during the severe dry season of 1964, and several cases of abortion were reported. In UGR a 95% pregnancy rate was noted for an unspecified sample of sows shot during July, and average prenatal litter size was three with very few females carrying five foetuses (none of the yearling females examined were pregnant); during August, 250 foetuses were recorded from 149 pregnancies, giving an average of only 1,68 foetuses per female, compared with 2,51 foetuses per female (216 foetuses from a sample of 86 pregnancies) during September. The very low prenatal litter size for the August sample probably reflects especially poor grazing conditions in a particular removal area. Nevertheless, the overall mean of 1,98 foetuses per female for the combined sample of 235 pregnancies during August and September of 1964 is markedly lower than the average of 3,21 foetuses per female recorded in the Complex for 1973 and 1974. The absence of corpora lutea counts for the 1964 sample prevents an assessment of the extent to which the small average prenatal litter size might have been due to a low ovulation rate rather than high mortality in utero.

In the desert country of Arizona, Sowls (1966) found that reproduction in the collared peccary is greatly affected by nutrition, and the pregnancy rate was highest in years of high winter rainfall and good food conditions; the percentage of young surviving in the population was also directly related to the amount of rainfall. Reproduction may also be adversely influenced by a lack of specific nutrients in the diet, as demonstrated for the domestic pig, where low intake of pantothenic acid (one of the B complex vitamins) resulted in abnormal frequency of oestrus and an increased incidence of reproductive failures during pregnancy (Ullrey, Becker, Terrill & Notzold 1955). Teer, Thomas & Walker (1965) found that both ovulation and conception rates of white-tailed deer in Texas were inversely related to population density, and concluded that high reproductive performance was dependent on adequate nutrition.

On the basis of a reproductive performance of 3,07 young per mature female per year and a 45,52% proportion of female offspring, the warthog population in the Complex was producing 1,40 female young per mature female per year during the study period. Clough (1969) found no indications of a decline of fertility with age among warthog sows that he examined in Uganda, and no signs of reproductive senescence were observed in Zululand. However, small sample size precludes a definitive statement on this aspect.

OVARIAN STRUCTURE AND DYNAMICS

The follicles

Classification of follicles into groups according to size was useful for illustrating growth changes at various stages of the ovarian cycle. Maximum numbers of large follicles coincided with the mating season in autumn, when follicles of ovulatory size exceeded 6 mm in mean diameter. Clough (1969) noted 7 to 8 mm as the diameter of follicles at ovulation for warthogs in Uganda, compared with 8 to 12 mm in the domestic sow (Anderson & Melampy 1967). Follicles destined to ovulate in the domestic sow reached an average diameter of 6,5 mm two days before oestrus (Burger 1952). Follicular atresia in warthog ovaries was a similar process to that described in other mammals (Mossman & Duke 1973).

The corpora lutea

Following rupture and collapse of the follicle walls around a central blood clot, the development of a corpus luteum at each site of ovulation is a rapid process in the warthog ovary. If pregnancy ensues, corpora lutea of 5,4 - 9,6 mm in mean diameter are maintained until term. In Uganda, Clough (1969) reported rapid growth of warthog corpora lutea to about 10 mm in diameter. Five corpora lutea in the ovaries of a bushpig from Ndumu Game Reserve, Natal, ranged from 7,8 to 9,9 mm in mean diameter. Corpora lutea in the domestic sow measure 8 - 9 mm in diameter within a week of ovulation, increasing to 10 mm or more if pregnancy follows, compared with 4 - 6 mm for newly formed corpora haemorrhagica (corpora lutea with central blood clot) (Anderson & Melampy 1967). During the first two weeks of development corpora lutea of pregnancy in the domestic sow are morphologically indistinguishable from those of the oestrous cycle; however, the latter subsequently regress rapidly in sows where the ova are not fertilised, and have diminished in diameter to 4 mm by the middle of the next oestrual period (commencing about 21 days after the first), and by ovulation during the following oestrus to 2 mm (Anderson & Melampy op. cit.).

Circulating progesterone is necessary for the maintenance of pregnancy in the domestic pig and is supplied by the corpora lutea, although in some mammals this supply may be augmented or replaced by placental progesterone (Perry 1971). In the domestic pig, plasma progesterone levels fall near the end of pregnancy, in advance of luteal regression (Masuda, Anderson, Henricks & Melampy 1967). The slight but significant decline in corpora lutea diameters of warthogs from about 40 days post-conception until mid-gestation, followed by an increase towards term (Fig. 30), is similar to the pattern found in giraffe (Hall-Martin 1975). In the collared peccary, which has a gestation period of 142 to 149 days, Sowls, Smith, Holtan, Moss & Estergreen (1976) noted a gradual but non-significant increase in luteal cell diameters as gestation progressed to 80 days, after which there was a decrease in diameter to 120 days and then a significant increase in size at 140 days. However, Hall-Martin (op. cit.) found that individual luteal cells of giraffe did not decrease in size when the total corpus luteum size was decreasing. Although size of luteal cells was significantly correlated with progesterone content of luteal tissue in the peccary, Sowls et al. (op. cit.) suggest that reduced secretion of luteal progesterone can be associated with a considerable concentration in luteal tissue and that the placenta might contribute increasingly to the maintenance of plasma progesterone levels during the last third of gestation. Notwithstanding the gradual increase in size of warthog corpora lutea during the latter half of gestation, the functional activity of the luteal cells could therefore be decreasing. Clough (1969) also found no macroscopically visible indications that warthog corpora lutea begin to regress before parturition. However, endocrinological interpretation of the inversion in corpora lutea size about mid-gestation must await more detailed investigation.

Corpora albicantia and regressing corpora lutea

In mammals where maintenance of pregnancy is dependent on at least some luteal function throughout pregnancy, labour is preceded by a fall in concentration of progesterone in the maternal blood, so the time of onset of labour is evidently related to factors controlling luteal regression (Liggins 1972). Although an explanation of these factors is beyond the scope of this study, the release of a uterine luteolytic agent (a prostaglandin), probably largely under foetal control via increased foetal hypophysial and adrenal activity, is implicated in terminating luteal activity and in triggering parturition (Anderson & Melampy 1967, Perry 1971, Liggins op. cit., Heap 1972).

After parturition the warthog corpus luteum degenerates rapidly (see also

Clough 1969) to form a small, brown-pigmented mass of scar tissue, the corpus albicans. As in the white-tailed deer (Cheatum 1949 , Teer et al. 1965), these scars are often compressed during the subsequent breeding season by adjacent development of large follicles and new corpora lutea, but they may persist throughout the succeeding period of pregnancy. In the wildebeest, Watson (1969) notes that older corpora albicantia thus compressed into layers are frequently so close to other corpora albicantia that counting them becomes unreliable in old animals, where they may persist in many ovaries for nine to 10 years.

In Uganda, Clough (1969) recorded a maximum of 16 corpora albicantia in the ovaries of a single warthog sow, and assumed that some were from more than one previous pregnancy or were the remains of corpora lutea of the cycle, if this particular female had several oestrous cycles before finally conceiving. A maximum of 23 corpora albicantia from one warthog was recorded in Zululand. Clough (1969) was unable to distinguish between corpora albicantia resulting from corpora lutea of a cycle and those resulting from corpora lutea of pregnancy. However, corpora albicantia originating from regression of corpora lutea of the cycle appeared unimportant in Zululand due to the dearth of atrophied corpora lutea of ovulation accompanying enlarged corpora lutea of early pregnancy.

Several studies of other ungulates have indicated that the scars of corpora lutea of pregnancy may be confused with scars of corpora lutea of ovulation and luteinised (unovulated) follicles, and that some scars are relatively less persistent than others (Robinette, Gashwiler, Jones & Crane 1955, Golley 1957, Teer et al. 1965). In the warthog ovary, positive differentiation between corpora albicantia of pregnancy and pigmented scars resulting from other sources was also impracticable. Only one instance of an accessory corpus luteum was recorded, and the absence of atrophied corpora lutea of ovulation accompanying enlarged corpora lutea of pregnancy of a subsequent oestrous cycle may reflect the high fertility of the warthog population, such that the first oestrus of the season almost invariably led to pregnancy. Although corpora albicantia resulting from sources other than regressing corpora lutea of pregnancy may be relatively uncommon in the warthog, the problem of recognising their origin plus the probable inflation of their numbers, due especially to persistence of more than one generation into the collecting period, render counts of these pigmented scars unreliable for estimating the incidence of ovulation. The mere presence of corpora albicantia is also not a certain indicator of a previous pregnancy, although this seems highly probable where corpora albicantia of a relatively large size class are present in numbers corresponding to the normal ovulation rate.

Significantly more corpora albicantia were present in the left compared with the right ovaries of Zululand warthogs, which supports other evidence (differential ovulation rate and ovary mass) indicating differential activity of the ovaries. Child et al. (1968) and Clough (1969) also found differential ovulation favouring the left ovary in Zimbabwean and Ugandan warthog populations, and Asdell (1964) states that the left ovary is slightly more active in the domestic pig.

Seasonal ovarian activity

During gestation the largest follicles rarely attained 3 mm in diameter. Following a gradual increase in largest follicle diameters during the early post-farrowing period, no further increase in average size of the largest follicles occurred throughout the remainder of the lactation period. The distinctly seasonal occurrence of large follicles and recent ovulations in the Zululand warthog population concurs with the pattern of ovarian activity reported in the Nagupande warthog population in Zimbabwe (Child et al. 1968). Although Clough (1969) did not analyse ovarian activity of warthogs in Uganda on a monthly basis, he found no indications of reproductive seasonality from eight observed cases of oestrus and analysis of foetal age in 16 pregnancies.

The females of several African mammals have oestrous cycles and may conceive while lactating, e.g. hippopotamus (Laws & Clough 1966), black rhinoceros (Goddard 1967), wildebeest (Watson 1969), Uganda kob (Morrison & Buechner 1971), white rhinoceros (Owen-Smith 1973), buffalo (Grimsdell 1973), giraffe (Hall-Martin 1975), zebra (Smuts 1976b). The mammary glands may be starting to regress at the time of ovulation, as in the wildebeest (Watson op. cit.), but oestrus and conception may occur during the period of maximal lactation, as commonly happens in the Uganda kob (Morrison & Buechner op. cit.). In many species of mammals however, lactation inhibits follicular development, oestrus and ovulation.

Unless the litter dies or is removed shortly after parturition, the domestic sow normally remains in anoestrus during lactation, with oestrus and ovulation occurring after lactation has ceased (Crighton 1967, Peters, First & Casida 1969); however, a post partum heat, usually not accompanied by ovulation, frequently occurs at about 44 hours after parturition but the time is variable (Burger 1952). In the warthog, ovulation did not occur during lactation and no lactating females were pregnant (see also Clough 1969). Conversely, in the collared peccary, oestrus and ovulation accompanied by successful mating normally occur during lactation, at earliest eight days after parturition (Sowls 1966). Post partum heat with ovulation permits the peccary to produce young at a faster rate than the warthog, which in Zululand ovulates about six months after parturition.

LACTATION

Duration

Roth (1965) found that weaning occurred at seven to 10 weeks of age in orphaned juvenile warthogs reared in captivity and was a critical period characterised by stagnation of development, "before the growth rate increased steadily after the change from milk to solid foods." Child *et al.* (1968) recorded lactation in shot warthogs up to four months after the last pregnancies, but considered that milk was probably not important to the juveniles after seven to nine weeks. Bradley (1968) observed a complete nursing period of about 150 - 160 days in Nairobi National Park, although nursing was supplemented at an early age with some grazing. According to Cumming (1975a), the juveniles of a tame free ranging sow in Zimbabwe were weaned at 21 weeks, but were already feeding for as long as their mother each day by the time they were 63 days old. The observations of Bradley and Cumming (*op. cits.*) agree with the evidence from Zululand, indicating the duration of lactation as about five months.

Milk composition

Faust (1961) has reported the composition at parturition of a milk sample from a warthog sow in Frankfurt Zoo, and Roth (1967) has described the composition of three samples (10, 17 and 25 ml) of early lactation warthog milk from Zimbabwe. Only total solids content was analysed for three samples of post partum milk from Zululand, giving values slightly lower than the 19,8 and 20,8% total solids measured in two samples of early lactation warthog milk from Zimbabwe (Roth *op. cit.*). Since milk composition varies at different stages of lactation (Ling, Kon & Porter 1961), the limited data available preclude adequate quantitative description of trends in the major constituents of warthog milk during early and established lactation.

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CHAPTER 6

DISTRIBUTION, ABUNDANCE AND POPULATION STRUCTURE

INTRODUCTION

Warthogs are widely distributed in the African savannas and woodlands and, as Kingdon (1979) points out, generally belong to a community that includes antbears, whose burrows profoundly influence the suitability of a locality for warthogs. Although Western (1975) classifies warthogs as water-dependent grazing animals, Dorst & Dandelot (1970) report their occurrence in the Sahel region where surface water is not available for six months of the year. Warthogs also occur in seasonally arid country in the Kalahari region of Botswana, where their moisture requirements might be supplied by feeding on succulent underground roots and rhizomes (Smithers 1971). In the moist, evergreen forests of the Aberdare Range, Kenya, warthogs graze in patches of montane grassland at altitudes of 2 100 - 2 400 m, overlapping with giant forest hogs (Hall-Martin pers. comm.), while Kingdon (1979) records warthogs living on the Shira Plateau, 3 000 m up Mount Kilimanjaro.

Although studies by Lamprey (1963), Field & Laws (1970), Jarman (1972), Monfort (1974), and Cumming (1970, 1975a) have provided some data on warthog abundance in relation to vegetation types, warthog preferences for habitats within their geographic range remain inadequately documented. Information on warthog population parameters, particularly sex ratios, is available from a variety of localities, and Spinage (1972) has provided life table data for a population in the Akagera National Park, Rwanda. Other notable studies of the age class structure of warthog populations are those of Bradley (1968) and Cumming (op. cits.).

Time taken up by the collection of post-mortem material from cropping prevented a comprehensive study of warthog distribution and abundance in the Complex, but largely qualitative observations over a two-year period, together with field sex and age classifications, provide some information on warthog population ecology and dynamics in relation to environmental resources and constraints.

METHODS

DISTRIBUTION AND ABUNDANCE

Warthog densities and habitat usage were not measured by systematic sampling. However, largely qualitative observations at all times of day in all types of vegetation, accumulated over a two-year period, permit an outline of some features of warthog distribution and abundance in the Complex, and provide some ecological background which may be beneficial to management.

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On a localised scale, satisfactory estimation of warthog densities is sometimes possible by intensive coverage of small areas from the ground. In HGR, warthogs grazing on short grass lawns within the extensive areas of open grassland on Hlaza Hill could be counted from vantage points opposite the hill slopes. With the aid of a telescope, certain individuals could be identified by features such as tusk shape and size, and most of the resident groups were recognisable by their sex and age composition. Many of the holes used or probably used by these individual warthogs and family groups had been located, and they apparently lived in quite small, overlapping home ranges and did not normally move beyond the adjoining slopes of the two neighbouring hills (Nkwakwa and Godeni), where other warthogs were resident. Several of the warthogs residing on Godeni were also individually identifiable and were not seen closer to Hlaza than the dip between the two hills. A more intensive study using the radio-tracking technique would be necessary to assess the full extent of movements and overlap between warthogs living on these hills. However, the availability on Hlaza Hill of a small water-seepage, preferred grazing areas, abundant holes and shady cover in clumps of bushes and patches of closed woodland and forest probably promoted largely sedentary habits among the local warthogs.

The consistency of repeated sightings of known individuals and groups on Hlaza Hill also indicated that a reasonably accurate estimate of total warthog numbers was possible. The census area was centred on the grassland and skirted by thicket, woodland and forest communities which, on the southern slopes particularly, comprised a natural boundary zone; a road was used to delimit the northern margins, although some of the warthogs utilising the favoured grazing areas in the grassland sometimes slept in holes just to the north of this road. During January, February and March 1974, the Hlaza warthogs were counted repeatedly, by scanning first one side of the hill and then the other, using a vehicle to travel rapidly between vantage points, and checking a few "blind" areas at the hill summit and in patches of forest by traversing them on foot.

In UGR, several foot transects were made during the 1974 dry season in an attempt to obtain some indication of warthog abundance in management areas south of the Black Umfolozi river. Management areas, delimited on the basis of catchment areas and the road network, are used for allocating controlled burning, erosion-reclamation measures and game removal. Nine management areas were sampled by walking at a steady pace, recording total time spent traversing each area and numbers of warthogs sighted. Transects were generally made between about 08h00 and 11h00, and 15h00 and 17h00, but were terminated during the very hot hours when it was known that many warthogs would have moved into the shade of thickets and trees, this behaviour rendering them less visible. Results were expressed as numbers of warthogs contacted per hour.

POPULATION STRUCTURE

During the period September 1973 to June 1975, data on warthog population composition in the Complex were collected monthly by random sampling from roads and on foot, classifying warthogs according to sex and three age classes (juvenile, yearling and adult), which can be distinguished in the field throughout the year (see Chapter 2). Subadults (2 - 3 years old) were classified separately from adults whenever they could be distinguished. By virtue of the short well defined farrowing season in Zululand, 1 November was taken as the start of the warthog annual cycle and the date on which animals from one age class pass through to the next.

The accumulated population sample includes an unknown number of repeated sightings of the same individual warthogs or warthog groups. Where an identifiable individual or group was seen several times during any one month, only one sighting was included in the monthly sample. Changes in composition of known groups through recruitment, mortality or dispersal, were thus included in successive monthly samples, if the group was resighted during more than one month.

Frequently sex, age and number of warthogs could not be determined, particularly because of dense vegetative cover. Moreover, sexing of juveniles is often difficult or impossible under field conditions. All sightings where the number of warthogs present was uncertain, and/or some individuals past the juvenile age class could not be distinguished as yearlings or adults, were discarded.

The data were supplemented by classifications made at waterholes in the Complex during the dry seasons of 1973 and 1974. Some comparative data were obtained from a sample classification of warthogs drinking at two waterholes in MGR during July 1973. Skulls collected from warthogs during cropping in the Complex were used to estimate approximate ages on the basis of dental criteria described in Chapter 2, thereby providing an indication of the influence of cropping on population age structure.

RESULTS

DISTRIBUTION AND ABUNDANCE

Warthogs are very widely distributed throughout almost the entire area of the Complex, but are virtually absent in the extensive forest stands of north-western HGR. However, they use holes and seek shade within the forest margins and in smaller clumps of forest and closed woodland. Their occurrence in all other habitats in the Complex is indicative of their ability to live in a wide range of vegetation types, including dense woody vegetation, so long as grassy glades are available. In closed Spirostachys africana woodland and Euclea

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divinorum thicket, the grass Dactyloctenium australe was widely utilised by warthogs. Although warthogs favour short grass areas, they did not appear averse to moving through or sometimes feeding in medium to tall grass cover, often taller than themselves.

The distribution of warthog density in the Complex, like the distribution of total grazing pressure, is uneven, as suggested by the results of transects walked in management areas south of the Black Umfolozi River during the 1974 dry season (Fig. 35, Table 29). Several variables may influence the results of such transects and they should be considered as no more than a rough index of relative abundance of warthogs during that period. The high number of warthogs sighted per hour in management area no. 28 may partly reflect the presence of water in a large pan (Dadethu). Warthogs were noticeably scarce in extensive areas of tall mature grass cover with few or no short grass patches, e.g. Matshemnyama Hill.

TABLE 29. Warthog density index transects conducted on foot during the 1974 dry season in the area of Umfolozi Game Reserve south of the Black Umfolozi River.

Dates	Management area	Time spent (min.)	Total number of warthogs sighted	Sightings per hour
74-09-16	25	230	4	1,0
74-08-26 74-09-04 74-09-06	27	360	33	5,5
74-09-06 74-09-12 74-09-19	28	395	52	7,9
74-10-06	29	180	13	4,3
74-09-17	30	220	20	5,5
74-10-05	31	260	28	6,5
74-09-15	34	240	17	4,3
74-09-20 74-09-21	35	220	9	2,5
74-09-10 74-09-11	36	240	20	5,0

Within management area no. 36, an extensive portion of the Meva basin has been badly degraded for years. Acacia grandicornuta and Pappea capensis are

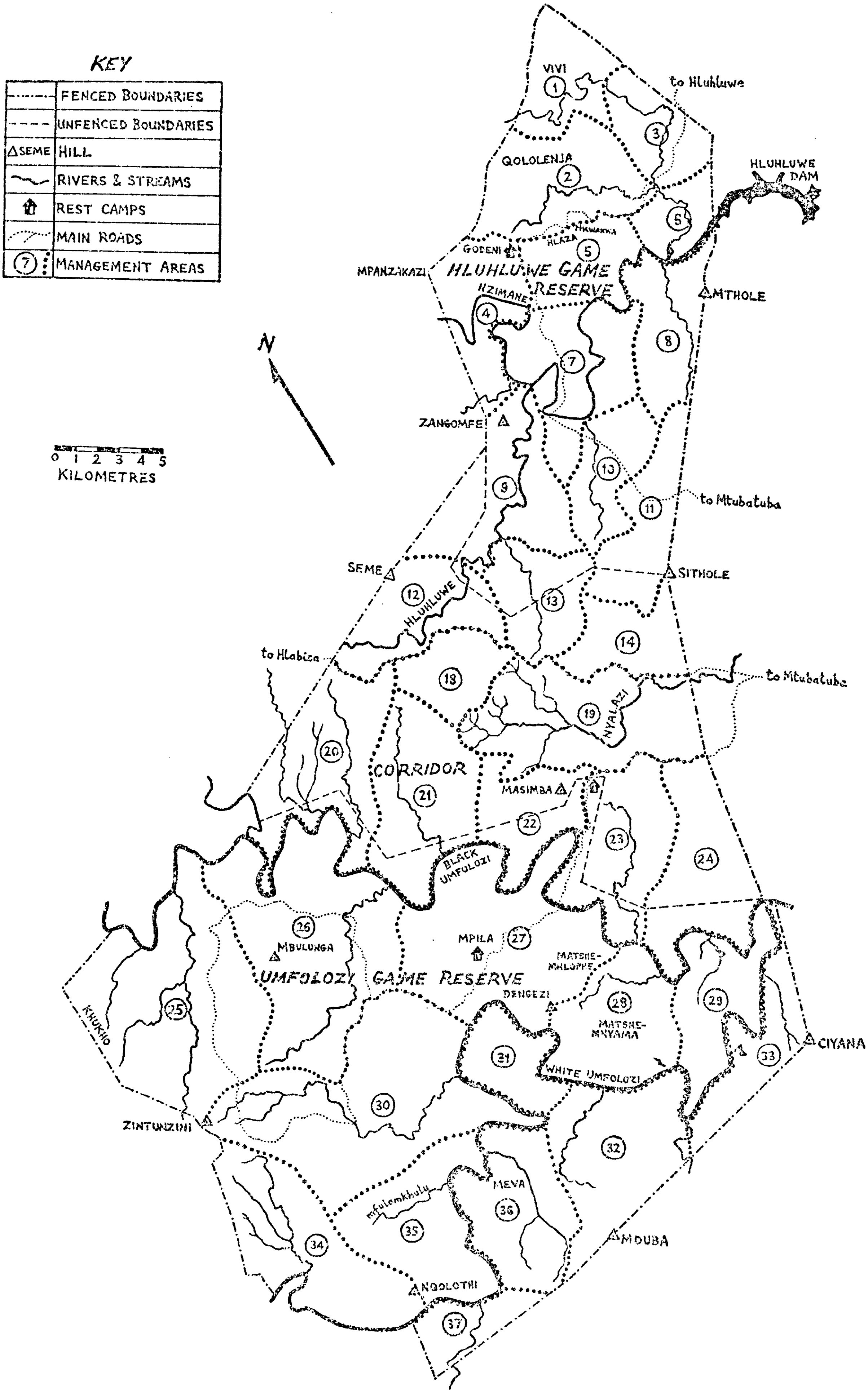

FIG. 35. The Hluhluwe-Corridor-Umfolozi Game Reserve complex showing management areas, delimited on the basis of catchment areas and the road network.

the dominant trees and Azima tetracantha and Asparagus spp. are conspicuous in the herb layer, but the grass cover is virtually absent; no warthogs were encountered here, which was probably due partly to the lack of food, as some warthogs were seen in the fringing areas where a grass cover is still present. However, the numbers of warthogs and other grazing species in the area may be related more to movement patterns concerned with drinking than to habitat. Over successive dry seasons, ungulates "funnelling" through the Meva basin to drink from the White Umfolozi River have probably contributed significantly to the disappearance of the grass cover.

Probably the highest year-round warthog densities in the Complex during the study period were found in the northeast of HGR, particularly in management areas numbers 3,5 and 6 and parts of 2, and in the southern half of UGR (management areas 27, 28, 29, 31, 32 and parts of 30, 33, 34, 35 and 36). In these areas the minimum average density during the study period was probably about 4 warthogs /km^2. Densities peak after the farrowing season, when local densities may be extremely high. On Hlaza Hill, HGR, intensive observations during the first three months of 1974 indicated a density of 35 - 40 warthogs/km^2. Warthog densities in HGR appeared to be lowest in the southwestern portion, to the extent that they were infrequently encountered in some areas.

Although warthog population densities throughout the Complex have yet to be accurately determined, it was probably only in the southern half of UGR that high warthog densities largely overlapped with areas allocated for game removal during 1974, on the basis of habitat degradation (Fig. 36). However, other grazers have also contributed to the pattern of area overgrazing, and in some areas the scarcity of warthogs during the study period could reflect heavy removal in the past.

POPULATION STRUCTURE

Sex and age classifications of samples of warthogs were initially obtained from observation hides at waterholes, recognising only two age categories, viz. juveniles and individuals older than 12 months. A sample of 61 warthogs classified at Munywaneni waterhole in HGR during June 1973, comprised 52,5% males (all ages), while 45,2% of individuals older than one year (n = 42) were males. At Bube and Msinga waterholes, MGR, males comprised 43,4% of a sample of 83 juvenile, yearling and older warthogs classified during July 1973; however, only 21,4% of individuals older than one year (n = 28) were males. The results of subsequent field classifications, based mainly on sightings of warthogs from roads and on foot, are shown in Tables 30 & 31.

Because warthog piglets spend most of their first month in holes, the

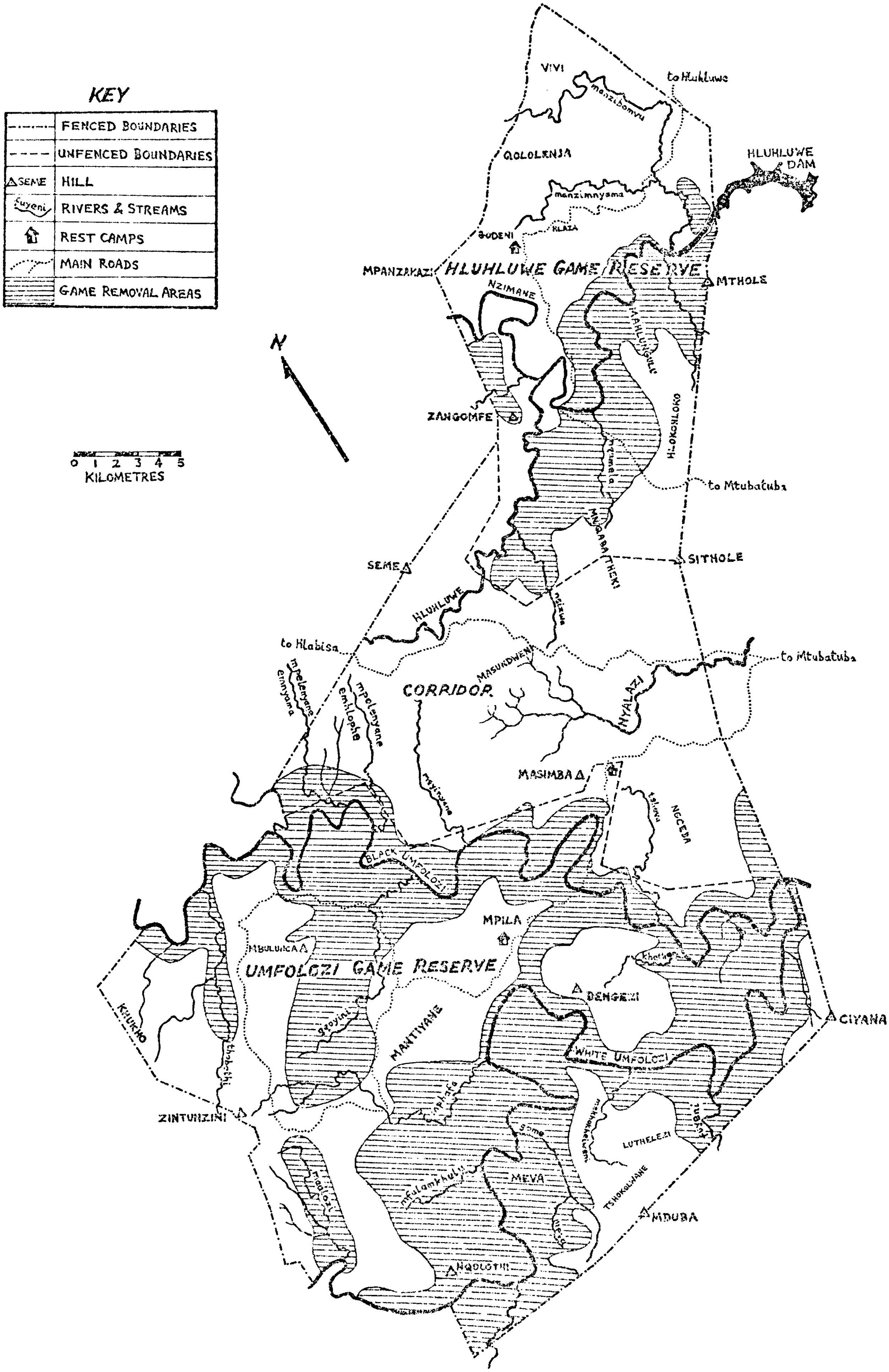

FIG. 36. The Hluhluwe-Corridor-Umfolozi Game Reserve complex showing areas assigned for game removal in 1974, on the basis of habitat degradation (from map compiled by R. Porter in 1974 : Natal Parks Board records).

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TABLE 30. Sex and age classifications of warthogs in the Hluhluwe-Corridor-Umfolozi Game Reserve complex, based on sightings from roads and on foot, for each two-month period between September 1973 and June 1975.

MONTHS AND YEAR	NUMBER OF WARTHOGS CLASSIFIED										RATIO		Number of ad.♀♀ with juveniles	Number of juveniles	Litter size
	Juveniles			Yearlings			Adults			Total	Juv./Ad.	Yrlg./Ad.			
	♂♂	♀♀	Unsexed	♂♂	♀♀	Unsexed	♂♂	♀♀	Unsexed						
1973															
Sep.-Oct.	9	11	3	5	3	3	7	21	0	62	0,82	0,39	11	17	1,55
Nov.-Dec.	1	3	25	14	12	3	17	32	6	113	0,53	0,53	13	29	2,23
1974															
Jan.-Feb.	16	19	92	13	17	8	25	77	2	269	1,22	0,37	59	127	2,15
Mar.-Apr.	22	28	66	15	18	0	34	72	6	261	1,04	0,29	45	92	2,04
May -Jun.	27	30	11	10	9	0	22	34	0	143	1,21	0,34	29	64	2,21
Jul.-Aug.	28	29	44	19	13	0	21	58	4	216	1,22	0,39	48	101	2,10
Sep.-Oct.	36	42	78	37	34	2	50	84	2	365	1,15	0,54	68	139	2,04
Nov.-Dec.*	5	5	87	22	29	7	28	66	4	253	0,99	0,59	39	94	2,41
1975															
Jan.-Feb.	18	20	64	12	21	0	17	43	2	197	1,65	0,53	39	102	2,62
Mar.-Apr.	13	15	40	8	17	0	21	31	0	145	1,31	0,48	29	68	2,34
May -Jun.	19	22	72	20	37	0	44	60	0	274	1,09	0,55	50	113	2,26
Total	194	224	582	175	210	23	286	578	26	2298	1,12	0,46	430	946	2,20

* a sounder of one adult ♀ with three neonates, sighted on 74-10-29, has been included in the Nov.-Dec. sub-sample.

TABLE 31. Sex and age classifications of warthogs seen at waterholes in Umfolozi Game Reserve during August and September 1974.

DATES	LOCALITY	NUMBER OF WARTHOGS CLASSIFIED								RATIO		Number of ad.♀♀ with juveniles	Number of juveniles	Litter size
		Juveniles			Yearlings		Adults		Total	Juv./Ad.	Yrlg./Ad.			
		♂♂	♀♀	Unsexed	♂♂	♀♀	♂♂	♀♀						
15,16,31 Aug., 2 Sep.	Bekapanzi	14	22	0	25	21	26	25	133	0,71	0,90	16	36	2,25
20 Aug., 20 Sep.	Mphafa	3	1	0	3	4	6	5	22	0,36	0,64	1	4	4,00
19,23 Sep.	Dadethu	5	8	20	5	6	2	10	56	2,75	0,92	10	27	2,70
Total		22	31	20	33	31	34	40	211	0,99	0,86	27	67	2,48

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concomitant delay between birth and observation of piglets in the field precludes an accurate assessment of natality in the field. Juvenile : adult ratios (Table 30) tended to be higher during January - February, after the farrowing season, when juveniles are following their mothers whenever they leave the hole. Data from cropping during the study period indicated a mean prenatal litter size of 3,21 (n = 52 pregnancies) for warthogs in the Complex (Chapter 5). Since average litter sizes during January - February of 1974 and 1975 were 2,15 and 2,62 respectively (Table 30), early post-natal mortality would have been of the order of 18 - 33%. However, the monthly samples contributing to the data in Table 30 may be rather small and subject to a degree of sampling variation which possibly obscures trends in some population parameters.

Survival of juveniles to the end of their first year may be estimated from average litter size and the juvenile : adult ratio in September - October. Excluding the 1973 data because of small sample size, the average litter size of matriarchal sounders in September - October 1974 was 2,04 and the juvenile : adult ratio was 1,15. Assuming all mature sows had produced an average of 3,21 piglets each, the decline in litter size by September - October indicated a juvenile mortality of 36,4%. Excluding adult males from the juvenile : adult ratio gives an average litter size of 1,83 juveniles per adult female in September - October (when juveniles are 10 - 12 months old). Since the minimum farrowing rate was 95,5% (Chapter 5), this ratio becomes 1,92 juveniles per adult female for sows that farrowed, but includes sightings of juveniles without an adult female (particularly during October, when sows about to farrow start deserting their young of the previous year). Thus mortality during the first 10 - 12 months, as calculated from the difference between mean prenatal litter size and the juvenile : adult female ratio in September - October (after excluding non-breeding females), was 40,2%.

Limited evidence suggesting considerably lower juvenile mortality rates in certain localities of northern HGR and on Mpila Hill, UGR, was obtained from resightings of identifiable family units (Table 32), and it is perhaps noteworthy that lion activity in these areas was virtually absent or minimal during the study period. Of the total sample of 49 piglets from known sounders, 40 survived to at least six months of age, indicating a mortality rate of 18,4%. However, the true mortality rate was undoubtedly higher since some litters would have been slightly smaller when first recorded than at birth. Judging by the excess number of enlarged teats on the udders of four of the sows when first seen with juveniles, the sample probably comprised at least 54 piglets at birth, indicating a minimum mortality of 25,9% during the first six months. Considering only those litters with piglets surviving to 12 months of age, the loss of six piglets from an original cohort of 23 corresponded to a

TABLE 32. Survival of warthog piglets from identifiable family units in the Hluhluwe-Corridor-Umfolozi Game Reserve complex, based on observations of 15 litters during their first year.

Family no.*	Litter size when first recorded†	Date of first observation	Mortality up to last re-sighting	Age attained by surviving piglets (months)
Ia	4	73-12-03	2	12
Ib	3	75-01-03	2	6-7
II	1	74-01-02	0	6-7
III	3	74-01-15	0	7-8
IV	3	74-02-04	0	6-7
V	4	74-02-10	2	12
VIa	6	74-03-26	1	12
VIb	3	75-01-27	0	7-8
VIIa	4	74-04-30	0	12
VIIb	4	75-01-07	0	7-8
VIIIa	3	74-05-12	1	12
VIIIb	3	75-01-26	0	7-8
IXa	2	74-06-09	0	12
IXb	3	74-12-06	1	7-8
X	3	75-01-21	0	6-7

* distinguished by a suffix where the same sows were observed subsequently with a new litter.

† does not necessarily correspond to litter size at birth.

mortality rate of 26,1%.

Although many yearlings leave the family groups, the ratio of yearlings : adults in September - October provides a measure of yearling survival, or recruitment to the adult class. The sample of 365 warthogs classified from roads and on foot during September and October 1974 (Table 30) comprised 156 juveniles (42,7%), 73 yearlings (20,0%) and 136 adults (37,3%). The difference between recruitment into the yearling class (juvenile survival) and recruitment into the adult class a year later provides an indication of yearling mortality. The juvenile : adult ratio in September - October 1973 was 0,82 and the yearling : adult ratio at this time one year later was 0,54, indicating about 34% mortality of yearlings. However, the September - October 1973 sample was small (23 juveniles, 11 yearlings, 28 adults) and so may have been unrepresentative of population age structure. The September - October 1974 classification is based on a much larger sample, but the disparity between the juvenile : adult ratio of 1,15 (yearling recruitment) and subsequent yearling : adult ratios during 1975 (yearling survival) suggests that yearling mortality during 1975 probably exceeded 50%.

Because of the difficulty of distinguishing older subadults from adults in the field, changes in subadult : adult ratios were considered unreliable for estimating mortality within the 2 - 3 year age class. However, the observed subadult : adult ratio of 0,46 in November - December 1974 was in accord with the yearling : adult ratio of 0,54 for September - October 1974.

Sex ratios of yearling and older warthogs combined (Table 33) showed a preponderance of females, averaging 61,7%, throughout the study. A large proportion of juveniles observed in the field could not be sexed, and the ratio for those classified by sex was not significantly different from parity (Table 34). Sexual parity before birth was shown by foetuses (78 males, 67 females, 22 indeterminate) from 52 sows cropped in the Complex during 1973 and 1974. The sex ratio in yearling warthogs was not significantly different from parity, but a significantly disparate sex ratio in favour of females was found in subadults (i.e. 2 - 3 years) and adults. Sex ratios of adults varied considerably during the year (Table 35); the proportion of adult males was highest during the mating season, but declined subsequently.

Results from warthog capture operations in the Complex during the dry season of 1972 (Table 36) provide sex ratios similar to those obtained from field classifications. In order to check the validity of the finding that females predominate in the adult segment of the population, game guards in HGR were instructed to record the numbers and sexes of warthogs older than the juvenile age class (i.e. 12 months +), seen in the course of their routine foot patrols. During August and September 1974, they classified warthogs

TABLE 33. Sex ratios for warthogs older than 12 months in the Hluhluwe-Corridor-Umfolozi Game Reserve complex during 1973, 1974, and 1975 (pooled data for classifications from roads, on foot and at waterholes).

	Year	Number of warthogs classified	Sex ratio ♂♂:♀♀	χ^2	P
A	1973	153	40,5:59,5	5,50	$<0,02$
B	1974	945	38,4:61,6	50,75	$<0,001$
C	1975	331	36,9:63,1	22,87	$<0,001$
	Overall	1429	38,3:61,7	78,53	$<0,001$

For H_0, A = B = C, χ^2 = 0,62, d.f. = 2, $P>0,70$

TABLE 34. Sex ratios of warthogs in different age classes for all warthogs classified in the Hluhluwe-Corridor-Umfolozi Game Reserve complex between September 1973 and June 1975 (pooled data for classifications from roads, on foot and at waterholes).

Age class	Number classified	Sex ratio ♂♂:♀♀	χ^2	P
Juveniles	471	45,9:54,1	3,23	$>0,05$
Yearlings	449	46,3:53,7	2,43	$>0,10$
Subadults	227	42,7:57,3	4,80	$<0,05$
Adults	711	31,4:68,6	98,77	$<0,001$
Adults + subadults	938	34,1:65,9	94,67	$<0,001$

TABLE 35. Sex ratios of adult + subadult warthogs in the Hluhluwe-Corridor-Umfolozi Game Reserve complex at different times of the year (pooled data for classifications from roads, on foot and at waterholes between September 1973 and June 1975).

	Months	Number classified	Sex ratio ♂♂:♀♀	χ^2	P
A	Nov.-Dec.	143	31,5:68,5	19,64	$<0,001$
B	Jan.-Feb.	162	25,9:74,1	37,56	$<0,001$
C	Mar.-Apr.	158	34,8:65,2	14,58	$<0,001$
D	May -Jun.	160	41,3:58,7	4,90	$<0,05$
E	Jul.-Aug.	129	36,4:63,6	9,50	$<0,01$
F	Sep.-Oct.	186	34,9:65,1	16,86	$<0,001$

For H_0, A = B = C = D = E = F, χ^2 = 9,30, d.f. = 5, $P<0,10$

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sighted according to sex, whenever possible (Table 37). The resultant sample was also characterised by a significant preponderance of females.

TABLE 36. Sex ratios of warthogs (all age classes) captured in Hluhluwe and Umfolozi Game Reserves during the 1972 dry season (unpublished Natal Parks Board records).

Locality	Number of warthogs captured	Sex ratios	χ^2	P
HGR	46	41,3 : 58,7	1,39	$>0{,}20$
UGR	412	41,7 : 58,3	11,22	$<0{,}001$
Overall	458	41,7 : 58,3	12,61	$<0{,}001$

TABLE 37. Sex ratios for warthogs older than 12 months in Hluhluwe Game Reserve, as recorded by game guards on routine foot patrols during August and September 1974.

Month	Number of warthogs classified	Sex ratios	χ^2	P
Aug.	89	27,0 : 73,0	18,89	$<0{,}001$
Sep.	87	34,5 : 65,5	8,38	$<0{,}01$
Overall	176	30,7 : 69,3	26,27	$<0{,}001$

DISCUSSION

DISTRIBUTION AND ABUNDANCE

Published density figures for warthog populations (Table 38) indicate that despite their high reproductive propensity, warthogs seldom attain a commensurately high density, except locally. In Yankari Game Reserve, Nigeria, where the warthog population exceeded that of any other ungulate species, Henshaw (1975) attributed the numerical dominance of warthogs to their high reproductive rate and a scarcity of large predators. While the importance of predation and other population limiting factors may vary, densities of warthogs also reflect their small average group size and lack of large aggregations. The high wet season density of warthogs on Hlaza Hill in HGR may partly be associated with the good cover of palatable grasses, and although probably not exceptional, exceeds the highest local seasonal density of 28 warthogs/km^2 recorded by Cumming (1970, 1975a) in the Sengwa Wildlife Research Area,

TABLE 38. Warthog densities (warthogs per km²) in various localities.

Country	Locality	Warthog density		Source
Nigeria	Yankari Game Reserve	0,59		Henshaw (1979)
Upper Volta	Arli Nat. Park	2,96		Green (1979)
Cameroon	Bouba Ndjida Nat. Park	1,20		van Lavieren & Bosch (1977)
Zaïre	Virunga Nat. Park			
	Rwindi-Rutshuru plain	1,0 - 1,2		Bourlière (1965)
	Semliki plain	1,3		
	Rwindi-Rutshuru plain	2,46		d'Huart (1971
	Garamba Nat. Park	0,13		Bourlière (1965)
Rwanda	Akagera Nat. Park			
	Central area	0,9		Bourlière (1965)
	Various habitats	0,31 - 4,87		Monfort (1974
Uganda	Rwenzori Nat. Park			
	Lightly grazed area	0,04		Petrides & Swank (1965)
	Moderately overgrazed area	0,85		
	Heavily overgrazed areas	2,66 and 7,61		
	Various habitats (4 years)	0,02 - 7,62		Field & Laws (1970)
Kenya	Nairobi Nat. Park			
	Entire park (4 years)	1,35 - 1,99		Foster & Kearney (1967)
	Short grass area	14,5		Bradley (1968)
	Entire park	3,9		
Tanzania	Tarangire Game Reserve (4 years)	0,85 - 1,37		Lamprey (1964)
	Serengeti ecosystem	1,7		Sinclair (1977)
Zambia	Kafue Nat. Park (Ngoma area)	0,23		Dowsett (1966)
Zimbabwe	Henderson Ranch	1,31		Dasmann & Mossman (1962)
	Wankie Nat. Park			
	Main Camp	2,32		
	Robins Camp	13,13		
	Victoria Falls Nat. Park	2,59		
	Sengwa Wildlife Research Area (8 years)	2,32 - 5,13		Cumming (1975a)
	Mopane vlei (over 5 years)	10,62		
	Baikiaea woodland (5 years)	0,27		
	Kariba Basin	3,96		Child (1968)
	Middle Zambezi Valley	April	October	Jarman (1972)
	Riverside	0,2	5,6	
	Mid-floodplain	-	4,8	
	Mopane/floodplain ecotone	0,6	5,7	
	Buffalo Range Ranch (game section)	4,37		Taylor & Walker (1978)
S. Africa	Kruger Nat. Park	0,21		Pienaar (1969)

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Zimbabwe. High densities after the farrowing season could be expected to decline through mortality; shifts in feeding grounds and dispersal induced by social factors may also influence local densities.

Direct comparison of the density figures in Table 38 is difficult as many were derived by different census methods without critical assessment of their accuracy. In areas with dense cover, densities of warthogs may be considerably underestimated, and Child (1968) noted that their aptitude for remaining hidden in small patches of scrub is not generally recognised. The 1979 aerial survey of the Kruger National Park showed an average density of 0,15 warthogs/km^2, but if areas where no warthogs were counted (13 779 km^2) are excluded from the total area sampled (17 096 km^2), an average density of 0,76 warthogs/km^2 is indicated (National Parks Board records). However, these figures could probably be doubled to give reasonable estimates of absolute density, judging by Melton's (1978a) assessment of undercounting bias in aerial censuses conducted over an area of comparable vegetative cover.

For certain types of vegetation, aerial surveying may provide useful information on overall warthog distribution but, as a census technique, it is subject to large counting errors (Melton 1978a, b, van Lavieren & Esser 1980), depending particularly on weather, time of day, and density of the vegetative cover. As Melton (1978b) has indicated, a reappraisal of census techniques is necessary "to find those most suited to produce absolute density estimates and indices of trends in density." Although the data on warthog dispersion in the Complex are inadequate, the area generally provides favourable warthog habitat.

Petrides (1974) reported evidence from Uganda that warthogs became more numerous as overgrazing increased, and suggested that their distribution in Africa is often associated with overgrazed landscapes. In the Complex, areas of short grass cover comprising mainly stoloniferous and leafy species were favoured grazing locations of warthogs, wildebeest, white rhinos and other ungulates, and intensive area selection was particularly noticeable on the fertile bottomlands. While grazing pressure may stimulate grass productivity and encourage stoloniferous grasses, an excessive level and frequency of defoliation becomes detrimental and the hazard of soil erosion is increased.

Although Zululand warthogs cropped some taller grasses up to a height of about 50 cm, their preference was predominantly for short grasses, so that there appears to be considerable justification for Petrides (op. cit.) terming the warthog a "successional species." However, locally overgrazed areas were probably less attractive to warthogs during the dry season, especially where there was only a scanty stubble of dry grass adjoining areas of taller grass with a good supply of rhizomes. Warthogs reduced dietary competition with

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other grazers during the dry season by feeding on grass roots and tiller bases, which they sometimes dug up over wide areas. By exploiting the translocated nutrients in the root systems of perennial grasses, warthogs ameliorate the structural and chemical changes in grass forage that limit the dry season food supply.

Resightings of identifiable warthogs in the Complex (see Chapter 7) suggested that their movements were generally very localised within rather small home ranges throughout the year. During the wet season, when warthogs grazed a wide variety of grasses, the flush of new growth would encourage sedentary habits. The change in feeding strategy and diet during the dry season probably enables warthogs to maintain strong home range fidelity. Apart from daily movements, in some instances possibly over fair distances to water and wallows, there were no indications of extensive seasonal movements, and no concentrations of warthogs were noted on patches of green grass near rivers. In a Zimbabwean warthog population, Cumming (1970, 1975a) found evidence of localised seasonal shifts in feeding grounds and core areas of home ranges, and inferred that habitat heterogeneity was an important requirement, especially in view of limitations placed on movements by warthogs' dependence on holes. Cumming suggests that the apparent familiarity of warthogs with the precise location of suitable holes within their home ranges is an adaptation to the selection pressure of predation. Average home range size may therefore reflect a balance between metabolic requirements and the survival value deriving from familiarity with an area that is not too large.

In the Complex, holes were much more numerous than warthogs in all but a few restricted localities, where dense thickets or rock crevices often provided suitable alternative night-time shelters. The adequate choice of holes allowed warthogs to circulate although some types of holes were used more frequently and over longer periods, which may partly reflect durability in relation to soil type. Overall warthog density during the study period was probably not limited by a shortage of holes. However, the often localised distribution of favoured holes, good feeding areas and wallows may contribute to spatial variations in density of warthogs apparent even within the same general habitat type.

Where surface water was available within or near their home ranges, individual warthogs and family groups probably drank at least once daily during the dry season. High ambient temperatures were also an inducement to frequent wallowing. At the peak of the dry season, no points within the Complex are more than about 8 km from a water source – a distance which, especially when compounded by terrain, could restrict utilisation of some areas by warthogs, unless they were able to obtain succulent forage. Evidence of warthogs digging up and eating small succulent tubers of an unidentified dicotyledonous plant was found in one locality in HGR. It is therefore possible that warthogs with home ranges furthest from water could obtain some of their dry season moisture requirements from certain plant sources. However, the traffic of warthogs to and from certain waterholes during the dry season gave the impression that some warthogs could be travelling several kilometres to drink, which might involve leaving the normal areas of occupancy of their home ranges for a few hours.

Elsewhere in Africa, warthogs have been recorded living in areas seasonally without water. Within the Rukwa Valley, Tanzania, Vesey-Fitzgerald (1960) observed warthogs remaining in areas which contain "absolutely no surface water" during the dry season, while in the outlying parts of Yankari Game Reserve, Nigeria, Henshaw (1979) found that warthogs "remained tied to their home ranges despite the absence of water for much of the year." Evans (1979) found that warthogs in Mwabvi Game Reserve, Malawi, were probably "relatively independent of free water and obtained their water from roots of dicotyledonous plants which they were often observed to dig up in open grassland." In Akagera National Park, Rwanda, Monfort (1974) considered that water had a vital influence on warthog distribution, and warthogs were most numerous near water. Further investigation, especially in regions with a limited hydrographic system, could show that water dependence in the warthog varies with the local availability of succulent plants.

POPULATION STRUCTURE

The estimated 36 - 40% mortality of piglets during their first year may be attributed almost entirely to natural factors, since few juveniles were shot during the study period and poaching was considered negligible. During 1974, the ratios of juveniles/adults did not change significantly between January - February and September - October (Table 30), which suggests that adult mortality proceeded at much the same rate as juvenile mortality. Cumming (1975a) concluded that warthog age and sex ratios derived from field classifications do not provide a very satisfactory basis for estimating some population parameters. In the Complex, realistic estimates of farrowing percentage and litter size at birth were obtained from cropped warthogs (Chapter 5). However, as Cumming (op. cit.) has indicated, the rate of adult mortality may markedly influence estimates of percentage juvenile mortality based on the proportion of juveniles per adult at different times. Thus changes in litter size of family groups based on field classifications also need to be related to mortality of adult sows, particularly where many litters are accompanied by more than one sow (in such sounders the maternal origin of juveniles is often impossible to establish). Since adult warthog mortality in the Complex could not be directly measured, it must be accepted that mean litter size per sow in September - October may be a biased estimate of juvenile survival.

In Nairobi National Park, Kenya, Bradley (1968) was able to monitor litter sizes of 19 identifiable warthog family groups from about two to six weeks after birth until the surviving piglets attained an average age of seven months; mortality during the first six months was estimated as 48,4% of the original cohort of 62 piglets. Although not accounting for some neonatal mortality, observations of litter size within identifiable family groups, commencing as soon as the piglets start appearing from the burrows, probably provide a reasonably accurate measure of juvenile mortality. Because juveniles remain with their mothers until virtually the end of their first year, any piglet which disappears from the rest of the family group can be regarded as most probably dead.

For an expanding warthog population along the Chobe River, Botswana, Child, Roth & Kerr (1968) recorded a mean litter size of 3,40 for piglets up to six weeks old; since the number of juveniles per adult female averaged 1,74 almost a year later, a juvenile mortality rate of 48,8% may be inferred. In Zimbabwe, Child _et al_. (_op. cit_.) reported juvenile mortality exceeding 95% among warthogs marooned on an overcrowded island in Lake Kariba, while in the Nagupande tsetse control area, they estimated at least 25% survival of piglets to the age of 12 months. For a warthog population in the Sengwa Wildlife Research Area, Zimbabwe, Cumming (1975a) estimated annual recruitment of juveniles from farrowing percentages (the proportion of mature sows that had bred) and average litter sizes, recorded at the time when piglets were first observed outside the holes where they were born; juvenile mortality, inferred from the ratios of juveniles : adult female shortly before the subsequent farrowing season, varied between 10% and 64% per annum, and was not correlated with population density.

Clough, cited by Spinage (1972), estimated mortality of 50% in the first year of life in the warthog population he studied in Rwenzori National Park, Uganda. Spinage (_op. cit_.) applied the same factor in constructing a life table derived from a collection of 451 warthog skulls representing natural deaths in Akagera National Park, Rwanda. Monfort (1974) estimated sex and age composition of the warthog population in Akagera National Park from sample counts; his data on survival correspond to a mortality of 74% in juveniles up to 11 months.

Good recruitment of juveniles to the warthog population in the Complex was indicated by the high farrowing percentage and large average litter size at birth. Since mortality of piglets during their first year was only moderate in comparison with reported rates elsewhere, recruitment into the yearling age class was substantial. The large base of juveniles that characterised the population age structure is particularly apparent when the sample classification derived from counts during September and October 1974 is compared (Table 39) with similar data for Akagera National Park, where farrowing occurs from mid-September to mid-November with a peak in October (Monfort 1974).

In comparison with older warthogs, juveniles may be more prone to mortality because of their limited body temperature control (Sowls & Phelps 1966), and there is also some evidence that weaning is a critical period (Roth 1965). Predation undoubtedly may account for a large proportion of juvenile warthog losses, and in Nairobi National Park, Rudnai (1974) considered that many newborn piglets are killed by lions. Mortality patterns in declining warthog populations marooned on islands in Lake Kariba showed that juveniles were most sensitive to environmental stress, while adult survival was last to be affected (Child 1968). Juvenile mortality rates provide a very important indicator of "demographic vigour" (Caughley 1977). Although population trends cannot easily be predicted, an increase in juvenile mortality may herald a downward trend in the rate of population increase (of which it is a major component); with due consideration of habitat conditions, rainfall cycles might also give a useful indication of probable trend in certain regions. The high reproductive rate of warthogs, if not offset by proportionate mortality, would allow rapid population growth during periods of favourable environmental conditions. However, since the average lifespan is probably short compared to the potential longevity, periods of markedly increased juvenile mortality could be expected to produce population fluctuations of considerable amplitude within a relatively short time.

Natural mortality patterns for yearling and older warthogs in the Complex are difficult to assess because the population has been subject to prolonged removal. As part of a game management programme to alleviate habitat degradation, warthog control shooting was started during 1957, initially in HGR, but also including UGR from 1959 onwards. Subsequently, warthog control shooting continued every year, extending also to parts of the Corridor, and supplemented by live capture from 1966 onwards. Warthog control in the Complex reached a peak in 1964 when over 3 000 were shot. During the 16 years from 1957 to 1972, the total number of warthogs removed from the Complex was 27 087, of which only 722 were captured (unpublished Natal Parks Board records). Most of the control shooting has been non-random with respect to sex and age classes. Except for some older juveniles, piglets were not usually shot, and mature sows were normally exempted from at least shortly before the farrowing season probably until well after the piglets had been

TABLE 39. Comparison of warthog age classifications shortly before the farrowing season for populations in Akagera National Park, Rwanda, and the Hluhluwe-Corridor-Umfolozi Game Reserve complex, S.Africa.

Months & year	Locality	Number of warthogs classified	Age composition of sample (%)			Author
			Juveniles	Yearlings	Adults	
Sep. 1969	Akagera	191	20,7	18,3	61,0	Monfort (1974)
Sep.-Oct. 1974	Complex	365	42,7	20,0	37,3	Mason (present study)

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weaned. Old warthogs with fine tusks were also generally excluded from cropping.

Control shooting during the study period was certainly not random, even excluding that proportion of sex and age classes deliberately collected for investigation of growth, reproduction and other parameters. Since the skulls collected from cropping were largely unrepresentative of the sex and age structure prevailing in the population, they cannot be used to estimate age class frequencies (based on dentition criteria) and to construct a life table. Skulls were collected from less than half of the total number of warthogs cropped in the Complex during the study period. The dentition of these skulls was later examined to check age classes assigned in the field to the freshly shot warthogs. Adult warthogs were further classified into four age classes using criteria of tooth attrition, corroborated wherever possible by incremental layering in dental cementum (Chapter 2).

The sex and age composition of the 385 shot warthogs from which skulls were collected (Table 40) suggests that yearling, subadult and young adult warthogs were bearing the brunt of cropping. Of 366 warthogs at least one year old, 26,0% were yearlings, and 82,2% were between one and five years old. For cropped warthogs at least two years old (n = 271), 35,1% were subadults and 27,7% were estimated 3 - 4 years old. The large proportion of yearlings in the cropped sample tends to support indications from field classifications of live warthogs that yearlings suffered considerable annual mortality, probably exceeding that of juveniles. However, the data do not allow a distinction to be drawn between mortality arising from natural factors and mortality from control shooting. Bradley's (1968) data on age class structure of the warthog population in Nairobi National Park, where mortality patterns were not complicated by cropping, suggest disproportionately higher losses within the yearling and subadult age classes than in subsequent year classes. Natural mortality among yearling warthogs is undoubtedly influenced by social factors which result in dispersal of yearlings away from their mothers, although bonds between an adult female and usually one of her female offspring may persist.

The selective emphasis inherent in control shooting in the Complex has probably been fairly consistent in the past, although earlier records of warthogs removed were largely unclassified according to sex and age class. Thus the extent to which control shooting may have influenced warthog population structure remains uncertain. Besides favouring warthogs in the juvenile and old age categories, control shooting has been male-biased, a situation which Attwell (1978) also reported for wildebeest culling in the Complex. During 1967 when sexes were recorded for 600 out of a total of 692 warthogs shot in

TABLE 40. Sex and age composition of shot warthogs from which skulls were collected during cropping in the Hluhluwe-Corridor-Umfolozi Game Reserve complex between June 1973 and June 1975.

Age class	Number of warthogs	Sex composition		% of total
		Males	Females	
Juvenile	19*	8	7	4,9
Yearling	95	51	44	24,7
Subadult	95	50	45	24,7
3-4 years	75	32	43	19,5
4-5 years	36	15	21	9,4
5-10 years	54	20	34	14,0
10 years +	11	7	4	2,9
Total	385	183	198	100,1

* including 4 unsexed specimens.

UGR and the southern Corridor, the ratio of males to females was 340 : 260, which was significantly different from parity (χ^2 = 10,7, $p<0,01$).

Although females comprised 58,0% of adult warthogs (n = 176) from which skulls were collected during the study period (Table 40), this ratio has been weighted by some selective sampling associated with research objectives. In fact the overall sex ratio of warthogs culled in the Complex during the study years (Table 41) was significantly biased (χ^2 = 110,7, $p<0,001$) towards more males, which comprised 64,5% of the total number classified by sex (n = 1 325). Excluding three months during 1973 when warthogs captured (n = 61) were not classified by sex, the capture records for 1973 and 1974 (Table 41) indicate a preponderance of females in the live population, which accords with results from field classifications; of the 278 captured warthogs classified by sex, females significantly outnumbered males (χ^2 = 23,0, $p<0,001$) by 28,8%.

Selective culling has probably resulted in considerable depression of the male segment of the warthog population in the Complex, although there are indications that differential mortality is a natural phenomenon in warthogs. Besides considerations related to stage of the breeding cycle and development of the young, further selection for mature males probably arises because they are larger than females and so more desirable for ration distribution to game guard camps. Cumming (1970) has argued that African hunters engaged in control operations are more likely to select an adult male from a sounder with less conspicuous members, and also select more males because they are more solitary than females and usually less wary, and so are more readily shot. This could

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TABLE 41. Numbers and sexes of warthogs removed from the Hluhluwe-Corridor-Umfolozi Game Reserve complex by control shooting and live capture during 1973, 1974 and 1975.

YEAR	CONTROL SHOOTING Males	Females	Unsexed	Sub-total	LIVE CAPTURE Males	Females	Unsexed	Sub-total	TOTAL WARTHOGS REMOVED
1973	347	171	11	529	77	130	61	268	797
1974	434	268	0	702	22	49	0	71	773
1975*	73	32	0	105	0	0	0	0	105
1973-1975	854	471	11	1336	99	179	61	339	1675

* removal figures recorded to the end of May.

explain discrepancies between warthog sex ratio data from field observations and shot samples, e.g. for yearling and older warthogs on Henderson Ranch, Zimbabwe, Dasmann & Mossman (1962) obtained a sex ratio of 42,2% males : 57,8% females (n = 45) from field counts compared with 51,9% males : 48,1% females (n = 27) in a shot sample.

Notwithstanding a sex ratio of unity at birth, Brooks (1975) found that differential mortality characteristically operates against males in impala. Evidence of disproportionate mortality of males has also been reported in springbok (Crowe & Liversidge 1977), and Brooks (op. cit.) considered that depression of the sex ratio may result from differential responses to various socially and environmentally induced stress factors. After recording a sex ratio near unity at birth for warthogs in Nairobi National Park, Bradley (1968) found a change in the sex ratio in favour of females among yearlings and subadults, which he attributed to relatively higher mortality among males after leaving their mothers.

Records of adult warthog sex ratios from other areas of Africa (Table 42) suggest that a preponderance of females is commonly a natural condition. As the sex ratio at birth for warthogs in the Complex was close to parity and there were no indications of differential dispersion affecting sex ratios observed in the field, it is thus unlikely that the disparate sex ratio of subadult and adult warthogs results solely from male-biased culling.

In respect of field classifications, Child, Roth & Kerr (1968) suggest that there may be an inherent bias against observing single adult males, whereas adult females could be over-represented because family units are more conspicuous. They considered that sex ratios of adults normally approach parity, and further suggested that warthogs are monogamous (see also Frädrich 1974), which implies that a 1 : 1 sex ratio amongst adults should be observed in the field during the mating season. This was not supported by Cumming (1975a) who found a preponderance of females during the mating season in a warthog population undisturbed by culling. Evidence from the Complex (Table 35) also showed a significant preponderance of females at this time, although courting males may be more conspicuous because of their behaviour patterns, and there were no indications of monogamous pairing. The marked decline in numbers of subadult and adult males seen after the mating season was also recorded by Cumming (1975a) in Zimbabwe, and suggests increased mortality during the dry season. Moreover, there are grounds for suspecting that natural differential mortality is an important cause of the decrease in the proportion of males during and after the 2 - 3 year age interval (Table 34). Social factors that may predispose males to higher mortality are examined first.

Family units are disrupted during or shortly before the farrowing season

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TABLE 42. Comparative sex ratios of adult warthogs from field classifications in various regions.

Country	Locality	Age categorisation	Sex ratio ♂♂:♀♀	Source
Zaîre	Virunga National Park	Adult	34,2:65,8	Bourlière (1965)
	Virunga National Park	24 months+(n=482)	51,0:49,0	d'Huart (1971)
Rwanda	Akagera National Park	Adult (n=178)	46,6:53,4	Monfort (1972, 1974)
Kenya	Nairobi National Park	Adult (n=254)	31,5:68,5	Foster & Kearney (1967)
	Nairobi National Park	24 months+(n=59)	44,1:55,9*	Bradley (1968)
Botswana	Chobe Game Reserve	24 months+(n=272)	36,4:63,6	Child, Roth & Kerr (1968)
Zimbabwe	Sengwa Wildlife Research Area	24 months+(n=7892)	40,2:59,8	Cumming (1975)
	Sengwa Wildlife Research Area	36 months+(n=5018)	33,8:66,2	Cumming (1975)
S.Africa	Hluhluwe-Corridor-Umfolozi Game Reserve complex	24 months+(n=938)	34,1:65,9	Mason (present study)
	Hluhluwe-Corridor-Umfolozi Game Reserve complex	36 months+(n=711)	31,4:68,6	Mason (present study)

* recorded just after the farrowing season.

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when the pregnant sows of matriarchal sounders desert their young of the previous year. The one year old siblings of these litters generally remain together, forming transient heterosexual sounders, but one or more (particularly females) may rejoin their mothers about one to two months after the latter have farrowed. Mother-daughter associations, originating when usually one yearling female rejoins the mother and her most recent litter, commonly persist through at least the subsequent mating and farrowing seasons. Some sounders which contain two or three females, each of which has bred in the same season, thus represent extended families. Bonds between females and their male offspring are less durable and the minority that rejoin their mothers after farrowing generally leave during the subsequent mating season, when they are about 18 months old and have just attained sexual maturity. Limited evidence indicated that a few males may remain loosely attached to matriarchal sounders even longer, although probably not beyond about 30 month of age. However, most males leave their mothers as yearlings and temporarily accompany siblings or join a bachelor group. Most yearling females become pregnant at about 18 months, but males probably contribute little to population recruitment until they are about 30 months old, and even then may be less successful in competition with older males for mating priority.

Survival of females might be enhanced because relatively more females remain attached to their mothers for 12 to 18 months and longer. After leaving the matriarchal sounders, yearling males would have to find alternative holes to spend the night in and consequently might incur higher mortality. According to Bradley (1968), male warthogs spend much of their second year with either a sibling or an adult male and seem likely to suffer relatively high mortality during their "first solitary wandering phase" away from their mothers. Cumming's (1975a) data on home range behaviour suggest that yearling and subadult males form the main dispersive element of a warthog population. However, direct evidence that natural sex-linked mortality occurs initially among yearlings is lacking. In the Complex, solitary adult and subadult males were an important social class but the incidence of solitary yearling males was low, which concurs with the findings of Cumming (op. cit.) for an undisturbed warthog population in Zimbabwe. From about two years of age, males are often solitary and although they may temporarily associate with other males during the day, they apparently tend to spend the night alone (see also Bradley 1968). Notwithstanding uncertainty about social and environmental influences on survival in the yearling class, natural differential mortality probably becomes particularly important from about two years of age onwards because of the response of subadult and adult males to the onset of night.

In the Complex, subadult and adult males generally retired to holes or other night-time shelters considerably later than most family groups and were sometimes abroad well after dark. Matriarchal sounders are probably more dependent on holes than subadult and adult males, which have been found at night lying up alone in dense grass and in thickets. One adult male that was followed after dark bedded down in long grass close to a hole containing a mature sow that was probably near oestrus. Such behaviour may render male warthogs more susceptible to predation. In Zimbabwe, Cumming (1975a) found some adult male warthogs spending the night in slight depressions and in dense grass and he recorded a lion killing one in just such a situation after dark. Factors which predispose males of many prey species to heavier lion predation have been outlined by Bertram (1978). Male warthogs preoccupied in agonistic encounters or fighting, or possibly wearied after the competition for females during the mating season, may be particularly vulnerable to predation. Whatever the reasons for the marked dry season decline in sightings of males, Cumming (1975a) suggests that warthogs generally may be more susceptible to predation during the dry season when they are forced into medium and tall perennial grasslands to feed on rhizomes. In such cover, the short stature of warthogs would be a handicap in keeping watch for predators.

Mitchell, Shenton & Uys (1965) found that lions killed more male than female warthogs (24 ♂♂ : 7 ♀♀, $\chi^2 = 9{,}32$, $P < 0{,}01$) in the Kafue National Park, Zambia. However, records of warthogs killed by lions in the Kruger National Park, S. Africa, showed no specific sexual bias (Pienaar 1969). No significant selection by lions for male warthogs was evident in kill records from the Sengwa Wildlife Research Area, Zimbabwe (Cumming 1975a). Nevertheless, as Cumming (op. cit.) has noted, existing records are inadequate and the possibility that a disparate sex ratio in warthogs may arise from greater predation on males requires further investigation. Data on warthog sex ratios at birth are also inadequate (Chapter 5) and the possibility cannot be excluded that sex ratios at birth might be related to environmental conditions and population density.

Although the sample classification of warthogs at waterholes also indicated a sex ratio favouring females in the adult age class, the disparity was considerably less marked than for the data from road and foot sampling. The reliability of the waterhole records may be influenced by small sample size, and it is not known whether the frequency of drinking by adult male and female warthogs is the same. Nevertheless, the results of a survey of game utilising Bube waterhole in MGR during April 1965 also indicated a preponderance of female warthogs; excluding juveniles, the sex ratio for 155 warthogs recorded at this waterhole was 26,5% males : 73,5% females (University of

Natal Wildlife Society Project Report : Newsletter No. 4, 1965).

Factors governing warthog dispersion and numbers in the Complex require more intensive investigation, although evidence reported by Cumming (1975a) for a Zimbabwean warthog population suggests that predation and density dependent changes in fecundity are important in natural population regulation. Cumming (op. cit.) found that farrowing percentage was inversely related to population density during the preceding mating season, but concluded that predation, "probably acting in a density independent manner, was a major limiting factor and largely responsible for observed fluctuations in warthog population density." In the Complex however, the dry season food supply, particularly during drought years, could well overshadow the undoubtedly significant role of predation in limiting warthog numbers. Baker (1978) found that animals without seasonal migrations showed considerable mortality through starvation at the end of the dry season, and in most species this mortality was greater than that due to predation.

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CHAPTER 7

ECOLOGY, SOCIAL ORGANISATION AND BEHAVIOUR

INTRODUCTION

Leuthold (1977) stated that social organisation in a species results from all social interactions and spatial relations among members of a population. In reviewing the social systems of ungulates, Estes (1974), Geist (1974) and Jarman (1974) noted a relationship between the type of social organisation and ecological parameters, and attempted to take both ecological and ethological observations into account when formulating hypotheses. Owen-Smith (1975) emphasised the adaptive significance of behavioural strategies that promote individual survival and mating success, so that the genetic basis of such behaviour tends to prevail in the population; he pointed out that for higher mammals in particular, "tactics can be modified in relation to prevailing ecological circumstances, resulting in a variability of expression both in terms of behaviour and social organization that may at first appear confusing." Social organisation may undergo pronounced cyclic changes in seasonally reproducing populations, reflecting the influence of local environmental conditions.

Costs and gains are inherent in the adoption of particular behavioural and social strategies, which may be a compromise between different selection pressures. Comparative studies of warthogs in different parts of their environmental range might highlight some of the constraints that have influenced their behaviour, social system and ecological adaptations. Several studies have contributed to a better understanding of the functional relationships between behaviour and ecology of warthogs, but as yet there is no consensus concerning their social organisation. As regards the other two African suids, the position of the bushpig in the spectrum of ungulate social organisation requires clarification, but considerable information is available on giant forest hog social structure and behaviour.

The first field studies on the behaviour and ecology of warthogs were carried out in West Africa (Bigourdan 1948, Guiraud 1948). More recently, Henshaw (1975, 1979) described basic features of warthog ecology in Nigeria, while in the Virunga National Park, Zaïre, d'Huart (1971a, b, 1975, 1976, 1978) studied aspects of the ecology, biology and behaviour of warthogs and giant forest hogs, and in neigbouring Rwanda, Monfort (1974) examined spatial distribution and population structure of warthogs in the Akagera National Park.

In East Africa, Geigy (1955) made observations on warthog behaviour, social groupings and ecology in the Ulanga district, Tanzania, while investigating the vectors of relapsing fever, and Lamprey (1963) gathered information on habitat preferences in Tarangire Game Reserve. Subsequently, more detailed behavioural studies have been made in Nairobi National Park by Frädrich (1965, 1967, 1974) and Bradley (1968), while in Rwenzori National Park in Uganda, Clough (1969) studied warthog reproduction and noted a few features of their ecology, Field (1968, 1970, 1972) studied feeding preferences, and Clough & Hassam (1970) recorded daily activity patterns.

Evans (1979) recorded the broad pattern of habitat utilisation by warthogs in Mwabvi Game Reserve, Malawi. Further south, Simpson (1964) made limited observations on warthog behaviour in Wankie National Park, and Child (1968) and Jarman (1972) included behavioural and ecological aspects during their studies of large mammal populations in the Zambezi Valley. The long term study by Cumming (1970, 1971, 1975a) in the Sengwa area of Zimbabwe is the most comprehensive account of warthog ecology and behaviour to date, confirming and amplifying many earlier observations, particularly those of Frädrich (1965) and Bradley (1968). Cumming examined population structure and distribution, activity and movement patterns, social behaviour and communication as well as diet and mode of feeding.

Kingdon (1979) has reviewed information and made perceptive observations on the behavioural ecology of the African suids and has made a significant contribution to the interpretation of their functional and comparative anatomy in terms of ecological adaptation.

Information on behaviour in relation to environmental factors is pertinent to understanding warthog social organisation and population dispersion in terms of density of distribution in various habitats. The present study was concerned with basic features of the behavioural ecology of Zululand warthogs, as part of a wider investigation, with a view to providing a better policy for management and a basis for future research.

METHODS

CAPTURE AND MARKING OF WARTHOGS

Since the possibility of recognising individual animals greatly facilitates study of movements and social relationships, an effort was made to capture and mark some warthogs in HGR. During 1973, several attempts were made to capture warthogs at night by placing nets over or in front of the holes in which they sleep, and then inducing them to bolt out by stamping over the chamber of the hole, poking a long flexible stick into the hole or throwing earth clods inside. Capture was also attempted on wet rainy mornings, when warthogs remain in their holes. Due to problems experienced with this technique, warthogs were subsequently captured during daytime with the assistance of the Game Capture Unit of the Natal Parks Board, using drive nets.

Normally, live capture of warthogs from areas within the Complex scheduled for game removal is undertaken during the dry season at waterholes. Drive nets are set up near the pan and warthogs arriving to drink and wallow are chased into the nets by members of the capture team, dispersed in hiding near the nets. When nets are set away from pans for capture and removal of other game, some warthogs may also be caught. During the wet season, the widespread distribution of water in small pools throughout the Complex renders capture at waterholes not worthwhile, since warthogs disperse to the many watering points.

The warthogs that were marked for later identification were caught during the wet season by driving them into a long line of nets, erected in several successive localities. This exercise was far less productive in terms of warthogs caught per given expenditure of time than if it had been conducted at waterholes during the dry season. Nevertheless, nine warthogs were caught and marked with colour-coded ear tags in both ears (Plate 4j) between 73-10-20 and 73-11-14, in the north-east of HGR. Rotating plastic ear tags were used with paired strips (approximately 3 or 4 x 8 cm) of woven nylon ribbon ("Sterkolite") attached. Ages of the nine warthogs (both sexes) marked were estimated as about 12 months (two individuals), about 24 months (four individuals) and over three years (three individuals). Three of the females marked were judged to be in an advanced state of pregnancy.

INDIVIDUAL RECOGNITION

Individuals could not easily be distinguished by facial features and the technique could only be used on a small scale in localised areas. Apart from thick vegetation which restricted visibility, warthogs in many areas were too nervous to allow for close and prolonged observation. Although Bradley (1968) could recognise almost all the warthogs in an approximately 32 km^2 study area within Nairobi National Park, using photographs showing the pattern of ear notches, tusk length and shape, and wart shape and angle, this was facilitated by the warthogs using a much smaller short grass area within his study area as their primary feeding grounds.

Except in rare cases, for example an adult female with double upper left canines, most of the recognition features were not outstanding, but were useful within the limited areas where known individuals were normally seen. During the last year of the study several free-ranging warthogs on Mpila Hill in UGR became habituated to my approaching them fairly closely on foot. Towards the end of the study two family units in particular, within whose home ranges my caravan was parked, were readily accompanied by myself in the field. Provided reasonable care was taken, they were little influenced by my presence.

Such warthogs provided valuable insight into basic daily patterns of activity, feeding style, behaviour, movements and use of holes. The locations of many of the warthog holes on Mpila Hill became known and certain holes were visited periodically to investigate their use.

BEHAVIOURAL ECOLOGY

Field observations on food selection, use of holes, daily activity, social aggregations and behaviour were made throughout the study period, from a vehicle and on foot (see Chapter 1). Some information on warthog diet, disease and parasites was obtained from culled specimens.

RESULTS AND DISCUSSION

CAPTURE AND MARKING OF WARTHOGS

During nocturnal capture attempts, several areas with a dense distribution of likely holes were visited and hole after hole was tried, but without success. This indicated that there were many more holes than warthogs to use them, and emphasised the need to locate holes being utilised. A further prerequisite was to observe warthogs enter particular holes for the night.

Even when a net is placed over an occupied hole, there is a possibility of the warthogs remaining inside, especially if the hole is deep, which happened on one occasion when two sows and five piglets could not be induced to flee despite provocation for 20 min. Where holes occur close together, they should all be netted or blocked in case they are connected or the one in use has been wrongly identified. Cumming (1970, 1975b) advises blocking of supernumerary entrances and possible exits prior to capture in such instances. Two capture attempts on rainy days narrowly failed when, in one instance, four warthogs evacuated a hole shortly before the net could be positioned, while on the other occasion, two sows escaped underneath a small hoop net held at the mouth of their burrow.

Cumming (1970, 1975a, b) also found that attempts to catch, even at well-used holes, without seeing warthogs enter invariably failed, largely because warthogs used a number of holes and seldom used the same hole for many consecutive nights. Attempts to capture warthogs at their holes were relatively few and although unsuccessful, perseverance with this method along the lines described by Cumming would undoubtedly have yielded better results, especially after the experience gained of warthog behaviour in relation to holes.

Apart from a small hoop net, a length of drive net was used in most of the capture attempts, but the tunnel-net design of Cumming (1975b) appears eminently more suitable. In 125 captures reported by Cumming (_op. cit._), only seven warthogs were left in holes, but periods spent waiting for warthogs to emerge when capture was successful varied from a few minutes to more than 24 h, and attempts to flush them out were not always successful.

Several cases of spinal injury to warthogs resulting from incorrect handling have occurred during capture and removal operations in the Complex. This is apparently a consequence of holding a captured warthog by the hind feet and lifting the hindquarters off the ground, so that the animal's mass is largely supported by the forelimbs. One person may then propel the warthog slowly forwards for a short distance in wheel-barrow fashion, without any danger from the warthog's tusks. Lifting the warthog's hindlegs too rapidly or too high could dislocate or even break the vertebral column, through this being strained upwards. In February 1974 an adult male that had been troublesome at Godeni Camp in HGR was captured for translocation to another part of the reserve, but was first brought to the author for marking. This boar had been handled in the manner described and, unknown at the time, the spine was broken in two places (Plate 10a). Upon being unbound and released, the warthog was unable to use the hindlimbs and so was shot.

The ear tags were not conspicuous in the field, particularly in tall grass and dense bush, and the colours tended to become obscured by dirt or mud. One tag, in the left ear of an adult female, was known to have torn out; this was first noticed 43 days after she was marked. Only 11 resightings of tagged warthogs were recorded, the last on 74-01-28, and involving only three different individuals, with one, three and seven resightings respectively. All resightings were well within a kilometre of the site of marking.

Child (1968) mentioned the ease with which warthogs lost ear tags, while Cumming (1970) also recorded a high loss of ear tags and found that conventionally marked warthogs in his study area were seldom seen during the first 2½ years of his study. However, radio tracking as done by Cumming was not feasible during the Zululand work.

FOOD SELECTION

Warthogs in the Complex are essentially grazers and favour areas with lawn-like swards, which they help to maintain through their close cropping. Although short grasses with a high ratio of leaf to stem are preferred, warthogs do sometimes feed in areas of medium to tall grass (as high as or higher than an adult warthog) but, apart from the seed-rich inflorescences of some tall grasses, the parts selected are usually within about 50 cm of ground level.

Stomach samples covering every month of the year were collected during cropping in the Complex from over 200 warthogs of both sexes, mostly older

PLATE 10

(a) Partially skinned back of an adult warthog boar captured in HGR showing locations (arrowed) where the spine had been broken apparently as a consequence of lifting the hind feet off the ground to propel the animal in wheel-barrow fashion.

(b) Yearling male warthog aged about 12 months, chewing on a warthog skull. (UGR, 74-11-10).

(c) Alluvial terrace of White Umfolozi River showing large tract churned up by warthogs foraging for grass rhizomes. (Mndindini area, UGR, 74-10-05).

(d) Shallow excavations scooped with the snout by a warthog foraging for grass rhizomes in fairly hard soil. (UGR, 74-06-10).

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than 12 months. Quantitative analyses of these samples according to plant species and parts have not been done. However, qualitative visual examination of stomach contents at the time of collection indicated that grasses form by far the major part of warthogs' diet. Direct observation of live animals supported this conclusion and warthogs were never seen browsing off the leaves and twigs of shrubs or trees, and nor were such items observed in stomach contents.

When feeding warthogs were shot, freshly ingested material was sometimes collected from their mouths and several grass species were identified from large pieces of leaf blades, sheaths, stolons, rhizomes or inflorescences. Some grass species observed eaten by warthogs or identified from mouths and stomachs are listed in Table 43.

The grasses listed in Table 43 do not represent the full range of species utilised by warthogs in the Complex, since they are based on limited identifications from a few conspicuous parts of easily recognisable grass species found in the mouths or stomachs of cropped animals, and occasional identifications from direct observation of plants eaten. Microscopic examination of fragments in stomach samples should at least double the number of grass species in this list. Nevertheless, observations suggest that favoured species include *Urochloa mosambicensis*, *Panicum maximum*, *Panicum coloratum*, *Chloris virgata*, *Digitaria argyrograpta*, *Sporobolus nitens*, *Sporobolus smutsii*, *Cynodon dactylon* and *Dactyloctenium australe*, most of which are short tufted or stoloniferous mat-forming grasses. The stoloniferous *Dactyloctenium australe* is mainly restricted to shaded woodlands where it often forms fairly extensive lawns, and was readily grazed during both the wet and dry seasons. The short, largely stoloniferous lawns on riverine alluvia, where *Cynodon dactylon* is the dominant grass of open and less heavily shaded parts, were extensively utilised by warthogs during the dry season.

Warthogs in UGR were observed uprooting and eating the swollen basal stems and leaves of the small sedge *Cyperus obtusiflorus* during both the wet and dry seasons. Fallen fig fruits (mainly *Ficus sycomorus*) from trees growing along the banks of rivers and streams were readily eaten and about a dozen warthog stomachs examined during summer and autumn contained large quantities. Approximately half the stomach fill (4,8 kg wet mass) of one adult male was estimated to comprise fig fruits. Fallen marula (*Sclerocarya caffra*) fruits were also eaten and even their hard woody kernels were swallowed after being cracked by the warthog's molar teeth into smallish fragments.

One observation (August 1974) of warthogs eating the fallen fruits of *Ziziphus mucronata* was recorded in UGR. Small numbers of fruits of *Euclea schimperi* were noted in a few stomachs from HGR and one stomach from UGR

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TABLE 43. Records of grass species eaten by warthogs in the Hluhluwe-Corridor-Umfolozi Game Reserve complex, derived from examination of post-mortem material and direct observation of feeding (May 1973-June 1975).

	SOURCE OF RECORD		SEASON IN WHICH RECORDED *	
GRASS SPECIES	Culled hogs	Direct observation	Wet Season	Dry Season
Dactyloctenium australe	X	X	X	X
Chloris virgata	X	X	X	X
Chloris gayana		X		X
Panicum maximum	X	X	X	
Panicum coloratum		X	X	X
Urochloa mosambicensis	X	X	X	X
Cynodon dactylon	X	X	X	X
Sporobolus nitens	X	X	X	X
Sporobolos smutsii		X	X	X
Sporobolus pyramidalis		X		X
Digitaria argyrograpta	X	X	X	X
Digitaria eriantha		X		X
Setaria sphacelata		X	X	X
Themeda triandra	X	X	X	X
Eragrostis superba		X		X
Rhynchelytrum repens		X	X	
Bothriochloa insculpta	X			X
Paspalum sp.		X	X	
Paspalidium sp.		X	X	X
Aristida sp.		X		X

* Wet season = October-March
Dry season = April-September

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contained a few seeds from Berchemia zeyheri fruits. On Ntabamhlophe Hill in HGR an area was investigated where warthogs had been reported digging up and eating small succulent tubers during summer; on the soft sandy soil of the Acacia burkei woodland were numerous shallow excavations, attributed to warthogs digging with their snouts. Several tubers or portions of them were found in the excavations and an unsuccessful attempt was made to grow some for later identification. The tubers apparently belonged to a rambling dicotyledonous plant, but the aerial portions of the single plant located were dead and withered. During the 1981 dry season in the Kruger National Park, warthogs were observed eating the swollen rootstocks of the dicotyledonous weeds Brayulinea densa and Alternanthera pungens, which they dug up with their snouts after scraping aside the spreading, prostrate stems. Apart from fig and, to a lesser extent, marula fruits, which compared to grasses are of restricted availability both temporally and spatially, preliminary visual examination of stomach contents suggested that dicotyledonous material was rare in the diet of Zululand warthogs.

A few additional plants recorded eaten by warthogs in HGR (Hitchins 1968b) are listed as follows, together with the portions ingested: Digitaria swazilandensis (culms, leaves), Phragmites communis (young shoots), Malvastrum sp. (stem, leaves), Sida rhombifolia (stem, leaves), Strychnos spinosa (fruit). Unusual food items eaten by warthogs in the Complex and reported by staff in Natal Parks Board records (unpublished) include portions of live barbel (Clarias sp.) that were stranded in a drying-up pan, fresh white rhino dung, and shards of bones (a large male was seen crunching an approximately 9 cm long portion of impala metacarpus with his molar teeth, and swallowing the pieces).

During the present study osteophagia was observed on about a dozen occasions when warthogs, particularly juveniles, chewed skulls (Plate 10b) and fragments of bones. No pieces of bone were noticed in any of the stomachs examined. Field (1970) recorded warthogs in Uganda engaging in both osteophagia and geophagia, but the latter was not observed in Zululand. However, Henshaw & Ayeni (1971) and Henshaw (1975) reported warthogs in Nigeria frequently visiting natural mineral licks where they avidly ate the soil, biting the material with their incisors and feeding without pause normally for 5 - 15 min and occasionally for longer than 25 min. Although a high frequency of osteophagia and geophagia may indicate deficiencies or imbalances of nutritional minerals (particularly phosphorus and calcium) in the diet (Langman 1978), Cumming (1970, 1975a) suggests that the behaviour of chewing bones may, in young warthogs, be a function of "teething". Bradley (1968) reported warthogs chewing on the ends of bones, sticks and even stones, and he observed geophagia on many occasions.

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Reports indicate that warthogs may eat a range of unusual items. In West Africa, Bigourdan (1948) recorded that the diet of warthogs comprised grass, roots (especially of aquatic plants), fruits (especially wild figs), and occasionally eggs, snakes, lizards, insects and even carrion. Field (1970) observed coprophagia or dung eating, in tame warthogs, mostly involving warthog dung, although that of buffalo, elephant, waterbuck and francolin (Pternistis sp.) was also taken, and the younger warthogs readily ate dead rats. On a single occasion witnessed by Bradley (1968), a group of warthogs spent eight minutes eating rhino dung. Monfort (1974) also mentions the occurrence of coprophagia, especially in old males. Geigy (1955) observed juvenile warthogs eating the rotten remains of a bird, and a warthog in the Luangwa Valley, Zambia, was observed drinking blood from a freshly killed elephant (Dowsett 1969). In the Kruger National Park, a warthog boar was observed devouring a hare that had been recently killed on a road (unpublished National Parks Board records).

Flesh and carrion may be eaten occasionally by warthogs in Zululand, but are almost certainly insignificant in the diet compared to the year-round importance of grass. Cumming (1970, 1975a) concluded that the diet of warthogs is very largely herbivorous rather than omnivorous, although both he and Child (1968) confirmed that warthogs occasionally eat meat and animal remains. However, Child (op. cit.) found that even when warthogs were starving on islands in Lake Kariba, they made little, if any, use of the abundant carrion available, but relied on grass. In South West Africa, warthogs on a farm in the area between Outjo, Kamanjab and Khorixas commonly come to a site where carcasses of domestic stock found in the veld are deposited, and feed on the carcasses (Jordaan pers. comm.). Although this could be a form of pica behaviour reflecting nutritional deficiencies, Geigy (1955) states that warthogs readily eat carrion. In Wankie National Park, Zimbabwe, Wilson (1975b) reported an observation of a large male warthog which chased three cheetahs off an impala carcass and proceeded to feed on the carcass; he also recorded warthogs coming to feed on the flesh and intestines of cropped impala. Warthogs thus undoubtedly retain some of the suid disposition to feed from carcasses, even if infrequently.

Numerous studies confirm the importance of graminaceous material in the diet of warthogs. Based on 291 records of plants observed being eaten by warthogs in Tarangire Game Reserve, Tanzania, selection for grasses was 82%, and the range of plants involved 17 species of grasses, three species of sedges, five species of herbs and woody herbs, two species of shrubs and woody ramblers, and the fruit of one species of tree (Lamprey 1963). In Nairobi National Park, observation of feeding warthogs indicated that they

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are predominantly grazers (Frädrich 1965, Bradley 1968). Quantitative studies by Field (1968, 1970, 1972) involving observation of tame warthogs and analysis of stomach samples, confirmed that grasses were by far the major component of the diet of warthogs in Rwenzori National Park, Uganda; large monospecific mats of Sporobolus homblei were particularly favoured as grazing sites.

Feeding records, predominantly from tame animals, indicated that warthogs in the Sengwa area of Zimbabwe feed mainly on the foliage and rhizomes of grasses, and regularly dig below the surface during the dry season to obtain rhizomes (Cumming 1970, 1975a). Child (1968) also presented evidence from Zimbabwe that grasses comprise the bulk of warthog food, and Wilson (1975b) identified 12 species of grasses eaten by warthogs in Wankie National Park. Smithers (1971) records that warthogs in Botswana feed mainly on grasses and the underground rhizomes of grasses, and are partial to freshly sprouting grass on burnt patches. In the Timbavati Private Nature Reserve, eastern Transvaal, Hirst (1975) listed eight species of grasses observed to be eaten by warthogs, which generally preferred short-grass savanna in this locality.

Henshaw (1975, 1979) observed that food selection of warthogs in Nigeria varied seasonally and reflected the habitat types where their home ranges were located; although grasses and grass rhizomes were the primary foods, warthogs sought out the roots of Cochlospermum tinctorum throughout the year and warthogs living on floodplains also selected sedges. Vogel (1978) assessed dietary habits of southern African ungulates from the carbon isotopic composition of their bone collagen, and concluded that warthogs are predominantly grazers. This result was corroborated by findings in Kenya, where analysis of carbon isotopic ratios in warthog faecal samples indicated that warthogs selected between 88 and 95% of their vegetative diet from plants belonging to the C_4 photosynthetic system, i.e. grasses (Tieszen & Imbamba 1980).

Seasonal trends in diet

Visual examination of stomach contents and observation of feeding warthogs suggested a definite seasonal variation in the proportions of different grass components selected by warthogs in the Complex. During the wet season the bulk of material in the stomachs apparently comprised grass leaf blades and sheaths, with portions of stolons and stems occurring as a smaller fraction. Large numbers of grass seeds were evident in some stomachs collected during January and February, but constituted a relatively minor fraction of stomach fill; warthogs were observed to ingest seed-rich inflorescences at this time, and the species involved include Chloris virgata, Urochloa mosambicensis,