Reproduction in the male warthog *Phacochoerus aethiopicus* from Zululand, South Africa

D.R. Mason

Mammal Research Institute, University of Pretoria, Pretoria

Parameters of male sexual function in warthogs *Phacochoerus aethiopicus* were investigated using material from cropping operations in Zululand. Based on the occurrence of spermatozoa and elongating spermatids in the seminiferous tubules, attainment of sexual maturity was recorded at about 17 to 18 months of age when minimum mass of paired testes is about 25 g and body mass about 45 kg. Minimum values recorded for mean tubule diameters of adults were already attained by some yearlings at 16 and 17 months of age. Although yearling males were observed to display sexual interest in females, probably few participate in breeding because of competition from older, larger males. As indicators of sexual function, testes mass and seminiferous tubule diameter showed a regular seasonal fluctuation, first becoming manifest among yearlings. However, the mean and maximum values of these parameters continued to increase until about three years of age.

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Parameters van geslagsfunksie in vlakvarkbere *Phacochoerus aethiopicus* is ondersoek deur die benutting van materiaal vanaf bevolkingsbeheermaatreëls in Zoeloeland. Gebaseer op die teenwoordigheid van spermatozoa in die tubuli seminiferi van die testis is bere geslagsryp op 17 tot 18 maande en dan is die minimum massa van die gepaarde testes omtrent 25 g en liggaamsmassa omtrent 45 kg. Minimum waardes vir buisdeursneë onder volwassenes is alreeds deur sommige diere op 16 en 17 maande bereik. Alhoewel jaaroud bere gesien is wat geslagsbelangstelling in sôe toon, neem hulle waarskynlik min deel aan paring as gevolg van kompetisie deur die ouer en groter bere. Testismassa en buisdeursnit toon 'n reëlmatige seisoenskommeling wat alreeds by die jaaroud groep waarneembaar is alhoewel die gemiddelde en maksimum waardes van hierdie parameters aanhou toeneem tot ongeveer drie jaar oud.

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D.R. Mason
Present address: Department of Research and Information, Kruger National Park, Private Bag X402, Skukuza, 1350 Republic of South Africa

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Under seasonal climatic conditions, the occurrence of breeding seasons in warthog *Phacochoerus aethiopicus* populations has been widely reported, e.g. Fairall (1968), Child, Roth & Kerr (1968), Smithers (1971), Wilson (1975), Cumming (1975), Sheppe & Haas (1976), Boshe (1981), Rodgers (1984). 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 (J-P. 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) and Rodgers (1984). Clough (1969) 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.

Male warthog reproductive biology in Zululand was investigated using material from population control shooting in the Hluhluwe-Corridor-Umfolozi Game Reserve complex, which covers an area of 897 km^2 in the foothills of the first escarpment west of the Zululand coastal plain. Climatically the region is characterized by a hot summer rainy season from October to March inclusive, and a cooler dry season from April to September.

Material and Methods

Reproductive tracts were collected from 155 male warthogs shot in the Hluhluwe-Umfolozi complex between June 1973 and June 1975, and from 16 males shot in Mkuzi Game Reserve (a generally drier locality some 30 km to the north-east) between July and September 1973. Each testis and the paired epididymes were weighed 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 counter-stain. 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.

Where reproductive parameters were related to age, the

latter was determined using criteria described by Mason (1982, 1984). Four age classes of warthogs were distinguished, viz. juvenile (birth – 12 months), yearling (12 – 24 months), subadult (24 – 36 months) and adult (older than 36 months). Since warthogs in Zululand have a short, clearly defined farrowing season from about mid-October to early December (Mason 1982), the ages of warthogs within the first three year classes could be deduced to within about two months by extrapolating back to an approximate mean farrowing date (1 November).

Results

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 *vs* 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 (Figure 1) shows a fairly uniform increase until a body mass of about 45 kg is attained, and thereafter a wide range in testes mass. Growth in mass of the paired testes with age is illustrated in Figure 2. Testicular development below 12 months of age is inadequately represented owing 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 1), examination of the scatter in Figure 2 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 Figure 3. Minimum values recorded for mean

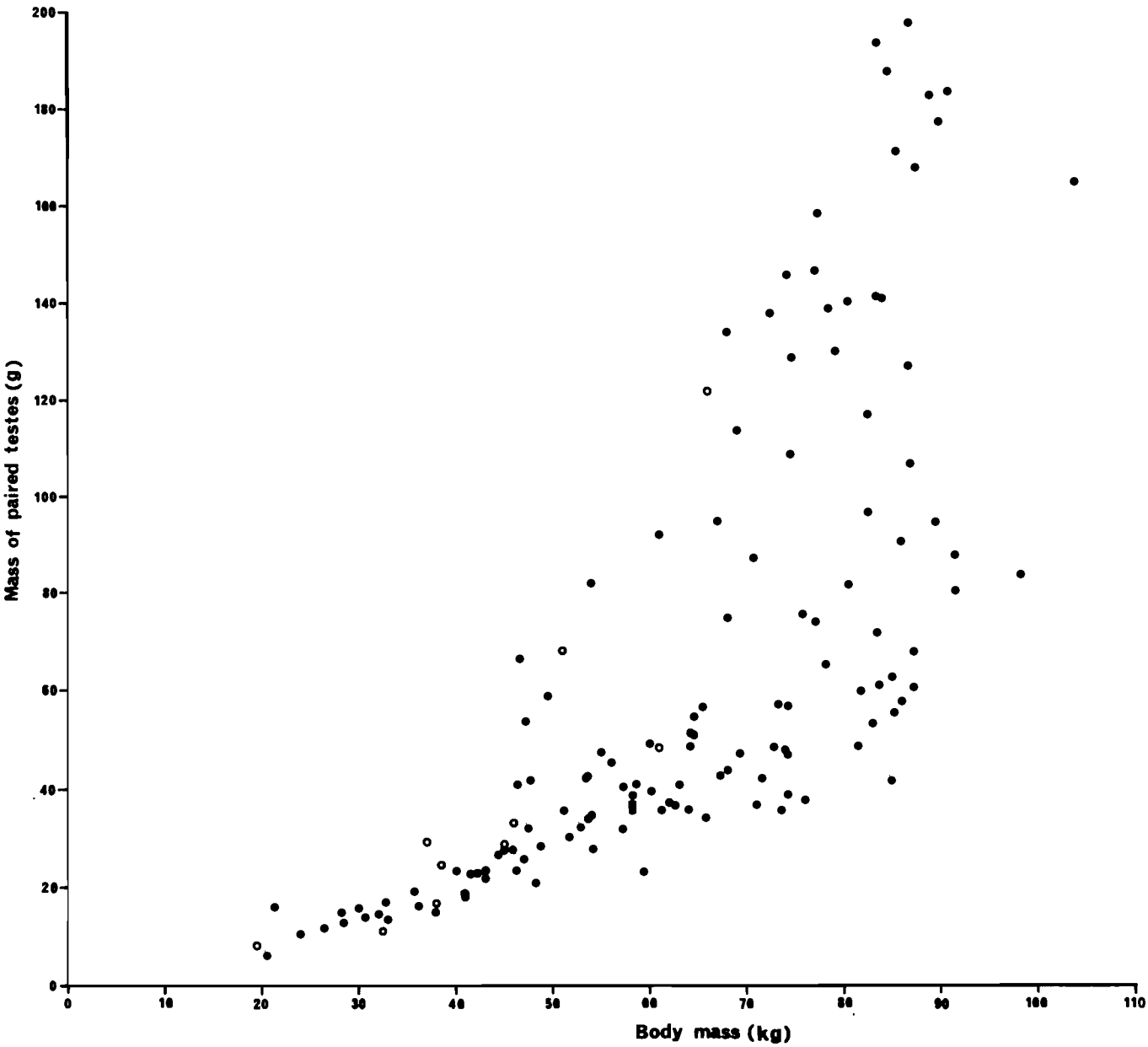

Figure 1 The relationship between testes mass and body mass of warthogs from Zululand (● = Hluhluwe-Umfolozi; ○ = Mkuzi).

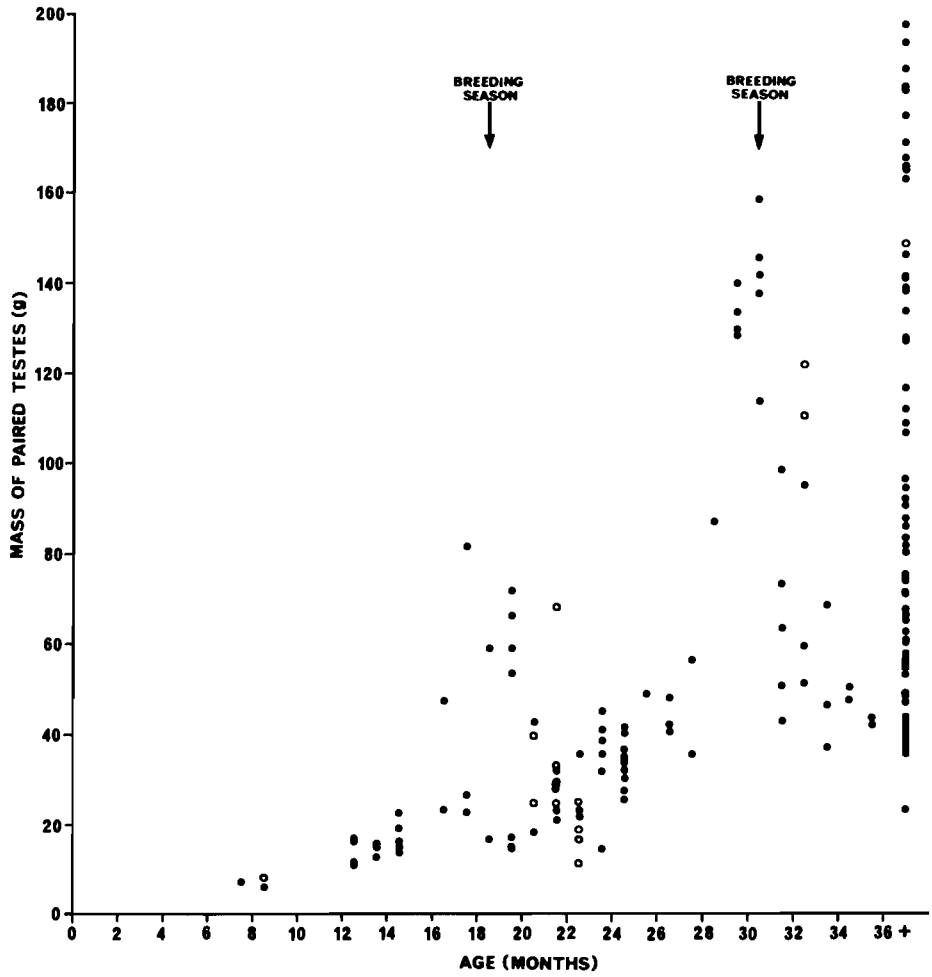

Figure 2 Growth in mass of warthog testes with age (n = 168; ● = Hluhluwe-Corridor-Umfolozi Game Reserve complex; ○ = Mkuzi Game Reserve).

Table 1 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[a]	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

[a] Including one juvenile from Mkuzi Game Reserve.

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 1 & Figure 3). The pattern of wide variation in tubule diameter within the yearling and subadult age classes, 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 (Figure 4), 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 2).

Spermatozoa and elongating spermatids were first observed in the seminiferous tubules of yearling warthogs from the Hluhluwe-Umfolozi 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 Umfolozi Game Reserve on 15 April 1975, contained spermatozoa in numbers estimated at $1{,}24 \times 10^9$ and $1{,}34 \times 10^9$ per ml in the left and right epididymes respectively (H.M. Dott pers. comm.). The masses of paired testes and epididymes of this animal were 81,6 and 9,4 g respectively. Round spermatids were

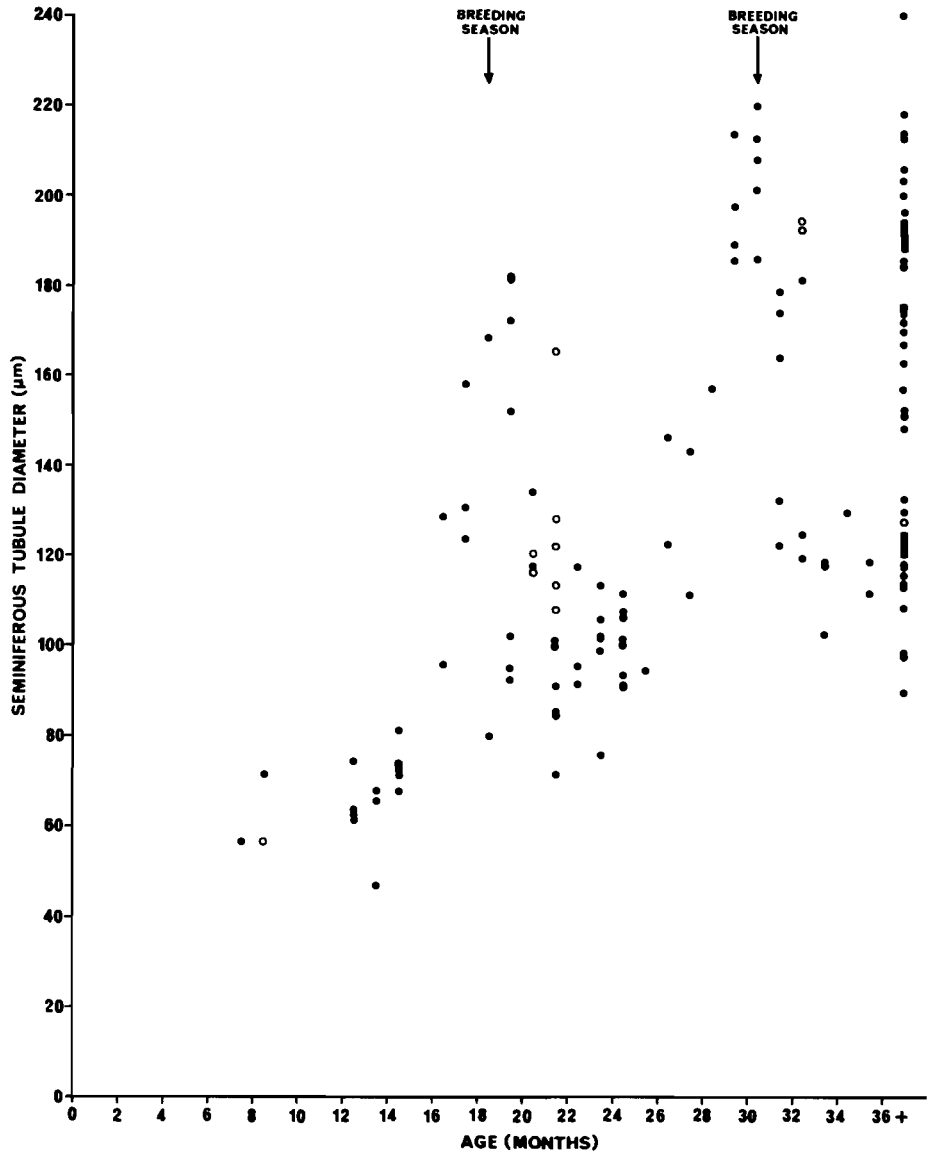

Figure 3 Variation in mean seminiferous tubule diameter of warthogs with age (n = 146; ● = Hluhluwe-Corridor-Umfolozi Game Reserve complex; ○ = Mkuzi Game Reserve).

already present in the tubules of two yearlings (paired testes masses of 23,2 and 47,4 g) collected 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 2) 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 (Figure 4e) 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 7 September 1974 in Umfolozi Game Reserve. The next highest values for paired testes mass

Table 2 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

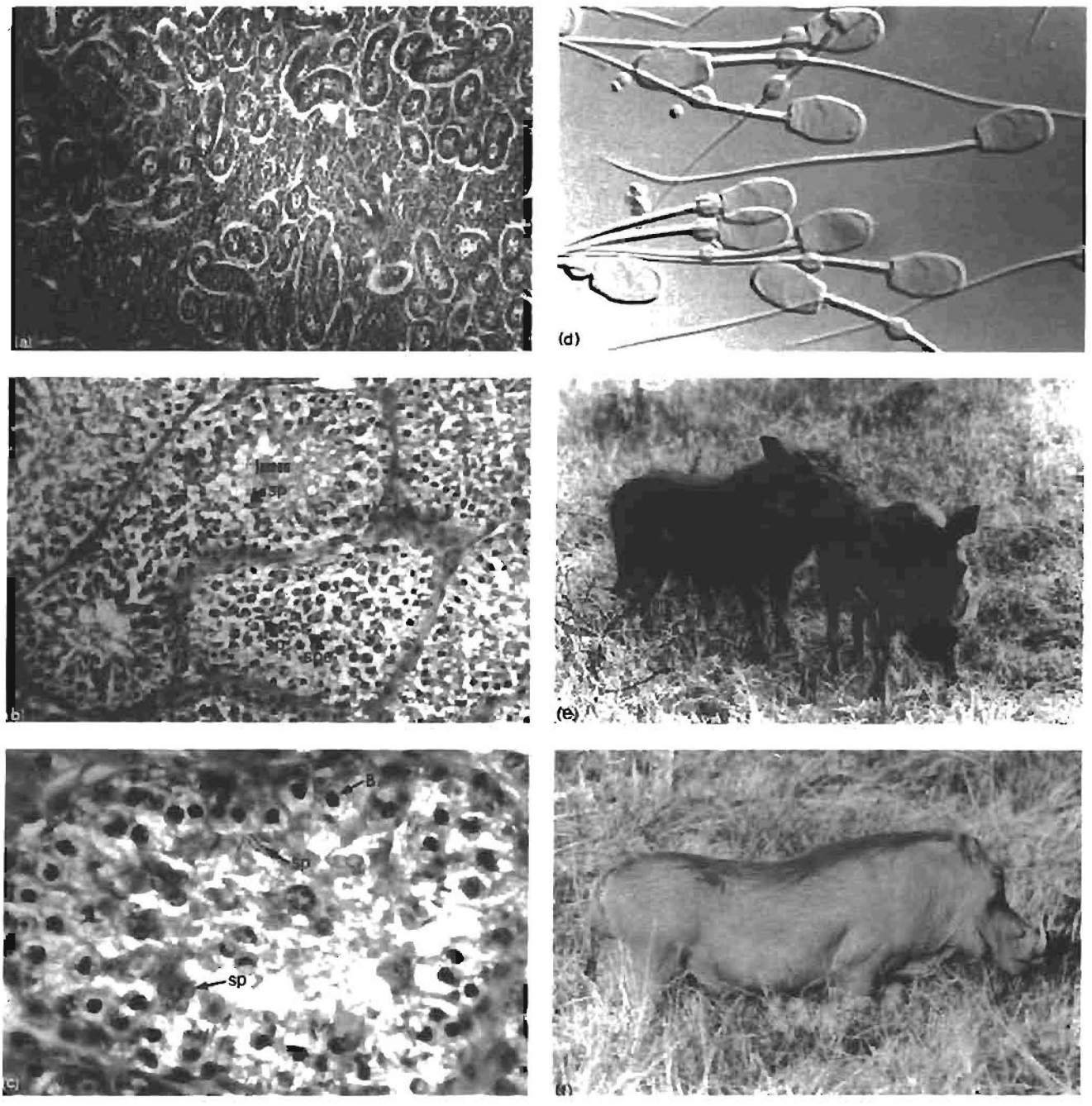

Figure 4 (a) Section of testis from a 12-month old immature warthog showing grouping of seminiferous tubules and abundant intertubular tissue. 6 μm, haematoxylin & eosin (× 63). (b) Section of testis from a mature yearling warthog aged about 19 months showing large seminiferous tubules with numerous primary spermatocytes (spe) and bundle formation of spermatids (sp). Type B spermatogonia (B) are located along the basement membrane. 6 μm, haematoxylin & eosin (× 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 (× 400). (d) Warthog spermatozoa (× 1 800). (e) Yearling male sniffing the enlarged vulva of a yearling female which was probably in late oestrus. (Umfolozi Game Reserve, 5 June 1975). (f) Adult male with swollen and protruding testes during the mating season (Hluhluwe Game Reserve, 19 April 1974).

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 Hluhluwe-Umfolozi 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 Mkuzi Game Reserve 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 2), the tubules of males in the older age

classes (estimated over 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 (Figures 5 & 6) with maximal values during March, April and May, when mating occurs. Mean testes mass increased four-fold from the minimum 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 (Figure 4f), 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 2) indicated that yearling males are fertile at this time.

The relationship between paired testes mass (y) and seminiferous tubule diameter (x) illustrated in Figure 7, is given by the regression equation $y = 0{,}00249x^{2{,}05213}$ and has a good correlation coefficient (r = 0,9156) that is highly significant ($p < 0{,}001$). However, the scatter for mature

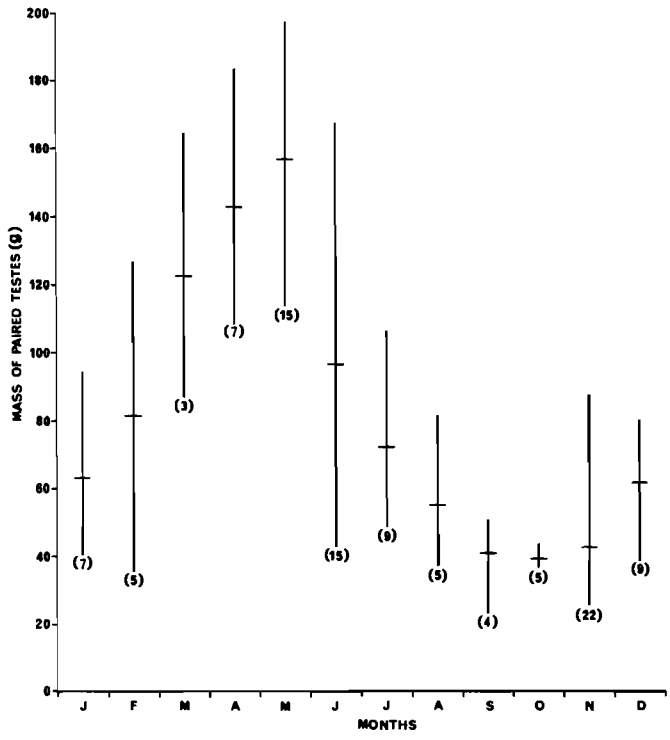

Figure 5 Seasonal change in combined testes mass of warthogs (at least two years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973–May 1975 (range — vertical line; mean — crossbar; monthly sample size is shown in brackets).

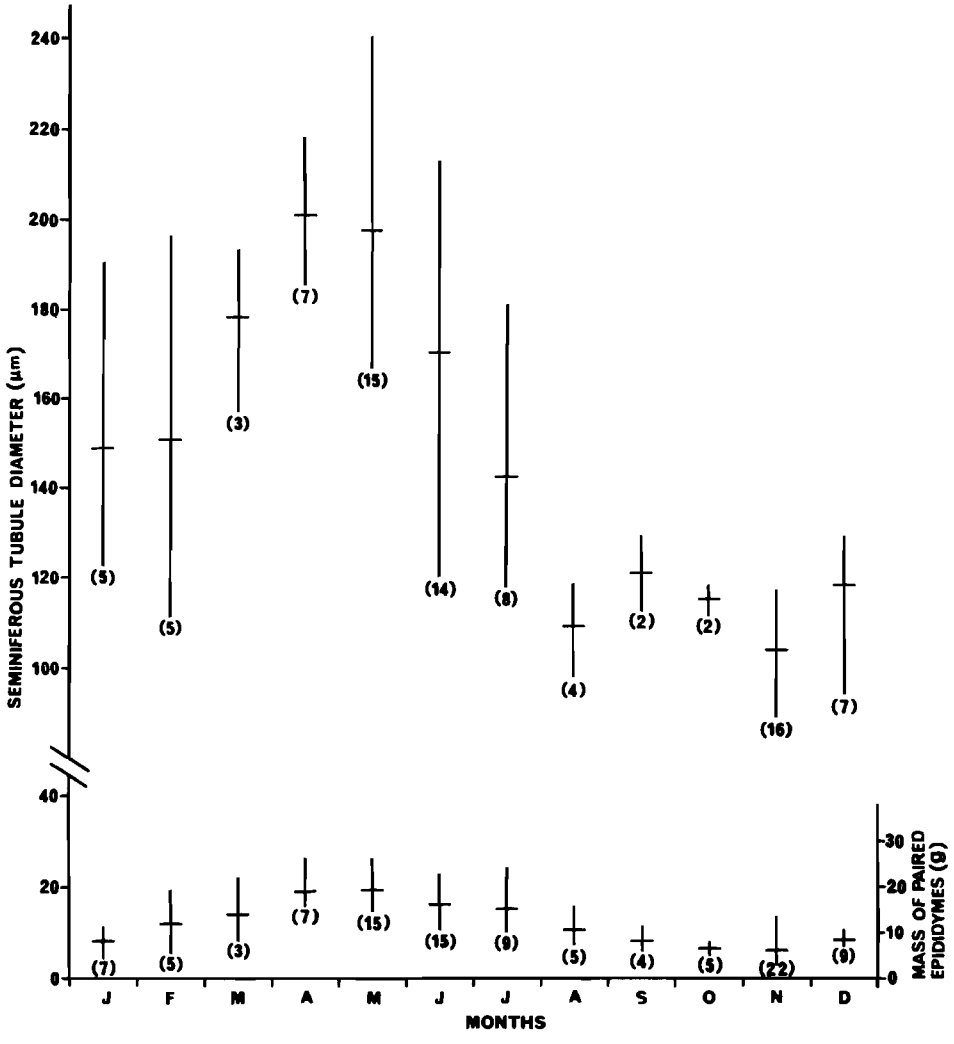

Figure 6 Seasonal change in seminiferous tubule diameter and combined epididymes mass of warthogs (at least two years of age) from the Hluhluwe-Corridor-Umfolozi Game Reserve complex, June 1973–May 1975 (range — vertical line; mean — crossbar; monthly sample size is shown in brackets).

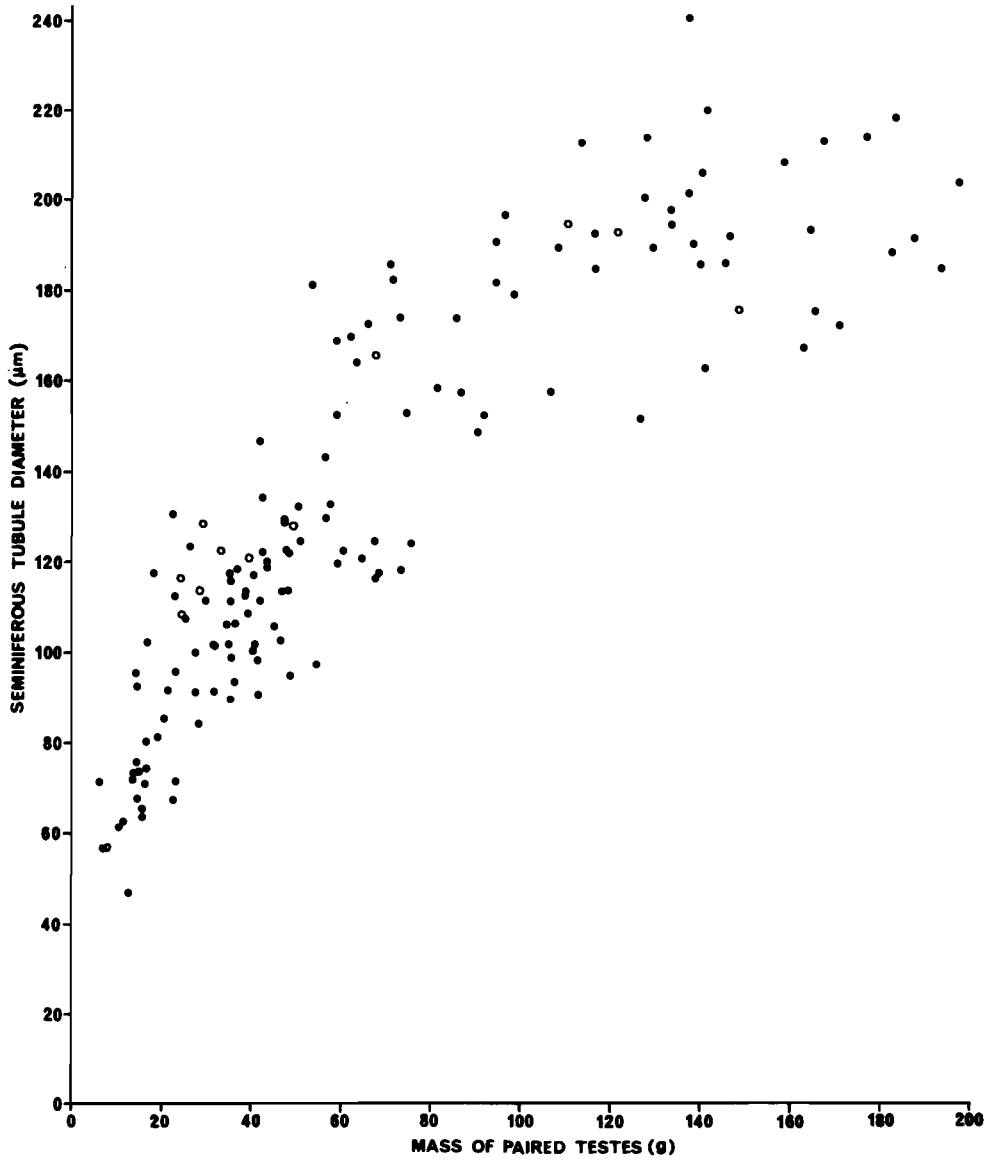

Figure 7 Scatter diagram of mean seminiferous tubule diameter plotted against combined testes mass for 134 warthogs from the Hluhluwe-Corridor-Umfolozi Game Reserve complex (● = Hluhluwe-Corridor-Umfolozi Game Reserve complex; ○ = Mkuzi Game Reserve).

animals is such that testes mass can decline markedly with little or no concomitant change in tubule diameter.

Discussion and Conclusions

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 *Loxodonta africana* (Hanks 1972, 1973), African antelope (Skinner, van Zyl & Oates 1974), hippopotamus *Hippopotamus amphibius* (Skinner, Scorer & Millar 1975), zebra *Equus burchelli* (Smuts 1976) and giraffe *Giraffa camelopardalis* (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 a Tanzanian warthog population at the northern limit of the unimodal rainfall belt of southern Africa, adult boars also exhibited seasonal testicular atrophy, of the order of 50% in mass of combined testes and epididymes by the end of the dry season (Rodgers 1984).

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 *Aepyceros melampus* 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 *Hylochoerus meinertzhageni*, Parkes (1966) drew attention to the clumped grouping of seminiferous tubules and the high proportion of intertubular secretory tissue distributed in large confluent blocks (Figure 4a). Apart from these features, the basic cellular composition of the warthog 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 *Syncerus caffer* (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 (1969) 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 of combined testes and epididymes recorded by Clough (1969) for a single warthog was 264 g, compared with a maximum of 223,5 g in Zululand warthogs. Skinner *et al.* (1975) found that testicular size of mature hippopotami in the 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. Under the bimodal annual rainfall regime in equatorial Uganda, there is also some evidence that warthogs may maintain higher body masses than in Zululand. Warthog boars aged at least three years (n = 56) averaged 79,6 kg in the Hluhluwe-Umfolozi complex, compared with 84,7 kg for adult boars (n = 71) weighed by Clough & Hassam (1970) in the Queen Elizabeth National Park, Uganda. However, such inter-population comparisons can be misleading and evidence of geographical variation in average size of warthogs remains inconclusive (Mason 1982).

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 (1975) 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 Hwange (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 2). 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 15 April 1975 in Umfolozi Game Reserve, and ranged from $1{,}23 \times 10^9$ to $9{,}17 \times 10^9$ sperm per ml for a single epididymis (H.M. Dott pers. comm.).

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