Observations on Growth and Ageing of Warthog, *Phacochoerus aethiopicus* (Pallas, 1766)[1]

By H. H. Roth

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Population studies of Large African Mammals require more knowledge of growth in captive known-age individuals for comparison with growth and ageing criteria, established from material derived from game harvesting and Tsetse Control Hunting operations. This allows a better interpretation of such results, which, together with the desire to investigate further the patterns of mammalian body development led to the present study. Detailed records were taken from five warthogs, *Phacochoerus aethiopicus* (Pallas), which were captured at an age of 2—3 weeks, and reared in captivity subsequently. Two of these were lost at the age of $2^1/_4$ and $6^3/_4$ months; but three survived and were observed for almost 2 years.

All five warthogs originated from different sows, two from Wankie National Park, two from the Nagupande River (Central Zambezi drainage) in Southern Rhodesia, and one from the Fort Jameson District in Northern Rhodesia. Each individual was weighed at frequent intervals and the following measurements were taken with the animal laid on its side:

1. Length of head and body: between pegs at the anus to the tip of the snout of the extented head;
2. Shoulder height: between pegs at the highest point of the withers and the sole of the fore foot;
3. Length of the tail: from the second tail vertebra to the tip of the tail;
4. Length of the hind foot: from the calcaneus to the tip of the extended hoof;
5. Length of the ear: from the notch to the tip of the ear;

Interpretation of these records required they be compared with average warthog weights and body measurements, which were obtained from warthogs in the Nagupande Area and are broken down in rough age classes in Table 1. Further, the different feeding conditions of each captive individual had to be taken into account.

Weight increase

Figure 1 shows the increase in weight of the experimental warthogs expressed as a function of age. The gain in weight was not steady in the course of body development. During the first 6—7 weeks (i. e. 2—9 weeks of age) the sucklings only put on about 30—100 grms per day.

Towards the end of this early suckling stage the young animals seemed to undergo a crisis during which development stagnated before the growth rate increased steadily after the change from milk to solid foods. Roth (1964) has also recorded this set back of growth towards the end of the suckling period and well before weaning in the porcupine *(Hystrix africaeaustralis)*. Here the decrease occured, despite an almost doubled milk intake, and was interpreted as the result of the nutritional insufficiency of pure milk at this stage of physical development. The body weight increased mar-

[1] Frau Dr. h. c. Erna Mohr zum 70. Geburtstag in freundschaftlicher Verbundenheit.

kedly only after the change to vegetable food was completed. Nutritional effects were not investigated in detail in the warthog experiment, but the stagnation of growth also definitely began while the hoglets were still on whole milk. As warthogs No. 3 and 4 continued to get whole milk mixed with maize the stagnation could not possibly have been the result of the dietetical change and it is interesting to note that this apparent physiological crisis coincides with the period of highest youth mortality (BIGOURDAN, 1948), and that hoglet No. 4 died for no obvious reason during this critical stage. MOHR (1960) quotes Russian investigations into youth mortality of the European boar *(Sus s. scrofa)* which also showed that 20% of all wild piglets die during the first three month of life.

Growth in the experimental hoglets reached a maximum increase of 120—270 grms per day when they were between 2 and 7 months of age. The average gain per week during this period in the extreme case of No. 3 was 1.9 kg with peaks of more than 3.5 kg. Towards the end of the first year the weight increase declined to an average of 45—152 grms per day or 1.1 kg per week in No. 3. Whereas this decline continued, during the first half of the second year in No. 3, a new surge in the growth of boars No. 1 and No. 5 was detected; the daily gain in these animals increased from 90 to 141 and 45 to 63 grms respectively. BIGOURDAN (1948) describes the growth of two warthogs, and his figures, although generally lower, confirm the same gain pattern: 43 grms per day at 1—2 month; 83—108 grms per day at 2—6 months and 50—61 grms per day at 6—12 months.

Figure 1 shows that all the weight curves follow a similar course during the first 3—4 months, but from this age, weight increases differed greatly between the three surviving hogs. This variation is explained by the difference in the rearing conditions:

No. 1 (and No. 2) were kept in concrete stables and initially suffered from diarrhoea. They did not receive "pet" attention and remained very nervous and frigh-

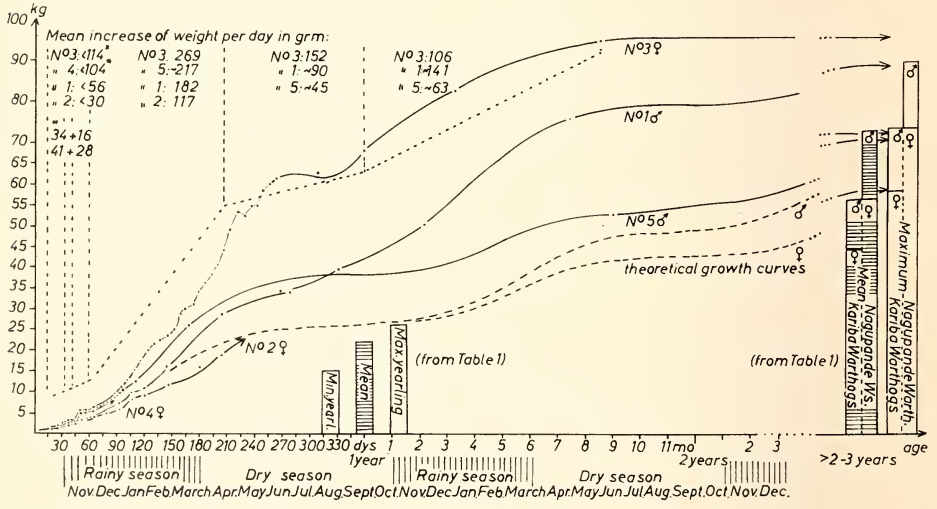

Fig. 1. Weight increase in *Phacochoerus aethiopicus.* The weight increase of the experimental animals (full curves) is compared with the theoretical weight increase of freerangig hogs (dotted curves) as would follow from the mean weights in Table 1. All weight figures are related to seasons in the bottom scale. For the arithmetical calculation of weight increase in the experimental animals during comparable periods some values had to be taken from the graphs. These interpolated figures are marked ~. All values of the first period are maximum figures because the initial very slow weight gain is not included in the calculation.

tened. They were very soon put onto a diet consisting purely of pressed domestic pig cubes. These conditions delayed early development somewhat compared with the other warthogs. After nine months the boar (No. 1) was put together with No. 3 in an open enclosure and the beneficial effect of this change is manifest in the growth curve.

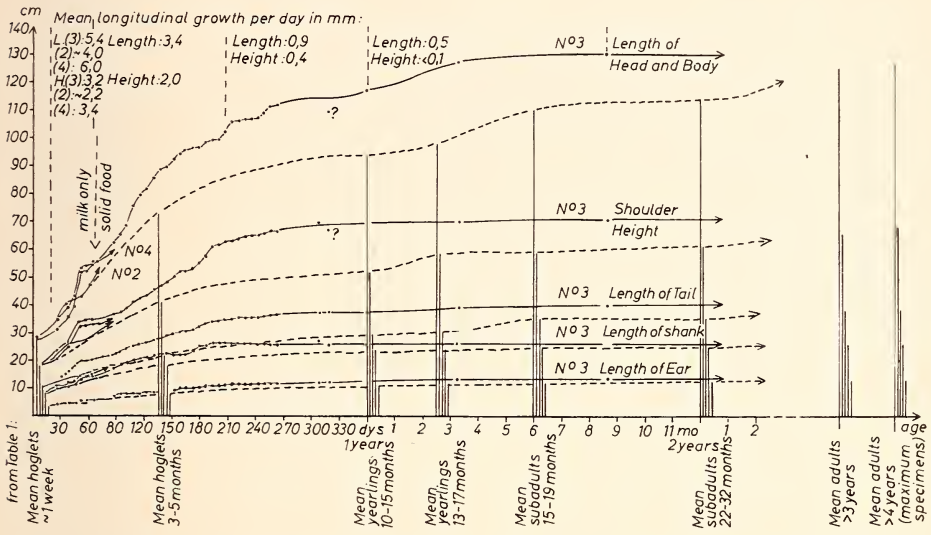

Fig. 2. Growth of ♀♀-*Phacochoerus aethiopicus* (Nos. 2, 3, and 4). The growth of the experimental animals, differentiated as head and body length, shoulder height, length of tail, length of shank, and length of ear (full curves), is compared with the theoretical growth of free-ranging hogs (dotted curves). This was established from the mean figures shown in Table 1 and entered into Figures 2 and 3 as vertical lines for each age group. The numbers of free-ranging animals measured in each age group are given in brackets. The ~ marked figures for the mean longitudinal growth per day were calculated by interpolation from the curves.

No. 3 (and No. 4) were reared as free living pets and received maximum care and they were fed for 6 weeks (i. e. to an age of about 7—8 weeks) with pure whole milk. The surviving female (No. 3) was then fed with maize porridge, prepared with milk, for another 5 months and consumed up to 100 lbs of maize per month. The change to ordinary pig meal at 7¼ months caused a slight loss of weight, whereupon feeding was reversed to maize porridge, now prepared with water only. After transfer to the experimental enclosure at 9 months this animal was fed the same ready made pig meal as No. 1 and the change to a less fattening diet is again reflected in the growth curve.

No. 5 was also a household pet and initially was fed on milk, but it was then weaned to natural grasses; thus the rearing of this animal resembled natural conditions most closely.

In Table 1 mean weights of free living warthogs from various areas as given by Bigourdan (1948), Junor (1960) and Child (1963) have been compiled and are broken down in rough age classes for comparison with the weights recorded for the experimental hogs. The birth weight of *Phacochoerus aethiopicus* varies, according Bigourdan (1948), between 480—620 grms in litters of four and 850—800 grms in twins; but Wilson (1964) has recorded maximum foetus weights of 680—795 grms in a litter of four. These figures are comparable with the averages in the Nagupande

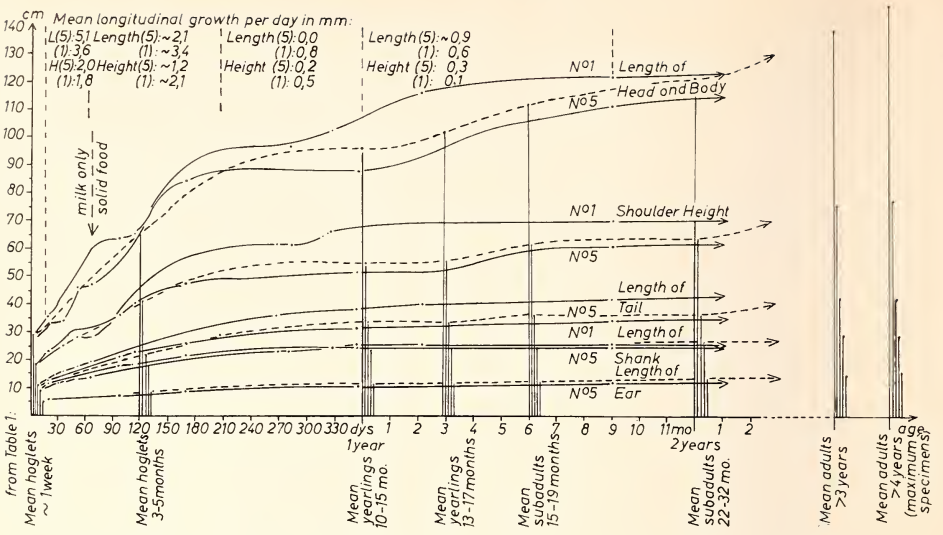

Fig. 3. Growth of ♂♂-*Phacochoerus aethiopicus* (Nos. 1 and 5). For the calculation of the mean longitudinal growth per day during comparable periods most values had to be taken from the graphs and the mean figures given are only approximate. The ratio between length and height development during the first period becomes more narrow the more of the earliest growth is included.

area for 3—10 days old hoglets (Tab. 1) and the initial weights of the experimental animals (Fig. 1). The maximum and minimum weights of Nagupande yearlings as given by CHILD (1963) are entered in Fig. 1; they even range considerably below the growth curve recorded for the more naturally fed boar No. 5. All three experimental animals had gained far more weight at one year than free living warthogs. This is particularly true of No. 3 which already weighed 68 kg, the weight of a fully grown sow, after one year and ultimately reached 95 kg. BIGOURDAN (1948) associates the mean adult weight of 70 kg with 3—4 year olds and only records figures of 90—110 kg for 7—15 years old boars. Females are 15—20% lighter and the heaviest one he recorded was only 80 kg.

In relating the normal weights a theoretical growth curve was established (Fig. 1). This curve follows closely the gain in weight recorded by BIGOURDAN (1948) for two young warthogs which weighed 1.7 kg at 1 month, 3.0 kg at 2 months, 4.5—6.0 kg at 3 months, 13—16 kg at 6 months and 22—27 kg at 12 months. Unfortunately no further weights are given and the conditions under which these warthogs lived are not stated. If the body development recorded in this study is compared with the theoretical growth curve and BIGOURDAN's figures it is evident that warthogs No. 1 and 3 grew very rapidly and abnormally early, and that free living warthogs develop much slower and over a more extended period.

Factors causing this difference are believed to be seasonal food stringencies and parasite invasion. The initial development in the wild population is as rapid as in the captive animals, but growth is undoubtedly retarded during the first dry season, and very probably again during the subsequent two dry seasons before full size is reached. Although all the growth of all the experimental hogs indicates the first year's reduction, artificial feeding largely compensated for the deficiency which seems to occur under natural conditions. A comparison of the weight curves of No. 1 and 3 warthogs with No. 5 confirm this consideration.

Figure 4 manifests the significance of parasite infestation for the European boar (Sus s. scorfa). All warthogs in the Nagupande aera were found to harbour very numerous intestinal nematodes (Strongyloidea) and although pathological lesions were not noted it seems more than likely that such enormous worm burden did retard development in juveniles. The excreta of the experimental warthogs were examined regularly for worm eggs, during the entire period and the complete absence of eggs indicated they remained worm free. The same difference also applied to tick, lice and flea infestations, all of which very common and heavy under natural conditions at Nagupande.

Fig. 4. 6—8 months old European Boar *(Sus scrofa scrofa):* both animals are litter mates of the same age, but the right hoglet was heavely infested with lung worms *(Metastrongylus spec.).* (Aufnahme Dr. H. H. Roth)

Body Growth

Figures 2 and 3 show the linear development in the experimental warthogs expressed as a function of age, and differentiated as the lenght increase of head and body, and the growth of the shoulder height, tail, shank and ear. As opposed to the weight increase, which followed a sigmoid curve, longitudinal growth was already most rapid during the first 2 months and then decreased gradually. During early rapid growth the head and body grew longer at an average of 3½—6 mm per day, and the shoulder height increased approximately 2—3½ mm daily. The graphs of linear growth show a similar temporary slowing down as suckling tapers off and after weaning i. e. at 7—10 weeks of age, as observed and commented on with respect of weight increases. The difference of longitudinal growth between the three warthogs is not as marked as in weight increases. The well-fed No. 1 and 3 continued their initial rapid growth during the following 5 months at 3½ and 2 mm per day respectively; they had reached a much larger size earlier than the grass fed No. 5, before the growth of all decreased to almost a standstill during the general depression period at 7—10 months of age. At the end of the first year and beginning of the second year longitudinal growth was accellerated and this corresponded with the increased weight gain at this period. However, the growth increase was only marked in the horizontal dimension i. e. in the length of head, body and tail, and occured mainly in the two males. The length and height increased at a different rate. Beginning with a ratio of less than 2:1 the growth in the horizontal dimension continued at a higher rate than the increase of the body height, so that the ratio became more than accelerated 2:1 during the second half of the first year. The second period of growth was characterized by a much wider ratio of 3—6:1 for length: height development.

The normal body measurements of warthogs are given in Table 1 and are entered in Fig. 2 and 3 as mean values for hoglets of approximately 1 week and of 3—5 months age, for yearlings just about one year old and somewhat older ones, for subadults of about 1½ years and of approximately 2—2½ years age, and for adults older than 3 years and maximum specimens. At 3—4 months the body dimensions of the experimental warthogs, excepting the virtually fattened No. 3, were still similar to free-ranging hoglets. After one year No. 3 was considerably larger than average yearlings

Table 1 **Mean Weights and Body Dimensions**

Area of Origin	Approx. Age	Specimens measured Sex	No.	Body Weight kg	(lbs)	Length of Head & Body cm	(inch)	Length of Tail cm	(inch)
West Africa	Yearlings (>7—10 months)	♂	2	18.5		82.9		26.0	
		♀	2	13.0		74.5		—	
	(known age: 12 months)	♂	1	30.0		97.0		—	
		♀	1	32.0		97.0		—	
	Sub-adults (24—32 months)	♂	5	50.0		116.5		33.0	
		♀	2	43.5		114.5		—	
	Adults (3—4 years)	♂	3	69.0		127.0		34.0	
		♀	1	66.0		130.0		—	
	(4—6 years)	♂	3	84.7		137.9		36.0	
	(>4 years)	♀	3	73.7		129.0		—	
	Max. Specimens (known age: 7—15 years)	♂	5	98.2		142.8		—	
Southern Africa: Lake Kariba August, 1959	Adults (>2 years)	♂	6	56.5	(124.3)	—		—	
		♀	19	44.8	(98.6)	—		—	
	Large specimens only	♂	2	74.1	(163.0)	—		—	
		♀	3	59.0	(129.7)	—		—	
	Max. specimens only	♂	1	76.4	(168.0)	—		—	
		♀	1	68.2	(140.0)	—		—	
Southern Africa: Nagupande River October, 1962	Yearlings (10—13 months)	♂	8	22.3	(49.0)	91.7	(36.06)	32.6	(12.81)
		♀	5	22.4	(49.2)	95.9	(37.75)	30.2	(11.88)
	Max. Yearling	♂	1	28.2	(62.0)	97.2	(38.25)	32.4	(12.75)
		♀	1	27.3	(60.0)	94.6	(37.25)	32.4	(12.75)
	Min. Yearling	♂	1	15.0	(33.0)	90.8	(35.75)	31.1	(12.25)
		♀	1	18.6	(41.0)	85.8	(33.75)	24.8	(9.75)
	Adults (>2 years)	♂	4	73.4	(161.5)	138.4	(54.50)	44.2	(17.38)
		♀	7	55.6	(122.3)	117.5	(46.25)	39.5	(15.56)
	Large specimens only (>3 years)	♂	2	85.9	(189.0)	151.6	(59.69)	48.0	(18.88)
		♀	4	61.2	(134.7)	119.7	(47.16)	37.8	(14.94)
	Max. specimens only (>4 years)	♂	1	90.0	(198.0)	165.1	(65.00)	49.5	(19.50)
		♀	1	74.1	(163.0)	121.7	(47.88)	35.0	(13.75)

of Phacochoerus aethiopicus *Table 1*

Shoulder Height		Pelvic Height		Shank Length		Ear Length		Girth		Reference
cm	(inch)	cm	(inch)	cm	(inch)	cm	(inch)	cm	(inch)	
47.0		—		—		—		60.8		Bigourdan (1948)
43.0		—		—		—		55.0		
54.0		—		—		—		73.0		
—		—		—		—		73.0		
63.2		—		—		—		86.1		
62.5		—		—		—		79.0		
72.3		—		—		—		96.5		
—		—		—		—		88.0		
74.0		—		—		—		103.8		
72.0		—		—		—		100.0		
79.6		—		—		—		109.0		
—		—		—		—		—		Junor (1960)
—		—		—		—		—		
—		—		—		—		—		
—		—		—		—		—		
—		—		—		—		—		
—		—		—		—		—		
56.0	(22.06)	56.0	(22.06)	24.0	(9.44)	11.3	(4.44)	—		Child (1963)
52.3	(22.59)	52.1	(22.50)	23.2	(9.13)	11.0	(4.31)	—		
59.1	(23.25)	60.3	(23.75)	25.1	(9.88)	10.8	(4.25)	—		
52.1	(20.50)	52.1	(20.50)	24.1	(9.50)	11.4	(4.50)	—		
56.5	(22.25)	55.3	(21.75)	24.8	(9.75)	12.1	(4.75)	—		
49.5	(19.50)	50.8	(20.00)	22.2	(8.75)	9.6	(3.75)	—		
71.6	(28.19)	68.8	(27.06)	27.8	(10.94)	13.2	(5.19)	—		
65.4	(25.75)	64.3	(25.31)	24.8	(9.82)	12.9	(5.06)	—		
77.2	(30.37)	71.6	(28.15)	28.6	(11.25)	13.7	(5.38)	—		
66.5	(26.17)	65.5	(25.81)	25.1	(9.88)	13.0	(5.10)	—		
78.1	(30.75)	73.0	(28.75)	29.2	(11.50)	14.6	(5.75)	—		
64.2	(25.25)	62.3	(24.50)	26.0	(10.25)	13.1	(5.13)	—		

Table 1 Continuation

Area of Origin	Approx. Age	Specimens measured Sex	No.	Body Weight kg	(lbs)	Length of Head & Body cm	(inch)	Length of Tail cm	(inch)
Southern Africa: Nagupande River Oct./Nov. 1962	Hoglets (~ 1 week)	♂♀	2	0.7—0.9		28.2	(11.13)	10.4	(4.07)
	(~ 2 weeks)	♂♀	2	1.2—1.25		31.3	(12.35)	10.8	(4.25)
Southern Africa: Nagupande River Nov. 1962— April 1964	Hoglets (3—5 months)	♂	1	—		64.8	(25.50)	21.6	(8.50)
		♀	2	—		73.3	(28.87)	21.6	(8.50)
	Yearlings (11—15 months)	♂	5	—		100.2	(39.45)	36.2	(14.25)
		♀	2	—		89.6	(35.25)	28.9	(11.38)
	Yearlings (13—17 months)	♂	6	—		101.7	(40.08)	33.7	(13.25)
		♀	2	—		97.8	(38.50)	31.1	(12.25)
	Subadults (15—19 months)	♂	3	—		112.2	(44.17)	36.8	(14.50)
		♀	3	—		109.2	(43.00)	35.2	(13.83)
	Subadults (22—30 months)	♂	13	—		126.2	(49.67)	38.3	(15.07)
		♀	9	—		113.4	(44.67)	35.1	(13.82)
	Adults (2—3½ years)	♂	22	—		128.7	(50.66)	39.7	(15.64)
		♀	18	—		117.0	(46.06)	37.2	(14.64)
	Large specimens only (> 3 years)	♂	11	—		137.6	(54.17)	42.2	(16.60)
		♀	11	—		121.8	(47.96)	38.8	(15.25)
	Max. specimens only (> 4 years)	♂	4	—		149.6	(58.88)	42.9	(16.88)
		♀	2	—		127.6	(50.25)	40.7	(16.00)

Age categories, which are defined "only" are compiled from individuals extracted from the preceding age category. "Minimum and maximum yearlings" are included in the preceding yearling category.

and had reached yearling size already at 6 months. Warthog No. 1, although much heavier than any yearling had grown to the maximum size recorded for free-living yearlings, and No. 5 remained within the range shown by such yearlings (Fig. 2).

Fig. 2 shows that the very well fed No. 3 had reached the physical proportions of an average adult already by 9—12 month, and was larger than any known maximum specimen at the early age of 21 months. Boar No. 1 needed 11—14 months and No. 5 20—24 months to grow up. The mean values for fully adult and old males suggest,

Continuation Table 1

Shoulder Height		Pelvic Height		Shank Length		Ear Length		Girth		Reference
cm	(inch)	cm	(inch)	cm	(inch)	cm	(inch)	cm	(inch)	
18.1	(7.10)	18.7	(7.44)	8.3	(3.28)	3.8	(1.47)	—		Child (1963)
20.8	(8.15)	19.7	(7.75)	9.2	(3.59)	4.2	(1.79)	—		and author.
—	—	40.6	(16.00)	17.8	(7.00)	8.9	(3.50)	—		Taken by
40.6	(16.00)	41.2	(16.25)	18.2	(7.25)	8.2	(3.18)	—		author
56.1	(22.06)	55.0	(21.69)	25.7	(10.10)	11.9	(4.68)	—		
48.6	(19.13)	49.5	(19.50)	24.1	(9.50)	10.7	(4.38)	—		
56.2	(22.13)	57.8	(22.79)	25.8	(10.13)	11.8	(4.63)	—		
59.1	(23.25)	59.5	(23.38)	24.2	(9.50)	11.8	(4.63)	—		
62.0	(24.41)	63.7	(25.06)	25.0	(9.82)	12.6	(4.92)	—		
60.8	(23.92)	59.3	(23.33)	25.0	(9.83)	12.3	(4.83)	—		
68.0	(26.75)	65.7	(25.87)	26.8	(10.52)	13.6	(5.37)	—		
61.5	(24.22)	60.7	(23.89)	24.5	(9.66)	12.8	(5.04)	—		
70.4	(27.72)	67.4	(26.55)	27.3	(10.74)	13.8	(5.42)	—		
63.2	(24.86)	61.7	(24.27)	25.3	(9.94)	13.2	(5.17)	—		
75.0	(29.54)	71.4	(28.12)	28.2	(11.10)	13.9	(5.46)	—		
65.1	(25.61)	63.4	(24.92)	25.9	(10.20)	13.3	(5.25)	—		
77.5	(30.50)	74.8	(29.44)	28.4	(11.19)	13.7	(5.38)	—		
69.2	(27.25)	67.3	(26.50)	26.1	(10.25)	12.8	(5.00)	—		

however, that the two captive boars will continue to increase mainly in body length, but also in shoulder height for some time.

Apart from the discussed linear dimensions the girth measure is important for weight estimations in the field and for age classification of hogs older than two years. Bigourdan (1948) has tried to adapt Crevat's formula for measuring geometric weight to warthogs and states that with a slight alteration of the coefficient he was able to estimate weights within an error of 3—4 %. In this study only few girth measures were taken. No. 3 and 4 warthogs measured 25.5 and 23.0 cm respectively at 4—5 weeks and the girth of No. 3 had increased to 107—109 cm when 21 months old. No. 1 measured at the same age only 100—102 cm.

Pattern of Growth

Although the intensity of growth varied between the experimental warthogs the produced data allow the following generalisations: During the initial suckling period all longitudinal growth is rapid and weight increases very slowly. After the critical weaning stage at about 7—10 weeks, which is characterized by a general set back in development, the increase of body weight becomes more rapid than linear growth. While gaining volume the body stretches more than it grows higher. The vertical growth consists mainly of the elongation of the extremities, as reflected by the measurements of the hind foot, but also of an actual increase of body diameter. Whereas the ultimate shank length is reached earliest increases in shoulder height, in both sexes, continue for somewhat longer. It is important, however, to note that apart from the development of the withers in boars (see below) the vertical development was finalised before the full body length was reached. The prolonged longitudinal growth of head and body was also manifest in the continued growth of the tail. The size of the ear also increased a little after the vertical development had ceased.

Bigourdan (1948) states that male hoglets grow more rapidly than females, already after weaning, and from then on would have an increasing physical advantage. This observation was based on the growth of two individuals; because of the different rearing conditions no conclusion can be drawn in this respect from the present study. A comparison of the mean body measurements of yearlings of the two sexes in Tab. 1 seems to confirm that male yearlings are generally a little larger than females, although Child's sample rendered almost the same mean weights for both sexes. The difference is, however, insignificant for field observations and true sexual differentiation does not occur before one year. This becomes evident from Table 2 in which the development of the withers, as expressed by the difference between pelvic and shoulder heights, is compared for both sexes. The withers are poorly developed in yearlings but become very prominent in fully grown boars of more than 3 years age when they are about 4 cm high. In females there is a regressive tendency and fully grown and old sows have less withers than subadults. Another definite secondary sexual feature, apart from the tusk growth and size, are the warts. The infraorbital warts grow much larger in males and the supraoral ones hardly develop at all in the female. Sexual differentiation in the observed captive boars began with about 15—18 months. Tab. 1 shows that adult males in the Nagupande area were generally more than 20% heavier than females. This was also true for the warthog population weighed by Junor (1960) on

Table 2

Development of the withers in *Phacochoerus aethiopicus*

Approx. age	Difference between Shoulder and Pelvic Height.			
	No.	Mean in ♂♂	No.	Mean in ♀♀
Yearlings (10—15 months)	13	(0.7—) 0.3 cm.	7	(0.6—) —0.1 cm.
Yearlings (11—17 months)	6	(±0—) 0.3 cm.	2	(±0—) —0.3 cm.
Subadults (15—19 months)	3	(0.8—) ±0 cm.	3	1.3 cm.
Subadults (22—30 months)	14	(2.5—) 2.9 cm.	12	(1.8—) 2.5 cm.
Adults (> 3 years)	12	(3.7—) 4.4 cm.	12	(2.1—) 2.3 cm.
Max. specimens (> 4 years)	5	(3.7—) 4.6 cm.	3	1.9 cm.

Compiled from measurements of Table 1 excluding some doubtful ones; figures in brackets include doubtful measurements i. e. those individuals for which considerably greater pelvic than shoulder height was recorded; these measurements are amended in this compilation to ± 0 difference of shoulder to pelvic height.

islands on Lake Kariba under conditions of extreme starvation. On an average the male body is 10—20 % longer and becomes 7—15 % higher depending on the age class.

The growth of the head was not examined in this study. BIGOURDAN (1948) shows, however, that the ratio between zygomatic width and length of the skull is less than 1:2 (< 50 %) in young and subadult warthogs, but increases to more than 1:2 (50 bis 62 %) in old individuals. It follows that the initially more rapid longitudinal development of the head is completed before the head has grown to its full broadness. In the final stage it represents about 15—18 % of the body weight. In one juvenile male of 44 kg body weight the head was weighted and found to be 14—14.5 % of the total weight.

Apart from the physiological pattern the warthog seems to be subject to a seasonal variation. Being a monoestrous species warthogs in Southern Rhodesia are always born shortly before or just after the beginning of the rainy season (Sept.—Dec.). The first rapid development of the hoglets therefore coincides with the nutritionally most favourable time of year. The comparisons of the initial development rate and the average size and weight of yearlings suggests that growth is gradually reduced to almost nothing during the second half of the first year which is characterized in Rhodesia by most unfavourable environmental conditions of the dry season. The theoretical growth curve in Fig. 1 has to rise considerably from the one-year-mark if it is to reach the point which indicates graphically the ultimate size of an average adult. If this renewed growth is taken as equal linear increase towards the final weight the graph would suggest a continued and prolonged growth almost as intensive as the first year's development. Since this is very unlikely it follows that the growth pattern of the second and third year resembles that of the first year, the intensity of growth becoming less during every rainy season. As shown above the development of all but one of the experimental warthogs is to be regarded as abnormal. Nevertheless each individual does show a characteristic depression of the weight curve as well as of linear growth during the first dry season followed by a renewed increase during the second rainy season. The growth curve of No. 5, however, which was fed naturally, is definitely confirmative of a seasonal growth pattern.

Physical and Sexual Maturity

BIGOURDAN (1948) considers warthogs to be grown up at 3 years of age. Further body development continues, however, gradually and full physical maturity, particularly in boars, is not reached before 4 years. After 8 years symptoms of high age and senility develop, but BIGOURDAN (1948) has recorded possible weight increases up to 12—15 years. The longevity is given as 20 years, although warthogs in captivity usually do not live longer than 12 years (maximum 16½ years) (MOHR, 1960). Comparing carefully maximum weights with figures of average adults, BIGOURDAN (1948) comes to the conclusion that the normal life expectancy is 3½—4 years, as compared with 2—3 years only in the more heavily hunted European boar. In his opinion this difference accounts for the fact that *Phacochoerus aethiopicus* has not always been clearly recognised as a species only about half the size of the European wild pig. As shown above the experimentally kept warthogs were fully grown up already after 1—2 years due to the optimal rearing conditions. Although in size hardly distinguishable from older adults the poorly developed tusks, warts, mane, and the withers and testicles (in the boars only) did reveal that the animals were still juvenile i. e. physically immature. It was found in this study that the milk canines are shed at about 6 months age and that the tusks then develop in both sexes at more or less the same rate up to 20—21 months. At this age the upper tusks of No. 1 measured from the

gum to the tip along the convex curve 8,3 cm and along the concave curve 4,4 cm, in No. 3 the measurements were only 6—9 and 3,8 cm. In the males the base of the upper tusk was already much wider (2,5—3 cm ♂) than in the female (< 2 cm ♂). This means that only about 3—4,5 cm actually protruded from the lip which is hardly noticeable on distance in the field. GEIGY (1955) gives several pictures of known age warthogs of 2 years from East Africa in which the tusks seem to be even less developed. According to STOCKLEY (1950) the average tusks of adult boars in Kenya are rarely less than 28 cm (11 inch.) long, growing often up to 38 cm (15 inch.). Considering even that these measurements may have been taken from the extracted teeth the difference of tusk sizes between two year-olds and adults is significant and well visible in the field. The infraorbital warts started developing at about 12 months and had grown to a height of only 3—4 cm in the males and 1—1.5 cm in the female after 20—21 months. The supraoral warts had grown only in the males to approx. 1.5 cm. BIGOURDAN (1948) has described the maximum size of warts in fully adult individuals as being 10—12 cm. Whether or not the warts are a reliable age indicators is still to be investigated in a larger material. The testicles started bulging out visibly from about 12—15 months on and measured about 4—6 cm in length at 20—21 months. Dark pigmentation of the scrotum was already conspicuous at this stage. The average testicle size of adult boars is about 7—8 cm (CHILD, 1963).

These indications of physical immaturity, of course, do not include necessarily that the hogs had not yet attained sexual maturity. On the contrary, the first symptoms of heat were observed in the female already at the early age of 7—8 months (early May 1963). A closer vaginal inspection in July and August showed that the juvenile still (or again — after having been joined with the young boar) discharged colourless mucus from the slightly hyperaemic vulva. This had definitely ceased in October. In May 1964 oestrous was again observed and the young boar repeatedly attempted to serve the female. The mating at this early age of 17—19 months was, however, unsuccessful; BIGOURDAN (1948) states also that sexual maturity is normally reached at 20 months. This would confirm that warthogs produce their first offspring at the end of the second year, or after three years.

Rough Ageing in the Field

Age classification of warthog populations in the field are relatively easy because of the distinct breeding period of this species (September—December). More accurate assessments will have to be based on the analysis of skull samples for which dental ageing criteria are being prepared by CHILD et al. (1965). For observational age classification, however, the following rough criteria are suggested as a result of this study:

1. Body size in relation to the accompanying sow.
2. Ratio of body length to body height.
3. Development of tusks and warts.
4. General physical appearance.

The application of these criteria to various age classes is summarized in the following key:

Hoglets of current year (up to 3 months): less than 30—35 cm shoulder height and less than 55—60 cm head-and-body length: i. e. any hoglet which has not grown much higher than half the shoulder height and half the head-and-body length of the mother is less than 3 month old.

Hoglets of preceding year (up to 9 months): more than 35—40 cm shoulder height, but not taller than 45—55 cm, and more than 60—65 cm head-and-body length, but not

longer than 85—95 cm: i. e. juveniles which are definitely taller than half the shoulder height and longer than half the head-and-body length of the mother, but may have reached approx. 3/4 of the adult dimensions, have to be considered older than 3 months and less than 1 year; they were born in the preceding year and in reproductivity studies may be recorded as "yearlings".

Yearlings (up to 1 1/4 year): ranging between 48—58 cm shoulder height and 90 to 100 cm head-and-body length: i. e. juvenile warthogs which are only little, but visibly smaller than adults — they may have reached 4/5 of the adult dimensions — are ± 1 year old.

Subadults (1 1/2—2 years): more than 60 cm shoulder height and at least 110 cm head-and-body length, but without conspicous tusks and warts, the withers and testicles being still poorly developed: i. e. subadults are not distinguishable anymore by body size alone, but the general physical immaturity as described above allows to classify them as 2 year-olds.

Adults (3—5 years): as compared with juveniles and subadults head and body have stretched and are almost twice as long as the shoulder height; body volume, withers and mane are well developed; the upper tusks protude in both sexes conspicously from the lip, at least 8—10 cm; the infraorbital warts have also grown out markedly to about 8—10 cm.

Old (senile) adults (> 8 years): the body has fattened to a more cylindrical shape and the back is hollowed to saddle profile; tasks have maximum size, but are frequently knotched and blunted; the mane hair is diminished and the skin around the eyes is wrinkled and slack; the upper warts have thickened and are sometimes hanging down, whilst the lower ones are very broad, and cracked; the front trotters have grown very long and, as a rule, impress also firm ground, producing thus a very distinct spoor (quoted according Bigourdan, 1948).

Summary

Five captive warthogs were weighed and measured at frequent intervals between 1 and 21 months of age. From these recordings the growth rate and pattern of body development in *Phacochoerus aethiopicus* are established and discussed in detail. For the interpretation of the obtained records these are compared with average weights and body measurements which were taken from wild warthogs; they are broken down in rough age classes and are compiled in Tab. 1. The comparison shows that there is a great difference between the artificially reared hogs and the wild population. Free-ranging warthogs grow much slower and develop over a longer period. Development appears to be markedly depressed by seasonal food stringencies and parasite invasions.

Warthogs are normally grown up at 2 1/2—3 years when they also have become sexually mature; but full physical maturity is not reached before 3—4 years. The secondary development of tusks, warts, withers and testicles and their significance for the ageing of subadults are discussed. As a result of this study rough criteria for observational age classification of warthog are suggested and a simple key for ageing in the field is given.

Zusammenfassung

Fünf gefangen gehaltene Warzenschweine wurden regelmäßig während eines Alters von 1 bis 21 Monaten gewogen und vermessen. Anhand dieser Daten werden Wachstumsgeschwindigkeit und die Gesetzmäßigkeiten der Körperentwicklung von *Phacochoerus aethiopicus* festgelegt und im einzelnen erörtert. Um die erhaltenen Daten zu deuten, werden diese mit Durchschnittsgewichten und -körpermaßen verglichen, die von wilden Warzenschweinen genommen worden waren, in Altersklassen aufgeteilt und in Tab. 1 zusammengestellt sind. Der Vergleich ergibt einen erheblichen Unterschied zwischen den künstlich aufgezogenen Schweinen und der Wildpopulation. Freilebende Warzenschweine wachsen viel langsamer und entwickeln sich über einen längeren Zeitraum. Die Entwicklung scheint dabei stark beeinträchtigt zu sein durch jahreszeitlich auftretende Futterknappheit und durch Parasiteninvasionen.

Warzenschweine sind normalerweise mit 2½—3 Jahren erwachsen und sind dann auch schon geschlechtsreif geworden; die volle körperliche Reife wird jedoch nicht vor 3—4 Jahren erreicht. Die sekundäre Entwicklung der Hauer, Warzen, des Widerrists und der Hoden, und deren Bedeutung für die Altersbestimmung von jungerwachsenen Warzenschweinen, wird erörtert. Als Ergebnis der vorliegenden Studie werden grobe Anhaltspunkte gegeben für Altersbestimmungen von Warzenschweinen bei der Feldbeobachtung, und ein einfacher Bestimmungsschlüssel ist hierfür angefügt.

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Author's address: Dr. rer. nat. Dr. med. vet. Harald H. Roth, Department of National Parks and Wildlife Management, Salisbury, S. Rhodesia