Koedoe 24: 169-185 (1981)

RELATIONSHIPS BETWEEN REPRODUCTION AND ENVIRONMENT IN THE HIPPOPOTAMUS *HIPPOPOTAMUS AMPHIBIUS* IN THE KRUGER NATIONAL PARK

G. L. SMUTS
Natal Parks, Game and Fish Preservation Board
P.O. Box 622
Pietermaritzburg
3200

I. J. WHYTE*
Department of Research and Information
National Parks Board of Trustees
Private Bag X402
Skukuza
1350

Abstract — Hippopotamus *Hippopotamus amphibius* reproduction in the Kruger National Park, Republic of South Africa, is described and compared with that of other populations in Africa and with captive reared specimens. Information collected during drought and pluvial periods indicates that adult hippo cows react to adverse environmental conditions (reduced shelter in pools, overcrowding and food scarcity) by marked declines in conception rates (from 36,7% — 5,6%). Indirect evidence indicates that when environmental conditions are unfavourable calf survival is improved by extending the period of lactation and by calves suckling more than one cow. During favourable years some calves mature early (♂♂, 2 years, and ♀♀ 5 years) but generally sexual maturity is attained at six and 9-10 years for males and females respectively. The calving interval, when environmental conditions are favourable, is about two years and reproductive senescence and sterility are insignificant factors. The population sex ratio is 1:1. Hippos appear to be typical K-selected species. Environmental constraints have caused them to adopt a low reproductive rate and high survival rate and consequently a close adjustment to the long-term carrying capacity of the environment.

Introduction

Hippopotami *Hippopotamus amphibius* are dependent on water for shelter during the day. This, together with their related nocturnal feeding habits and the

* *Reprints obtainable from I. J. Whyte*

unpredictable nature of the climatic regime in semi-arid parts of Africa, places certain constraints on the population dynamics of the species. Food and shelter are, for example, likely to become severely limiting under certain conditions, whereas population growth is apparently not influenced markedly by disease or direct predation. It is relevant to understand how evolution has equipped the hippopotamus to cope with these situations.

Using reproduction and population data collected during hippo cropping operations in the Kruger National Park (KNP), Republic of South Africa, and by comparing these with similar published data from other parts of Africa we will attempt to explain:

(i) how environmental conditions and sampling methods can account for different population sex ratios;

(ii) the extent to which environmental conditions influence various aspects of male and female reproduction; and

(iii) some evolutionary implications of hippo behaviour and population dynamics.

During the peak drought period of 1970-71 at least 150 hippopotami died in the Letaba and Olifants rivers of the KNP (Anon. 1971). These deaths resulted from a combination of malnutrition and exposure, or from wounds sustained during fights. To avoid similar die-offs and the over-utilization and trampling of grazing areas during future droughts, it was decided to crop these hippopotamus populations to maintain them at approximately their post-drought numbers (Joubert & Pienaar 1973). By late 1973 populations had increased markedly and cropping was initiated in 1974. Recovery of the hippopotamus populations after 1971 was linked to improved habitat conditions following a period of above average rainfall which started in 1972 and continued up to 1979. The only previous cropping operation was during the 1964 drought when 104 hippopotami were shot in the Letaba River (Pienaar, Van Wyk & Fairall 1966).

Materials and Methods

Between May 1974 and August 1975 data were collected from 225 hippopotami cropped in the Letaba River, Olifants River and in Orpen dam in the KNP (Table 1). Animals were shot during May, June, August and September of 1974 and during August 1975. Sex data only were available for an additional 238 hippopotami shot in the Crocodile, Olifants and Letaba rivers during 1976 and 1977. Hippopotami were selected along the rivers depending on their group size and accessibility to the recovery team. Animals were shot randomly in the water as they surfaced. Samples of between six and 19 were taken from one locality per day. In a few instances, it was possible to remove entire groups, depending on group size and available escape routes. Dead animals were removed from the river soon after they reappeared on the surface. On land they were numbered, degutted and sexes established. Reproductive material was removed, weighed and examined in the field with ovaries and testes being preserved, sectioned and examined later as described by Smuts, Hanks & Whyte (1978). Females were tested for milk or colostrum and sperm smears were taken from the slit epididymides of males. Ages were assessed as described by Laws (1968).

Calving season was estimated by using foetal weights and calculating conception dates as described by Huggett & Widdas (1951). An average birth weight of 42,14 kg was calculated from records in the literature (Burton 1962; Laws & Clough 1966; Pienaar *et al.* 1966; Young 1966) and the gestation period was assumed to be 240 days (Asdell 1946; Kenneth & Ritchie 1953).

Using the gestation time of 240 days, t_0 (the time during which the embryo would be too small to weigh) was calculated at 48 days (Huggett & Widdas 1951). Data from the same months of different years were pooled to give an average frequency distribution of births versus month of the year. Birth data from small calves collected during the cropping operations were used to augment the data for the months of birth and together these were compared with monthly precipitation. Rainfall data were taken from three permanent stations within the KNP that were closest to the areas of collection. Rainfall data collected between September 1973 and August 1975 were used.

Results

Sex Ratios

The localities and sexes of the 225 hippopotami cropped during 1974-75 and the 238 cropped during 1976-77 are given in Tables 1 and 2, respectively. Sex ratios for different age classes (1974-75 hippopotami) are given in Table 3.

Table 1

Localities and sex ratios of 225 hippopotami of all ages cropped in Kruger National Park during 1974 and 1975

Locality	1974		1975		1974 +1975		Females %	Chi-square value	P-value
	♂	♀	♂	♀	♂	♀			
Letaba River	23	44	19	39	42	83	66,4	13,45	<0,005
Olifants River	28	48	—	—	28	48	63,2	5,26	<0,025
Orpen Dam	3	7	4	10	7	17	70,8	4,16	>0,05
Totals	54	99	23	49	77	148	65,8	22,40	<0,005

Male Reproduction

Growth of the left and right testes for 76 hippopotami together with information on spermatogenesis are shown in Fig. 1. Epididymal smears show that sperm production commences at an early age (Table 4). The first spermatozoa were, however, only found in seminiferous tubules at five years of age when the combined testes weight was 189 g. According to seminiferous tubule histology the median age at the start of spermatogenesis was six years, and, at this age, the combined testes weight was approximately 266 g (Fig. 1), and mean seminiferous tubule diameter approximately 160 µm (Fig. 2). Because of the limited months of collection it was not possible to investigate seasonality in male hippopotami.

Table 2

Localities and sex ratios for 238 hippopotami of all ages cropped in Kruger National Park during 1976 and 1977

Locality	1976		1977		1976 + 1977		Females %	Chi-square value	P-value
	♂	♀	♂	♀	♂	♀			
Crocodile River	27	49	4	10	31	59	65,6	8,71	<0,005
Olifants and Letaba rivers	20	45	30	53	50	98	66,2	15,56	<0,005
Totals	47	94	34	63	81	157	66,0	24,27	<,005

Table 3

Sex ratios for different age classes of hippopotami cropped in Kruger National Park during 1974 and 1975

Age Class (years)	Males	Females	Females (%)	Chi-square value	P-value
Prenatal	16	16	50	—	—
0-5	17	23			
6-10	15	16			
11-15	5	12			
16-20	9	5			
0-20	46	56	54,9	0,98	>0,05
21-25	4	21			
26-30	19	35			
31-35	7	27			
36-43	1	9			
21-43	31	92	74,8	30,25	<0,005
0-43	77	148	65,8	22,40	<0,005

Female Reproduction

Growth in weight of the ovaries of non-pregnant hippo cows is almost linear (Fig. 3). Ovaries from primiparous females indicated that the first really noticeable increase in follicle size (>10mm) started at six years of age. However, since one six-year-old cow was pregnant (Table 5), puberty probably commences at five years of age in certain cases. The average age at sexual maturity is 9-10 years (50% pregnant) and aparently all females are sexually mature at 11 years (Table 5 and Fig. 3).

Table 4

Presence of epididymal sperm in 76 hippopotami cropped in Kruger National Park during 1974 and 1975. (Months sampled = May, June, August and September)

Age (years)	Number of hippopotami Sperm present	Sperm absent	Total
1	0	4	4
2	1 (very few)	1	2
3	1 (few)	2	3
4	1 (few)	4	5
5	1 (few)	1	2
6	3 (many)	0	3
7	3 (many)	0	3
8	2 (many)	0	2
9	4 (many)	0	4
10+	48 (many)	0	48

Fig. 1. Growth in weight of hippopotamus testes with age (n = 76). ○ = no spermatogenesis; ◑ = slight spermatogenesis; ● = full spermatogenesis.

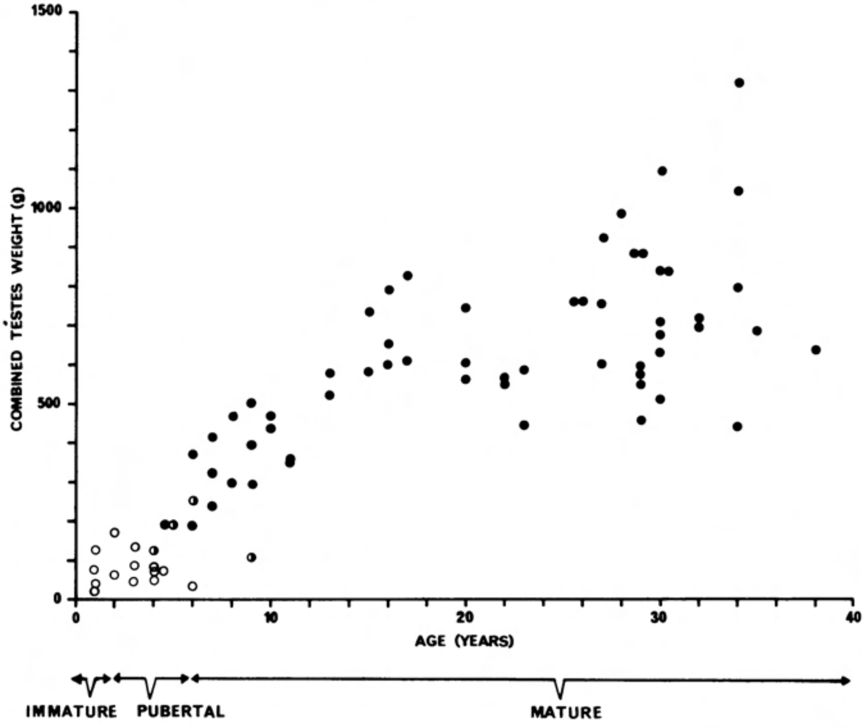


Fig. 2. Growth of seminiferous tubules in hippopotami (n = 70).

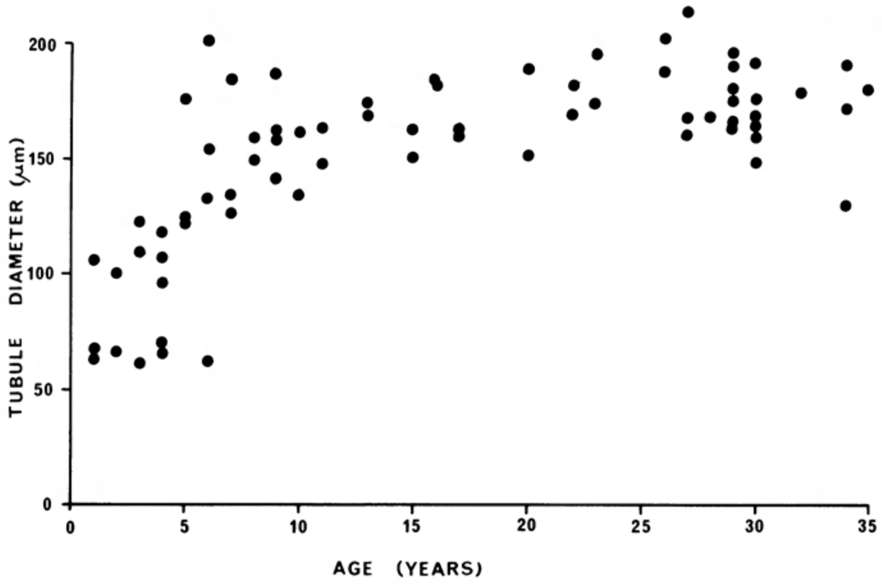
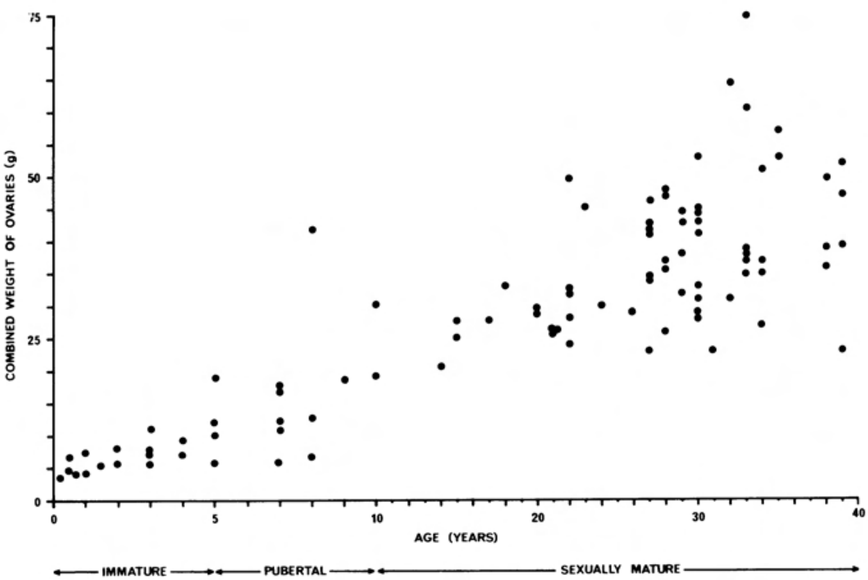


Table 5

Reproductive activity for a sample of 147 hippopotamus cows shot in Kruger National Park during 1974 and 1975

Age or age group (years)	Pregnant and/or lactating		
	n	No	%
1	9	0	0
2	5	0	0
3	3	0	0
4	2	0	0
5	4	0	0
6	2	1	50,0
7	5	0	0
8	5	1	20,0
9	1	0	0
10	3	2	66,0
11-15	11	11	100,0
16-20	5	5	100,0
21-25	22	22	100,0
26-30	35	32	91,4
31-35	26	24	92,3
36,43	9	8	88,9

Fig. 3. Growth in weight of hippopotamus ovaries with age (n = 95 non-pregnant cows).



One of 109 adult cows (11+ years old) was sterile. The ovaries of this 15-year-old were bilaterally hypoplastic (combined weight = 2,5 g), there were no follicles present and the tissue consisted chiefly of densely interwoven smooth muscle fibres (Imes **pers. comm.*). It is possible that ovarian atrophy had been brought on by vascular impairment since schistosomes had caused severe blood vessel lesions. A 25-year-old pregnant female had one abnormal ovary (687,0 g), which was grossly diagnosed as a teratoma, while the other ovary 54,5 g was normal (Imes *pers. comm.*). Most common tissue in the abnormal ovary was pseudostratified ciliated columnar cells resembling respiratory epithelium. Underlying the mucosa were typical mucus glands associated with respiratory mucosa. There were also spicules of cartilage present.

Accepting a gestation period of about eight months the mean calving interval for sexually mature cows (11+ years old) may be estimated by first calculating the duration of anoestrus (x) as follows (*vide* Hanks 1972):

---

*G.D. Imes
Zoonotic Pathology Division
Armed Forces Institute of Pathology
Washington D.C.
U.S.A.

$$\frac{\text{Number non-pregnant}}{\text{Number pregnant}} = \frac{x}{\text{length of gestation period}}$$

$$x = \frac{8(69)}{40} \text{ months}$$

$$= 13{,}8 \text{ months}$$

mean calving interval interval = x + 8 months

$$= 21{,}8 \text{ months}$$

Foetal implantation occurred on the same side as ovulation and ovarian activity was the same on both sides with 20 corpora lutea on the left and 20 on the right.

Aspects of hippopotamus reproduction for different periods (1964 and 1974-75) and different areas (KNP and Queen Elizabeth National Park, Uganda) are compared in Table 6.

Table 6

*Comparative reproductive data for adult female hippopotami from Kruger National Park and Queen Elizabeth National Park, Uganda**

Reproductive State	Kruger Park 1974-75		Kruger Park 1964**		Queen Elizabeth National Park 1961-63	
	No	%	No	%	No	%
Visibly pregnant	40	36,7	2	5,6	160	24,7
Lactating	85	78,0	20	55,6	389	59,9
Simultaneously pregnant & lactating	22	20,2	0	0	40	6,2
Sterile	1	0,9	0	0	0	0
Neither pregnant nor lactating***	7	6,4	14	38,9	140	21,6
Either pregnant or lactating or both pregnant and lactating	102	93,6	22	61,1	509	78,4
Sample size	109		36		649	

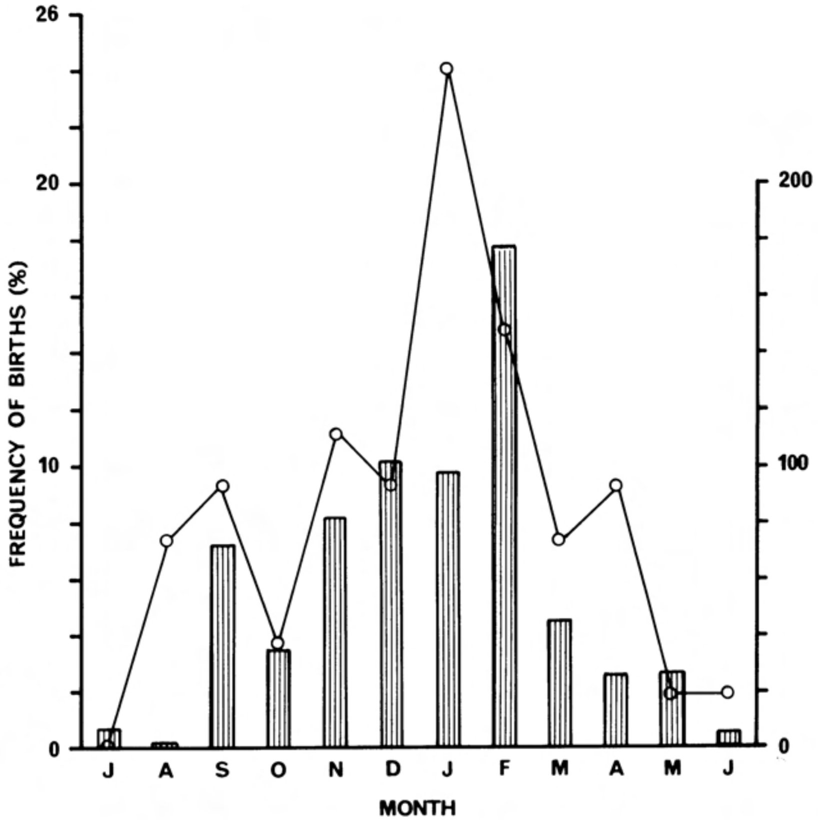
* Laws & Clough (1966)
** Pienaar *et al.* (1966)
*** This group includes animals with recent ovulations, *i.e.* true conception rates may be higher than those shown in the table.

Using previously described information the Huggett and Widdas regression equation describing foetal growth for hippo was:

$$y = -8{,}698 + 0{,}1812x$$

Figure 4 shows the relationship between expected birth and rainfall over a three year period.

Fig. 4. Average frequency distribution of births in hippopotamus cows (graph) and its correlation with monthly rainfall (histogram).



Discussion

Sex Ratio

Data in Tables 1 and 2 are remarkably consistent (63,2 - 66,4% of the population are females) for different rivers and different years of collection. The sex ratio (1 ♂♂: 1.9 ♀♀) for the whole sample (n = 463) is, however, different to the 1:1 ratio obtained by Pienaar *et al.*, (1966) in 1964 (n = 104 hippopotami of all ages). Since the actual shooting was random in both studies it is likely that the different population sex ratios resulted as follows:

i) During 1964 study, hippo were collected during an extremely dry period. The Letaba River stopped flowing and the Olifants reached its lowest recorded level in at least 70 years. Pools suitable for hippo habitation were limited and overcrowded. It is likely that because of severe competition for shelter there was no segregation of sexes or age classes with the result that shooting was automatically random with respect to the whole population.

ii) Between 1974 and 1977, however, the population had dispersed along the rivers as there were sufficient suitable pools available. Under these favourable environmental conditions normal population segregation took place with large herds (schools) generally consisting of one or two large (prime) bulls, sub-adult cows, and adult cows with their offspring. Old and young bulls tended to occupy smaller, apparently less favourable wallows. Since localities with large herds were selected where possible during the cropping operation, one would expect more females to be taken. Bere (1959) and Laws & Clough (1966) have shown that there is a definite tendency for males to congregate in small wallows while the associated lakes have a preponderance of females. Verheyen (1954) also found that hippopotami have a social structure in which males hold harems and other mature males are evicted. Strikingly similar results to those from the KNP have been reported for the Luangwa River in Zambia by Marshall & Sayer (1976). They found that when herds were cropped the sex ratio was 1 ♂ : 1,6 ♀♀ compared to unity when an effort was made to crop scattered individuals and small groups as well.

Table 3 indicates that between birth and 20 years of age the sex ratio is not significantly different from a 1:1 ratio. Here, nevertheless, the reduced number of young bulls relative to cows is almost certainly due to the sampling method previously described. The sex ratios of the first four groups of age classes indicate that young bulls start leaving the herds shortly after 10 years of age.

Although fighting amongst hippo is a mortality factor (Attwell 1963; Laws & Clough 1966; Pienaar *et al.* 1966) it is not known to what extent the sexes are influenced individually. Current evidence, however, indicates that sex ratios for all age classes together is close to unity for wild populations.

Age Structure and Age Determination

The small sample (Table 3) precludes a meaningful interpretation of age structure. Table 3 indicates that there are few individuals in age classes 11-15, 16-20 and 21-25 and a large number in age class 26-30. Large proportions of 26-30 year olds have also been reported by Marshall & Sayer (1976) and are evident in the data of Sayer & Rakha (1974). The first-mentioned authors have suggested that there is an anomaly in the technique used for estimating age. All three studies employed the technique of Laws (1968). This technique is based on the allocation of mean chronological ages to 20 groups of hippo and has not been verified by known-age material from a wild population. A similar technique described for elephant by Laws (1966) has recently been found to produce anomalies (Fatti, Smuts, Starfield & Spurdle 1980). As is the case with elephant, it is possible that errors are due to incorrect allocation of chronological ages. This could easily occur, especially in the older age classes, since Laws only had six known-age skulls (15-43 years old) all from captive reared animals. Laws (1968) suggested that: "Subsequent work may lead to refinements but in the meantime there is available an age scale based on objective criteria which can be used to analyse hippopotamus populations."

In contrast to the work of Laws (1968), Pienaar *et al.* (1966) used growth data from captive reared animals to estimate age. The differences between the two studies are extensive. According to Pienaar *et al.* (1966) hippos weighing between about 770-950 kg are 30-42 months old. Looking at age and sex specific hippo weights given by Marshall & Sayer (1976), who used the system of Laws (1968) for estimating age, one finds that animals of this weight are between seven and eight years old, a minimum age difference of four years. Evidence given by Laws (1968) on the validity of his method of age estimation and data provided by Marshall & Sayer (1976) indicate that despite certain defects the system of Laws (1968) is the most reliable method published so far. Finally, since Pienaar *et al.* (1966) used body weights to estimate the ages of young hippo, adverse environmental conditions before and during the time of their collection would have caused ages to be underestimated considerably. At the time of their study nothing had been published on hippo age determination.

Male Reproduction

Autolysis is generally a problem in hippos due to a long interval between death, removal and fixation of testis material. This probably accounts for sperm being located in epididymal smears but not in histological sections of the testis from the same animal. It is clear though (Table 4) that spermatogenesis commences at an early age (2 years) and that young bulls are sexually mature at six years of age. Puberty extends from age two to five. Although young bulls are mature at six years it is unlikely that they breed in the wild until they are considerably older. Combined testes weights for young males reach the adult weight range by eight years of age but the asymptotic weight is only reached at 25-30 years (Fig. 1). In instances where most or all of the individuals in a large school were shot, the "herd bulls" (largest males) were between 26 and 34 years of age. There were generally one or two of these big males per herd.

Laws & Clough (1966) found that 50% of the hippo bulls in their large sample were mature at five years of age when looking at the presence of spermatozoa in the epididymis (range = 4-11 years). Boulière & Verschuren (1960) report a captive male hippopotamus in the Antwerp Zoo which had a fertile mating at an age of about three to four years. Similarly Dittrich (1976) provides evidence showing that sexual maturity in male hippopotami in captivity ranges from about 2,5 - 7,25 years of age. Data thus indicate that under the present conditions hippo bulls in the KNP are sexually mature at an early age similar to captive animals. It is unlikely, however, that wild young bulls are allowed to breed effectively until they are considerably older and it seems probable that psychological maturity in the wild is only attained at about 20 years of age.

Puberty and Sexual Maturity

The gradual increase in size of the ovaries of non-pregnant hippo cows (Fig. 3) is largely due to increased follicular activity during puberty and later to the presence of corpora lutea in various stages of regression.

Although the average age at sexual maturity for the KNP hippoptami (9-10 years) was similar to those given by Laws & Clough (1966) (9,5 years-Uganda) and Sayer & Rakha (1974) (11 years-Zambia), full reproductive capacity was reached earlier in the KNP (11 years) than in Uganda (20 years) or Zambia (20 years). These differences are possibly related to the excellent habitat conditions experienced throughout the KNP since 1972.

Details from hippo cows reared in captivity show that some are fertile at an early age (2 years 3,5 months; Dittrich 1976). These results are similar to those reported by Pienaar *et al.* (1966) (mature in third year and calve in fourth year) but indicate sexual maturity at an earlier age than the findings for other wild populations where the system of age determination described by Laws (1968) was used. As mentioned in the preceding section, we believe that the rough system used by Pienaar *et al.* (1966) is invalid and as such cannot be compared with other published work. Further, assuming that Pienaar *et al.* (1966) estimated ages incorrectly, and that Laws (1968) is correct, then the statement of Pienaar *et al.* (1966) should read that cows mature in their seventh year and calve in their eighth. This would be compatible with our findings especially if one considers that the 1964 hippo were collected during and after a severe drought period, which would have caused maturity to be delayed. Although Laws & Clough (1966) state that the realistic range for puberty is 7-15 years, their "Table 1" shows that the range for puberty is actually 3-17 years with one three-year-old and three four-year-olds out of samples of 28 and 20 respectively, being sexually mature. In our study there were only five animals in the 3-4 year group (Table 5) and the first pregnancy occurred at about five years of age. In contrast to Dittrich (1976) we conclude that hippo in the wild can, and sometimes do, start breeding at an early age similar to those in captivity, but that this early breeding is restricted to a small minority. The possible influence of nutrition and social behaviour on reproduction are discussed later in this paper.

Reproductive Senescence and Sterility

Table 5 shows that there is a slight drop in reproductive activity in the old age classes. Both the oldest cows (43 years) were, however, pregnant. Breeding into old age has also been recorded by Laws & Clough (1966) and Marshall & Sayer (1976).

Since the ovaries of only one adult cow in a sample of 109 indicated sterility (0,09%) this aspect is of little consequence to the population as a whole. The same appears to be the case for other populations, since no cases were found in the literature.

Calving Interval and Lactation

The calculated calving interval of 21,8 months indicates that under the reigning conditions hippo cows in the study area calve approximately once every two years. A two year cycle has also been suggested by Laws & Clough (1966) who add that lactation lasts for 10-12 months and anoestrus for four months. However, when applying the same formula we used to the data of Laws & Clough (1966) the following is obtained:

$$\text{Anoestrus (x)} = \frac{8\ (\text{number non-pregnant})}{\text{number pregnant}} = \frac{8\ (489)}{160}$$

$$= 24{,}5 \text{ months}$$

$$\text{and thus mean calving interval} = x + 8 \text{ months}$$

$$= 32{,}5 \text{ months}$$

These results indicate that under the conditions experienced in Queen Elizabeth Park, hippo were only calving every third year and not every second year as suggested by Laws & Clough (1966).

The conception rate of 36,7% obtained in our study is the highest figure published to date, and considering the good habitat conditions is probably close to the maximum. A slightly higher rate could have been obtained had more material been collected just prior to the main calving season. However, in an animal with a calving season which, despite an obvious peak, still spans the whole year (see next section) the months of collection have relatively little effect on assessing approximate conception rate (Smuts 1976).

When looking at other work on hippo reproduction one is tempted to conclude that some authors have doubted the validity of their own field data. Laws & Clough (1966), for example, suggest that the high percentage of lactating females (55,9), relative to those pregnant (24,7), is due to biased selection of their study specimens. The present study and all others undertaken to date (Laws & Clough 1966; Pienaar *et al.* 1966; Mackie 1973; Marshall & Sayer 1976 and Hancock 1978) clearly show that conception rates for hippo are low (20-36,7%) when compared to other large herbivores with gestation periods of similar duration. Similarly, where figures for lactating hippo cows are given, these are always considerably higher than conception rates.

The high percentage of lactating hippo cows in a population can be due either to a naturally long period of lactational dependence, or to calves suckling more than one adult female, *i.e.* calves may be suckling females without young of their own. Although the last statement may seem unlikely it has been documented (Laws 1969) for the African elephant *Loxodonta africana.* Additionally, in two instances from our study where entire groups of hippo were destroyed in one locality on the same morning, there were fewer calves than lactating females. When looking at shot samples, when all animals in a group were shot, one finds that there are always considerably more lactating females than 0-5 year old calves, the ratio being roughly one calf to two or three lactating females (see Tables 3 and 6 and Marshall & Sayer 1976). The ratio becomes even more disparate when younger calves (0-2 years) only are considered. Although young calves are difficult to shoot and also take longer to float than older animals, it is unlikely that only one out of every two or three shot is retrieved. The data at our disposal show that there are more lactating females than suckling calves and thus that a certain percentage of individual calves are suckling from more than one female. Hopefully future studies will help to clarify this matter.

In view of the above discussion the annual calving rate of 66% suggested by Marshall & Sayer (1976) for hippo from eastern Zambia must be viewed with caution, especially when one considers that only 34% of their adult females were pregnant. It would be impossible for hippo to achieve an annual calving rate of 66% unless conception rates were considerably higher.

Seasonality of Breeding

Although data were pooled to produce Fig. 4 it seems likely that births are correlated with rainfall as has been reported by Laws & Clough (1966). Further analysis indicated that 70% of all births occurred during the six wet months (October — March) when 80% of the precipitation occurs.

Reproduction and Environmental Stress

Data on puberty, sexual maturity, and average conception rates for hippo cows in different and in the same wild populations indicate that these animals are sensitive to deteriorating environmental conditions. The following illustrate this point:

i) Conception rates in the KNP increased from 5,6% in 1964 to 36,7% in 1974/75, during a drought and a pluvial period, respectively (Table 6). At the same time the percentage of lactating females rose from 55,6% — 78,0% and those simultaneously pregnant and lactating from 0 — 20,2%. In both studies the hippo were collected during the same time of the year (May — August 1964 and May — September 1974-75) and from the same general area.

ii) In Queen Elizabeth Park conception and lactation data were intermediate to those in the KNP (Table 6) as were, apparently, habitat conditions (Bere 1959; Laws & Clough 1966).

iii) The previously mentioned late ages at which full reproductive-capacity is achieved in Uganda and Zambia (20 years) (both areas overpopulated with hippo) when compared to the KNP in 1974-75 (11 years).

iv) The earlier age at which breeding commences in captivity (Dittrich 1976) is most probably related to improved nutrition and reduced social stress.

During times of nutritional stress one can expect many facets of somatic development to be retarded and the chances are that hippos are influenced more severely than are other large herbivores, the possible reasons being:

a) They are almost exclusively nocturnal grazers with the result that feeding time cannot be extended much to cope with food shortages.

b) They are dependant on deep accessible pools for shelter during the day. During drought conditions the availability of these pools becomes a severe limiting factor. As water levels drop in rivers hippo are forced to congregate in the remaining suitable pools. These gradually become overcrowded and fouled with excreta. Intraspecific interactions increase, while at the same time animals are forced to move greater distances to find suitable grazing. Associated herbivores further aggravate the situation through their feeding and drinking habits. The net effect is that energy expenditure exceeds energy intake and growth and reproduction are influenced.

It appears that environmental constraints have caused hippo to adopt a reproductive strategy which includes a long intercalving period, late age at maturity, and a 1:1 population sex ratio. These attributes are typical of animals with a low reproductive potential and when one includes longevity and the high probability of survival of calves, hippo conform well to the requirements of a "K-selected" species. The possibility that hippo calves have an extended period of lactation dependence during environmental stress or that possibly they suckle more than one female indicates an adaptation to contain mortality and is further support for this strategy. On the other hand the short gestation period, when compared to large mammals such as elephant (22 months) or the white rhino *Ceratotherium simum* (15 months) (Kenneth & Ritchie 1953), should not be seen as an adaptation to increase reproductive rate but may rather be an adaptation to the aquatic environment which provides conditions for the calf similar to those for the foetus in the uterus. This environment, together with nocturnal feeding, reduce the influence of harsh temperatures and dessication and from the standpoint of energy demand, it is "cheaper" to let the calf walk than for the cow to carry it in her uterus. In association with low predation rates, these factors reduce the need for precocious young and hence greater birthweights and longer gestation periods.

In conclusion it seems that the reproductive strategy of the hippopotamus is well adjusted to the climatic fluctuations so typical of the semi-arid parts of Africa. Here they have traded the ability to exploit transient environments for the ability to maintain relatively stable populations with low rates of increase, low rates of mortality, and a close adjustment to the long-term carrying capacity of the environment. In most instances where their population behaviour is to the contrary, the direct or indirect influence of man appears to be implicated. The 1970-71 die-off in the KNP, for example, was accentuated through the reduced flow in the rivers resulting from large dams and farming activities upstream. The status of hippo populations throughout Africa is likely to become more threatened in future, particularly as farming activities increase, thereby reducing grazing areas, river flow during critical times of the year, and inevitable siltation of river systems associated with agricultural and industrial expansion.

Acknowledgements

We thank the National Parks Board of Trustees for permission to publish this paper and for providing facilities in the laboratory and field. The late Mr. J. de Kock helped during field operations. Thanks are extended to Messrs. L. Wagener, E. Wood, J. Marais, L. Mangane, P. Chauke, J. Sithole and P. Nkuna. Thanks are also due to the Natal Parks, Game and Fish Preservation Board for laboratory facilities and to Mrs. A. L. Ludbrook who undertook the histological work. Mrs T. I. E. Anderson and Miss B. W. Tathan kindly typed and retyped the manuscript.

REFERENCES

ANON., 1971. Annual Report. Department of Nature Conservation 1970-71. National Parks Board of Trustees.

ASDELL, S.A. 1946. Patterns of Mammalian Reproduction. New York: Comstock.

ATTWELL, R. I. G. 1963. Surveying Luangwa Hippo. *Puku* 1: 29-50.

BERE, R. M. 1959. Queen Elizabeth National Park: Uganda. The hippopotamus problem and experiment. *Oryx* 3: 116-124.

BOURLIÈRE, F. and J. VERSCHUREN. 1960. Introduction a l'écologie des ongules du Parc National Albert. *Explor. Parc natn. Albert. Inst. Parcs. Nat. Congo Belge, Bruxelles.*

BURTON, M. 1962. *Systematic Dictionary of Mammals of the World.* London: Museum Press.

DITTRICH, L. 1976. Age of sexual matruity in the hippopotamus *(Hippopotamus amphibius). Int. Zoo Yb.* 16: 171-173.

FATTI, P., G. L. SMUTS, A. M. STARFIELD, and A. A. SPURDLE. 1980. Age determination in African elephants. *J. Mamm.* 61: 547-551.

HANCOCK, P. 1978. Dynamics of an overutilized area in the Ndumu Game Reserve, Tongaland. M.Sc. thesis, Univ. of Natal.

HANKS, J. 1972. Reproduction of elephant *(Loxodonta africana)* in the Luangwa Valley, Zambia. *J. Reprod.Fert.* 30: 13-26.

HUGGET, A. St. G. and W. F. WIDDAS. 1951. The relationship between mammalian foetal weight and conception age. *J. Physiol* 114: 306-317.

JOUBERT, S. C. J. and U. de V. PIENAAR. 1973. An aerial census of elephant, buffalo and other large game in Kruger National Park. Memorandum, National Parks Board of Trustees.

KENNETH, J. H. and G. R. RITCHIE. 1953. Gestation periods. A table and bibiliography. Technical communication No. 5. *Commonwealth Bureau of Animal Breeding and Genetics.* Edinburgh.

LAWS, R. M. 1966. Age criteria for the African elephant *(Loxodonta a. africana). E.Afr.Wildl. J.* 4: 1-37.

LAWS, R. M. 1968. Dentition and ageing of the hippopotamus. *E.Afr. Wildl.J.* 6: 19-52.

LAWS, R. M. 1969. Aspects of reproduction in the African elephant *(Loxodonta africana). J. Reprod. Fert.* Suppl. 6: 193-217.

LAWS, R. M. and G. CLOUGH. 1966. Observations on reproduction in the hippopotamus *(Hippopotamus amphibius* Linn.) *In:* Rowlands, I. W. (Ed). *Comparative Biology of Reproduction in Mammals.* London: Academic Press.

MACKIE, C. S. 1973. Interations between the hippopotamus *(Hippopotamus amphibius* L.) and its environment on the Lundi River. Thesis, University of Rhodesia.

MARSHALL, P. J. and J. A. SAYER. 1976. Population ecology and response to cropping of a hippopotamus population in eastern Zamiba. *J. App.Ecol.* 13: 391-403.

PIENAAR, U. de V., P. VAN WYK and N. FAIRALL. 1966. An experimental cropping scheme of hippopotami in the Letaba river of the Kruger National Park. *Koedoe* 9: 1-33.

SAYER, J. A. and A. M. RAKHA. 1974. The age at puberty of the hippopotamus *(Hippopotamus amphibius* Linn.) in the Luangwa river in eastern Zambia. *E. Afr.Wildl.J.* 12: 227-232.

SMUTS, G. L. 1976. Reproduction in the zebra mare *(Equus burchelli antiquorum)* from the Kruger National Park. *Koedoe* 19: 89-132.

SMUTS G. L., J. HANKS and I. J. WHYTE. 1978. Reproduction and social organization of lions from the Kruger National Park. *Carnivore* 1: 17-28.

VERHEYEN, R. 1954. Monographie éthologique de l'hippopotame *(Hippopotamus amphibius* Linn.) *Explor.Parc natn.Albert. Inst. Parcs. Nat. Congo Belge, Bruxelles.*

YOUNG, E. 1966. Nutrition of the hippopotamus *(Hippopotamus amphibius). Afr.Wildl.* 20: 165-167.