REPRODUCTION IN THE UGANDA DEFASSA WATERBUCK, *KOBUS DEFASSA UGANDAE* NEUMANN

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(Received 16th April 1968, revised 10th June 1968)

Summary. The reproductive organs of the defassa waterbuck are similar to those of *Caprinae*. There appeared to be a seasonal fluctuation in testes weight, the lowest weight occurring in the driest month of the year. The female is poly-oestrous and monotocous and can conceive at the first *post partum* oestrus. Ninety-two per cent of implantations occurred in the right uterine horn but the left ovary was more active than the right. The highest incidence of births appeared to be correlated with the two wet seasons. The lowest incidence of conceptions appeared to be correlated with the lowest maximum temperatures. The possible relevance of temperature to sexual periodicity is discussed.

INTRODUCTION

There is little information on reproduction in the waterbuck, *Kobus* sp., other than Heape's observation (1901) on the length of di-oestrus in *K. ellipsiprymnus*, Gerhardt's (1933) description of the penis and Amoroso, Kellas & Harrison Matthew's (1954) investigation of placentation in *K. defassa*. There have been several comments on times of calving in different parts of the continent, and Kiley-Worthington (1965) and Spinage (1968) have described reproductive behaviour.

The present observations were made on the Uganda defassa waterbuck, *Kobus defassa ugandae* Neumann, in the Queen Elizabeth Park in western Uganda, which is situated between longitudes 29°45'E and 30°15'E, and latitudes 30'S and 15'N. The climate is semi-arid with an average rainfall at Mweya, the Park headquarters, of 670 mm (26.4 in.) per annum, with dry periods from December to February and June to July.

MATERIALS AND METHODS

Between August 1963 and April 1967, fifty-nine males and eighty-two females were killed and the reproductive organs obtained. The ages of the animals were determined by the methods outlined by Spinage (1967).

Large organs and foetuses were weighed in the field. Small foetuses were fixed in 10% formalin and weighed in the laboratory. Pieces of testis and

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epididymis were fixed in Susa fluid, and pieces of seminal vesicle and mammary gland in 10% formalin. Ovaries were fixed in 10% formalin and afterwards sliced transversely with a razor blade into approximately 1-mm sections. The number of follicles visible to the naked eye was counted and diameters of corpora lutea and follicles of about 5 mm or more were measured with calipers. Corpora albicantia were counted.

Histological sections were cut at 5 to 8 μ . Testes and epididymides were stained in Heidenhain's iron haematoxylin alone, and all other tissues were counterstained with eosin using standard procedures.

Ova were recovered by sectioning the Fallopian tube.

Some animals were captured by using immobilizing drugs (Short & Spinage, 1967) and were released after recovery.

RESULTS

THE MALE

General description of the adult reproductive organs

The adult testes had a mean combined weight of 147.9 ± 4.5 g, and the epididymides had a mean combined weight of 37.3 ± 6.0 g. Adult testis weight was reached in the 5th to 6th year and did not appear to decline thereafter (Table 1). The seminal vesicles were lobulated and had a mean weight of 21 g. The ampullae of the vasa deferentia weighed approximately 7 g.

TABLE 1

MEAN PAIRED WEIGHTS OF TESTES, EPIDIDYMIDES, SEMINAL VESICLES AND AMPULLAE OF THE VASA DEFERENTIA FOR EACH YEAR OF AGE

Age (years)	Sample size	Mean paired wt of testes (g)	Mean paired wt of epididymides (g)	Sample size	Mean paired wt of seminal vesicles (g)	Mean paired wt of ampullae (g)
1	8	4	2	1	1.4	0.7
2	6	38	19	—	—	—
3	4	108	13	—	—	—
4	2	68	14	—	—	—
5	10	127	23	2	15.4	4.7
6	7	143	24	1	20.9	10.2
7	8	151	42	3	25.7	5.1
8	4	148	51	3	21.2	6.4
9	3	155	22	1	18.1	6.2
10	5	151	27	3	18.3	7.1
11	2	138	52	—	—	—

The penis was of the fibro-elastic type similar to that of the ram. The glans was pigmented and bore the urethral orifice at the extremity of a urethral process; this process was extended in the erect penis. The preputial opening was situated about 25 cm anterior to the testes and the extended penis would probably reach about 15 cm beyond this point.

Histology of the testis and epididymis

The foetal testis had descended to the scrotal entrance by the 111th day of gestation, where it remained until after birth. The germinal cells in a 179-day foetus were similar in size to those found in a male in which spermatogenesis had not commenced, but the foetal gonad contained more interstitial tissue. The development of the testis is summarized in Table 2. All adult testes showed active spermatogenesis without any apparent decline in testis tubule diameter

TABLE 2
DEVELOPMENT OF THE TESTIS

Age	Sample size	Histological appearance of the testis	Mean diameter of seminiferous tubules (μ)	Appearance of epididymis
179-day foetus	1	Seminiferous tubules without lumina	50	No contents
$\frac{1}{2}$ yr	2	Tubules without lumina, primary spermatocytes in division	40	No contents
1 yr	5	Some tubules with lumina, some spermatozoa present	50	No contents
$1\frac{1}{2}$ yr	3	Many tubules with lumina, spermataids present, spermatozoa rare	110	Few spermatozoa and debris
2 yr	2	Many tubules with lumina, few spermatozoa	110	No contents
3 yr	4	Most lumina with spermatozoa	160	Packed with spermatozoa
4 yr	2	Active spermatogenesis in all tubules	160	Packed with spermatozoa
5 yr	5	Active spermatogenesis in all tubules	170	Packed with spermatozoa
6 yr	4	Active spermatogenesis in all tubules	190	Packed with spermatozoa
7 yr	6	Active spermatogenesis in all tubules	190	Packed with spermatozoa
8 yr	1	Active spermatogenesis in all tubules	160	Packed with spermatozoa
9 yr	1	Active spermatogenesis in all tubules	180	Packed with spermatozoa
10 yr	3	Active spermatogenesis in all tubules	180	Packed with spermatozoa
11 yr	1	Active spermatogenesis in all tubules	180	Packed with spermatozoa

TABLE 3
MONTHLY CONDITION OF TESTES IN ADULTS 6 YEARS OF AGE AND OLDER

Month	Sample size	Mean paired wt of testes (g)	Mean paired wt of epididymides (g)	Mean seminiferous tubule diameter (μ)
January	3	166.7	26.6	215 (2)
February	4	152.5	77.5	197
March	3	156.7	63.3	174 (1)
April	3	162.3	27.7	206 (2)
May	0	—	—	—
June	3	138.3	31.0	169 (1)
July	6	117.4	25.9	186 (3)
August	7	136.8	14.8	178 (2)
September	3	126.0	25.7	180
October	2	155.0	35.0	197
November	2	160.0	25.0	167
December	2	155.0	60.0	193 (1)
Mean $\pm$ S.E.		147.9 $\pm$ 4.5	37.3 $\pm$ 6.0	187.5 $\pm$ 4.7

Figures in parentheses after last column refer to sample size where this differs from column 2.

or testis weight with age. Spermatozoa were first observed in the testis at 1 year and in the epididymis at 1½ years. Only a few cells were found in the latter at this age, but by the 3rd year the epididymides of all healthy males were packed with spermatozoa. There was no significant difference in testis tubule diameter per month ($P > 0.05$). Testis weight showed an apparent seasonal fluctuation ($0.05 > P > 0.025$), the lowest weight being recorded in the driest month, July, but the monthly sample was small (Table 3).

THE FEMALE

General description of the adult reproductive organs

The female reproductive tract was similar to that of the ewe and had a mean weight of 230 g ($n = 7$) in non-pregnant animals. The overall length from vulva to the curve of the cornua was about 30 cm and the vagina measured about 14 cm in length. The ovaries had smooth surfaces interrupted by the reddish swelling of the corpus luteum when present, and the smaller vesicle-like swellings of the follicles. The mean weight of the left ovary, 2.81 g, was significantly greater than that of the right, 2.36 g ($n = 80$; $0.05 > P > 0.025$). Mean dimensions of the left ovary were $21 \times 17 \times 13$ mm, and those of the right $21 \times 15 \times 11$ mm.

Development of the ovary to puberty

The ovaries of a 51-day *ante partum* foetus were small in size and consisted of germinal cells and connective tissue. Those of an 18-day *ante partum* specimen showed hypertrophy due to the development of Graafian follicles (Pl. 1, Fig. 1), weighed 0.50 g and 0.49 g, and measured $10 \times 9 \times 9$ mm each. Regression appeared to occur after birth. A female approximately 5 months old (weighing 43.6 kg) had ovaries weighing 0.26 g (L) and 0.21 g (R); they also contained Graafian follicles but apparently had a greater amount of connective tissue (Pl. 1, Fig. 2). A female of about 6 months, weighing 51.7 kg, had ovaries of 0.60 g (L) and 0.35 g (R), with much larger follicles reaching 4 mm in diameter. No animals less than 1 year old ($n = 9$) showed signs of corpora albicantia, and they were present in only two out of twelve animals aged 1 to 2 years.

In the 1st year of life, the mean paired ovary weight was 1.02 g and rose to 2.3 g in the 2nd year; pregnant animals in their 2nd year had ovaries exceeding 3 g. By the 3rd year, mean adult ovary weight was reached.

The mature ovary

The follicle. Follicular development appeared to remain constant throughout life, the mean number of follicles per ovary being twenty-six (Table 4). Text-fig. 1 shows that the follicles were probably also produced at a constant rate throughout most of the period of gestation, the apparent rise at parturition not being significant ($P > 0.05$). The number of follicles exceeding 5 mm in diameter, which averaged 1.4 per pair of ovaries, showed a rise at the beginning of pregnancy followed by a steady decline to nil at full term, and developed again in the *post partum* period (Table 5). The largest Graafian follicle measured 11 mm in diameter.

PLATE 1

FIG. 1. Section of ovary of 222-day-old foetus showing Graafian follicles. Scale equals 1 mm.

FIG. 2. Section of ovary of approximately 5-month-old female showing an apparent reduction in ovary size and number of follicles. Scale equals 1 mm.

The corpus luteum. When the ovum was in the two-cell stage the corpus luteum was 6 mm in diameter and had attained 10 mm by the time that the four- to eight-cell stage was reached, with rapid occlusion of the lumen. The corpus luteum of pregnancy was maximum in size by the 30th day and remained constant in size until full term. After parturition regression occurred rapidly. No accessory corpora lutea were found.

TEXT-FIG. 1. Ovarian changes during pregnancy. Top: Scatter diagram of number of follicles per pair of ovaries. Centre: Mean number of follicles > 5 mm diameter. Bottom: Mean diameter of the corpus luteum, vertical lines represent range. The broken line suggests the behaviour of the Graafian follicle at ovulation showing collapse in size after the ovum is extruded. The size of the corpus albicans is shown at 21 days *post partum*.

Sections of ninety-nine corpora lutea were examined histologically. Theca lutein cells could not be distinguished. The cytoplasm of the luteal cells appeared to undergo an increase in vacuolation towards full term but it was not readily apparent. Some luteal cells were darkly staining with dark nuclei having the appearance of pyknosis.

Corpora albicantia counts varied from nought in a 9-year-old animal to ten

in a 10-year-old. There was no correlation between the number of observed corpora albicantia and the expected number of pregnancies (Table 6).

Counts of corpora lutea plus corpora albicantia per ovary showed that the left ovary was 1.2 times more active than the right.

TABLE 4
MEAN NUMBER OF FOLLICLES VISIBLE TO THE
NAKED EYE PER PAIR OF OVARIES FOR EACH
YEAR OF AGE

Age (years)	Sample size	Mean no. of follicles	Range in no. of follicles
1	9	26	16 to 41
2	12	26	10 to 48
3	2	26	13 to 39
4	6	35	15 to 76
5	8	27	13 to 45
6	4	26	14 to 38
7	9	23	12 to 43
8	2	22	5 to 38
9	6	29	19 to 42
10	8	27	13 to 46
11	3	31	8 to 50
12	5	19	8 to 28
13	1	> 35	
14	7	25	13 to 54
Mean $\pm$ S.E.		27 $\pm$ 1.2	12 to 45

TABLE 5
DEVELOPMENT OF THE CORPUS LUTEUM AND NUMBER OF
FOLLICLES > 5 MM IN DIAMETER DURING GESTATION

Days of pregnancy	Sample size	Mean no. of follicles	Mean diameter of CL (mm)	Range of diameter of CL (mm)
0	10	0.8	11.4	6.0* to 16.0
0 to 30	6	1.6	15.6	14.0 to 19.0
31 to 60	7	2.3	14.9	13.0 to 17.0
61 to 90	16	1.6	14.8	13.0 to 16.0
91 to 120	2	1.5	17.2	16.0 to 18.5
121 to 150	10	1.0	15.1	13.0 to 17.0
151 to 180	8	0.5	15.2	13.5 to 16.5
181 to 210	12	0.2	14.6	12.5 to 17.0
211 to 240	8	0	16.6	13.5 to 22.0
Post partum	3	0.7	12.0	11.0 to 14.0

* Recent ovulation, egg in two-cell stage.

Duration of reproductive activity

The average female life-span was estimated to be about 13 years (Spinage, unpublished data); one exceptional animal, calculated to be 18½ years old at death, gave birth 2 months before she died although the calf was lost within 2 weeks.

TABLE 6
MEAN NUMBER OF CORPORA ALBICANTIA
FOR EACH YEAR OF LIFE

Age (years)	No. of animals	Mean no. of corpora albicantia	Range
1	9	0	0
2	12	0.4	2 to 3
3	3	0.7	0 to 2
4	8	1.5	0 to 3
5	9	2.0	0 to 6
6	7	1.5	0 to 3
7	11	2.0	0 to 4
8	3	2.0	1 to 3
9	6	3.0	0 to 5
10	9	4.0	2 to 10
11	4	2.5	1 to 4
12	5	4.5	3 to 8
13	1	4.0	
14	7	4.0	1 to 6

Post partum oestrus

Two marked females were killed at 61 and 62 days *post partum*, respectively. The first, aged 10 years, was not pregnant and the ovaries contained a corpus luteum 11.5 mm in diameter. The corpus albicans of the previous ovulation was 6.5 mm in diameter and pale yellowish in colour.

The second animal was 12 years old and bore a foetus estimated to be 43 days old. The corpus luteum was 13.0 mm in diameter and eight corpora albicantia were counted.

Two animals in their first pregnancies, with foetuses aged 72 and 176 days, had no corpora albicantia. The evidence from the second animal suggested that conception could sometimes take place at the first *post partum* oestrus, and the evidence from the two primiparous females suggested that conception could take place at the first oestrus.

Pregnancy

Implantation. Of the forty-seven animals examined, implantation had taken place in the left uterine horn in four cases and in the right in forty-three, a preference for implantation in the right of 92%.

Placentation is of the cotyledonary, syndesmochorial type. Cotyledons were well formed by the 43rd day. Their number varied from twenty to forty-eight.

Foetal development. In the male, dark-coloured papillae of the horn primordia appeared by the 67th day. By the 111th day, vibrissae were present on the snout and eyelids and the testes were above the scrotum. Both sexes were fully hirsute by the 181st day. The eyes opened about the 190th day and in the final week preceding parturition the first incisors may have cut the gum.

Of the sixty foetuses older than 30 days which could be sexed, thirty were male and thirty female.

No twins were seen. In none of the animals was it possible to obtain an accurate record of gestation length.

Birth prediction

The date of birth of a foetus was predicted by using the method of Huggett & Widdas (1951). Thirty-two days was chosen for the x intercept for the following reasons. Female Y120 gave birth on 9th December 1966 and was killed on 9th February 1967, 62 days *post partum*, when the foetus weighed 1.87 g ($\sqrt[3]{W} = 1.2$). Y139 was killed 104 days *post partum* and had a foetus weighing 88.5 g ($\sqrt[3]{W} = 4.4$). If $\sqrt[3]{W}$ is plotted against days of gestation with a t_0 of 32 and 48 days, the maximum $\sqrt[3]{W}$ being 25 at 240 days (the heaviest recorded foetus was 14.2 kg and gestation has been given as 240 days for *K. ellipsiprymnus* (Spector, 1956) and 243 days for *K. defassa* (Dekeyser, 1955), then the expected gestation period for known foetal weights can be predicted (Text-fig. 2).

TEXT-FIG. 4. Distribution of births of waterbuck in the Queen Elizabeth Park predicted from foetal weights (top) and observed newborn calves (bottom). Cross-hatched sections in top diagram show births from animals collected in August and September which may bias the result.

The closest correlation is obtained with a t_0 of 32 assuming Y139 passed 42 days *post partum* before conceiving again. This could have meant two oestrous cycles of 21 days, Heape (1901) giving a cycle length of 21 days for *K. ellipsiprymnus*.

Female Y120 gave birth on 16th April 1965, 11th February 1966 and 9th December 1966, giving two *post partum* intervals of 61 days. Y112 calved on 7th March 1966 and had calved again by 15th January 1967. She was killed on 6th March 1967, which should have been 65 days *post partum*; she was still not pregnant, although she had recently ovulated and had a regressing corpus albicans.

The dates of birth of seventy-two foetuses were predicted (Text-fig. 3). Of these, nine were from the Semliki River Valley and have been omitted from subsequent analyses. Of the remaining sixty-three (three of which were neonates), 43% were collected in August and September in connection with other studies. The sample was, therefore, biased for the months of August to April

TEXT-FIG. 5. Correlation of seasonal distribution of births and conceptions with mean rainfall, mean minimum and mean maximum temperature.

against May to July. The total number of predicted births showed that parturition occurred throughout the year, but with two peaks correlated with the two wet seasons and a marked decline in the June–July dry season (Text-fig. 4). Assuming an equal chance of being born in any month of the year, this distribution was significant ($0.05 > P > 0.025$). If the bias is removed ($n = 63$ to 21)

then the distribution is no longer significant. Fifty-one, observed newborn calves showed a similar pattern with a significant decline during the dry seasons. Adding the 'unbiased' figures to the observed births showed a highly significant decline ($P < 0.001$).

The latter data were converted to time of conception. Conceptions were then plotted against the 10-year average monthly rainfall for Mweya, and against mean monthly minimum and maximum temperatures recorded from 1965 to 1966. The closest correlation was found with the drop in maximum temperature, least conceptions occurring when the mean maximum temperature failed to rise above 27.9° C (April and November, see Text-fig. 5).

The mammary gland

The female has two pairs of inguinal teats. The mammary gland weighed approximately 40 g in the adult virgin female and reached a weight of nearly 2 kg when full of milk. Colostrum was produced at least 23 days before estimated parturition and was a thick, sticky yellowish liquid in the unsuckled gland. Regressed glands due to calf loss were common but no case of mastitis was observed ($n = 24$).

The quiescent gland consisted of much connective tissue and fat cells. Lactating glands had distended alveoli and secreting acini with a single-layered epithelium. The examination of histological sections could only reveal whether a gland recorded in the field as not lactating was in fact active. If lactating tissue was not found in section then it was not possible to say whether the animal was lactating without having examined most of the gland.

In a continually breeding animal like the waterbuck the adult should be permanently lactating except when she stops feeding the calf at heel to produce colostrum for the next birth.

DISCUSSION

Pregnancy

An asymmetrical preference for implantation is probably not unusual in wild ungulates. It has been recorded in the dikdik, *Rhynchotragus kirkii* (Kellas, 1954), Uganda kob, *Adenota kob* (Buechner, 1961) and impala, *Aepyceros melampus* (Mossman & Mossman, 1962).

Statements such as "Twins perhaps not infrequent" (Ansell, 1960) are probably due to the fact that calves often associate so that two may be seen following one female. Riney & Kettlitz (1964) record an instance of twins in *K. ellipsiprymnus*, whilst an oft-quoted reference is that of Frechkop (1954) who found three embryos in a female, a rare departure from normal as the waterbuck is undoubtedly monotocous.

Sexual periodicity

Although it has long been known that some African ungulates appear to breed throughout the year whilst others are more seasonal, there is little information to date upon sexual periodicity. Small reliance can be placed upon sub-

jective estimates of calving periods as movement of observers in many parts of Africa is restricted during the wet seasons, giving bias to observations.

Laws & Clough (1966) found in the hippopotamus, *Hippopotamus amphibius*, taken from the same area as the waterbuck, that peaks in numbers of births were correlated with peaks in rainfall, the distribution being similar to that of the waterbuck. In both species gestation length is the same; peaks in numbers of births occur in similar months and least numbers occur in June and July. The least numbers of conceptions also occur in October to November in both species, but the hippopotamus did not show a decline during April corresponding to that of the waterbuck.

As there are, on average, 5 dry months and 7 wet months in the year, the question first to be answered is whether, assuming an equal chance of conception or birth occurring in a wet or a dry month, the distribution of conceptions/births is due to chance. Analysis shows that, for both species, the unequal distribution is significant ($0.05 > P > 0.025$). Thus, in the waterbuck, 11% more conceptions in the dry seasons gives 22% more births in the wet seasons.

Testis weight appeared to show some cyclic fluctuation with minimal weights occurring in July, but there was no apparent correlation with rainfall fluctuations nor with fluctuations in numbers of conceptions. This may be due to the small sample size ($n = 38$) for Clough (1966) found in the hippopotamus, using a sample size of 245, that testis weight fluctuated randomly. But he found a correlation between testis activity, as measured by the relative numbers of different stages of spermatogenesis, and conceptions. In the waterbuck, the monthly sample was considered too small to justify such an analysis. As in the hippopotamus, there was no apparent correlation between testis tubule diameter and numbers of conceptions.

In relation to sexual periodicity, it can be assumed either that natural selection has operated to favour births at the most propitious time of the year, this being a teleological assumption in the absence of any knowledge of survival rates; or, that some environmental factor has a direct effect upon mating or conception. The former alternative is obviously inflexible for, if the seasons change, the young will be born at the wrong time.

In the waterbuck, there is as yet no evidence to suggest that dry seasons are unfavourable for calves. The numbers of conceptions were highest when the conditions were driest, and lowest just before the rainfall tailed off, or when the wet seasons were having their maximum effect. Amount or quality of food as a factor influencing conception is therefore a debatable question.

Photoperiodism, an important factor in sexual rhythms in temperate zones, is unlikely to constitute a factor as day length on the equator is constant to ± 2 min throughout the year. Times of sunrise and sunset vary 30 min between February and the end of October but show no obvious correlation with the numbers of births or numbers of conceptions.

The difference between minimum and maximum mean temperatures at Mweya ranged from 5.0 to 12.1°C . During the months when conception in the waterbuck was lowest, the maximum temperature failed to rise above 21.2°C on some days, whilst the minimum temperature dropped to 16°C . Although these temperatures are within the accommodation range of waterbuck (Taylor

& Spinage, unpublished data), the fluctuation to which they are exposed is much more marked than is indicated by minimum and maximum mean temperature records. Whether temperature is a factor influencing sexual periodicity in the waterbuck is at present open to question, but the study of temperature as a causative factor in tropical sexual rhythms would seem to warrant more investigation than it has so far received.

ACKNOWLEDGMENTS

I am grateful to Dr R. M. Laws for his advice and encouragement in this project and to the Nuffield Unit of Tropical Animal Ecology for providing facilities. I am also grateful to the Director and Trustees of the Uganda National Parks for permitting this work to be carried out in the Queen Elizabeth Park, and to the Science Research Council of Great Britain who financed the project. I also wish to thank Miss B. O. Vidler who kindly cut most of the histological sections. Finally I am grateful to the Zoological Society of London for providing facilities at the Wellcome Institute of Comparative Physiology.

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