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REPRODUCTIVE PHENOMENA DURING THE *POST PARTUM*–PRECONCEPTION INTERVAL IN THE UGANDA KOB

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Summary. Female Uganda kob antelope conceive while lactating maximally and may continue lactating to 180 days of pregnancy. Udders of lactating females exceed 450 g in weight; in non-lactating adults, udders weigh < 300 g. The uterus is grossly involuted by 20 to 30 days post partum, declining from about 1000 g to <100 g. Immature ovarian follicles of 2 to 5 mm diameter occur at about the same rate both in pregnant and non-pregnant adults. Mature follicles > 5 mm in diameter are absent in the last 60 days of gestation and are rare in the first 20 days post partum. Follicles in oestrous females become >8 mm, increasing to 11 mm at ovulation which may commence at about 10 days post partum. Some females may conceive at this time. Seven females conceived at <65 days post partum. Post partum females commonly have up to four or five oestrous cycles before conception. Many oestrous periods recur at 6- to 13-day intervals and are accompanied by ovulations resulting in accumulations of small CL which begin to regress before reaching maturity. These brief dioestrous intervals are thought to result from premature regression of cyclic cL brought on by increased secretion of oxytocin induced by various sensory stimuli associated with the territorial mating grounds to which oestrous females go to mate.

INTRODUCTION

A previous article (Buechner, Morrison & Leuthold, 1966) concerning reproduction in the Uganda kob, Adenota kob thomasi (Neumann) gave a preliminary report on several aspects of reproduction and territorial mating behaviour. It was shown that although post partum anoestrous intervals may be short and apparently not prolonged by lactation, conception may be preceded by several recurrences of oestrus, even at unusually brief intervals, and by the proliferation of small, partially developed but regressive cl. Since then, cl morphology has been described in detail (Morrison, 1971) and the overall data have been elaborated to interpret more completely the reproductive events occurring in the post partum-preconception interval.

This African antelope is characterized by an arena or lek type of territorial

mating behaviour found in some avian species such as sage grouse and prairie chicken (Buecher, 1961a). The larger arenas or territorial mating grounds contain thirty to forty breeding males defending individual mating territories. Mating occurs throughout the year and oestrous females remain on the mating ground for about 24 hr, moving with impunity from one territory to another while the males remain bound to their individual territories. Mating rarely occurs off the territorial mating ground. Under these conditions, it was possible to observe the mating behaviour of animals captured and tagged for individual recognition (Buechner, 1963; Buechner & Schloeth, 1965).

The female kob gives the impression of being almost continuously pregnant and the present article is concerned with the reproductive characteristics associated with or influencing the length of interval between parturition and the ensuing return to pregnancy. It is also concerned with the possible cause of the small, regressive cyclic cL of ovulation and the correlation between accumulations of these cL and oestrous periods repeated at unusually brief intervals of 6 to 13 days.

MATERIALS AND METHODS

The collection of kob and the circumstances and methods of study have been described previously (Buechner et al., 1966; Morrison, 1971). In brief, 197 pregnant and 144 non-pregnant females were collected at various times in 1957 to 1958 and 1962 to 1964. Some females were marked individually to facilitate observations on behaviour. Females of known and unknown breeding histories were collected from all stages of reproduction, providing a foetal growth curve and information on lactation, uterine condition and ovarian morphology.

Although the subject here concerns post partum-preconception aspects of reproduction, certain information from pregnant females that is related to the reproductive characteristics of non-pregnant females is included to illustrate features in transition or overlapping between the two states.

Morphological characteristics of CL studied by histological methods described previously (Morrison, 1971) were correlated with behavioural evidence where appropriate for analysis.

RESULTS

Lactation

Lactation inhibits follicular development, ovulation and oestrus in many species of mammals (Perry & Rowlands, 1962) but does not always do so in kob. Over half the non-pregnant females collected while in oestrus and over half the pregnant females up to 180 days of gestation were lactating (Table 1). After 180 days of pregnancy, lactation diminished markedly because of the weaning or death of fawns. The lesser incidence of maximal lactation in oestrous females compared to non-oestrous females suggests that oestrus is favoured by the cessation of lactation, though it is more probable that it reflects the small size of the sample of non-pregnant females. The high proportion of lactating

females in early gestation indicates that suckling has little influence on oestrus and ovulation.

Additional evidence for ovulation and conception in lactating females existed in Females 137 and 156 (Table 2) which were found to contain newly

Table 1

Lactation in 237 parous female kob collected throughout the reproductive cycle

No. of females in conditions of lactation						
No lactation	Minimal lactation	Maximal lactation	Total females			
10	7	7	24			
4	7	18	29			
55	25 6	49 5	129 55			
	No lactation	No lactation Minimal lactation 10 7 4 7 55 25	No lactation Minimal lactation Maximal lactation 10 7 7 4 7 18 55 25 49			

^{*} Calculated with growth curve derived from known-age foetuses (Buechner et al., 1966).

Table 2

Weights of udders and uteri and size of largest follicle at known and estimated intervals <20 days post partum

Female No.	Post partum interval to death (days)*	Uterus wt (g)	Udder wt (g)†	Largest vesicular follicle (mm)
47	<1	1311	900	4.0
138	1 to 2	730	850	3.0
79	2 to 4	585	150	3.0
392	2 to 4	511	794	3.0
92	2 to 4	395	825	5⋅0
103	2 to 4	366	1075	2.0
159	2 to 4	260	960	4.0
200	5 to 10	190	652	4.0
115	5 to 10	139	764	6.0
137	5 to 10	128	740	4.0‡
156	10 to 20	90	714	4.0\$

^{*} Estimated from condition of uterus (see text) except Female 47 whose still-born twins were found immediately after parturition and before elimination of the afterbirth.

§ Accompanied by one each of Class-A and Class-B cl.

formed cyclic cL of Classes A and B at <20 days post partum and also in six lactating females listed in Table 3 which had conceived at 65 days, or less, post partum. Udders of lactating females included in Tables 2 and 3 averaged 727 ± 38 g in weight, compared to 120 and 150 g in the two non-lactating females.

[†] All lactating maximally except Female 79 which was not lactating. ‡ Accompanied by Class-B cL (defined previously by Morrison, 1971).

By 222 to 233 days of gestation, the udder weights of nine gravid, non-lactating females averaged 263 ± 51 g. In nine other females at 234 to 245 days (very close to term), udders weighed 633 ± 143 g, the largest having recrudesced to 1589 g. Milk was extruded easily from three of the largest udders and they appeared capable of nursing immediately after parturition.

Preconception events following parturition

Regression of CL of pregnancy. Hammond (1927) found that CL of pregnancy in cattle remain at full size for 30 to 60 days post partum, and he believed they prevent ovulation from commencing. In kob, CL of pregnancy remain at full size $(11.6\pm0.02 \text{ mm})$ until parturition but immediately after parturition they diminish rapidly in size and undergo extensive histological degeneration (Morrison, 1971) which begins in the final 4 weeks of gestation. The CL of pregnancy measured 7.3 to 10.8 mm, with a mean of 8.5 ± 0.44 mm, in ten

Table 3 weights of udders and uteri, sizes of largest follicles, and post partum intervals to conception at known post partum intervals of $>\!20$ days

Female No.	Reproductive condition	Parturition to collection (days)	Parturition to conception (days)	Udder wt* (g)	Uterus wt (g)	Largest vesicular follicle (mm diam.)
404 469 428 420 435 418 413 430 433	Non-gravid Embryo microscopic Embryo microscopic Non-gravid Embryo microscopic Embryo microscopic Embryo microscopic 50 days pregnant† 48 days pregnant†	20 25 27 30 46 58 69 100 113	10 to 15 12 to 17 31 to 36 43 to 48 54 to 59 50 65	539 653 454 549 696 624 120 510 794	50 95 120 105 142 150 80 292 396	6·0 7·0 5·0 6·0 8·0 7·0 None 7·0 5·0

^{*} All lactating maximally except Female 413 which was not lactating.

females collected within 10 days post partum. After 10 days post partum, the regressing CL of pregnancy measure <5 mm.

Involution of the uterus. The uterus involutes rapidly after parturition in the kob. Female 47 (Table 2) was collected within about 1 hr post partum. The extraembryonic membranes were still present in the uterus. Females 404 and 469 (Table 3) were collected at known intervals of 20 and 25 days post partum, respectively. Nine other females were collected at intervals estimated to be from 1 to 20 days post partum (Table 2) according to the extent of their uterine regression interpolated between that of Females 47, 404 and 469. The uteri of Females 47 and 138 contained fully developed and pedunculate caruncles, the largest of which measured 40 mm in diameter. The foetal membranes of Female 138 were expelled but much mucus and blood remained in the uterine lumina. At 2 to 4 days post partum, the caruncles were slightly reduced though still highly pedunculate. Less mucus or blood remained in the uterus. The caruncular peduncles were greatly reduced at 5 to 10 days but the caruncles projected

[†] Calculated with growth curve derived from known-age foetuses (Buechner et al., 1966).

10 mm into the lumina. Blood or mucus remained only in traces. At 10 to 20 days, mucus and blood were absent. The caruncles had regressed into flattened plates which extended 5 to 10 mm into the uterine lumina. At 20 to 30 days, the caruncles were <5 mm in height and much reduced in diameter; the largest had regressed to <30 mm in diameter. The weights of the uteri in these females decreased rapidly, declining from over 1000 g at parturition to about 100 g at 10 to 20 days. These conditions suggest that the uterus may be sufficiently regressed to accept implantation within 3 weeks of parturition.

Follicular development. The onset of oestrus and ovulation in ungulates is dependent on the development of mature Graafian follicles at the end of the post partum anoestrus. Immature follicles, 2 to 5 mm in diameter, vary slightly in number in most kob. Oestrus females may contain twenty-five to thirty immature follicles, but other non-pregnant and pregnant adults have twelve to twenty immature follicles regardless of length of gestation or state of lactation.

One or two maturing follicles 5 to 8 mm in diameter occurred in each of seventy-nine females at <100 days of pregnancy. The incidence declined to <25% in seventy-three females at 100 to 180 days. Maturing follicles were absent in thirty-five females collected after the 180th day of pregnancy. At <20 days post partum, only two follicles of this size range (Females 92 and 115, Table 2) were found among eleven females. Two other females collected at 5 to 10 days post partum, however, had new CL of Classes A and B which would have required fully mature follicles. After 20 days post partum, maturing follicles became more abundant, especially in oestrous females, occurring in over 70% of a sample of fifty-four females.

The maximum size of follicles at ovulation exceeds 9 mm. Six oestrous females each had one follicle measuring 8 mm and two others each contained a 9-mm follicle. None of these follicles appeared to be at the point of ovulating. A female collected at 15 min *post coitum* contained an 11-mm follicle which probably would have ruptured within a few hours.

Seemingly, there is a quiescent period for maturing follicles during the final 60 days of pregnancy and through the first 10 days *post partum*. The onset of ovulation is correlated with growth of mature follicles at the termination of the quiescent period.

Onset of ovulation and oestrus. One female exhibited weak oestrous behaviour 10 days after parturition and provided the only example of a known post partum interval to renewed mating activity. The presence of new CL in females collected at estimated and known post partum intervals indicates that ovulation can occur as early as 10 days post partum. Females 137 and 156 (Table 2) had new CL of Classes A and B at 10 to 20 days post partum. Females 469 and 428 (Table 3) had full-sized CL of pregnancy when collected at 25 and 27 days post partum, respectively. They were estimated to be 10 to 15 days pregnant. Back dating the estimated duration of pregnancy in these females puts the post partum interval to conception at 10 to 15 days in Female 469 and 12 to 17 days in 428. In an earlier paper (Buechner et al., 1966), the age of the CL in Female 469 was listed as 4 days and the minimum post partum interval to conception was given as 21 days.

Recurrent ovulation and oestrus. The proliferation of small cyclic CL and their

relationship to oestrous periods repeated at brief intervals are of primary concern here. The incidence of these CL is illustrated in Table 4. No new CL were present at <10 days post partum. The few Class-D and Class-E CL present at this time are carried over from before the recently ended pregnancy. After 10 days post partum, CL in Classes A, B and C are abundant and CL in Classes D and E become more numerous as regressive CL of Class C fail to mature and go through the regressive characteristics of Classes D and E (Morrison, 1971). After a female develops mature CL of pregnancy, small CL of Classes A, B and C are absent. All cyclic corpora that originate before the ovulation of conception regress through Classes D and E by 200 days of pregnancy, and most are regressed into Class F by 221 days.

Of the fifty-three non-gravid females of > 10 days post partum (Table 4), only eight females lacked new CL of Classes A to C. Twenty females had a single corpus of either Class A, B, C or D. Among the remaining twenty-five females, multiple corpora occurred in various combinations. Twenty-one females had

Reproductive condition	No. of	Average occurrence of corpora/female by class*						
	females	A	В	С	D	E	F	
Non-gravid, < 10 days post partum Non-gravid, > 10 days post partum Oestrous Non-oestrous	9				0.22	0.11	1.67	
	24 29	0·29 0·24	0·25 0·48	0·75 0·62	0·96 0·79	0·46 0·21	2·38 1·45	

Table 4
OCCURRENCE OF CORPORA LUTEA IN NON-PREGNANT, PAROUS FEMALES

two corpora of some combination of Classes A to D, three females had combinations of three corpora, and one female had a corpus of each class from A to D. In any combination, no two corpora were of the same class.

Seven of the oestrous females had ovulated very recently and were on the mating ground after having formed a Class-A cl. The incidence of Class-A cl might have been considerably higher if the other seventeen oestrous females had been collected a day or two later, allowing them time to ovulate and develop a new Class-A cl. This would have added five more combinations of two cl, six more combinations of three, and one more combination of four cl. The combination of a Class-A and a Class-C cl occurred more frequently than any other, especially when potential Class-A cl from ovulations in oestrous females are included.

Daily observations disclosed a succession of visits to mating territories by the females listed in Table 5. Females in the first group (Nos. 416 to 9/3) were immobilized and marked on the mating ground while in oestrus during the first observed visit of each animal. Females 20/6, 507 and 413 were also non-gravid and immobilized but were not in oestrus and were in feeding herds when captured away from the territorial mating grounds. Subsequently, they appeared in oestrus on the mating ground at intervals of 8 to 21 days after capture. Female

^{*} Criteria for each class described by Morrison (1971).

413 had given birth on the day before her capture. The initial visits of Females 458, 29/3 and 515 came at considerable intervals after being captured while pregnant. In the interim, they had completed gestation and parturition. Females 411, 488 and 494 were never immobilized and were identified by natural markings. The first visit listed for each female was the first observed; unobserved visits may have preceded some of these.

The intervals between successive visits were of lengths that fell into three

Table 5

Female uganda kob observed on successive visits to territorial ground*

Female No. and reproductive condition at initial capture or initial observation	Days from initial observation or capture to first visit and successive visits to territorial mating ground (intervals in parentheses)								
	1 st visit	2nd visit	3rd visit	4th visit	5th visit	6th visit	7th visit		
Captured by immobilization during oestrus on TG 416 447 442 9/3	0† (6) 0† (13) 0† (20) 0† (13)	6 (6) 13† (13) 20 (7) 13†	12† (6) 26‡ 27† (8)	18 (12) 35‡	30 § (6)	36§ (13)	49‡		
Captured by immobilization off TG, non-oestrous 20/6 507 413	8† (27) 21§ (26) 10¶ (24)	35† 47‡ 34§ (20)	54						
Captured by immobilization off TG, pregnant 458 29/3 515	154† (6) 219 (6) 251§ (5)	160 (7) 225 256†	167† (21)	188†					
Not captured, observed in oestrus on TG 411 488 494	0† (6) 0† (10) 0¶ (13)	6† (29) 10† 13†	35 (5)	40					

^{*} TG = territorial mating ground. Note: this table is a revision of Table 1 in Buechner et al. (1966). † Copulation observed.

§ Intense oestrous behaviour occurred but copulation was not observed.

¶ First visit was 10 days post partum.

natural categories: (1) a range of 5 to 8 days occurred in eleven intervals, six of which were 6 days in length. The 5-day interval in Female 515 indicates a minimum interval length. She returned to the mating ground on the 6th day also, when she actually copulated. Oestrus usually lasts about 24 hr (Beuchner et al., 1966); Female 515 probably entered oestrus on the 5th day but was not sexually receptive until Day 6, (2) seven intervals ranged from 10 to 13 days with five intervals being of 31 days, (3) seven intervals ranged amodally between 20 and 29 days.

The unusual brevity of the 5- to 8-day intervals suggested either that oestrus was not occurring in some visits or that visits were recurring within oestrous

Conception inferred from age of foetus, female not seen on TG during final visit.

periods which lasted up to 8 days. If oestrus did last 8 days, a female would be expected to remain on the mating ground almost continuously rather than appear only at the beginning and the end of the period. Numerous observations revealed that oestrous females seldom stayed on a mating territory for more than 24 hr. With few exceptions, the territorial mating grounds were monitored daily to verify the absence of these females between visits. Copulation or intense sexual behaviour often took place in succeeding visits at these brief intervals, which clearly established that oestrus occurred. Females not seen copulating or evincing intense oestrous behaviour, such as mounting other females or demonstrating great excitement, were probably at the beginning or end of oestrus. They refused the male's attention but remained on his territory.

It was not possible to correlate exactly a cyclic cL of any particular class with a specific visit to the mating territory in all females. Six females were collected between 14 and 137 days after their final respective visits, by which times their cL had regressed beyond Class C and could not be differentiated by age. There was, however, at least one CL of Class D or older for each visit in all females except No. 416. She visited the mating ground seven times, copulating or exhibiting oestrus, but possessed only three cL, of Classes D to F. Either some corpora were obliterated or she had failed to ovulate during some of the visits to the mating ground. Female 411 provided a good example of correlation between CL and visits to the mating ground. She contained one CL of Classes A, B, C and D, and eight of Class F. She was on a territorial mating ground when collected, and the Class-A cr would have originated about 24 hr earlier. The Class-B CL originated from the third visit, 5 days previously. The Class-C CL must have resulted from an unobserved visit within the 29-day interval, otherwise it would have regressed to Class-D or older. The Class-D cl came from her second visit, and a Class-F corpus from her first visit.

DISCUSSION

The pattern of reproduction in the kob that emerges is one of an early return to oestrus and ovulation after parturition, with the possibility of conceiving after a post partum anoestrus as short as 20 days, the approximate length of a normal dioestrous interval in large ungulates. Conception may, however, be delayed by repetitions of infertile oestrous cycles.

The high incidence of cyclic CL accumulating in non-pregnant females indicates that ovulation is commonly repeated one or more times before conception in this population of kob. There is good evidence that many of these ovulations are accompanied by oestrus and that both recur at intervals of 6 to 13 days in many cases. The principal questions arising concerning these phenomena are why do cycles recur and why do many of them recur at such short intervals?

Some repetitions of cycles may have resulted from disturbance or from pathological conditions described by Buechner et al. (1966). Another hypothesis for recurrent cycles concerns the phenomenon of unilateral implantation in the right horn of the uterus. Although implantation of all foetuses was solely in the right uterine horn, CL of pregnancy were distributed equally between right and

left ovaries (Buechner, 1961b; Buechner et al., 1966). One possibility was that some of the blastocysts migrating through the left uterine horn to the right horn failed to survive the migration, and that subsequent ovulations were repeated from the left ovary until implantation succeeded. Non-pregnant females collectively possessed 104 cL of Classes A to E in the left ovary and 84 in the right. A chi-square test showed no significant difference (P>0.05) between ovaries; nevertheless, the preponderance of cL in the left ovary may indicate that blastocyst loss is a possible cause of recurrent oestrus, although it does not explain the short dioestrous intervals.

It has been shown that ovulation may commence as early as 10 days post partum. The uterus may not be capable of accepting implantation until considerably later in some females, in which case cycles may be repeated until conception succeeds. A final possibility is that the earliest ovulations may not be accompanied by a sufficiently intense behavioural oestrus for coitus to ensue. These alternatives seem the most feasible explanations for recurrent cycles. It seems unlikely, however, that disturbances or diseased uteri would be prevalent enough in the population to cause the common pattern of frequent ovulations as the present data indicate.

The remaining question is, why do ovulation and oestrus recur at 6- to 13-day intervals, resulting in accumulations of small, partially developed, regressive CL, rather than at intervals of approximately 21 days when the CL have time to regress before the next ovulation ensues and so occur one at a time? Intervals exceeding 13 days in length did occur (Table 5). Seven intervals ranged from 20 to 29 days. These may be actual interval lengths or may include shorter intervals between unobserved oestrous periods. Female 20/6 had an interval of 27 days between visits (during which copulation occurred) to the territorial mating ground during a period when the ground was monitored daily, but in the other cases, unobserved oestrus may have occurred. The longer cycles would be meaningful if they occurred only after a series of short cycles and just before conception, indicating that some deficiency is finally overcome, allowing a normal cycle and pregnancy to follow. However, interval lengths recurred in no regular sequence.

The short dioestrous intervals are possibly explained best by the rapid degeneration of the accumulating small cL described here and in a previous paper (Morrison, 1971). Rapid degeneration of cyclic cL in kob resembles the accelerated regression of cL artificially induced in sheep and cattle. Moore & Nalbandov (1953) found that a plastic bead 8 mm in diameter inserted in the ewe's uterus at the 3rd day of the oestrous cycle shortened the cycle to a mean of 8·2 days. Exogenous oxytocin injected into cattle during Days 3 to 6 inclusive of the oestrous cycle shortened the cycle length to 8 to 12 days (Hansel & Donaldson, 1964). No information concerning events happening on the 3rd day of the kob's cycle is available, but their dioestrous intervals averaged 8·6 days.

Armstrong & Hansel (1959) described corpora lutea formed from oestrous cycles altered by oxytocin injections in cows. These CL were remarkably similar to the regressive Class-C CL of the kob. Hansel & Wagner (1960) found that uterine dilatation during the first 7 days of the cycle caused shortened dioestrous

intervals of 8 to 12 days in a large proportion of cows and heifers, and infusion of 2 to 5 ml of raw semen or the sediment of centrifuged semen and preputial fluid into the uteri of heifers at oestrus often caused a return to oestrus between Days 6 and 13 of the cycle accompanied by marked inhibition of development in CL which contained few normal luteal cells.

Oxytocin secretion increases naturally during lactation (Folley, 1956) or from massaging the vulva and cervix in cattle (Hays & VanDemark, 1953). Various exogenous stimuli are known to cause uterine contractions and letdown of milk in bovines (VanDemark & Hays, 1952; Folley, 1956). In the ewe, ovulation is hastened by the presence of the ram (Riches & Watson, 1954; Schinkel, 1954) which may be attributed to oxytocin released by sensory stimulation (Greep, 1961; Lehrman, 1961).

These findings indicate that oestrous cycles may be shortened and CL may be prevented from maturing normally by physiological conditions related to oxytocin secretion resulting from various sensory stimuli. Release of oxytocin near the time of oestrus in the kob may result from a variety of visual, auditory, olfactory, and tactile stimuli associated with the activity on the territorial ground, and may provide the mechanism through which the corpus luteum is prevented from maturing normally and the oestrous cycle is shortened. Female kob were within 1 km of their 'home' mating territory in 95% of 2713 observations on marked individuals (Buechner, 1963). Stimuli from the mating territory undoubtedly attract females approaching oestrus. The males often whistle loudly, frequently developing a chorus that can be heard for more than a kilometre, which seems to advertise the location of the mating ground and the readiness of the males to mate. The oestrous females can readily see the mating activity and smell the strong, barnyard-like odour at the territorial mating ground. When females enter the ground, they receive vulval and vaginal stimulation from the males. Many females are lactating copiously, presumably stimulated by increased secretion of oxytocin. The combination of stimuli functioning through oxytocin may be responsible for the regressed CL and short cycles.

Armstrong & Hansel (1959) and Malven & Hansel (1964) noted that oxytocin did not shorten cycles and inhibit CL growth in hysterectomized dairy heifers, indicating that an intact uterus is required for oxytocin to be effective. Hansel (1966) found that injections of purified bovine luteinizing hormone (LH) and other LH-containing preparations overcame the inhibitory effects of concurrently administered oxytocin on CL weight and progesterone content. Oxytocin apparently acts through the uterus to interfere with hypophysial LH secretion or with the effect of LH on the CL.

The significance of the short oestrous cycles in the kob and the mechanisms through which they are regulated are not yet clear and will require further research involving the physiological relationships of the uterus, hypothalamus, hypophysis and ovary.

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