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# OBSERVATIONS ON REPRODUCTION AND BREEDING BEHAVIOR OF THE AFRICAN ELEPHANT

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*Abstract:* Observations on the breeding behavior of the African elephant (*Loxodonta africana*) in Uganda show that some wild females begin to breed at approximately 7 years and all females breed by approximately 11 years of age. A declining population and lower annual increment of elephants south of the Victoria Nile River in Murchison Falls National Park are associated with an average postpartum preconception interval more than three times longer than the 24.1-month (*sic*) period reported in 1953 by Perry. The change in length of this interval is possibly a function of self-regulation in population numbers. At least in some parts of its range, the wild African elephant breeds throughout the year with no distinct seasonal acceleration. Corpora lutea present during early pregnancy are not replaced during a subsequent stage of pregnancy but are maintained throughout gestation and for about 2 months after parturition. Old or degenerate corpora lutea persist for at least 4.5 years postpartum. Apparently in some animals corpora lutea develop before conception, whereas in others, conception apparently occurs when corpora are established. At least two graafian follicles may ovulate and develop into corpora lutea within a short time. Cows have multiple mates, there is no prolonged male-female relationship, and frequently there is no fighting by bulls over females.

Information concerning breeding and reproduction of the African elephant is limited. One of the most extensive reports directed entirely to various aspects of reproduction of the African elephant is that of Perry (1953). His study is devoted largely to describing the female reproductive tract, and emphasizes ovarian characteristics. Recently, Johnson (1963) reported extensively on histological and quantitative characteristics of the testes of the African elephant. He includes observations on the teeth and pituitary gland, and presents evidence that suggests the possibility of individual cyclicality in reproductive activity of adult males. Short and Buss (1965) detected no progesterone in 11 corpora lutea from six African elephants in various stages of the estrous cycle and pregnancy, postulated a relatively short functional and long structural life of the elephant's corpus luteum, and suggested that some corpora lutea developed prior to conception.

The first three chapters of a monograph by Hill et al. (1953:11-67) on the elephant in East-Central Africa include general in-

formation on reproduction. The anatomy of the male reproductive system has been reported on by Mojsisovics (1879), Oudemans (1892), and Schulte (1937). Data on age at sexual maturity and duration of gestation are provided by Seth-Smith (1932), Hundley (1934), Burne (1943), and Flower (1943).

The African elephant breeds throughout the year, at least in those areas for which data are available. Krumbiegel (1943) and Ansell (1960) observed calves throughout the year. Perry (1953) noted fetuses of variable age in cows collected throughout the year in Uganda. Buss and Brooks (1961) and Buechner et al. (1963) found no evidence of seasonal peaks in parturition and concluded that breeding occurs throughout the year in Uganda. Considering that environmental conditions within the African elephant's extensive range are highly variable, and that information has been secured from a limited part of this range, the possibility of seasonal breeding in some areas cannot be ruled out.

The purpose of this study was (1) to study structures of 120 pair of ovaries from

elephants considered to be of potential breeding age, (2) to study mating behavior of wild elephants in the field, and (3) to study mating behavior of elephants in captivity. Of the elephants collected, 109 were from near and south of Murchison Falls National Park in Northwest Uganda and are considered to be the savanna subspecies (*Loxodonta a. africana*). Eleven were collected on the Semliki plains off the northern tip of the Ruwenzori Mountains in northwest Toro District, Uganda, and are of the forest subspecies (*L. a. cyclotis*).

The term *family unit* refers to an adult female and its offspring, or two or more closely related females and their offspring. These units usually number from 4 to 15 individuals, their activities are closely coordinated, and large bulls seen with them are generally attached loosely and temporarily.

A *herd* is defined here as a group of elephants consisting of two or more coordinated family units, usually accompanied by bulls.

The term *corpora lutea* in this report refers to yellow structures formed from follicles which ovulate and from follicles which luteinize without ovulating; these yellow structures are histologically similar.

The term *corpora rubra* refers to reddish brown structures that represent degenerate corpora lutea and show retrogressive changes histologically in the nature of fibrous involution. A microscopic section of a very old terminal corpus rubrum is shown by Perry (1953, Fig. 27) who states, with our concurrence, that ". . . it is almost indistinguishable from the surrounding stroma in a stained section."

The techniques of Johnson and Buss (1965) for estimating age of male African elephants have been used for the elephants in this study. Emphasis was placed upon molariform replacement rate as well as the

extent of tooth wear. Data on total body length and height at shoulder were used as supplementary aids. Molariform replacement rate, which would seem to have a higher correlation with age than anatomical size, probably does not vary significantly between sexes. Although an average difference in body size probably occurs between males and females of the same age, this difference would be less during early than late life. Accuracy is probably within 1 year for elephants up to 10 years of age; thereafter accuracy would become progressively less.

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tion on the elephants in the Portland Zoo. Douglas R. Wise, Cambridge University, assisted with the field work in Uganda for 3 months.

## OBSERVATIONS OF OVARIAN STRUCTURES

### First Breeding

Evidence indicates that the wild African elephant sometimes begins to breed at an age of approximately 7 years. Two medium-sized females, No. 12 (3,264 lb) and No. 13 (3,000 lb), were collected from a herd of 22 elephants during early morning of September 12, 1958, near Butuku in northwest Toro District, Uganda. The rest of the herd departed quickly, except a large, old cow that stood over one of the dead females (No. 12) and refused to leave. The defensive behavior this cow showed for the younger female suggested that the cow was the dead female's dam (see Buss 1961:145). This behavior proved to be typical and was often observed subsequently. All attempts to drive the cow from the dead female failed, and finally the cow had to be shot. We then discovered that a very recently born calf (No. 14) was with her in the tall grass, and we assumed that the old cow was the calf's dam, particularly since the cow was lactating and her nipples indicated recent nursing.

Dissection and examination of the old cow (No. 11, 5,590 lb) revealed a fetus which weighed 171 pounds; the calf (No. 14) which was nursing her weighed 173 pounds. Obviously the large cow, with a fetus estimated at 19 months of age (Fig. 1), was not the calf's mother, yet she was nursing and protecting it. Evidently she was either lactating when the calf (No. 14) was born or was stimulated subsequently to lactation by the presence of the calf.

Dissection and examination of the young female (No. 12) which the old elephant refused to leave revealed a 77-pound uterus with the endometrium only partially healed from recent calving. (In contrast, the uterus of No. 13, a nulliparous female of approximately the same age, weighed only 3.2 pounds.) No milk could be expressed from the mammary glands of No. 12, and dissection of her udder showed that she was not producing milk. Her right ovary (50 g) contained two corpora lutea which measured 25 and 22 mm in diameter; her left ovary (28.3 g) had no corpus luteum. There was no corpus rubrum or developing follicle in either ovary. We concluded, therefore, that this young female had given birth very recently to her first calf, and that the calf was nursing its pregnant grandmother.

The weight (3,264 lb) and the height at shoulder (6 ft 9 in) of female No. 12 were similar to the measurements of an 8.5-year female savanna elephant in the Zoological Gardens at Basel, Switzerland (E. Lange, letter dated November 10, 1959). The molariform status of No. 12 indicated an age of approximately 9 years. Subtracting 22 months for gestation results in an age at first breeding of roughly 7 years for this elephant.

Four savanna-type cows (Nos. 46, 53, 59, and 66) and their calves, varying in age from about 6 months to 5 years, provide additional information on first breeding. The age at first conception of these cows was obtained by subtracting a 22-month gestation period and a calf's age from the mother's age at the time of her collection. On this basis, the four cows conceived at about 8, 8, 9, and 10 years respectively.

Although some cows conceived when they were only about 7 years of age, others did not conceive until they were between approximately 10 and 11 years of age.

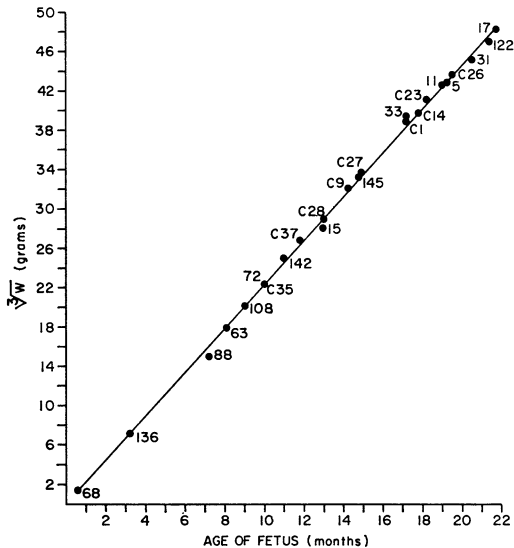


Fig. 1. Growth curve of 24 fetal African elephants calculated from Huggett and Widdas' formula  $W = a(t - t_0)$ . The average weight at birth is approximately 265 lb, the gestation period is assumed to be 22 months,  $t_0$  is taken as 0.17,  $a$  is taken as 0.0746, and  $t$  is calculated as days.

Eight cows (Nos. 39, 45, 97, 100, 103, 110, C9, and C55) were estimated to be about 8, 8, 8, 9, 8, 10, 10, and 8 years of age respectively. Their ovaries averaged 32.8 g and ranged from 15.6 to 49.5 g in weight. They contained no corpus luteum, no corpus rubrum, and developing follicles ranged from 1 to 5 mm in diameter except in one cow. Female No. C9, estimated at about 10 years of age, had ovaries weighing 48.8 and 49.8 g and containing developing follicles up to 7 mm in diameter, suggesting that she was approaching estrus. On this basis all eight cows were nulliparous.

All elephants that were at least 11 years of age in our series either were pregnant, were lactating and with nursing calves, or showed corpora rubra in their ovaries and were lactating, indicating that they had conceived at least once.

The sum of our observations on first breeding indicates that some wild African elephants in Uganda begin to breed at

approximately 7 years, and that all females have bred by approximately 11 years of age. Perry's statement (1953:106) that "... the wild African elephant may begin to breed at about 9 years of age ..." agrees with our observations and may be close to an average initial breeding age for the African elephant in Uganda.

#### Postpartum Preconception Interval

Evidence we obtained indicates that the interval from parturition to conception varies from approximately 9 months to approximately 4 years. An exceptionally short interval is indicated by data secured from a female forest elephant (No. 145) collected on April 17, 1964, on the Semliki plains. She was from a family unit of two cows with nursing young about 2 years of age. Milk was expressed readily by light pressure on her mammary glands, her nipples were freshly clean from nursing, and her udder weighed 12 pounds. Dissection revealed three large corpora lutea (21 to 26 mm diameter) and an 81-pound fetus estimated at approximately 14.8 months of age (Fig. 1). Her calf, therefore, was not more than about 9 months of age when she conceived.

On December 31, 1958, a family unit of five savanna elephants was collected soon after the unit had separated from a herd of at least 25 animals. The only females in the unit were two large cows (Nos. 53 and 54) that were lactating freely. The protective and defensive behavior displayed by these two lactating cows for the two youngest elephants in the family unit (Nos. 51 and 55) indicated that the young were progeny of the two cows.<sup>1</sup> This conclusion is supported by the parallelism of the size (1,796 and 1,805 lb) and estimated age (about 4 years) of these young elephants

<sup>1</sup> For a description of the behavior of the elephants in this family unit see Buss (1961:145).

to the size of corpora rubra (1 to 6 mm diameter) and the number of corpora rubra (14 and 18) in the cows' ovaries. Collectively, these behavioral and anatomical observations indicate that a postpartum period of about 4 years had elapsed.

The long postpartum period for these two cows provokes several questions. What is the average prevailing postpartum pre-conception period for the Murchison population, and does the length of this period change in the wild African elephant as population density changes? Evidence as to the average interval between parturition and conception may be obtained by comparing the relative numbers of pregnant and nonpregnant cows collected from the Murchison population. Our collection series of 120 adult cows includes 25 pregnant individuals, 93 animals classified as being in lactation anestrus, and 2 individuals judged to be in estrus. The distribution of pregnant to nonpregnant adult females may be regarded as a binomial where  $n_1 + n_2 = 1$ , and where  $n_1$  is the average gestation period and  $n_2$  is the average interval from parturition to conception. Using  $n_1$  as 22 months, the best estimate of  $n_2$ , applying Fisher's method of maximum likelihood, is 81.8 months (6.8 years), and the 95 percent confidence limits are 77.8 and 85.8 months. Perry (1953:107) used this same technique and on the basis of 31 pregnant to 34 nonpregnant adult females estimated 24.1 (*sic*) months as the most likely average interval between parturition and a subsequent conception. Thus it appears (1) that the postpartum period of about 4 years for Nos. 53 and 54 was not exceptional, and (2) that the prevailing average postpartum pre-conception interval for the Murchison population has indeed changed during the last decade, being more than three times as long as the one reported by Perry (1953:107).

The elephants south of the Victoria Nile River in the Murchison Falls National Park area are very crowded and compete for forage with buffaloes (*Syncerus caffer*) and hippopotamuses (*Hippopotamus amphibius*). In addition, the elephants are hemmed in closely by the Nile River, Lake Albert, two controlled hunting areas, and highways used by continually increasing numbers of hunters. Actually, the continual constriction of this elephant range appears to approach pen conditions. As a result, the range has been progressively and severely overutilized (Buss 1961, Buechner and Dawkins 1961). Aerial counts conducted in the Murchison area during 1963–64 showed that elephants declined by about 1,000 during the last 5 years, and the calves in the population decreased from about 7 or 8 percent in 1957–59 (Buechner et al. 1963:52) to approximately 6.0 to 6.5 percent (I. O. Buss and J. M. Savidge, typed ms. in files). From these observations we conclude (1) that the declining populations and lower annual increment in elephants south of the Victoria Nile River in Murchison Falls National Park are associated with an average postpartum pre-conception interval more than three times as long as that reported for 1947 to 1950 by Perry (1953), and (2) that the lengthening of this period possibly functions to self-regulate elephant population numbers.

#### Distribution of Breeding Dates

Observations of copulations (discussed in detail below) and conception dates extrapolated from fetuses of estimated age indicate that elephants in Uganda breed during every month. A fetal growth curve for 24 fetuses from the 25 pregnant elephants in our collection series (Fig. 1) has been calculated by using the formula proposed by Huggett and Widdas (1951) and

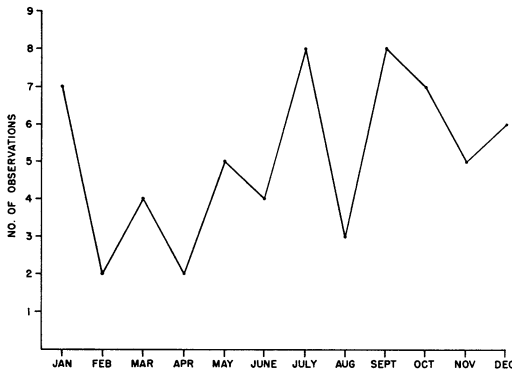


Fig. 2. Distribution of 61 breeding dates for Uganda elephants.

used by Perry (1953:101). When the estimated ages of these fetuses are subtracted from the respective dates on which the pregnant females were collected, a series of 24 breeding or conception dates, 11 dates of observed copulations, and deduced breeding dates from 26 fetuses obtained in Uganda and reported by Perry (1953) have been plotted and are presented in Fig. 2. Perhaps not all the 11 dates on which copulations were observed represent actual conception dates. Nevertheless, copulation probably is close to conception time. From the distribution of the 61 breeding dates presented in Fig. 2 it is seen (1) that breeding occurred throughout the year, and (2) that more elephants bred from July to November than at other times—this probably has no significance and reflects the few data available.

This information on distribution of breeding dates plus supporting evidence by Krumbiegel (1943), Ansell (1960), Buss and Brooks (1961), and Buechner et al. (1963) is conclusive that at least in some parts of its range the wild African elephant breeds throughout the year with no distinct seasonal acceleration.

### Longevity of the Corpus Luteum

In the laboratory the 120 formalin-fixed ovaries were wiped lightly with a paper towel, weighed to the nearest  $\frac{1}{40}$  gram, dissected, and the maximum diameter measured to the nearest mm. The ovary was then sliced into sections approximately 3 mm thick by starting at the free edge of the ovary and slicing parallel to but not toward the major axis of the hilum. In each section, the corpora rubra, graafian follicles, and corpora lutea were identified, counted, and the maximum diameter of each structure measured to the nearest mm. These structures, particularly the multiple corpora lutea (see Perry 1953), were then studied in relation to the reproductive cycle and to behavior of the elephants observed immediately prior to their collection.

An indication of the corpus luteum's longevity may be gained by tracing its size-maintenance through time. In Fig. 3 data are presented on maximum diameter: (1) of corpora lutea from 24 pregnant elephants, (2) of corpora lutea from 5 lactating cows collected with their calves up to about 6 months after parturition, and (3) of corpora rubra from 5 lactating cows collected with their calves from about 21 to 36 months after parturition. The upper end of each vertical line in Fig. 3 represents the maximum diameter of the largest corpus luteum (corpus rubrum of Nos. 73, 46, 38, 66, and 13) of both ovaries from a particular elephant; the lower end represents the maximum diameter of the smallest corpus luteum (corpus rubrum of Nos. 73, 46, 38, 66, and 13) from the same elephant. The lines in Fig. 3 for the 24 pregnant elephants are arranged from left to right according to gestational stage which was ascertained from fetal age (see Fig. 1), and the lines representing the 10 postpartum animals are arranged from parturition time to the right, according to the age of their calves.

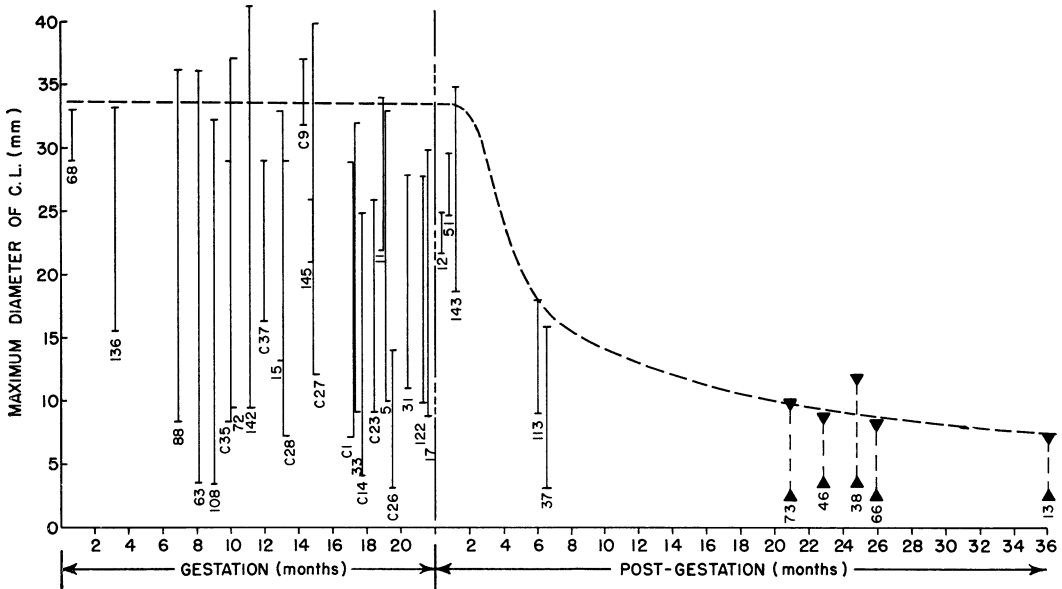


Fig. 3. Maximum diameters of corpora lutea from 24 pregnant and lactating elephants, and corpora rubra from 5 cows at approximately 21 to 36 months following parturition.

The curve in Fig. 3 (drawn near the maximum size of corpora lutea and corpora rubra) shows that corpora lutea were maintained throughout gestation and for a postpartum period of about 2 months. By approximately 6 months after parturition the corpora lutea had regressed significantly, and by about 21 months only corpora rubra were found. Thereafter, the rate of involution was very slow. Two cows (Nos. 53 and 54, discussed under "Postpartum Preconception Interval") collected about 4 years after parturition had corpora rubra from 1 to 6 mm in diameter. These data indicate that one set of corpora lutea lasts not only throughout pregnancy and for about 2 months after parturition, but also that the degenerate corpora lutea persist for at least 4 years postpartum. Short and Buss (1965) studied ovaries from six elephants and suggested that the corpus luteum persists structurally for a long time.

Perry (1953:134) states that "... one set of corpora lutea does not last throughout

pregnancy. Instead, it appears that those which are found in the ovaries in the earlier stages of pregnancy are replaced, usually near mid-term, by a very similar set, . . ." If this conclusion were valid, the degenerate remains of the first set should be readily distinguishable as corpora rubra in ovaries from young cows: (1) in late stages of their first pregnancies, or (2) in early postpartum stages with their first calves. Animals which were apparently in these categories were a pregnant cow (No. C14) and two postpartum females (Nos. 12 and 37), estimated at 8, 9, and 11 years of age, respectively.

The calves of Nos. 12 and 37 were estimated to be 2 weeks and 6 months of age, respectively (Fig. 3). Each cow was too young to have conceived more than once. Their ovaries contained no corpora rubra. The right ovary of No. C14 contained 7 corpora lutea, 4 to 21 mm in diameter; her left ovary contained 5 corpora lutea, 5 to 25 mm in diameter. The right ovary of No.



Table 1. Ovarian structures in three adult elephants.

ANIMAL	CORPORA LUTEA*	CORPORA RUBRA	DEVELOPING FOLLICLES	REMARKS
No. C44	14 (6-27)	6 (2-5)	14 (1-5)	Savanna type, 12 years of age, not pregnant, not lactating.
No. 140	6 (5-30)	none	12 (2-7)	Forest type, 9 years of age, not pregnant, not lactating.
No. 68	2 (29, 33)	7 (3-8)	9 (1-3)	Savanna type, very old, pregnant, fetus 3 weeks of age (3.5 g), lactating freely.

\* Numbers in parentheses indicate diameters in mm.

12 contained 2 corpora lutea, 25 and 22 mm in diameter; the left ovary had no corpus luteum. Additional information is provided by data from postpartum female No. 66 which we estimated at 10 years of age, and her calf which was estimated at 26 months of age when both were collected. Although No. 66 was not in an early postpartum stage, and her ovaries contained no corpus luteum, there were only 5 corpora rubra (4-8 mm diameter) in her right ovary, and only 3 (2-6 mm diameter) in her left ovary. The small number of corpora rubra suggests that she had only one set of corpora lutea.

Evidence that a single set of corpora lutea is maintained throughout gestation may also be seen by comparing the average number of corpora lutea during the first half of gestation with those during the second half. Counts of corpora lutea were obtained for 24 pregnant elephants. The average number of corpora lutea for 7 females in the first half of gestation was 6.6; the average number for 17 females in the second half of gestation was 6.2.

On the basis of this evidence we conclude that the corpora lutea present during early pregnancy are not replaced during any subsequent stage of pregnancy but are maintained throughout gestation and for about 2 months after parturition.

#### Estrus

Information concerning the period during which corpora lutea are formed was obtained from three cows (Table 1).

The 14 corpora lutea (6 to 27 mm in diameter) of No. C44, and the 6 corpora lutea (5 to 30 mm in diameter) of No. 140, must not have begun to develop simultaneously. Possible explanations include: (1) a series of silent heats (ovulation occurring without behavioral estrus), and (2) a number of estrous cycles accompanied by infertile matings (Perry 1953:123). All the corpora lutea of these two elephants were, by their macroscopic and histological appearance, too recent to be construed as regressing or degenerate corpora lutea of the preceding pregnancy. Since neither No. C44 nor No. 140 was pregnant, all corpora lutea developed prior to conception.

These data support those reported by Short and Buss (1965) suggesting that some corpora lutea develop before conception. This may not always be the case, as suggested by the fact that No. 68 had two large, similar-sized corpora, and a fetus about 21 days of age (Fig. 4). In this case, a fertile mating apparently occurred about when the corpora lutea were established.

The left ovary of No. 68 weighed 44.3 g, measured 66 × 53 × 22 mm, and contained no corpus luteum. The right ovary weighed 74.4 g, measured 68 × 63 × 30 mm, contained four follicles from 1 to 2 mm in diameter, and contained two light-yellow corpora lutea that measured 29 and 25 mm in diameter (Fig. 4). These corpora lutea will be referred to as A and B respectively.

Both A and B had a protuberance which Perry (1953:131) “. . . regarded as mark-

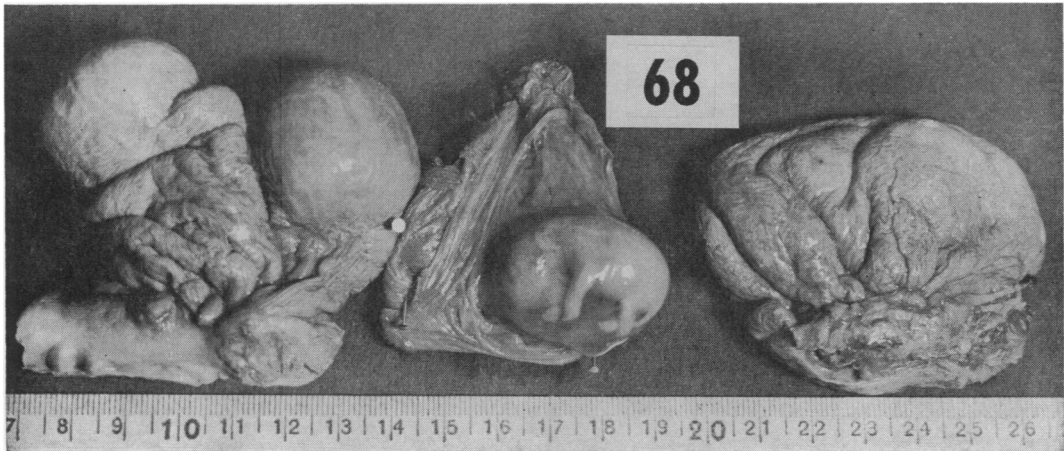


Fig. 4. Ovaries, and embryo approximately 21 days of age, from elephant No. 68.

ing the point of rupture. . . ." Histological sections cut through the protuberances and the centers of the corpora lutea revealed lutein cells that stained a very pale color, even when the normal staining time was doubled. The general color of the corpora lutea was distinctly more pale than a corpus luteum of similar size at or near the time of parturition. In comparing the histology of the two corpora lutea, no difference was detected in degree of vacuolation among lutein cells, they did not appear foamy, and they showed no evidence of fatty degeneration. In certain areas of the slides the lutein cells tended to be arranged radi-

ally in a linear order (Fig. 5). The connective tissue formed a close-meshed reticulum surrounding the luteal cells and near the center of the corpora lutea a fibrous central mass completely obliterated the original central cavity (Fig. 6). Vascular ingrowths were apparent throughout the sections, being particularly conspicuous near and proximal to the protuberances (Fig. 7). Blood cells were apparent in some vessels, but other vessels appeared as clear areas with a single-cell epithelial lining. The three largest blood vessels of A measured 0.11, 0.07, and 0.05 mm in diameter; the three largest vessels of B mea-

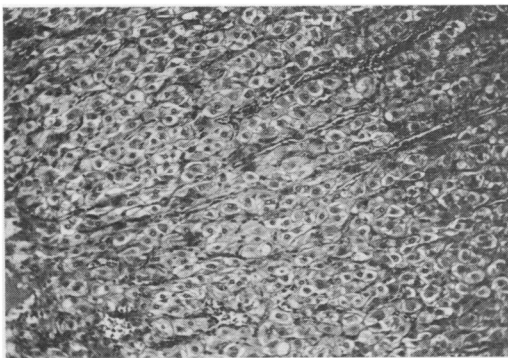


Fig. 5. Section of corpus luteum 68A showing linear arrangement of lutein cells.

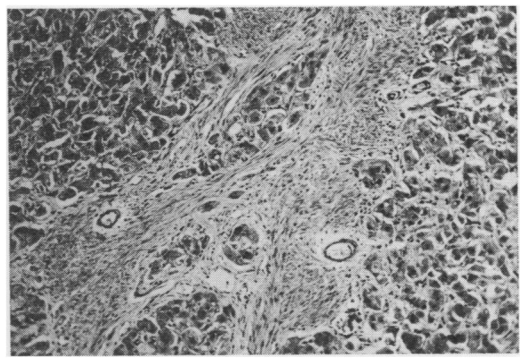


Fig. 6. Connective tissue mass near center of corpus luteum 68B surrounded by large nucleated lutein cells.

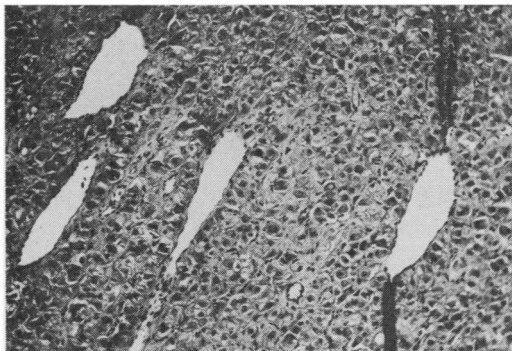


Fig. 7. Section of corpus luteum 68B showing development of vascular system among lutein cells near and proximal to the protuberance.

sured 0.95, 0.26, and 0.20 mm in diameter.

Collectively, these data indicate (1) that corpora lutea 68A and 68B were indistinguishable, (2) that both were relatively young but mature structures of similar age, and (3) that both had developed from follicles that ovulated within a short period of time.

#### OBSERVATIONS OF MATING BEHAVIOR

Elephants were observed copulating on 11 occasions in Uganda between August, 1958, and October, 1964 (Table 2). Additional observations of behavior related to mating were obtained during this time. Copulation was first observed on August 15, 1958. Four bulls, each estimated at eight to 9,000 pounds and with tusks of approximately 25 to 40 pounds on each side, were following a large cow when first seen at about 9:20 AM. Although the four were of similar body and tusk size, one was slightly larger and obviously dominated the other three.

The larger, dominant bull remained near the cow. Occasionally he chased away one of the subordinate bulls. Once when he was challenged, the sound of head-butting and tusk-clashing indicated the intensity of the encounter. At about 9:50 AM the dominant bull returned to the cow, and

with trunk and tusks held lengthwise on the cow's back, attempted to mount her. The cow moved ahead slowly and gave no visible response to the bull's attempt, which was unsuccessful. As the bull attempted to mount, one of the subordinate bulls rolled on the ground.

Forty minutes later the dominant bull swung his head over the cow's rump, and with trunk and tusks held lengthwise on her back mounted and achieved coitus. No form of courtship behavior was observed during the 2-hour period. The animal's movements were slow and the female remained passive during copulation.

On July 13, 1963, at about 7:30 PM, while one of us was watching a family unit of 14 elephants, a bull mounted a cow, but weak light prevented assurance that coitus was achieved. The cow did not stand still and probably was not receptive. The bull kept following the cow, attempted to mount several times, but probably was not successful.

During mid-forenoon of the following day, in almost the same place, copulation was completed. The similarity of size-classes among the 14 elephants which comprised the only family unit in the area during both days indicates that the same elephants were involved.

A rather loosely assembled herd of 75 elephants was closely observed from 11:30 AM until 12:50 PM on July 28, 1963. Family units were recognized as they detached themselves temporarily from the herd and fed independently or moved away. Throughout the period of observation no estrous cow was seen. There was no evidence of precopulatory play, defense of a particular cow, or close following of any cow. Among the 11 large bulls distributed widely throughout the herd, none showed antagonism or demonstrated dominance toward other bulls.

Table 2. Summary of observations on 11 elephant copulations, Uganda, 1958-64.

DATE	TIME	PROJECTED DATE OF PARTURITION	NO. OF ELEPHANTS IN GROUP	LOCATION
May 9, 1964	11:00 AM	March 9, 1966	338	Izizi River, near escarpment
July 13, 1963	7:30 PM	May 13, 1965	14	Q.E. Park, near Mweya on peninsula
July 14, 1963	9:00 AM	May 14, 1965	14	Q.E. Park, near Mweya on peninsula
July 28, 1963	1:10 PM	May 28, 1965	75	Izizi River, near park boundary
July 28, 1963	1:30 PM	May 28, 1965	40-50	Izizi River, near park boundary
August 15, 1958	10:30 AM	June 15, 1960	5 (1F)	Weiga River, near escarpment
September 14, 1963	11:30 AM	July 14, 1965	9	Q.E. Park, near Kazinga Channel
September 22, 1961	6:30 PM	July 22, 1963	300-350	Chambura River, Toro District
October 23, 1964	6:15 PM	August 23, 1966	5	Paraa Lodge, M.F.N. Park
November 29, 1963	6:30 PM	September 29, 1965	25-40	Igisi Hill, near park boundary
December 20, 1963	4:30 PM	October 20, 1965	25 + 15 nearby	M.F.N. Park, near Joliya River

At 1:10 PM, a medium- to large-sized bull mounted a large cow at the edge of the main herd 35 yards from our observation point. Once again there was no courtship behavior. The bull suddenly raised his head above the cow's rump, lowered his trunk and tusks in a typical fashion onto her back, mounted, and in slightly less than a minute achieved coitus. The cow continued to feed throughout the interaction. When a second cow with a 1- to 2-year-old calf approached within about 25 feet, the bull charged her but stopped abruptly as he neared her.

A second copulation was observed on July 28, at 1:30 PM, approximately  $\frac{1}{4}$  mile away. Among a herd of 40 to 50 elephants feeding and moving slowly through tall grass, a bull of approximately 9,000 pounds was seen chasing a small cow. She ran rapidly from near the center to approximately 50 yards from the herd. The bull pursued her closely, bellowed several times, and finally succeeded in getting his tusks on her back. Then she stopped and the bull raised his forelegs and seized her in a copulatory embrace. Copulation followed quickly. As soon as he dismounted, the cow returned slowly to the herd with her tail held nearly straight and her back humped slightly more than usual. The

bull walked slowly back to the herd. Other elephants in the herd, including large bulls, showed no aggression or interest toward either of the pair. Both elephants were soon mixed in the herd, feeding and moving as though the event had not occurred.

Mating behavior observed during September 13 and 14, 1963, differed widely from the behavior recorded on July 28. At approximately 8:30 AM on September 13 five family units, including four large bulls, were converging on a narrow, flat strip bordering a channel where they came to drink. Two family units had joined up in a mud wallow about  $\frac{1}{2}$  mile from the channel. The elephants in the other units were grazing and moving toward the flat strip. As one of the converging units reached the strip, a bull joined the unit and with his trunk examined the genitalia of three cows (see Fig. (vii)i, Kühme 1963:130) without provoking any reaction from them. The bull did not examine the oldest-appearing cow with a young calf, and a young adult bull in the unit showed no excitement. After his brief and perfunctory examination, the intruding bull moved about 150 yards to another family unit and repeated his examination. Failing to find a cow in estrus, the bull walked to the mud wallow and rolled with some of the elephants from

the two units that had assembled there. According to Kühme (1963:117) when elephants were excited “. . . sexually by members of their own species, and had not been able to find a satisfactory outlet, they preferred to roll in damp hollows . . . .”

On September 14, 1963, the same five family units and attendant bulls seen the previous day were observed drinking from the channel. At 10:15 AM they started toward an area of short grass and scattered clumps of shrubs. At 11:30 AM two adult males and one adult female in a family unit of nine elephants became involved in a fight. The bulls appeared equal in size and both carried approximately 25-pound tusks. One lighter colored bull seemed to dominate the other; the cow occasionally butted either one. Fighting subsided, but 5 minutes later it began with renewed vigor between the bulls. The cow began to feed, but after 4 minutes she stopped feeding and approached the fighting bulls. The dominant bull soon mounted her but was promptly “unseated” by the other. Fighting was renewed and the subordinate bull driven away. He retired about 25 yards and had a dust bath, leaving the light-colored bull and the cow facing each other butting heads and entwining trunks. The light-colored bull now had his penis extended and erect. The cow seemed only partially receptive; however, the bull finally positioned his tusks lengthwise along her back and, after following her about 10 paces, mounted and achieved coitus. Within 2 minutes all the elephants in the family unit were feeding peacefully. The six elephants not involved in the interaction remained passive.

Just before noon on September 14 a bull at the edge of the channel repeatedly attempted to mount a small cow that would not stand still. After pursuing the cow for about 4 minutes, the bull gave up and be-

gan to drink from the channel. The cow moved rapidly away from the water and toward the channel embankment. Part way up the slope she met another bull coming toward her. This second bull also attempted to mount her but she fled. He then chased her for about 2 minutes during which he made several semi-mounts. At this point, a third elephant of unknown sex intervened. This elephant was probably a female since no extended penis was visible. She chased the second bull away from the small cow which then escaped. After the bull left, the intervening elephant became passive.

William M. Longhurst, who conducted big game investigations in Uganda as a Fulbright Scholar, observed elephants mating about ½ hour before dark on September 22, 1961. Longhurst had moved to within approximately 50 yards of a long file of about 300 to 350 elephants strung out against the skyline beyond the edge of a patch of forest. Cows, relatively young elephants, and adult bulls appeared to be in the herd. No precopulatory behavior was seen, yet a brief 5- to 10-second copulation occurred. The elephants were walking slowly, and the receptive cow continued her slow gait throughout the event. The other elephants seemed to pay no attention; however, from Longhurst's position he could observe the file of elephants for a space of perhaps only 30 yards through an opening in the trees, and so missed any pre- or postcopulatory behavior that might have occurred.

The promiscuity of sexual behavior in the cow elephant was well demonstrated by an observation reported by Roger Wheeler (letter dated March 11, 1965), Superintendent of Murchison Falls National Park. On October 23, 1964, a family unit of three cows and a calf were observed moving toward the main lodge at Paraa. A bull from a nearby group of three bulls followed

closely behind the family unit, and at approximately 6:15 PM he mounted a cow and copulated, remaining mounted for 45–60 seconds. Soon another bull from the same group arrived and, after driving off the first bull without difficulty, mated with the same cow.

On May 7, 1964, when this same family unit had been observed searching through the waste bins near the lodge, the calf had very small tusks and was estimated at 15 months of age. Since the calf's mother was observed mating about 5.5 months later (October 23, 1964), she came in estrus approximately 20.5 months following parturition.

During a steady rain, a herd of 25 to 40 elephants was observed moving slowly through 10-foot *Combretum* on November 29, 1963. The low visibility prevented an accurate count of the various-sized animals as they fed and moved about in the screening vegetation. Observations had nearly ended at 6:30 PM when directly ahead of us a large bull mounted an average-sized cow. The cow did not move, and judging from the position assumed by the bull during the last moments of the mount, copulation was successful. The other elephants in the herd, including at least two other large bulls, appeared passive.

In midafternoon of December 20, 1963, a herd of 24 elephants was observed feeding near a family unit of 15 elephants. The herd of 24 elephants included two large bulls and a relatively small adult bull. They moved freely and amicably within the herd. At approximately 4:30 PM one of the large bulls in the herd of 24 elephants rose on his hind legs and mounted a cow. She remained still throughout the 50-second copulation. As on some former occasions when large bulls were nearby, these bulls, as well as the other nonparticipants, appeared entirely passive.

A herd of 338 elephants was observed while an aerial count of elephants was being made on May 9, 1964. From an altitude of 600 feet the herd appeared to be moving very slowly, probably feeding and resting. At 11:00 AM as altitude was reduced to 400 feet, a bull well within the herd mounted a cow. The cow remained still during the brief interaction. The bull moved slowly away from the cow after dismounting. At a distance of approximately 50 feet he stopped, raised his head, and pointed his trunk upward. The receptive-appearing stance of the cow, the typical copulatory position assumed by the bull, and bull's deliberate departure after dismounting, suggested that copulation was successful.

#### OBSERVATIONS OF ELEPHANTS IN CAPTIVITY

Four female Asiatic elephants (*Elephas maximus*) were captured as wild juveniles in southeast Asia when they were approximately 1 year of age. These females and a large Asiatic bull, now live in the Zoo at Portland, Oregon, where the following supplemental observations were obtained.

Female A mated when she was about 7 years of age (July 13, 1960) and 635 days or 21 months later (April 14, 1962) gave birth to a 225-lb male calf. Female B mated in June, 1960, January 18, 1961, and February 2, 1961, when she was approximately 10 years of age and delivered a 185-lb calf on October 3, 1962. The large bull copulated with Female C when she was 4 years of age and at irregular intervals thereafter, even after she was pregnant. Apparently Female C conceived between 6 and 7 years of age, for she delivered her first calf, a 155-lb male, on September 14, 1963, when she was approximately 8 years of age. Female D was about 6.5 years old when she was first observed to mate. Six

months later she copulated again, and after 31 days was observed copulating the third time. Since Female D delivered her first calf, a 240-lb female, on September 24, 1963, when she was approximately 9 years old, she was between 7 and 8 years of age when she conceived the first time.

These ages at first conceptions (6-7, 7, 7-8, and 10 years) and observations of widely variable copulatory behavior by captive Asiatic elephants are very similar to our data for wild African elephants. The observations of multiple copulations, and of the wide range in number (2 to 15) and size of corpora lutea during pregnancy, suggest that there may be one or several successive estrous periods that lead to conception. Perry (1953:128) also suggested that where relatively large numbers of corpora lutea occurred the successive "generations" were produced during a series of estrous cycles. The observations of captive Asiatic and wild African elephants indicate mating promiscuity. There was no prolonged male-female relationship, and frequently there was no fighting by bulls over females. The members of family units, except large bulls, appeared to be bonded closely.

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