REPRODUCTIVE CYCLES OF TWO *CERCOPITHECUS* MONKEYS

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Summary. Reproductive cycles of female vervets and Sykes' monkeys living in caged breeding groups were followed over 2 years, using a vaginal lavage technique. Both species showed menstrual cycles, and both showed leucocyte peaks in mid-cycle which were assumed to be associated with ovulation. Vaginal cornification patterns were dissimilar in the two species. Sykes' monkeys showed some limitation of copulation to an oestrous period but this was not at a constant stage in the cycle. Vervets appeared to be in continuous oestrus. The gestation period of vervets was confirmed at 165 days and that of Sykes' at about 140 days, which was correlated with a slower rate of development in the infant Sykes'. The caged Sykes' showed two breeding seasons annually, conceptions occurring in the dry seasons but free-living animals are reported as having one breeding season a year. Vervets had a single, long birth season as in the wild but not at the same time as nearby wild groups and not apparently associated with wet or dry seasons.

INTRODUCTION

Menstrual cycles are generally assumed to be the same throughout the primates, according to the review by Zuckerman (1930). Detailed information, however, is practically confined to a very small group of species, all Anthropeidea: man and the chimpanzee, and of the family Cercopithecidae, some macaque species and the baboons. For the observations reported here, the two species of monkeys (*Cercopithecus mitis* and *Cercopithecus aethiops*) were chosen because they had no visible indication of the progression of menstrual cycles; this was necessary for theoretical reasons concerning the main, behavioural object of the study. The only information on reproduction in either species at that time, though both are fairly common in zoos and *Cercopithecus aethiops* is quite widely used in medical laboratories, was an estimate of 213 days for gestation in the vervet quoted by Zuckerman (1953), with the comment that it seemed unlikely to be correct, and a few records of overt vaginal bleeding in vervets at rather long and variable intervals (Butler, 1966; Zuckerman, 1932); thus, it seemed that an account of reproductive cycles observed in healthy breeding groups of

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these species would be of value. These two *Cercopithecus* species had many differences in the pattern of their reproductive cycles, suggesting that the long-accepted concept of menstrual cycle homogeneity may need critical review and some qualification. After the reproductive cycles of the individual have been described, i.e. the menstrual cycle and the long cycle of conception, gestation, and lactation, there remains the possibility of individuals being synchronized to give a species' reproductive cycle or breeding season. These observations provided some information on breeding seasons in open-air captivity at a latitude within the natural range of the species. Fortunately, both species have been studied in the field not far from the places of origin of these groups (Gartlan, 1969; M. A. Omar, personal communication) so it is possible to initiate a discussion of the whole area of modification of reproductive cycles in response to external stimuli in *Cercopithecus*.

Animals

The genus *Cercopithecus* is entirely African, with sixty-seven species (Napier & Napier, 1966) the majority of which are strictly animals of high forest; the vervet is exceptional in its open-country habitat, the Sykes' monkey more typical. The genus is a little more distantly related to the other large genera of the family (*Papio*, *macaca*, and *Cercocebus*, the baboons, macaques, and mangabeys) than these are to each other.

Sykes' monkey is a subspecies of the *Cercopithecus mitis* group, living in the mountain forests of Kenya. It has recently been accorded full specific rank as *C. albogularis* (Osman Hill, 1966) but though its whiter ruff makes it the most handsome race of the group, this is not a major difference. The vervet (grivet, green monkey) *Cercopithecus aethiops* is widespread in Africa, and again local races have distinctive characters and have been accorded specific rank within the superspecies, *C. aethiops*. For both groups, information about exact place of origin provides the best identification. These Sykes' monkeys were trapped in or near the Aberdare Mountains in Kenya, the vervets within a few miles of Kampala, Uganda. Data were collected from breeding groups of both species in Kampala (20 min N of equator) from July 1966 to October 1968. Individuals were strangers to each other and the groups had to be established before observations could be begun. The two groups were housed in identical outdoor runs, 27 × 10 × 9 ft, each divided into two sections connected by a small drop door normally left open. They were fed the same diet: broken wheat, ground-nuts, sweet potato, young elephant grass, and mixed fruit and vegetables from the local market which varied with the season. Mineral licks were always available, and each animal had a raw egg every week.

The Sykes' group included an adult male, two juvenile males, and six adult females, three of them nulliparous at the start of the study. One of the older parous females died of metritis following premature delivery after the first year of the study. Five infants were conceived, and three survived and lived with the group.

The vervet group included an adult male, a juvenile male and five adult females (one of which escaped, and had to be shot after 18 months of the study). Nine infants were born during the study: one died soon after birth, the rest lived with

the group. Another four successful pregnancies began just as the study was ending. In addition, there were three probable abortions but since early abortuses are always eaten, they were not confirmed.

METHOD

Saline vaginal lavages were performed on all adult females three times a week, except for those which obviously found the procedure uncomfortable in the last part of pregnancy, and for all mothers with infants less than 5 weeks old. Samples from mothers were resumed either at 12 weeks or when they were first seen mating, whichever was first. The method used was that of Hartman (1932) with some modifications. Smoothed soft polythene pipettes were used to take the samples. Group-living animals will not allow samples to be taken without restraint but a routine was established whereby males, infants and new mothers went into the other section of the cage at sample time and the remaining adult females were gently netted in an established order. While the sample was being taken, the presence of a seminal plug or visible blood and the general condition of the animal were recorded.

A drop of each sample was examined without further treatment in a cell-counting chamber. Leucocytes and erythrocytes were counted and spermatozoa noted as present or absent. Crystals, bacteria, broken cell debris, and trichomonads were noted. Epithelial cells were also counted at first but this was found to be unsatisfactory and for the last 15 months, only basal and parabasal cells were noted and cornified cells were estimated by the sedimentation technique of Hartman (1932). Samples were taken up in graduated pipettes and left overnight, and the amount of sediment recorded as a percentage of the total sample (usually between 1 and 2 ml).

RESULTS

CERCOPITHECUS MITUS

Menstrual cycles

A total of seventy-two cycles was recorded.

Blood. Menstrual bleeding was visible externally only once or twice throughout the study. Usually blood was not sufficient to tint the lavage to more than a pale straw colour (around 500 erythrocytes/ml) and many menstruations were represented by three or four successive samples containing erythrocytes at less than 200 cells/ml. Such bleeding episodes occurred at fairly regular intervals of from 19 to 57 days, with a median of 30 days, and more than half the cycles fell within 5 days of this. Between menstruations, samples containing red blood cells, usually in small counts, were found but only in a single sample in the series. These intermenstrual bleedings occurred in just over half of the cycles for which complete records were available. At such low cell densities, the possibility of leakage due to trauma caused by the sampling itself was constantly born in mind but, in retrospect, is not regarded as having been frequent. Text-figure 1 shows the incidence of intermenstrual bleeding in days preceding the next menstruation. The distribution is not random, but con-

centrated in the middle of the cycles, with a median at Day 16, 59% of the records falling between Days 18 and 10. Outlying records may have been mainly due to trauma.

Vaginal cornification. (Unfortunately, this was only recorded adequately in the last 15 months of the study so that only thirty-six cycles contribute information here.) Sediments of cornified cells were heavier in the second half of the cycle than in the first, though there was much variation from sample to sample. Text-figure 2 shows the mean sedimentation rates for each female, with the complete records for one female to illustrate the variability. Sediments from the beginning of cycles also tended to be high as cornified cells continued to be shed into the vagina during menstruation. Individuals varied in the amount of this early sediment, and in the amount of difference between the two halves of the cycle. Typically, there was almost no sediment between Days 5 and 15.

TEXT-FIG. 1. Sykes' monkey: incidence of leucocyte peaks and intermenstrual bleeding in vaginal lavages, dated with reference to the next menstruation. There was no peak detected in twenty of seventy-two cycles, and no intermenstrual blood in thirty-five.

This was followed by a fairly abrupt rise, sediments then remaining high until just before or just after the next menstruation. This is comparable to the changes in cornification in the baboon described by Gilman (1937).

Leucocytes. Leucocyte counts tended to be somewhat higher in several successive samples over the time of menstruation. A very sharp mid-cycle peak in leucocytes was detected in 72% of cycles. A typical peak would be a count about ten times the count either side of it. Since it was so abrupt, it is likely it could have been missed in many cycles on the alternate day sampling schedule. Text-figure 1 shows the distribution of leucocyte peaks with reference to the next menstruation. There is a peak at Day 14, with 71% of the records falling between Days 18 and 10. In a typical cycle, the leucocyte peak occurred in the same sample as, or the next sample to, intermenstrual bleeding and just at the changeover from low to high sediment readings. It seemed a legitimate inference that these peaks were in some way associated with ovulation, and so they were used in calculating when conceptions occurred (see later).

TEXT-FIG. 2. Sykes' monkey: mean sediment readings (vaginal cornification levels) through cycles of five individuals (O, B, R, G and W). All cycles also shown separately for W to illustrate variability. Stippled squares are single records of copulations in these cycles.

Spermatozoa. In Text-fig. 2, the incidence of copulation (as judged from the presence of spermatozoa in the sample and from observed ejaculations) is shown in relation to cornification changes in five individuals' menstrual cycles. One female showed a clear peak in copulation in the first half of the cycle, two showed less clear peaks in the second half, one showed no peak at all, and one had very few copulations recorded but those did fall in the first half of the cycle.

TEXT-FIG. 3. Sykes' monkey: copulations recorded at known interval before the next menstruation.

TEXT-FIG. 4. Sykes' monkey: summary of the typical incidence of cell types in the vaginal lavage during the menstrual cycle.

This last female was the most successful breeder. The animal with the clearest peak did not conceive.

The distribution of all 282 copulations which occurred in known menstrual cycles is shown in Text-fig. 3. Copulation did not occur in the early part of very long cycles and was somewhat more frequent in the middle than at the end of the cycle (the highest count was actually for Day 14). There was no clearly defined oestrus during the cycle, a stage at which all females might be

expected to mate. Each individual, however, showed a highly non-random distribution of copulation in time. They tended to mate in bouts of several days with intervals of several non-mating days between them and, at least for some individuals, these bouts of mating occurred at specific stages in the cycle but for each, the pattern was slightly different.

Other. Small square crystals occurred in the samples of some individuals, but were not associated with any particular reproductive state. Bacteria were more abundant in samples from the second half of cycles. Mucus, the occurrence of which is a useful indicator of cycle state in baboons and mangabeys, is inconspicuous in the *Cercopithecus* vagina.

In summary, the events in an idealized Sykes' monkey menstrual cycle, as seen by the vaginal lavage method, are shown in Text-fig. 4.

Conception, pregnancy and lactation (Table 1)

Gestation was calculated assuming that conception occurred about the time of the next leucocyte peak after the last clear menstruation, which happened between Days 15 and 21 of the cycles. This gave four pregnancies of around 140 days, and one of 127 days for a small infant which did not survive. In all cases, some bleeding occurred in the second week after presumed conception, which is assumed to have been the "placental sign" described by Hartman (1928) for the rhesus monkey. Parabasal cells were first recorded in three cases at about 7 weeks but a staining technique would probably have drawn attention to these earlier. Also starting in the 7th week in three cases, later in the other two, there was a sharp rise in leucocyte counts. Red cells in small amounts were frequently found in pregnancy samples appearing about the same time as the rise in leucocyte density. In only one case was sampling continued right through pregnancy and then the leucocyte levels dropped to normal about 2 weeks before birth. High leucocyte counts are usually taken to indicate infection, so it is worth reporting that none of the mothers showed any symptoms of sickness during pregnancy, except the mother of the premature infant. This mother received a bite wound which became infected a week or so before the birth and she died shortly afterwards.

This estimate of gestation is much shorter than would be expected by analogy with the better known Catarrhines: the Sykes' is roughly the same size as the rhesus, with a mean gestation of 164 days. The difference is perhaps related to the slow development of infant independence in the Sykes' (Chalmers, 1970). Sykes' infants did not leave their mothers in the first 4 weeks, whereas rhesus (Hinde, Rowell & Spencer-Booth, 1964) leave in the 1st or 2nd week.

Copulation was infrequent during pregnancy (twenty-one records) though, in two cases, there were copulation bouts after presumed conception, one after 3 weeks and one at 5 weeks. An oestrus occurring during early pregnancy was reported by Ball (1935) in the rhesus monkey.

The lactation interval was long. When sampling was resumed at 12 weeks, there was little vaginal activity. Samples were almost empty of cells, but contained a few parabasals. In all cases, spermatozoa were found in samples before there was any change in this picture and rises in leucocyte counts and cornifi-

TABLE 1
DATA ON CONCEPTION, GESTATION AND LACTATION IN SYKES' GROUP

<i>Female</i>	<i>Baby born</i>	<i>Estimated length of gestation</i>	<i>Date of conception</i>	<i>At conception: Leucocyte peak</i>	<i>Blood peak</i>	<i>Days after last menstruation</i>	<i>Placental bleeding from Day</i>	<i>No. of copulations during pregnancy</i>	<i>Copulation again after birth in Week</i>	<i>Parabasal cells first seen on Day</i>	<i>High leucocyte count from Day</i>	<i>Notes</i>
Blue	21/6/67	about 140	26/3/68	?	?	15 to 21	7 to 13	8	25	96(1)	60	Data for conception cycle incomplete: another copulation series 19 days after conception
	31/7/68	138	12/3/68	+	+	17 to 19	8 to 10	0	Baby died. Copulation first occurred 45 days later	44	44	Leucocytes down 18 days before birth
Maroon	18/11/67	127	16/7/67	+	0	Menstruation not recorded	13	5	Baby small, baby and mother both died	109(1)	97	Another bout of copulation 36 days after presumed conception
White	27/11/67	138	7/12/67	+	0	17	13	7	16	49	42	Cornification remained high in first 8 weeks of gestation
Orange	13/6/68	140	26/1/68	+	+	15	12	1	17	48	43	

cation rates followed. Regular menstrual bleeding did occur in these otherwise inactive animals.

There was a suggestion that conception might have been delayed by excessive maternal behaviour. At first, infants were allowed to leave the adults' cage freely, the mesh being too large to restrain them and by 5 months, they were hardly ever seen with their mothers. Under this regimen, the mother of the older

TEXT-FIG. 5. Sykes' monkey: mean monthly leucocyte counts (x) and sediment readings (●) for all cycling individuals, plotted over the rainfall at Kampala at the time (hatched area). C = conception, E = equinox.

infant conceived when it was 8 months old. Shortly after this, the infants were prevented from leaving the cage and they began to cling and suckle frequently, regressing to behaviour not seen for several months. The second mother did not then conceive when expected, though copulating frequently, and the first mother rejected her second infant when it was born and instead continued to suckle her older infant. This was clearly abnormal and a warning to those of us who study mother-infant interaction in captive animals.

Seasonality

Births only occurred in two periods, three in June to July, and two in

November. It is not, of course, possible to derive a seasonal breeding pattern from five births but, while taking samples, it was noted that both leucocyte counts and sediments sometimes became higher in all animals at about the same time, while continuing the intermenstrual fluctuations described earlier.

At Kampala, as is usual in the tropics, there are two wet seasons in the year, with peaks in April and November and troughs in February and August; being very near the equator, the amounts of rain that fall in the two seasons are almost

TEXT-FIG. 6. Sykes' monkey: mean frequency of copulation (each female could only score once in 1 day) and interaction frequency in daily 60-min observation periods in each month of the study. Rainfall, etc., indicated as in Text-fig. 5.

equal. The change in rainfall and the accompanying changes in vegetation are the most obvious seasonal changes; temperature and rainfall vary only very slightly. To illustrate a possible correlation between the cycle of wet and dry seasons and the changes in cell counts, the mean sediment reading in each month (from all samples from all non-pregnant animals) and the mean monthly leucocyte count were plotted over the rainfall at Kampala (Text-fig. 5). The number of samples with spermatozoa, divided by the total number of samples taken each month, and the mean number of social interactions in 60-min

observation periods are shown in Text-fig. 6. It will be seen that all these measures tended to be higher in dry seasons than in wet seasons and that conceptions occurred in dry seasons. (Leucocytes did not show the expected peak in the summer dry season of 1968. Perhaps in association, there were also no conceptions during that season).

TEXT-FIG. 7. Free-living Sykes' monkey: data kindly supplied by A. Omar, derived from 105 adult females shot in control work. (No records for April).

None of these measures was directly correlated with the rainfall which occurred in the same month, although the general periodicity of peaks and troughs was about the same. It seemed likely that, as suggested by Vandenberg & Vessey (1968), rainfall might affect the physiological processes through a change in the vegetation eaten by the animals and that this effect would take some time to manifest itself, so all measures were also plotted against the rainfall of the preceding month. Again, however, there was no correlation. It can be seen in Text-fig. 6 that the rainfall in a particular month was not very predic-

table, although the overall pattern is clear. Plants seemed to be governed in their growth pattern by other cues than rain, since a relatively small amount of rain in the month when rain should arrive had a disproportionately large effect, and even regularly watered garden plants grew more in the wet season. It must be assumed at this stage that the monkeys were also reacting to other cues or to changes in food plants which were only moderately dependent on rainfall.

Though annual breeding seasons are well established for many monkeys (Lancaster & Lee, 1965), the only suggestion of a twice-yearly season in the wild occurs in the rhesus monkey in Northern India (Prakash, 1962).

In a wild population of Sykes' monkey at Mugugu in the Aberdare Mountains in Kenya, Omar (personal communication) found a single breeding season with conceptions occurring in the 'small rains' of August to January and most births occurring just before the start of the heavy rains, in January to April (Text-fig. 7). These seasons did not correspond to either 'breeding season' of the caged group which came from the same area. Since breeding did not occur equally in the two wet seasons, the cues provided by one wet season must be different from the cues provided by the other, and a simple scheme of rain causing plant growth which increases monkey fertility is not adequate.

It is possible that the twice-yearly breeding in the caged group represented a change-over from an annual season before capture to a different annual season based on conditions at Kampala. There were no conceptions in August 1968, although copulation and cornification increased as expected. The relation of breeding to rainy seasons was different in the two areas, conception occurring during the rainy seasons and births before the rainy seasons in Muguga, while at Kampala conception occurred between the rains and births after the rains. Possibly, the dry season in warmer and more humid Kampala is most like the small rains in the Aberdares; possibly also the association of rain and breeding-seasons is not causal, but merely incidental. One thing is clear, that the breeding season is highly labile and susceptible to local conditions.

CERCOPITHECUS AETHIOPS

Menstrual cycles

Because the vervet group bred so successfully, only thirty-two complete menstrual cycles were recorded.

Blood. Menstrual bleeding (relatively high red blood cell counts in two to four successive samples) was rarely visible externally, though a little more often than in the Sykes' because the pale perineum of the vervet showed traces of blood more clearly than the slate-coloured skin of the Sykes'. Menstrual intervals varied from 25 to 46 days, with a median at 33 days, and 64% of cycles falling within 5 days of the median. Intermenstrual bleeding (usually a small cell count in a single sample) was usual, being recorded in twenty-six of the cycles. As can be seen in Text-fig. 8, most records were near the middle of the cycle, with a median at Day 16, and 73% falling between Days 11 and 19.

Vaginal cornification. Only twelve complete and two incomplete cycles were recorded and a diagram of the mean readings of these is shown in Text-fig. 9.

TEXT-FIG. 8. Vervets: incidence of leucocyte peaks and intermenstrual bleeding in vaginal lavages, dated with reference to the onset of the next menstruation. There were no peaks recorded in seven cycles, and no intermenstrual blood in six.

TEXT-FIG. 9. Vervets: mean sediment readings in fourteen cycles of five females, with distribution of copulations which occurred in these cycles.

TEXT-FIG. 10. Vervets: copulations which occurred at known intervals before the onset of the female's next menstruation.

TABLE 2
DATA ON CONCEPTION, GESTATION AND LACTATION IN VERVET GROUP

	Female	Baby born	Estimated length of gestation	Date of conception	At conception: Leucocyte peak	Blood peak	Days after last menstruation	Placentation bleeding from Day	Parabasal cells first seen on Day	High leucocyte count from Day	No. of copulations during pregnancy	Copulation started again after birth in Week
Snub	1	20/4/67	163	14/11/66	+	+	14	16	—	—	29	14
	2	5/1/68	160	31/7/67	+	+	13 to 15	12	30	60	16	11
	3	13/1/69	171	26/7/68	+	+	12	18	37	29	4(+)	? Birth after end of study
Big	1	29/3/67	167	10/10/66	0	+	13	16	—	56	7	14
	2	24/5/68	170	4/12/67	+	+	13	11	65	48	1	11
Toe	1	31/5/67	162	21/12/66	+	+	14	13	—	69	44	11
	2	3/7/68	158	26/1/68	(+)*	+	18	11	45	45	35	6
	3	28/2/69	161	29/9/68	+	0	12	15	—	—	11(+)	? Birth after end of study
New	1	4/10/67	169	17/4/67	+	+	13	24	20	20	12	5
	2	28/6/68	165	5/1/68	(+)	+	26	17	—	28	24	7
Red	1	4/6/67	142	20/1/67	+	0	18	10	—	70	15	23 days after small baby died at 8 days
		Mean:	165									

* Peaks were more like hummocks.

It was, however, clear that the sediments did not follow the same pattern as the Sykes'; if anything, sediments actually tended to be heavier in the first half of the cycle than in the second, the reverse of the Sykes' picture. Sediments were usually light in the vervets, and fluctuations small. (If, in this species, intermenstrual bleeding is consistently heavier than menstruation, the cycles would have been wrongly interpreted. At the time of going to press, this is regarded as unlikely.)

Leucocytes. Counts were higher over the time of menstruation, as in the Sykes', and again there were mid-cycle leucocyte peaks, whose distribution is shown in Text-fig. 8. The median was at 16 days before the next menstruation, but there was no clear peak, 64% falling between Days 11 and 19. In the vervets, intermenstrual bleeding was more regular than the leucocyte peaks, while the reverse was true for the Sykes'. There were also clear leucocyte peaks at the time of nearly all conceptions (see below).

Spermatozoa. Distribution of samples containing sperm cells in cycles for which sediment data were also available is shown in Text-fig. 9, and the distribution of 205 copulations which occurred at a known interval before the next menstruation in Text-fig. 10. There was a slight but non-significant drop in mating frequency towards the end of cycles but in general, healthy females showed spermatozoa in nearly every sample and could be regarded as being in continuous oestrus.

Conception, pregnancy and lactation

An average gestation of 165 days has recently been established for the vervet at the Institute of Comparative Biology at San Diego (R. B. Cooper, personal communication). Data on the twelve conceptions leading to live births which occurred during the study are given in Table 2. In all cases, there was either a leucocyte peak or intermenstrual bleeding between 12 and 24 days after the last recorded menstruation (no leucocyte peak in one case, no blood in two cases). This was followed between 10 and 24 days later by another series of samples containing red blood cells, invariably taken at the time as the next menstruation, but usually continuing longer and with smaller counts than in typical menstruation and subsequently presumed to be placentation bleeding. The appearance of parabasal cells in the samples 2 to 6 weeks after conception was the first hint of pregnancy in some cases, but some females conceived while still showing characteristic lactation interval samples, which include some parabasal, but few other, cells. The most useful sign of pregnancy (though palpation would presumably have given an earlier diagnosis) was a large increase in the leucocyte count, so that samples appeared to consist of nothing but a suspension of leucocytes; such increases began to occur between the 5th and 10th week of pregnancy. As in the Sykes', high leucocyte counts were not apparently associated with illness: in fact, the only female which was ill during pregnancy had very low counts at the time, and these became larger when she recovered. Only two females were sampled in late pregnancy and in these, leucocyte counts dropped to normal levels 2 and 4 weeks before birth. Small counts of red blood cells (never amounting to visible staining) were also frequent during mid-pregnancy.

The frequency of mating for some females hardly decreased during pregnancy. Although samples were not taken throughout pregnancy, 198 copulations with pregnant females were recorded, as compared with 376 with cycling females. Copulation was recorded in the week before birth but not in the first 4 weeks after birth. Births were uneventful and placentae were always eaten. Infants developed independence slightly faster than rhesus macaques and very much faster than the Sykes' monkeys (Chalmers, 1970) and correspondingly the lactation interval was very short. All females were copulating frequently by the 14th week, the earliest incidence being recorded in the 5th week.

Seasonality

Eleven births occurred between January and June, one was in July, and the remaining birth in October was to a female which was not in a group when the others were conceiving. Prospective birth dates for the three abortions also fell within this time. This long birth season included the driest and the wettest months of the year and could not be linked to seasonal changes at Kampala. It was similar in duration to the birth season found by Gartlan (1969) on Lolui Island about 70 miles away but the Lolui birth season extended from April to September. Struhsaker (1967) found an October to March birth season at Amboseli in Kenya.

Unlike the Sykes', there was no regular fluctuation in behaviour or cell counts in the vervets: sediment levels, leucocyte counts, copulations, and interaction frequencies were not related either to the twice-yearly wet and dry seasons or to the single annual breeding season of the monkeys. In part, this may merely reflect the inadequacy of the data. Since births occurred close together, there were 5 months for which no data was available because all animals were in late pregnancy or carrying small infants. This in itself, of course, represents a form of seasonality. It seems that vervets are so fertile that it would be necessary to keep a group of females with a vasectomized male to obtain adequate information on the possible occurrence of seasonal variation in vaginal histology.

DISCUSSION

The most striking result of this study is that two species of the same genus, kept in identical conditions in the same environment, should show differences in every aspect of their reproductive cycles: in their response to the environment in breeding seasons, in their behavioural changes during the reproductive cycles, and in their vaginal cell pictures. Neither species corresponded in breeding season to wild populations of the same species studied near their origins. This suggests a lability in reproductive cycles and an ability to respond to environmental factors which must be different for the two species. It follows that similarities of details of menstrual cycles between more distantly related species cannot be taken for granted and that where they are found, a corresponding similarity in environmental factors might be expected. These might be in the physical environment to which the species is adapted, or, perhaps more probably, in the social environment provided by the social organization typical of the species.

Day-length and temperature, which have been prominent controlling factors in studies of temperate species, are effectively eliminated in an equatorial environment, where the obvious seasonal change is in rainfall. Though this has been postulated elsewhere as a controlling factor in primate seasonal breeding (Vandenbergh & Vessey, 1968; Jewell & Oates, 1969) and though there was a general association of sexual behaviour with dry seasons in one species in this study, there was no good correlation in detail, suggesting that both rain and monkey cycles might be independently related to some third factor. The change in sediment and leucocyte counts with season in the Sykes' suggests the possibility of studying the breeding season without actually breeding monkeys, which could be very useful in experiments with these slowly-reproducing animals.

Within menstrual cycles, there was a notable lack of any defined oestrous period in the vervet and of any oestrous period that was shared by all individuals in the Sykes', though here individual females did have bouts of mating interspersed with inactive periods and these were related to their cycles, though differently for each individual. Both species went into anoestrus when carrying young infants. During pregnancy, copulation frequency in the vervet was not much affected, but Sykes' females mated only infrequently after conception.

It seems likely that sexual behaviour will be found to play a rather different rôle in the social organization of the two species and that both will differ from species like the baboons or mangabeys in which sexual behaviour is practically confined to sharply defined and relatively limited oestrous periods. (Behavioural data collected over the same period as the data presented may throw further light on this point.)

Leucocyte counts were found to be extremely useful in interpreting reproductive cycles in both species, but the lack of interest by vaginal histologists in such counts, suggests that they may not fluctuate so clearly in the better known primates. There was an association between high leucocyte counts and the presence of erythrocytes but the former were more dependable because erythrocytes were nearly always at very low densities. More particularly, the leucocyte peaks which appear to be correlated with ovulation seem potentially useful and the regular occurrence of high-count plateaux in mid-pregnancy requires further investigation since it was not apparently related to sickness in mother or infant.

Vaginal cornification patterns were different in the two species. Both had lower levels of cornification than rhesus or baboons and the vervet especially had small sediments with very little fluctuation. This may indicate a possible correlation between cornification levels and copulation patterns, with species which have intense bouts of frequent copulation needing more protection of the vaginal wall than those which mate 'little and often.'

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