COMPARATIVE FEATURES OF THE REPRODUCTIVE BIOLOGY OF HAMADRYAS BABOONS (PAPIO HAMADRYAS), GRIVET MONKEYS (CERCOPITHECUS AETHIOPS) AND Rhesus Monkeys (MACACA MULATTA)

By
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The primates, which until quite recently were considered exotic laboratory animals, are being ever more widely used in experiments designed to solve a number of medico-biological problems.

The experience of work with primates which is building up each year is not only indicating new and promising lines of investigation where primates must be used but also revealing the specific features of each species and its ecological and physiological peculiarities, thus making it possible to select the most suitable species for any particular type of investigation.

The rapid development of experimental primatology has made it imperative to study the important problem of the reproductive biology of various primate species. For research workers this problem is of dual interest. On the one hand thorough study of the reproductive process makes it possible to select the most suitable model for studying the physiology and pathology of reproduction in man. On the other hand elucidation of these questions makes it possible to put forward recommendations designed to rationalize the management and breeding of primates in captivity.

Comparison of data in the literature on the reproductive biology of primates with the material accumulated by the Sukhumi Primate Centre during its 45 years’ experience discloses a number of topical problems which require more detailed investigation or elucidation. The most important to our mind are:

458
(1) determination of the mean age at which females and males attain sexual maturity and of the factors which affect the establishment of sexual function in the two sexes;

(2) determination of the degree of variation in the age of first conception and the factors influencing the length of time between attainment of sexual maturity in females and the occurrence of the first and subsequent pregnancies; and

(3) determination of the degree of variation in the reproductive process in relation to age, season and acclimatization.

The many years of experience gained at the Sukhumi Centre indicate that to obtain a complete picture of the reproductive process, it is essential to evaluate all reproduction indices in relation to the features of inter-relationships within the monkey troops in captivity and the opportunities of those features to be manifested.

It seemed to us that it was precisely a comparative study of the characteristics of three primate species—hamadryas baboons, grivets and rhesus monkeys—from different geographical habitats that would enable us to settle and interpret a whole number of problems concerning the reproductive biology of primates in captivity.

First of all we shall give a short description of the main stages in the reproduction process in the order of their development.

The establishment and development of sexual function follow a different course in the three species of primate proposed for study. The basic stages in sexual maturation are most clearly marked in the hamadryas baboon. In that species there is a direct dependence of the age of sexual maturity on the weight achieved at two years of age (Fig. 1). Sexual maturation occurs in the overwhelming majority of the animals during the winter and autumn. The animals

![Graph](https://via.placeholder.com/150)

**Fig. 1.**

The weight of hamadryas baboon females at 2 years of age (white columns) and at the age of sexual maturity (black columns).

M = 7.6 kg, M₂ = 34.8 months.
usually reach the state of sexual maturity at 30.1 months. The more intensive growth in the first two years, the earlier the onset of sexual maturation. On the other hand rapid growth and early development of sexual function do not guarantee early pregnancy. For early pregnancy it is essential that the young female should attain a weight averaging 7.6 kg. In rhesus monkeys and grivets sexual maturation is earlier in its onset than in the hamadryas baboon but in the rhesus monkeys it depends on the season (Fig. 2). In hamadryas baboons the age of sexual maturity does not depend on the time of year but the menstrual cycles develop more quickly if the first swelling of the sexual skin occurs in spring or summer. A pronounced tendency to early sexual maturity in hamadryas baboon males and females is noted the last years with increase of baboon generations.

It is of great importance in evaluating reproductive biology to determine the limits of variability of the age of first pregnancy and to elucidate the factors which affect the course and outcome of that pregnancy.

In rhesus monkeys (Fig. 3) there is no clearly marked relationship between the age of first pregnancy and the age of sexual maturation, whereas in the hamadryas baboons (Fig. 4) and the grivets the first pregnancy occurs just as rapidly whatever the age of sexual maturation. Meanwhile, in all three species when sexual maturity is attained early, independently of the length of time which elapses between sexual maturity and the first pregnancy, that pregnancy has a pathological outcome more often than subsequent pregnancies. It is only in hamadryas baboons that the frequency of pathological outcome of pregnancy at the optimal age of sexual maturity decreases with an increase in the interval before first pregnancy. It must be assumed that the capacity possessed by the hamadryas baboon for regulating the dates of the onset of first pregnancy and

Fig. 2.
Sexual maturity in rhesus monkeys in various months of the year.
limiting mating, particularly in the early stages of sexual maturation, is characteristic of an animal community based on the harem principle, in which the laws of »domination – subordination« are in force. Only the animals which are prevented from mating by the troop possess an evolutionary advantage. Rhesus monkeys form harems once a year during the period of sexual activation and for them a constantly acting factor is their degree of maturity when the breeding season commences. In the first breeding season only those animals become pregnant which have achieved complete physical and physiological development by that time. In the others, pregnancy occurs during the following
season. This explains why in rhesus monkeys the interval from sexual maturity to the first pregnancy averages 15 months (240 observations). For hamadryas baboons and grivets it equals 10 months.

It should be noted that there is little information in primatological literature concerning the period between births in primates. Meanwhile the interval between giving birth and the beginning of the next pregnancy is the longest and most variable period and is characterized by the succession of such functional conditions as lactation and the re-establishment of sexual cycles. The mean length of the service period, *i.e.* the interval between giving birth and the next pregnancy, is very much the same in the females of the three species, equalling 10.5 months (500 cases) in baboons and grivets and 11.8 months (700 cases) in rhesus monkeys, although large individual variations are noted, especially in rhesus monkeys with late delivery.

In hamadryas baboons and grivets (Fig. 5), after the offspring are born, and have been breast-fed to the age of seven or eight months, menstrual cycles develop in two to three per cent, of the females three months after they have given birth. Eight months after birth the menstrual cycle has been re-established in 70 per cent of the females which have given birth at term. In rhesus monkeys the sequence of development of menstrual cycles after birth follows the same course as in hamadryas baboons. However (Fig. 6), the development of the menstrual cycles and the limits of variation of the service period are limited by the season in rhesus monkeys, which is not the case with baboons and grivets. This once again indicates that all forms of communication, including sexual relations, in rhesus monkeys are reflected in the structure of their communities. In that species the sexual activity of the males undergoes

![Graph showing terms of menstrual cycle development](image-url)

**Fig. 5.**
Re-establishment of menstrual cycles in hamadryas baboon females after labour at term.

\[n = 500 \ M \pm m = 7.8 \pm 0.07 \text{ months.}\]
The period before conception (months)
$M \pm m = 11.8 \pm 0.18$ (service-period), $n = 700$

Fig. 6.
Incidence of pregnancy occurrence after labour in rhesus monkeys.

periodical seasonal variations, so that they do not form stable communities like those of hamadryas baboons. It is for that reason that the service period in rhesus monkeys may be increased by a factor of many times if fertilization does not occur during the breeding season.

In a number of cases, under the influence of various factors, the length of the period until the development of the menstrual cycle and of the service period may vary appreciably, thus producing substantial changes in the reproductive process as a whole.

The author has found species differences in the times of development of the menstrual cycles and in the duration of the service period, depending in the first place on the age of weaning or death of the offspring, i.e. the duration of lactation and, in the second place on the time of the pathological outcome to pregnancy. In hamadryas baboons and grivets there is a clearcut relationship between the time of development of the menstrual cycles and the cessation of breast-feeding of the young. Weaning or death of the young immediately after birth causes rapid development of menstrual cycles and the onset of the next pregnancy (Table 1). The capacity of females to switch over from fulfilling their maternal functions to sexual activity depends directly on the duration of the period for which they breast-feed their young. The more protracted that period, the later the next fertilization occurs. Weaning of the offspring at the moment when menstrual cycles would naturally develop is most effective for the reproductive process and for increasing fertility. These phenomena occur in hamadryas baboons and grivets independently of the time of year. By making skilful use of this property it is possible to obtain two offspring from each female in the course of 14 months.
Table 1.
Terms of the onset of the subsequent pregnancy in hamadrays baboons depending on cessation of lactation.

<table>
<thead>
<tr>
<th>Subsequence of the sexual cycle in the weaning of the offspring</th>
<th>Te total number of weaned offspring</th>
<th>Subsequence of the menstrual cycle after the weaning of the offspring and the frequency of pregnancy</th>
<th>In distant terms</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Before menstrual cycle development</td>
<td>276</td>
<td>61.2</td>
<td>13.7</td>
</tr>
<tr>
<td>After the first cycle</td>
<td>108</td>
<td>22.2</td>
<td>15.7</td>
</tr>
<tr>
<td>2</td>
<td>81</td>
<td>8.6</td>
<td>9.8</td>
</tr>
<tr>
<td>3</td>
<td>54</td>
<td>1.8</td>
<td>29.6</td>
</tr>
</tbody>
</table>
This stage in the reproductive process has a somewhat different aspect in rhesus monkeys. In their case, the weaning of offspring in the course of the first four months of breast-feeding has a more or less marked effect on the development of sexual function (Fig. 7). In these primates the service period is 9.5 months on the average. It is only in a few individuals (roughly 10 per cent) that cessation of lactation in the first month leads to the speedy development of the menstrual cycles so that the next pregnancy occurs within one or two months. In other cases (we observed 550 of them), the next pregnancy occurs after 11–13 months, independently of the time at which lactation was stopped, i.e. two months later than when the offspring were weaned in the first four months of life. Hence, in male and female rhesus monkeys reproductive function obviously depends on a seasonal factor which has an evolutionary basis. This is not the case with hamadryas baboons and grivets. It is quite understandable that early weaning of the offspring does not in every case lead to a rapid second pregnancy, for at the time when the offspring are being weaned, males and females are beginning to experience a dying-down of sexual function and the relatively unstable community breaks up until the next active season. We saw a similar picture in those cases when pregnancy terminated in a pathological condition at various stages of foetal development. We found in this case also that the sexual status of the monkeys corresponded to the nature of troop organization and the ecological features of the species studied.

In hamadryas baboons and grivets ovulatory sexual cycles are restored immediately after termination of pregnancy and for three or four months after that time all females show a capacity for breeding (Fig. 8). The time it takes for menstrual cycles to develop does not depend on the season. However,
sexual function develops in females at different rates depending on the stage in foetal development at which pregnancy was terminated (Fig. 9). If pregnancy was interrupted in the early stages (up to three months), menstrual cycles begin again in almost 100 per cent of the females within 60 days. In cases of complications of pregnancy at later dates and particularly in the last month of foetal development, temporary amenorrhoea persists for longer.

Rhesus monkeys differ from hamadryas baboons and grivets in the mani-

**Fig. 8.**
Terms (months) of menstrual cycle re-establishment after the pathological outcome of pregnancy in hamadryas baboons.

**Fig. 9.**
Re-establishment of menstrual cycles and the duration of the service period in various terms of pregnancy pathology in hamadryas baboons.
festation of sexual function after a pathological outcome of pregnancy. A short service period occurs only in occasional individuals in which pregnancy was interrupted at the beginning of the breeding season, i.e. at early pregnancy term (Fig. 10). The females then manage to become pregnant again during that season. This, however, is rather exceptional, since the duration of the service period following pathological termination of pregnancy in most cases decreases progressively the nearer the termination of the pregnancy to the beginning of the breeding season. It must be noted that these features were investigated in primates kept in large groups in cages the whole year around.

In the light of the data obtained on variations in the service period the question of the effect of that period on the course and outcome of the next pregnancy is of interest.

The duration of the service period in hamadryas baboons after a normal birth does not cause any appreciable complication in the course of the next pregnancy, and the primates concerned do not lose the capacity for conception and normal foetal development. However, in cases when the service period is shortened by a pathological pregnancy, early onset of the next pregnancy is accompanied by a sharp increase in the risk of a second unfavourable outcome (Fig. 11). The danger of a second interruption of pregnancy is practically eliminated if four months elapse before its onset. In rhesus monkeys this phenomenon does not occur, since the length of the service period does not depend on the outcome of pregnancy but is largely determined by the seasonal nature of breeding. It is not known what mechanisms are responsible under conditions in their natural habitat for intensification of reproduction in the troop, but at the Primate Centre artificial shortening of the service period through early weaning of the young has proved an effective technique. It

![Graph showing duration of the service period (months) in rhesus monkeys after the pathologic outcome of pregnancy. M = 7.8 months.](image)

**Fig. 10.**

Duration of the service period (months) in rhesus monkeys after the pathologic outcome of pregnancy. M = 7.8 months.
The incidence of repeated pregnancy pathology (%) in different service periods in hamadryas baboons.

It seems to us that it is necessary to make some adjustments in our views in regard to the contradictory opinions expressed concerning the seasonal nature of breeding in various species of primate. First of all, when we talk of »seasonal nature« of breeding we mean a genetically determined succession of »active« and »dead« periods in primate reproductive activity. All the other factors which change the rhythm of reproductive activity in the course of the year do not constitute seasonal factors but give a false impression of being seasonal. This applies in particular to the breeding of hamadryas baboons. In them, as in grivet monkeys, analysis of factual material (1500 cases of pregnancy) seems to confirm the presence of seasonal factors. However, the first doubts as to whether the established breeding rhythm is truly seasonal in our Centre occurred when the following factors were considered. In the first place we

**Fig. 11.**
The occurrence of first and subsequent pregnancies in hamadryas baboons in various months of year. n = 1300.
found no seasonal features in the frequency of sexual maturation of the females. Secondly (Fig. 12), if seasonal features do exist and peak pregnancy occurs in summer (solid line), why is it that in young primiparous females, peak fertilization occurs in the winter months? (dot line). It can hardly be supposed that it is only climatic and feeding factors which act as basic regulators of this process. Later, we shall try to give an explanation of this phenomenon. Yet another factor of some importance should be taken into consideration in regard to the rhythm of breeding, and that is the time of weaning and the age at which offspring are weaned. In the Sukhumi Primate Centre 70 per cent of the offspring are weaned at the age of six to nine months, mainly in the spring and summer. Consequently the increase in female sexual activity in the summer is affected also by the age of weaning, which is adapted to the period of restoration to normal of the sexual cycles, and by the mass weaning in the summer period. Experimental weaning at different times of the year confirmed our assumption that the time of weaning brings about changes in breeding rhythm. A proof of the fact that the seeming change in sexual rhythms in hamadryas baboons and grivets during the course of the year is not seasonal in the true sense of that word is the finding that in winter and early spring the frequency of abortions and stillbirths is twice as high as at other seasons of the year. Second pregnancies in these females occur in the spring and summer months, thus artificially creating an appearance of »seasonalness« (Fig. 13).

As to the difference in breeding rhythm between young and adult females it seems to us that it is based on the laws governing troop inter-relationships and particularly on the principle of domination/subordination applied to sexual relationships between females with differing positions in the troop. As a result of these laws in any correlation between young and adult females in a group

Fig. 13.

Incidence of the pathological outcome to pregnancy and labour (%/

of the year in hamadryas baboons.

Month of the year

$\text{\%}$

$20$

$15$

$10$

$5$

$1$

$2$

$3$

$4$

$5$

$6$

$7$

$8$

$9$

$10$

$11$

$12$

$\text{Month of the year}$
dominated by one male, the adult females are in a privileged position, and the young females mate mainly in the winter time when the stronger females are either pregnant or feeding their young. If the structure of a troop is deliberately changed, pregnancy occurs in young females at the same rate all through the year. In rhesus monkeys (Fig. 14) none of the factors quoted above bring about changes in the breeding rhythm which has been established in the course of evolution. It should be borne in mind that these data are based on analysis of material regarding the distribution of dates of onset of pregnancies (700 pregnancies) in primates which have lived for many years in a large cage in a group consisting of one male with 25–30 females and newborn young.

Under laboratory conditions changes in the reproductive cycle of rhesus monkeys are possible if a combination of special circumstances is established, but this method is more laborious from the organizational point of view.

Thus, in a primate centre where rhesus monkeys are kept in troops, there is a comparatively clearly marked succession of periods of activation and damping-down of sexual activity. However, we are not inclined to think that the regular features observed in the research reflect in the same form the standard features of the reproductive biology of these species in their natural habitat. All stages in the reproductive cycle undergo alteration as a result of the introduction of primates under new conditions and the ways in which troop interrelationships manifest themselves in captivity. We became convinced of this when comparing the indices of breeding during acclimatization and habituation to new semidomestic conditions of maintenance.

Many years of experience in the Sukhumi Primate Centre makes it possible

\[\text{Fig. 14.}\]

Incidence of pregnancy occurrence (%) in various months of the year in rhesus monkeys.
to analyse breeding indices in imported monkeys and their subsequent progeny and to draw conclusions regarding the prospects of acclimatizing the species concerned.

On the basis of our observations it can be assumed that captivity and new environmental conditions do not cause much inhibition of sexual activity in imported primates. Confirmation of this is the ability of these sexually mature primates to mate and produce viable offspring on the average 14 months after they have been imported. A characteristic of all three species is the increase in fertility in every new generation, mainly through a reduction in the number of abortions and stillbirths to some extent.

Rhesus monkeys apparently possess greater adaptability, as is shown by the considerably lower incidence of pregnancy complications among them than among the baboons. The somewhat higher percentage of pregnancy and labour pathology in baboons, accompanied at the same time by a higher capacity for fruitful mating, depends in all probability on the different emotional status of the two species being compared. Hamadryas baboons are considerably more emotional in complex intra-troop relationships and in reacting to outside stimuli than rhesus monkeys.

As the animals grow accustomed to captivity, a tendency is seen towards a weakening of emotional reactions, which leads to a considerable decrease in the number of abortions in each generation, although the number of stillbirths remains unchanged. The variation in sexual function during acclimatization is vouched for further by the tendency noted for a shorter interval to elapse between the first swelling of the sexual skin and the development of regular menstrual cycles, and by the increase in the survival rate of the offspring, changes in the relative proportion of causes of death among the offspring and other indices reflecting the reproductive process in captivity.

In all we have available material descriptive of the reproductive function in eight generations of hamadryas baboons and six generations of rhesus monkeys. This bears witness to the successful acclimatization of these species of primate in the Sukhumi Primate Centre.

In terminating this brief review of material on the breeding biology of three primate species, we consider it our duty to mention that the data obtained are far from covering all the problems in this complex process. We trust that in the course of the discussion it will still be possible to deal with some aspects of age-related fertility, the organization of breeding in captivity, the sex-and-age structure of the colony and a number of other questions.

Summarizing the above mentioned I would like to say that our data reflect a statistical characteristic of the reproductive function of monkeys, which represents a complex of inner processes of the organism. Therefore in the studies on the selection of an adequate model it is necessary to consider the variety of forms of manifestations of reproductive function in monkeys in captivity.