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SOME ASPECTS OF REPRODUCTION AND SEXUAL BEHAVIOUR IN GENUS MACACA

ABSTRACT — Reproductive characters, natality, seasonality and sexual behaviour of the genus Macaca are examined on the basis of five years of studies of behaviour and biology of Macaca arctoides, M. mulatta, M. fascicularis and M. nemestrina in the Institute of Experimental Pathology and Therapy of the Medical Academy ofScie nces in Sukhumi, USSR. No clear-cut birth rate season was recorded in the species under study, as compared with populations living in the wild, in M. mulatta and M. fascicularis, however, marked peaks of natality, appear in spring and summer respectively. Neonate mortality increases during winter month. A long-term study has shown several important differences in sexual behaviour or its elements between Macaca arctoides and other species of the examined genus. Sexual behaviour of all examined species has proved to be closely connected with other types of behavoiur especially with social behaviour. Differences and similarities in reproductive parameters and sexual behavoiur among individual species are correlated with both the character of reproductive organs in the individual species and the quality of environment.

KEY-WORDS: Genus Macaca — Reproductive characters — Natality — Sexual behaviour.

In spite of the fact that genus Macaca belongs to one of the best known primate genera, both as laboratory objects and as well as animals living in the wild, the majority of investigations are in fact dealing with one or two species only and tend to generalize their results for the whole genus without a propter comparative basis, as recently correctly stated by Bernstein (1980). Answering the current need of synthesis of data we try to synthesize the recent finds on primate reproductive characters and the results of our own research of primate behaviour and biology together with gathering concentrate information about the largest possible number of Macaca species. This study should be taken as a preliminary one mainly for two following reasons. First, there is generally no systematic study covering all important reproductive characters and sexual behaviour as concerns the most importance species of the genus Macaca and, second, our data are also lacking in some important reproductive parameters and therefore, despite that we try to assimilate both reproductive and behavioural data, they are definitely not comparable with other studies.

MATERIAL AND METHODS

Reproductive and behavioural characters of four Macaca species (M. arctiodes, M. mulatta, M. fascicularis and M. nemestrina) have been examined since 1980 in the Institute of Experimental Pathology and Therapy in Sukhumi, Soviet Georgia, USSR (in the Sukhumi and Adler Branches). As the number of investigated individuals, the number of groups, as well as their location changed several times during the recent five years, all our data should be taken as approximative ones, serving for rough orientation about group size and structure. Generally all species

were reared in relatively large groups (30 to 80 individuals) in large secluded open-air areas (from 400 to 7000 m²). Stumptailed macaques (M .arctoides) were examined in the Sukhumi Branch. One group consisting of about 70 individuals was the subject of our study. The data on stumptailed macaques are the most complete. Pig-tailed macaques (M. nemestrina) were examined in the Adler Branch, rhesus macaques (M. mulatta) and crab-eating macaques (M. fascicularis) were studied botn in the Sukhumi and in Adler Branches but the reproductive characters mentioned in this study are based on the investigations of the three species in the Adler Branch. Reproductive characters of about 30 groups (more than 900 individuals) were examined in the Adler Branch since 1980. Data on natality were standartized by the average birth value per month. That makes possible a rough comparison of natality in the individual species. The climate in the region around Sukhumi is subtropical, typical of the Caucasian shores of the Black Sea, with summer temperatures regularly higher than 30 °C with very high humidity, and winter temperatures droping below −12 °C with occasional snow.

THE REPRODUCTIVE CHARACTERS OF GENUS MACACA

The first step in this study was to review data on reproduction of the Macaca species known till recently, to set up a framework for the comparison of species examined in our research. The basic reproductive characters (gestation length, length of estrous cycle, age at first breeding for females, age of sexual maturity of the females, and interbirth period) for Macaca species have been summarized in *Table 1.*

Some differences in the sources in reviwed data could be explained, in our opinion, on the basis of the variability of characters in the examined individuals and groups and by different environmental conditions or by the impossibility to make some complicated tests (biochemical or genetical) during the given research. Some differences in the length of estrous cycle are caused by the fact that in some Macaca species the bleeding phase of menstruation is rarely visible. The correct determination of menstruation cycle can be made only in the laboratory by a relatively complicated blood dip stick test.

Generally, it is worth to note, that the data presented by various authors are in good agreement. The delayed sexual maturation of stumptailed macaque females (M. arctoides) in the group studied in Sukhumi is probably caused by the climate of the Caucasian region of tne Black Sea coast.

NATALITY AND SEASONALITY OF FOUR MACACA SPECIES

The majority of populations of the Macaca species living in wild have clear-cut determined birth rate season. For example, the season of vanderu macaques (M. sylvanus) ranges from middle March till the beginning of August (Paul and Thompson, 1984

TABLE 1. *Data on reproduction of genus Macaca*

Species	Gestation length in days	Length of estrous cycle in days	Age at first breeding for females in months	Age at sexual maturity for females in months	Interbirth interval in days	References
Macaca fascicularis	162 160	28	46.3		390	Harvey et al. 1985 Valerio et al. 1969
Macaca fuscata	173	28 34	60	42		Harvey et al. 1985 Takahata, 1980
Macaca maurus	163					Harvey et al. 1985
Macaca mulatta	167 164	29	43.3 42	34	360	Harvey et al. 1985 Valerio at el. 1969 Bernstein, Gordon, 1977
Macaca nemestrina	167 174	42	47.3 48	35	405	Harvey et al. 1985 Tokuda et al. 1968 Hadidian, Bernstein, 1979
Macaca radiata	162	28				Harvey et al. 1985
Macaca silenus	171.8	39	60			Lindburg, lasley, 1985 Ramaswami et al. 1982 Green, Minkowski, 1977
Macaca artoides	179.6 177.5	29.4	65.6 58	59.5	288	Harvey et al. 1985 MacDonald, 1971 Vančatová et al. (in prep.) Trollope et al. 1975 Niewenhuijsen et al. 1985
Macaca sylvanus			46 60	46	945	Harvey et al. 1985 Burton, Sawchuk, 1982

and that of Japanese macaques (M. fuscata) from July to October (Nigi et al., 1980) or from Marcn to July (Kawai et al., 1967).

Females from the groups included in our study have no determined birth rate season. Birth rate was recorded throughout the year; however, some species are characterized by specific peaks of natality. No significant peaks were recorded in natality of M. arctoides and M. nemestrina (*Fig. 1*) as against M. mulatta and M. fascicularis (*Fig. 2*). The rhesus

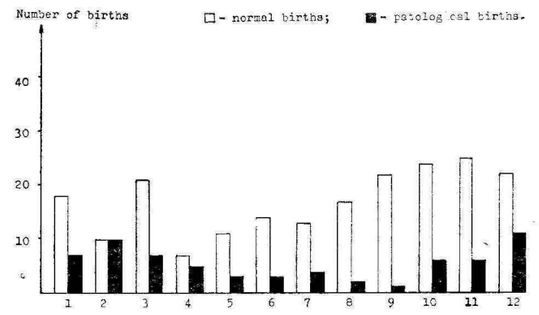

FIGURE 1. *Distribution of births over the year in Macaca nemestrina (1981—1985).*

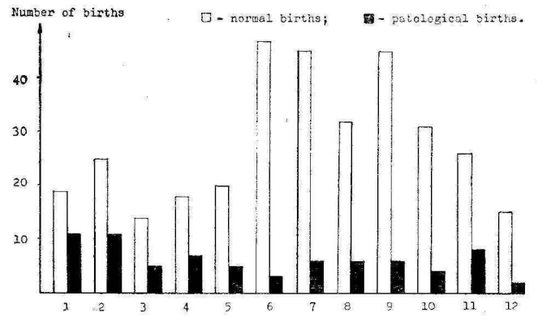

FIGURE 2. *Distribution of births over the year in Macaca fascicularis (1981—1985).*

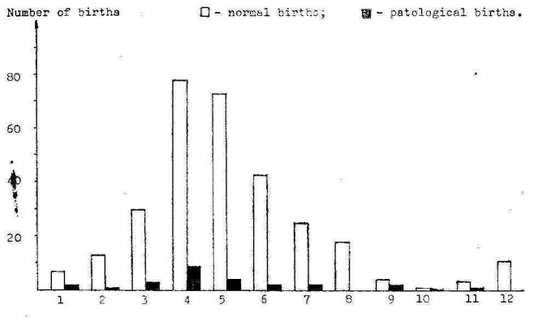

FIGURE 3. *Distribution of births over the year in Macaca mulatta (1981—1985).*

macaques have peak in the period April—June and (*Fig. 3*) the crab-eating macaques in the June—July period. Data on natality of the studied species were recorded from January 1981 to October 1985. As follows from the figures, neonate mortality and patnologies of the neonates are most frequent during cold months, e.g. from January to February in M. fascicularis, from December to March in M. nemestrina.

The reproductive characters of the females of M. mulatta older then 16 years living up to recent in Sukhumi are given in *Table 2.* The last delivery in the oldest female was recorded in the age of 25 years. This female is now 31 years (1.1. 1985). She had 14 deliveries, 11 times one neonate and three times twins. After Talbert (1968) females of M. mulatta have usually lost their menstruation in the age about 20—22 years and the maximal age suitable for reproduction is about 25 years.

TABLE 2. *Data on reproduction of the old females (Macaca mulatta)*

Females No.	Number of births	Patological pregnancy	Age (on 1. 1. 1985)	Age at the last births	Patological births
1 522	14		31	25	
1 957	11		29	22	2
3 935	5		25	20	
8 434	3		19	6	
8 144	3		19	7	
5 647	4	1	23	17	
5 511	3		24	8	1
7 646	12	1	20	18	1
10 046	12		17	17	
10 713	9		16	15	
9 205	6		18	17	
9 822	10	1	17	15	
3 935	5		25	20	
5 853	3		23	8	

SEXUAL BEHAVIOUR AND ITS PLACE IN THE BEHAVIOURAL PATTERN

A detailed description of sexual behaviour and its elements is far from the scope of our study, the preliminary results on sexual behaviour of Macaca arctoides have been published earlier (Čaljan and Vančatová 1984, Vančatová, Čaljan and Vančata, in prep). The main task of this study is to show some important features connected with sexual behaviour or its elements in the Macaca investigated species. For example, ejaculation usually occurs after one long copulation in M. arctoides while a series of several short copulations is necessary for one ejaculation in M. mulatta and only last one is efficient from the point of view of reproduction. Besides, M. arctoides males express various sounds as grin-lipsmacks, barks and chatters, during to copulation. Males of M. arctoides, in comparison witn other species, touch and clean their penis after ejaculation and eat the sperm. The tying of the pair after copulation

TABLE 3. *Distribution of births over the year in four species of macaques*

	Number of births	Month												$\bar{x}$	s
		1	2	3	4	5	6	7	8	9	10	11	12		
							Macaca mulatta (1981—1985)								
Distribution		7	13	30	78	73	43	25	18	4	1	3	11	25.5	26.41
%	309	2.29	4.25	9.80	25.5	23.9	14.05	8.17	5.88	1.31	0.30	1.00	3.59		
Standartiz.		0.27	0.51	1.18	3.06	2.86	1.69	0.98	0.71	0.16	0.04	0.12	0.43	1.00	1.04
							Macaca fascicularis (1981—1985)								
Distribution		19	25	14	18	20	47	45	32	45	31	26	15	28.1	12.01
%	337	5.64	7.42	4.15	5.34	5.93	13.95	13.35	9.50	13.35	9.20	7.72	4.45		
Standartiz.		0.68	0.89	0.50	0.64	0.71	1.67	1.60	1.14	1.60	1.10	0.93	0.53	1.00	0.43
							Macaca nemestrina (1981—1985)								
Distribution		18	10	21	7	11	14	13	17	22	24	25	22	17.0	5.95
%	204	8.82	4.90	10.29	3.43	5.39	6.86	6.37	8.33	10.78	11.76	12.25	10.78		
Standartiz.		1.06	0.59	1.24	0.41	0.64	0.82	0.76	1.00	1.29	1.41	1.47	1.29	1.00	0.38
							Macaca arctoides (1975—1981)								
Distribution		7	5	4	3	5	3	3	3	7	5	2	5	4.33	1.61
%	52	13.46	9.61	7.70	5.80	9.62	5.80	5.80	5.80	13.46	9.62	3.85	9.62		
Standartiz.		1.61	1.15	0.92	0.69	1.15	0.69	0.69	0.69	1.61	1.15	0.46	1.15	1.00	0.37

with ejaculation is another typical specific feature of M. arctoides, (*Table 3*).

Reproductive parameters play a very important role in the formation of behavioural patterns, especially of those of sexual, reproductive, parental and social behaviour. In no case should be taken the parameters as an exclusive part of any of the above mentioned types of behaviour and, consequently, sexual behaviour cannot be treated as an isolated type of behaviour. Quite in opposite it is an integral part of behavioural patterns. For example, Hinde (1974) stressed the fact that any generalization on sexual behaviour should be made very carefully with a broader analysis of behavioural patterns, namely for the two following reasons:

"First, sexual behaviour is not a clearly defined category but is closely related to many other aspects of social behaviour. Second, there is a great variability between species (but it may be in many cases simply the results of different reproductive parameters, as we have demonstrated), and even between the individuals of the same species, in nearly all aspects of sexual behaviour" (Hinde, 1974, p. 306).

For example, the elements of sexual behaviour were observed during our investigations not only in adult individuals but also in juveniles and sub-adults and they belong to various types of behaviour. Females of stumptail macaques (M. arctoides) are frequently observed to manipulate with genitalia of juvenile and sub-adults (e.g. sniffing at them, licking them). When juveniles or sub-adults pass the adults, they frequently stop and hold up their hind-limbs and demonstrate to the adults their urogenital region. Similarly, copulation behaviour without penis intromission plays a very important role in the constitution of social relations and hierarchies in all investigated species of the genus Macaca. Various elements of such copulation behaviour were found not only in adult males but also in females and sub-adult or juvenile individuals. Such contacts have not a sexual character and they are a typical expression of the dominant/subordinate social relations. Sexual behaviour in macaques is very frequently connected with some forms of aggressive behaviour. For instance we observed in one case that two fighting M. arctoides males copulated after the fight according to their dominance rank with one female. Within 1.5 hour the alpha male copulated 5 times and inferior male 2 times.

DISCUSSION AND CONCLUSIONS

Differences and similarities in reproductive parameters as well as various aspects of sexual behaviour among individual species seem to be in good correlation with specific features of reproductive organs and with the character of sexual dimorphism in given species of genus Macaca (c.f. eg. Kanegawa et al, 1971). But, according to our results, the character of reproductive parameters on the one hand and that of sexual behaviour and behaviour generally on the other are closely connected with the quality of the environment (Vančatová and Vančata, 1985, in press) and, consequently the environment plays a very important role in the formation of reproductive and behavioural patterns of a given population (cf. Vančatová and Vančata, 1985, in press). Some marked behavioural deviations appear under extreme environmental conditions especially in captivity. For example, an increase of homosexual relations and masturbation and a remarkable increase of direct agression could be observed in individuals living in small cages or secluded areas and behavioral impotence occures in males living in isolation for a long time.

Similarly, specific patterns of seasonality in the Macaca species reared in Sukhumi, i.e. the lost of strict seasonality typical for wild living populations, could be explained on the basis of environmental influences. Yet the differences in natality patterns among individual species also have shown that some features of sesonality are more or less preserved in some species and a precise evaluation of the environmental impact on seasonality of macaques natality would demand further thorough analyses. As it has been shown, the reproductive parameters are also closely correlated with the parameters of the environment and, consequently, the environment could be taken as a specific "transmittor" between reproductive parameters of the organism and relevant behavioural patterns.

Thus when examining any of the given problems or trying to find correlations between them ecological aspects of the topic should be taken into account. Such approach can help us to understand the reason of the variability of reproductive parameters and behavioural patterns both within species and among species but also in the determining of causes of reproductive and behavioural deviations in captivity and optimalization of breeding conditions in captive primates.

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