Reprod. Nutr. Dévelop., 1981, **21** (1), 59-68.

Annual plasma testosterone cycle and ejaculatory ability in the laboratory-housed crab-eating macaque (*Macaca fascicularis*)

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Summary. Six fertile and healthy adult *Macaca fascicularis* males were studied. Radioimmunological assay of the plasma testosterone, sampled without anesthesia in the afternoon at the beginning of each month, showed an annual hormone cycle with a maximum (16.7 $\pm$ 1.1 ng/ml) in the fall and a minimum (9.5 $\pm$ 0.9 ng/ml) in the spring (fig. 1). Using the ratio : number of ejaculations/number of trials, the ejaculatory ability of these animals (fig. 2) was estimated for 10 min in the presence of females between days 12 and 15 of their menstrual cycle. This ability showed no cyclic variation during the year.

Comparing the annual variation of testosterone levels in macaque males (*Macaca mulatta, Macaca arctoides, Macaca nemestrina, Macaca fascicularis*) and man, we found that, except for *Macaca arctoides* and *Macaca nemestrina*, the maximal simian levels always coincided with autumn and the minimal levels with spring in spite of the different rearing environments. (table 2).

After studying ejaculatory ability and plasma testosterone level in the intact macaque throughout the year and comparing it to the results obtained by Resko and Phoenix (1972), Phoenix *et al.* (1973) and Michael and Wilson (1974, 1975) studying castrated males, we believe that above a minimal level, variation in the plasma testosterone level does not affect male sexual behavior, at least as far as ejaculatory ability is concerned. Moreover, during this study we noted that above a maximal plasma testosterone level, varying with the season, the ejaculation rate may be depressed (fig. 3).

Introduction.

A mating season has been observed in macaques (non-human primates) living in their natural habitat or in an outdoor enclosure : *Macaca mulatta* (Conoway and Koford, 1964 ; Lancaster and Lee, 1965 ; Neuville, 1968 ; Vandenbergh and Vessey, 1968), *Macaca fuscata* (Tokuda, 1962 ; Hanby, Robertson and Phoenix, 1971 ; Eaton, 1972), *Macaca sylvana* (McRoberts and McRoberts, 1966), *Macaca fascicularis* (Gauquelin, 1968). However, there is no evidence of a restricted birth season in other macaques

raised in an outdoor enclosure (*Macaca arctoides* : Estrada and Estrada, 1976 ; *Macaca nigra* : Dixson, 1977), for births occur throughout the year.

When raised under stable photoperiod, temperature, humidity and diet, rhesus (*Macaca mulatta*) and Japanese (*Macaca fuscata*) macaques retain their seasonal breeding habits (Valerio, Pallota and Courtney, 1969 ; Nomura and Ohsawa, 1975 ; Aso *et al.*, 1977) characterized by a period of amenorrhea in the female (Riesen, Meyer and Wolf, 1971) and a decline in male sexual activity (Michael and Keverne, 1971) concomitant with a decreasing blood testosterone level (Plant *et al.*, 1974 ; Robinson *et al.*, 1975 ; Gordon, Rose and Bernstein, 1976 ; Michael and Bonsall, 1977).

Conversely, crab-eating macaques (*Macaca fascicularis*) in our laboratory, although raised in natural photoperiod at a constant temperature (Dang, 1977), reproduce regularly all year long, and ejaculation almost always accompanies copulation when the males have access to the females between days 12 to 15 of their menstrual cycle. We thus wished to determine if the male plasma testosterone level was stable throughout the year.

Material and methods.

Six fertile, healthy adult males imported from southeast Asia in 1972 were used in this study ; they were raised in the conditions previously described (Dang, 1977) : individual cages, natural photoperiod, relatively constant temperature (24 to 28 °C) and hygrometry, monkey chow occasionally supplemented with fruits and vegetables.

Blood samples were taken by puncture of the saphena or radial vein on days when there was no copulation ; the animal was not anesthetized but restrained in a holding cage with a movable side. All the animals had been accustomed to blood sampling for a whole year before the experiment began. The blood samples, taken in the afternoon between 2:30 and 5:30 p. m. at the beginning of every month for one year, were heparinized and centrifuged immediately. The plasma was stored at — 20 °C until assay. The next year, serial samples were taken from 4 of the 6 males every hour between 2:30 and 5:30 p. m. on one day in March and November to determine if the androgen level had changed during the afternoon.

Plasma testosterone was assayed by a radioimmunological method described elsewhere (Dang and Meusy-Dessolle, 1979). Assay sensitivity was about 5 pg/tube. Inter-assay variabilities were 7.9 p. 100 and 2.5 p. 100 for 6.8 ng/ml and 15,6 ng/ml respectively. Intra-variabilities were 6.2 p. 100 for 2.2 ng/ml and 2.1 p. 100 for 15.8 ng/ml. Mean « water blank » was 0.006 ng/ml. Mean recovery after extraction was 95 ± 0.9 p. 100.

Male ejaculatory ability was studied monthly in the presence of fertile adult females between days 12 and 15 of the menstrual cycle and determined during a 10-min period by the ratio : number of ejaculations/number of mating tests. The male was tested three times a day at minimum 2-hr intervals, each time with a different female. Less than 31 mating tests per month were practised on each male.

The statistical significance of the between-month differences was evaluated using Student's t-test.

Results.

The plasma testosterone pattern in each animal (a) and the mean (b) of the 6 animals sampled over a 1-year period are shown in figure 1. All except male MN (heavy line) showed a yearly androgen cycle : the testosterone level was maximal in September and October (16.7 $\pm$ 1.1 ng/ml) and minimal (9.5 $\pm$ 0.9 ng/ml) in the spring (March, April, May, June). It rose in April but there was no significant difference between March and April.

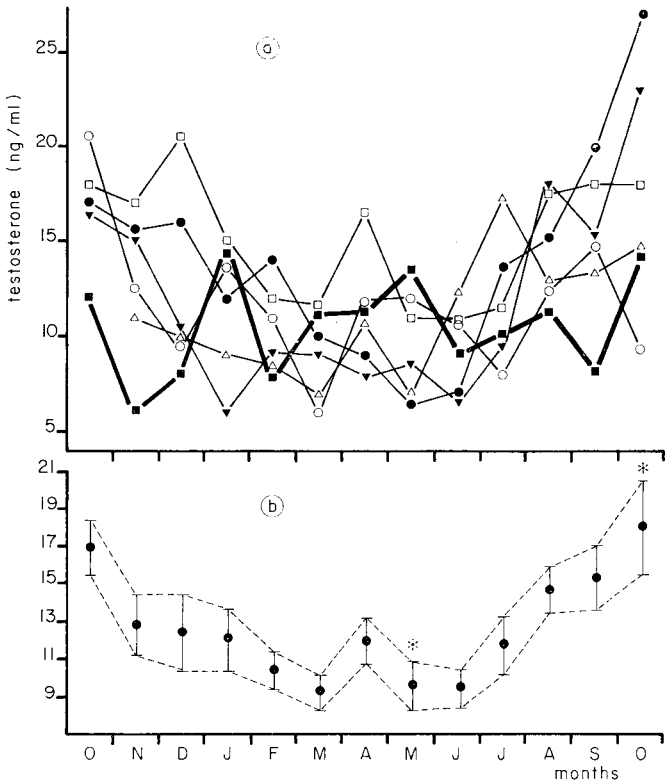

FIG. 1. — *Individual* (a) *and mean* $\pm$ SE (b) *testosterone levels of* 6 *males over a* 1-*year period.*
* Significant difference, $P < 0.02$.

The plasma testosterone levels of 4 males, sampled at 1-hr intervals between 2:30 and 5:30 p. m. on one afternoon in March and in November the next year, are given in table 1. During the afternoons of these two months, the levels were relatively stable in all the animals. The mean hourly levels of the 4 macaques for each of these months were not significantly different. As in the previous experiment, the mean level of the male MN was the lowest ; it should be noted that this animal was the youngest in size and body weight. The overall mean level for all the samples was significantly higher

TABLE 1

Plasma testosterone levels (ng/ml) *in 4 males measured at 1-hr intervals on an afternoon in March and in November*

Animals		2:30 p. m.	3:30 p. m.	4:30 p. m.	5:30 p. m.	$\bar{X} \pm$ SE
I	March	10.7	12.2	10.9	12.2	11.5 ± 0.4
	November.....	9.3	11.4	13.4	11.8	11.5 ± 0.8
N1	March	7.8	10.8	9.7	10.5	9.7 ± 0.7
	November.....	12.3	9.3	11.5	14.2	11.8 ± 1.0
N2	March	12.2	9.0	12.5	11.5	11.3 ± 0.8
	November.....	15.6	12.4	11.5	11.2	12.7 ± 1.0
MN	March	6.8	8.2	9.2	9.3	8.4 ± 0.6
	November.....	8.2	9.3	7.5	12.3	9.3 ± 1.0
$\bar{X} \pm$ SE	March	9.4 ± 1.3	10.0 ± 0.9	10.9 ± 0.9	10.6 ± 0.5	10.2 ± 0.4
	November	11.3 ± 1.6	10.6 ± 0.8	11.0 ± 1.2	12.3 ± 0.6	11.3 ± 0.5

in November (11.3 ± 0.5 ng/ml) than in March (10.2 ± 0.4 ng/ml). The statistical analysis of these results shows that they do not differ significantly from those of the 6 animals for the same two months in the previous year.

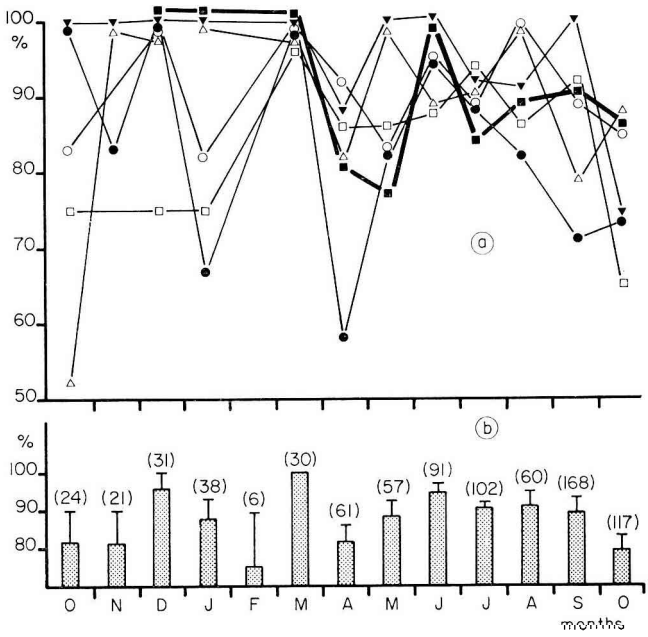

FIG. 2. — *Individual* (a) *and mean* ± SE (b) *ejaculatory rate of 6 males over a 1-year period.* ( ) *Total number of mating trials.*

The individual (a) or mean (b) ejaculatory ability of the males (fig. 2) did not follow an annual cycle concomitant with the plasma testosterone level.

We then divided the year into two periods according to the annual testosterone cycle : (i) August, September, October, November, December, January when the level was relatively high and (ii) February, March, April, May, June, July when the hormone level was low. We then correlated the monthly testosterone level of each animal with its monthly ejaculatory rate (fig. 3). In the first period (fig. 3*a*), we noted in all the animals that when the testosterone level was lower than 17 ng/ml, the ejaculatory rate fluctuated, sometimes reaching 100 p. 100 ; above this critical level, the rate also fluctuated but did not reach 100 p. 100. In the second period (fig. 3*b*), we observed the same phenomenon with a critical testosterone level of 11.5 ng/ml. In other words, *Macaca fascicularis* males could ejaculate more or less rapidly all year long. Above a critical maximal testosterone level (which is higher when the annual testosterone level is relatively elevated than when it is low), the ejaculatory ability was somewhat depressed during the first 10 min after the female was presented.

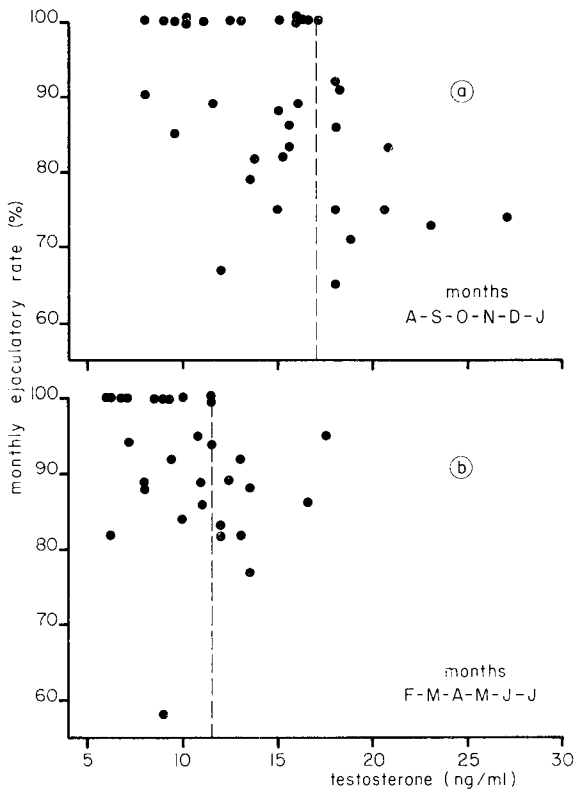

FIG. 3. — *Relationship between individual monthly testosterone level and individual monthly ejaculatory rate.* (a) First period when annual testosterone level is relatively high (August-September-October-November-December-January) ; (b) Second period when annual testosterone level is relatively low (February-March-April-May-June-July).

Discussion.

Macaca mulatta has a circadian testosterone cycle with a low level from 8 to 9 a. m. and a high level from 9 to 10 p. m. (Plant and Michael, 1971 ; Goodman *et al.*, 1974 ; Perachio *et al.*, 1977). Reinberg *et al.* (1975) observed that the plasma testosterone circadian acrophase in man varies as a function of the time of year so that regular sampling at the same time of day all year long is not valid for studying the annual cycle as they originally believed. The year-round circadian testosterone cycle has not yet been studied in the macaque. Assay of plasma testosterone sampled monthly in the afternoon in *Macaca fascicularis* shows an annual hormone cycle ; therefore, this data must be accepted with reservations until further study.

As noted by Bernstein, Rose and Gordon (1974), Eaton and Resko (1974), Phoenix, Dixson and Resko (1977), the restraint technique of sampling macaque blood does not seem to stress the animals very much. Moreover, our males were trained to be sampled for more than one year before the present experiment started.

A comparison of the annual testosterone cycle in different species of male macaques and in man (table 2) shows that, except for *Macaca arctoides* and *Macaca nemestrina*, maximal simian levels always coincide with autumn, while the minimal levels coincide with spring in spite of different rearing environments. Serum testosterone levels in laboratory-housed *Macaca arctoides* living in a constant environment were found to vary significantly throughout the year with peak levels in June and low levels in September (Slob, Ooms and Vreeburg, 1979) ; this chronology differs from that of some other primates. The case of *Macaca nemestrina* is intriguing. The males of that species, although raised in an outside enclosure, did not exhibit seasonal testosterone cycles ; nevertheless, their values varied around the mean level (Bernstein *et al.*, 1978).

Moreover, a comparison of the testosterone levels in different macaque species and in man (table 2) reveals that the minimal as well as the maximal levels in *Macaca fascicularis* are higher than in other species.

As to copulatory behavior, *Macaca fascicularis* in our laboratory ejaculate regularly all year long (Dang, 1977) ; their ejaculatory ability measured by our present method does not follow an annual cycle concomitant with the plasma testosterone level. In laboratory-housed *Macaca arctoides*, Trollope and Blurton-Jones (1975) did not find any definite period of male sexual inactivity during the year ; there was an annual serum testosterone cycle but the hormone levels did not correlate with ejaculatory behavior (Slob, Ooms and Vreeburg, 1979).

Our analysis indicates that once the blood testosterone level is between the minimum and the maximum, hormone level fluctuation no longer affects sexual ejaculatory behavior. Castration and supplementation experiments support this hypothesis. The testosterone level in the castrated male rhesus macaque is very low (Perachio *et al.*, 1977), and reduced or abolished ejaculatory behavior is restored after testosterone injection, but a high dose of this hormone cannot increase the sexual level above that observed before castration (Resko and Phoenix, 1972 ; Phoenix, Slob and Goy, 1973 ; Michael and Wilson, 1974). Likewise, injecting an intact male rhesus macaque with testosterone does not enhance its sexual performance (Phoenix, Dixson and Resko, 1977).

TABLE 2

Comparison of annual testosterone levels in man and macaque

Simian primates	Living conditions	Max. level (ng/ml)	Min. level (ng/ml)	Authors
Homo sapiens	in town	9.09 ± 0.42 Oct.-Nov.	6.40 ± 0.51 April-May	Reinberg and Lagoguey (1975)
	—	7.62 ± 2.16 July-Oct	6.31 ± 1.33 Jan.-April	Smals *et al.* (1976)
Macaca mulatta	laboratory	11.50 Sept.-Oct.	6.00 April-June	Plant *et al.* (1974)
	— id —	10.50 Sept.-Dec.	5.50 March-June	Michael and Bonsall (1977)
	— id —	11.50 July-Sept.	6.00 April-May	Beck and Wuttke (1979)
	— id —	15.5 ± 2.0 Sept.-Dec.	5.0 ± 0.5 April-June	Wickings and Nieschlag (1980)
	outside enclosure	12.00 Oct.-Nov.	2.00 March-June	Gordon *et al.* (1976)
Macaca nemestrina	outside enclosure	16.5 No seasonal fluctuation	9.0	Bernstein *et al.* (1978)
Macaca arctoides	laboratory	14.77 June	6.67-7.15 Aug.-Sept.	Slob *et al.* (1979)
Macaca fascicularis	laboratory	16.70 ± 1.10 Sept.-Oct.	9.50 ± 0.93 March-June	

Macaca fascicularis seems to have a given maximal testosterone level depending on the season ; above that level, the ejaculation rate may be depressed. It is interesting to correlate this result with those in the castrated male *Macaca mulatta* ; although injected with a daily constant dose (2 mg) of testosterone proprionate throughout the year, that simian displayed seasonal ejaculatory activity with a peak in autumn (Michael and Wilson, 1975).

Our animals ejaculate all year long because the females have regular menstrual cycles and only preovulatory females are chosen for testing male sexual activity. A female rhesus given estrogen may stimulate the copulatory activity of males in sexual rest (Vandenbergh, 1969). We do not know if the constant ovulatory menstrual cycles are due to the permanent round-the-year sexual activity of our males, but copulation cannot initiate ovarian activity in the female rhesus in seasonal rest (Vandenbergh and Post, 1976).

Reçu en mai 1980.
Accepté en septembre 1980.

Acknowledgements. — This research was supported by the DGRST, CNRS (L. A. 220) and UER Biomédicale Paris. We are grateful to Professors A. Delmas, J. Hureau and C. Thibault for their encouragement and discussion. Special thanks are due to Mrs. Alice Daifuku for help in editing this manuscript and to G. Aphaecix, R. Baret and M. Carpentier for the animal care.

Résumé. L'étude a porté sur 6 mâles *Macaca fascicularis* adultes, fertiles et sains, élevés au laboratoire. Le dosage radioimmunologique de la testostérone, dans le plasma obtenu à partir de prélèvements effectués dans l'après-midi, au début de chaque mois, sans anesthésie, a révélé un cycle annuel du taux de cette hormone avec un maximum (16,7 $\pm$ 1,1 ng/ml) en automne et un minimum (9,5 $\pm$ 0,9 ng/ml) au printemps (fig. 1). L'activité éjaculatoire de ces animaux en présence des femelles aux 12-15e jours de leur cycle menstruel, observée pendant 10 minutes et mesurée par le rapport : nombre d'éjaculations/nombre d'épreuves, ne varie pas d'une façon cyclique au cours de l'année (fig. 2).

En comparant le cycle annuel du taux de testostérone chez le Macaque (*Macaca mulatta, Macaca arctoides, Macaca nemestrina, Macaca fascicularis*) et chez l'Homme, nous avons observé chez ces simiens, excepté chez *Macaca arctoides* et *Macaca nemestrina*, que les taux maxima coïncident au même moment de l'année (automne), de même pour les taux minima (printemps) en dépit des différents environnements où ils vivent (tabl. 2).

Chez le Macaque, l'examen de l'activité éjaculatoire et du taux de testostérone plasmatique de l'animal entier au cours de l'année, comparés à ceux observés chez le castré (Resko et Phoenix, 1972 ; Phoenix *et al.*, 1973 ; Michael et Wilson, 1974, 1975) amène à penser qu'au-dessus d'un niveau minimum, la variation du taux de cette hormone n'affecte plus le comportement sexuel mâle, tout au moins en ce qui concerne l'activité éjaculatoire. De plus, au cours de cette étude, nous avons aperçu qu'au-dessus d'un taux maximum de testostérone, variable suivant la saison, on assisterait à une diminution de la rapidité à l'éjaculation (fig. 3).

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