

# Physical, hormonal and behavioural aspects of sexual development in the marmoset monkey, *Callithrix jacchus*

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**Summary.** Measurements of growth, plasma progesterone and testosterone levels, and copulatory behaviour were obtained from captive marmosets from birth until 600–800 days of age. Body weight and knee-to-heel length were similar for both sexes. Males exhibited a neonatal testosterone surge from 15–100 days and testosterone levels began to rise again, coincident with the growth of the testis, at about 250 days. The males were copulating by 400–500 days of age. Paired females were apparently ovulating and able to conceive from about 400 days. In peer groups, only the dominant female became pregnant, because subordinate females failed to ovulate.

## Introduction

The common marmoset, *Callithrix jacchus jacchus* (Napier, 1976), is a small, arboreal, South American primate. This monkey reaches puberty at about 15 months of age (Kingston, 1975), and the purpose of the present study was to define the physical, endocrinological and behavioural events of sexual development. Because animals of this sub-species exhibit little sexual dimorphism and females neither menstruate nor show any obvious physical signs of oestrus, detailed measurements of growth and of plasma progesterone and testosterone levels were required to act as criteria of development.

## Materials and Methods

Full details of the animals and their management have been reported elsewhere (Hearn, Lunn, Burden & Pilcher, 1975).

### *Physical measurements*

Measurements were taken of the body weight and knee-to-heel length in 20 males and 19 females at 10-day intervals from birth to 200 days, and then at 50-day intervals until 600 days. Adult size was considered to have been attained when there was no significant difference ( $P > 0.05$ ; Student's *t* test) between the young colony-bred animals and the adults caught in the wild ( $n = 40$ ; 20 males and 20 females). The length and width of the right testis in males and the width of the pudendal pad in females were measured with calipers. The pudendal pad, a secretory area (Epple, 1973; Hampton & Hampton, 1974), surrounds the vulva in females and the penis and scrotum in males and is used in marking objects (Epple, 1973) and during aggressive display (Stevenson & Poole, 1976). Testis volume was calculated by using the formula for the volume of an oblate spheroid ( $V = \pi \frac{1}{8} W^2 L$ , where  $V$  = volume,  $W$  = width and  $L$  = length). The mammary glands were examined for any signs of growth.

### *Blood sampling and hormone assays*

Blood samples (0.3 ml) were taken from the femoral vein between 09:30 and 12:30 h. A heparinized syringe was used with a 0.41 mm diameter (27 gauge) needle. Samples were collected at 15–30-day intervals from animals under 200 days old, and at 10-day intervals from males and 2–3-day

intervals from females over 200 days old for 2–4 months. The plasma was separated and stored at  $-20^{\circ}\text{C}$  until assayed. The frequency of sampling was sufficient to give adequate coverage of the female ovarian cycle of  $16.4 \pm 1.7$  days (Hearn & Lunn, 1975). All samples were assayed in duplicate.

Plasma progesterone concentrations in females were determined by a specific radioimmunoassay (Neal, Baker, McNatty & Scaramuzzi, 1975). The inter- and intra-assay variation was 11.3 and 4.2% respectively, with a detection limit of 2 ng/ml. Plasma testosterone concentrations in males were measured by the specific radioimmunoassay of Corker & Davidson (1978), with an antiserum, raised in a goat, against testosterone-3-carboxymethyl-oxime conjugated to bovine serum albumin. The antiserum cross-reacted significantly only with  $5\alpha$ -dihydrotestosterone (23.9%),  $11\beta$ -hydroxytestosterone (0.4%), oestradiol- $17\beta$  (0.2%) and androstenedione (0.1%). The inter- and intra-assay variation was 12.0 and 4.5%, respectively, with a detection limit of 1 ng/ml.

### *Pregnancy detection and breeding success*

Pregnancies were monitored either by radioimmunoassay of plasma progesterone concentrations or by transabdominal uterine palpation. Growth curves for the uteri of marmosets carrying single, twin and triplet fetuses have been reported previously (Hearn & Lunn, 1975; Hearn, 1978). The age of females at the time of their first conception was calculated from the date of birth of the first young in term pregnancies ( $n = 16$ ), assuming a gestation length of  $148 \pm 4.3$  days (Hearn & Lunn, 1975), or from the uterine diameter when the first pregnancy ended in a spontaneous abortion ( $n = 13$ ). The numbers of pregnancies and abortions and the relative success of rearing of young by colony-bred animals were recorded over a period of  $2\frac{1}{2}$  years. In calculating the percentage of offspring weaned and the occurrence of infant deaths, all stillbirths and the number of young in each set in excess of two were excluded because marmosets do not raise more than 2 offspring from each birth without artificial aid (Hearn *et al.*, 1975). Marmosets in our colony are normally weaned by 40 days of age and data from young dying before this age were analysed by using the Sign test (one-tailed; Siegel, 1956): for each pair or peer group,  $A - B = +1$  or  $-1$ , where  $A$  = the occurrence of no infant deaths (score 1) and  $B$  = the occurrence of one or more infant deaths (score 1).

### *Social groups*

Young marmosets were housed with their parents and siblings until 300–450 days of age, when they were removed to establish breeding groups. Because randomly paired colony-bred male and female marmosets have been slow to breed in other colonies (Kingston, 1975), three options were examined to determine the most efficient system for breeding: (1) young, unrelated marmosets were placed together to give 4 male–female pairs; (2) young male or female marmosets were paired with experienced adults of the opposite sex ( $n = 13$ ); (3) 15 peer groups were established, each comprising 6 unrelated young marmosets (usually 3 male and 3 female). After the initial part of the study, when they were at least 600 days of age, all of the females in social system (1), two in system (2) and three other females were placed with adult, experienced males because they had failed to conceive with their previous partners.

### *Behavioural observations*

*Pairs.* The animals were observed through a one-way mirror in an exercise cage of  $1.5 \times 1.5 \times 1.5$  m, supplied with branches, ropes, etc. Each pair was observed for 2 h/week for 10 weeks in the same exercise cage, with five observations at 12:00–14:00 h and five at 14:30–16:30 h. The times were chosen to avoid disturbance of the colony maintenance routine and to minimize diurnal variations in behaviour. Copulations (and other behaviour patterns to be reported elsewhere) were observed and recorded on an Esterline Angus pen recorder, and vaginal washings were examined daily for the presence of spermatozoa (Hearn & Lunn, 1975), except during Weeks 3, 4 and 8 of observation. Vaginal washings were also taken after observed copulation.

Observations of the pairs were carried out when the young marmosets were between 400 and 550 days of age, because marmosets are thought to become pubertal at about 450 days of age (Kingston, 1975). Young male–female pairs were established 100 days before observation began, while one female and two male youngsters were each paired with an adult of the opposite sex at the first observation period.

*Peer groups.* Dominant–subordinate interactions in 9 of the 15 peer groups were recorded in abbreviated notes. Dominant or subordinate status was assigned on the basis of interactions between pairs of animals as interactions involving 3 or more animals were rare. Any interactions involving food or water were excluded. The subordinate animal was identified from the following behaviour: ‘facial grimace’ (bared teeth gecker face; Stevenson & Poole, 1976); ‘submissive vocalization’, i.e. exaggerated forms of ‘tsik-tsik’, the infantile ‘ngä, ngä’ (Epple, 1968) and squealing; ‘flattened ear tufts’ (tufts flatten; Stevenson & Poole, 1976), and ‘fleeing’ the proximity of another animal (about 30 cm). The dominant animal was identified from behaviour associated with aggression: ‘vocal threats’ (erh-erh; Stevenson & Poole, 1976), ‘ear-tuft flicking’ (tuft flick stare; Stevenson & Poole, 1976), ‘genital presents’ (tail raised present; Stevenson & Poole, 1976) and ‘violent attacks’ (biting and clawing) at the subordinate animal. Dominant animals did not always respond aggressively, but they were easily identified from the direction in which the subordinate animal displayed its submissive behaviour (usually up to a maximum of 1 m). The dominant animal was given a score of ‘1’ against each animal it dominated for every dominant–subordinate interaction in which it was identified, and a single interaction could involve all the behavioural responses listed. An interaction was only considered as having terminated when the dominant animal started to interact with another animal in the group, when both animals lost sight of each other and the pursuit stopped, or when both animals ceased directing the particular behavioural response involved at each other.

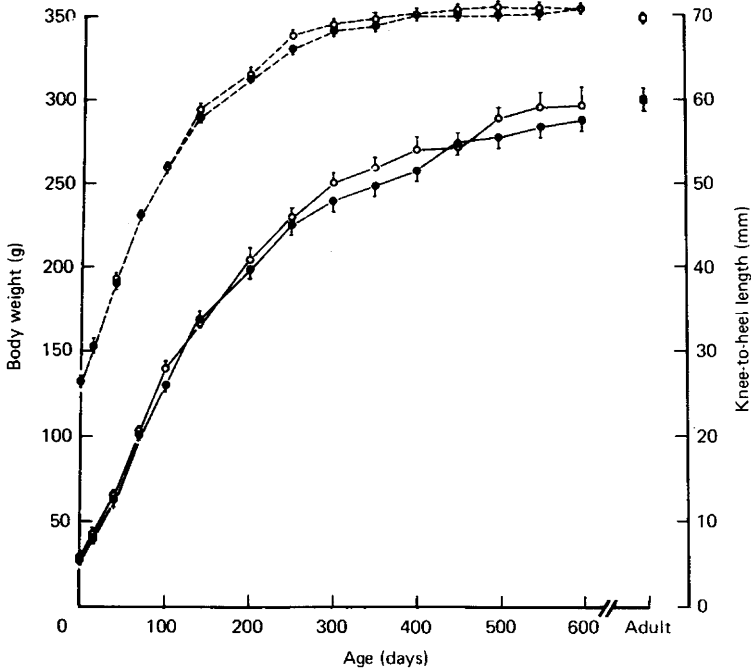
The peer groups were observed, without using a hide, in an exercise cage of  $2.0 \times 1.0 \times 2.0$  m connected by flexible ducting to their home cage of  $100 \times 50 \times 75$  cm (Hearn *et al.*, 1975). Cage sizes were identical in each of the four rooms used and the exercise cages remained connected to the home cages for 1 week after each group was set up. Each animal was identified by the colour of its ear tufts (normally white, but dyed with 1% Eosin Y (red) or 5% light green); the dyes did not affect their behaviour. Aggressive behaviour was rarely seen after the first 2–3 days, and so each group was observed for 1–2 h after the animals were placed together and for  $\frac{1}{2}$ –2 h the next day. Four groups were observed for 2–6 h, 2–3 months later. All observations took place between 11:00 and 16:30 h, and the animals under observation in the exercise cages were in full view of the 40–60 marmosets in the same room. Each peer group or pair had access to the exercise cage in their room at least once a week, and the exercise cages were cleaned every month, in keeping with the maintenance routine.

## Results

### Growth

Text-figure 1 shows growth curves for body weight and knee-to-heel length for marmoset monkeys from birth to 600 days of age, by which time adult size had been attained. There were no significant differences between males and females either in their adult weight or size, or in their rates of growth. Marmosets reached the adult body weight of  $300 \pm 6.6$  g (mean  $\pm$  s.e.m.,  $n = 40$ ) at 500–550 days, and adult knee-to-heel length of  $69.7 \pm 0.6$  mm at 300–350 days. The variation in knee-to-heel length between animals of the same age was low between birth and 300 days.

At birth, the pudendal pad is dark brown in both sexes and between 45 and 60 days of age it becomes a very light pink. Text-figure 2(a) shows the growth of the pudendal pad in female marmosets: there was considerable variation, but the adult pudendal pad width of  $20.1 \pm 0.5$  mm ( $n = 20$ ) was reached by about 425 days of age. There were no changes evident in the appearance of the mammary glands of female marmosets until after their first pregnancy.



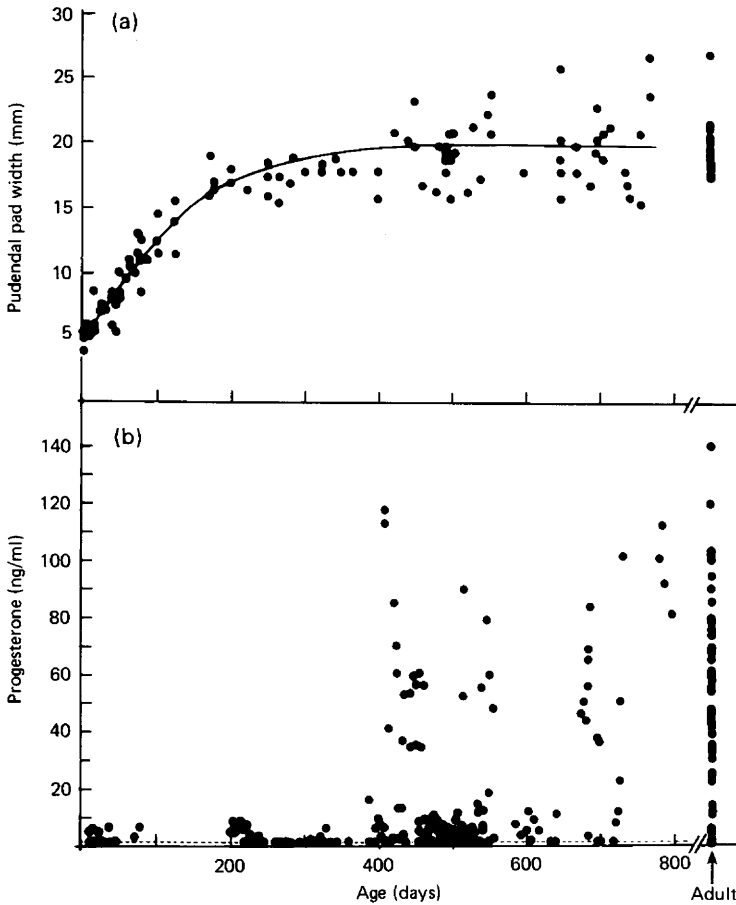
**Text-fig. 1.** Growth of male (●) and female (○) marmosets in captivity, determined from measurements of body weight (—) and knee-to-heel length (---). Values are mean  $\pm$  s.e.m. and at each point <200 days: maximum age range = 2 days, no. of males = 17–20, no. of females = 15–19; at each point >200 days, maximum age range = 18 days, no. of males = 10–20, no. of females = 9–19. The mean  $\pm$  s.e.m. body weight (■) and knee-to-heel length (□) of 20 adult males and 20 adult females are also shown.

The volume of the right testis in male marmosets from birth to 800 days old is shown in Text-fig. 3(a). The testes descend into the scrotum at 50–70 days of age and remain unchanged until 250 days (volume of right testis  $97.6 \pm 8.2$  mm<sup>3</sup>;  $n = 18$ ); they then grow rapidly and reach the adult size of  $729.6 \pm 25.3$  mm<sup>3</sup> ( $n = 20$ ) at 650–700 days of age. There is considerable variation between animals in the rate of growth, the time at which rapid growth of the testis commences, and the time at which adult testicular size is achieved.

#### *Endocrinology and fertility*

As shown in Text-fig. 2(b) plasma progesterone levels in female marmosets were at the limit of sensitivity of the assay ( $\leq 2$  ng/ml) before 400 days of age; values of 20 ng/ml or more were then obtained. These high progesterone levels usually follow ovulation in adult females, in which levels of progesterone in the luteal phase of the cycle can vary between 20 and 140 ng/ml for 7–8 days or more (P. Chambers & J. P. Hearn, unpublished data). The age at which females first conceived ranged between 335 and 974 days (Table 1), confirming that ovulation could occur from about 400 days onwards.

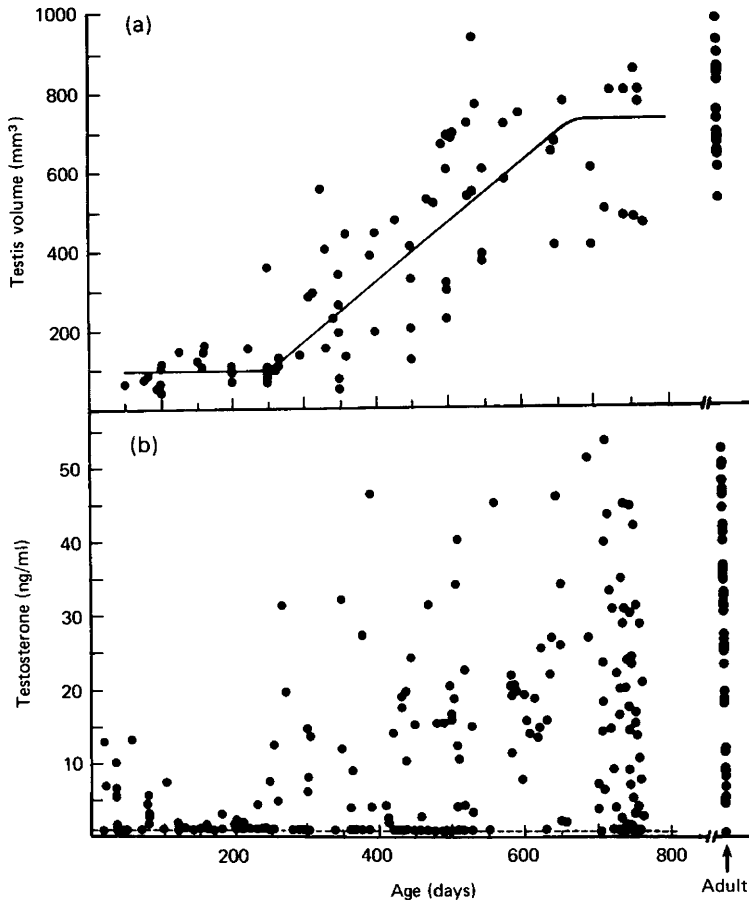
Testosterone levels (Text-fig. 3b) were elevated in neonatal males from Days 15 to 100, with peaks up to 13 ng/ml at about 40 days. Levels then declined to less than 3 ng/ml and remained unmeasurable ( $\leq 1$  ng/ml) while the volume of the right testis remained below 174.2 mm<sup>3</sup>. At about 250 days, testosterone levels rose sharply, coincident with the increase in testicular volume, to attain levels of 30–50 ng/ml which were in the upper part of the range for adult males. The earliest conception of a female paired with a juvenile male occurred when he was 450 days of age (Table 1).



Text-fig. 2. Measurements of (a) the width of the pudendal pad and (b) plasma progesterone concentrations in female marmosets. In (a) the adult values are from single measurements of 20 females; for the 53 measurements from the young females 31 females were measured once, 11 were measured at two and 11 at three different ages. In (b) the values are from 35 young females and 6 adults; the horizontal dashed line denotes the sensitivity of the assay (2 ng/ml).

### Sexual behaviour and breeding success

Details of the reproductive activity and breeding success of the marmosets in the three types of social group are summarized in Table 1. Definite copulations were identified when males reached 440 days of age. Chance observations of family groups showed that young males occasionally mounted their mothers from 250 days of age, the time when plasma testosterone levels and testis volume begin to increase (Text-fig. 3), although there was no evidence that these younger males ejaculated. All the pairs formed were seen to copulate, but the frequency of copulation was far greater when the male was sexually experienced: juvenile males had similar copulation frequencies with juvenile or adult females. Copulations between pairs or in peer groups were observed 4–49 days before spermatozoa were present in vaginal washings, except for pair 6 and two peer groups, when spermatozoa were found the same day. Copulations were also observed at least 4–185 days before the first conception was noted (Table 1). In the pairs, all adult females and 3 of the 6 juvenile females became pregnant, but only the experienced adult females successfully reared their young (Table 2). Two of the juvenile females spontaneously aborted and the other abandoned her young within 2 days of birth. Plasma progesterone concentrations remained low in 2 of the remaining 3 juvenile females (< 10 ng/ml), indicating



**Text-fig. 3.** Measurements of (a) the volume of the right testis and (b) plasma testosterone concentrations in male marmosets. In (a) the adult values are from single measurements of 20 males; for the 55 measurements from the young males 27 males were measured once, 22 were measured at two and 6 at three different ages. The sigmoid curve is fitted by eye. In (b) the values are from 62 young males and 7 adults; the horizontal dashed line denotes the sensitivity of the assay (1 ng/ml).

that they did not ovulate. Juvenile females, aged about 600 days and over, successfully reared their second and subsequent sets of young if they were removed from their original partners and paired with experienced adult males (Tables 1 and 2). Pregnancies in the peer groups were similarly successful (Table 2).

Of the three types of breeding systems, only young animals paired together and young females paired initially with experienced adult males were totally unsuccessful in rearing any offspring, partly due to a failure to conceive (Tables 1 and 2). The most successful combination was an adult female paired with a young male. While young females with peer groups and young females removed from their partners and paired with experienced adult males did not wean all their offspring, there was only a significant occurrence of infant deaths in the latter pairs (Sign Test: positive sign in 1 out of 8 pairs,  $P = 0.035$ , and in 5 out of 11 peer groups,  $P > 0.05$ ).

In 50% of young animals paired together, young males paired with adult females and peer groups, females took over 100 days to conceive for the first time after the pairs or groups were set up (Table 1). However, all young females removed from their original partners and paired with experienced adult

Table 1. Data pertaining to puberty in marmosets in different social groups

Social group	Age of male (days)				Age of female (days)			Time from formation of group to conception (days)			
	Type	Male	Female	No.	No. of observed copulations	At first observed copulation*	When sperm. first found in vaginal washings*		When ♀ conceived	At first observed copulation*	When first conceived
Pair	J	J		1	36	501	510	—	520	—	—
				2	4	495	—†	680	504	691	374
				3	23	508	517	—	527	—	—
				4	18	487	536†	567	499	579	222
Pair	J	A		5	14	499	511	503	(Adult)	(Adult)	25
				6	20	440	440	470	(Adult)	(Adult)	104
Pair	A	J		7	237	(Adult)	(Adult)	—	460	—	—
				8	NR	(Adult)	(Adult)	(Adult)	NR	335	10
Pairs	Ac	J		N = 9	NR	(Adult)	(Adult)	(Adult)	NR	753.1 ± 46.7 (545-974)	32.9 ± 6.2 (17-67)
Peer groups				N = 15	NR	475.8 ± 11.8‡ (439-558)	495.8 ± 26.6§ (439-558)	637.6 ± 24.3‡ (450-923)	426.0 ± 22.5 (343-461)	532.2 ± 6.5 (378-748)	116.3 ± 29.7 (8-463)

Values are mean ± s.e.m. (range).

J = young animals; A = adult animals, Ac = adult animals but not the original partner; NR = data equivalent to that for Pairs 1-7 not available.

\* No data for Pairs 1-4 for 100 days before observation: see text.

† The labia of these females were fused and were artificially opened at 507 and 530 days of age.

‡ n = 5.

§ n = 4.

males conceived within 70 days. There was a much higher number of spontaneous abortions (31) in the 51 pregnancies of the 29 young females than in the two experienced adults (0 in 6 pregnancies, Table 2). Of the first pregnancies of the young females, only 55% survived to term, and in 19% of these the young were abandoned within 1–2 days of parturition. None of the adults abandoned any set of offspring.

**Table 2.** Data pertaining to pregnancy and survival of offspring in marmosets in different social groups

Social group			No. of groups	No. of pregnant females	No. of pregnancies	No. of spontaneous abortions	No. of young born	Corrected no. of young born*	Young weaned (%)
Type	Male	Female							
Pair	J	J	4	2	2	1	2	2	0 (0)
Pair	J	A	2	2	6	0	17	12	12 (100)
Pair	A	J	2	1	2	2	0	0	0 (0)
Pair	Ac	J	9	9	32	18	31	27	17 (63)
Peer group			15	15	27	10	38	30	21 (70)

J = young animal; A = adult animal; Ac = adult animal but not the original partner.

\* Excluding all stillbirths and young in excess of two in each set; see text.

### *Reproductive inhibition*

In every peer group only the dominant female became pregnant. The other females did copulate with the males, but their low plasma progesterone concentrations (<10 ng/ml), over 2 months or more, indicated that they did not ovulate. When the peer groups were first set up, a dominant male (Male 1) and female (Female 1) were identified from the initial dominant–subordinate interactions. A ‘pair bond’ was established between the dominant male and female within a few hours, but not between any of the other members of the group. This pair bond was usually expressed (in qualitative terms) by the two animals frequently remaining within arm’s length of each other ( $\leq 10$  cm), following each other, huddling together and exhibiting intimate social grooming, courtship and copulatory behaviour. The pair bond did not completely exclude either the dominant male from copulating with other females, or the dominant female from copulating with other males. However, dominant males aggressively disrupted mounting of the dominant female by a subordinate male (3 instances), and on two occasions dominant females dislodged male partners mounting subordinate females. In one peer group the dominant male did not react to a subordinate male mounting the dominant female. Subordinate males also mounted subordinate females and spermatozoa were recovered from the vaginal washings, but these animals did not exhibit the intimate licking, tonguing and face-nuzzling mating behaviour of the dominant pair.

In an example of dominant–subordinate interactions from one peer group, a clear ranking order was achieved among the three males (Table 3). Male 3 started the aggressive behaviour in the group, and the only two reversals of assigned status occurred during the very first interactions between Males 1 and 3. In the peer groups Males 2 or 3 were usually the first to exhibit aggressive behaviour. Among the females, only the dominant female was clearly identified (Table 3). Female 2 was only scored as dominant to Female 3 in four out of the six interactions, and no clear ranking between these two was achieved. When all six animals were considered together, intra-sexual rank was not necessarily related to inter-sexual rank and no clear ranking order from 1 to 6 could be achieved. The dominant male and female ranked as dominant to all the rest, but about equal to each other, scoring 4 and 3 respectively. Male 2 was ranked as subordinate to the dominant pair, but dominant to all the rest. The rank order between Male 3 and Females 2 and 3 was not clear, mainly because they spent most of their time avoiding the dominant animals. There was no interaction between the dominant male and Female 2, but from her submissive behaviour towards the other dominant animals it was highly unlikely that she would be dominant to the dominant male.



**Table 3.** Dominance scores, determined from the numbers of interactions between dominant and subordinate animals, of 6 marmosets in a peer group

Dominant animal	Subordinate animal					
	Male 1	Female 1	Male 2	Male 3	Female 2	Female 3
Male 1		4	14	10	0	2
Female 1	3		15	29	19	30
Male 2	0	0		30	12	5
Male 3	2	0	0		1	0
Female 2	0	0	0	0		4
Female 3	0	0	0	0	2	

The scores below the diagonal line (2.8%) indicate reversals of assigned status.

After the first 2–3 days, usually following the removal of one of the subordinate animals because of persistent attacks from one or more dominant animals, the relationships in the peer groups were established and aggressive interactions virtually ceased. The dominant pair could be distinguished by their association (the male following the female, etc.) but no rank order between subordinate animals was evident. When young were born to the dominant female, they were frequently carried and cared for by the dominant and subordinate animals. There were no marked differences in carrying frequencies between subordinate animals (casual observations of the groups). After the young were weaned, the dominant female attacked one or more of the subordinate females, and consequently the peer groups were disbanded 2–3 months after the young were born. The dominant pair and their young were left in their own cage, while the remaining animals were removed and either separated into male–female pairs, or paired with an experienced adult of the opposite sex. All of the latter pairs copulated and spermatozoa were recovered from the vaginal washings within 5–13 days of pairing ( $n = 6$ ); 4 of the previously subordinate females became pregnant within 10–52 days of pairing, while plasma progesterone concentrations in the remaining 2 indicated that they ovulated within 31–34 days of pairing. Two of the pregnant females and one of the females that ovulated remained in the same room beside the dominant female.

### Discussion

The identical weight and skeletal development of males and females, and the lack of sexual dimorphism in the adults, is typical of a monogamous species (Short, 1977; Clutton-Brock, Harvey & Rudder, 1977), and is in agreement with the behavioural evidence for monogamy in the marmoset (Epple, 1967). These results are in contrast to those cited by Ralls (1976), who has indicated that marmosets are sexually dimorphic with respect to their ventral sterno-pubic length.

The physical and endocrinological development of marmoset monkeys is completed within 18–20 months, yet the marmoset still retains the typical primate characteristic of a delayed puberty when compared to other mammals of a similar size, such as the rat, which reaches puberty within 2–3 months (Tanner, 1962). The marmoset completes development in a much shorter time than the 5–7 years or more of the rhesus monkey, *Macaca mulatta* (van Wagenen & Catchpole, 1956), or the 4–8 years of the yellow baboon, *Papio cynocephalus* (Altmann & Altmann, 1970; Lister, 1975), and this may be correlated with its shorter life-span and smaller body weight (marmoset: 167–360 g, 12 years; rhesus macaque: 4.65–14.5 kg, 21.5 years; baboon species: 11–30 kg, 28–29 years; Napier & Napier, 1967). No clear relationship between body weight and pubertal age was achieved in female marmosets, in contrast to that found in rhesus monkeys (Wilén, Goy, Resko & Naftolin, 1977) and women (Frisch & Revelle, 1970), because females did not exhibit menarche and could be reproductively inhibited by dominant females.

Puberty in the marmoset is best described as a period rather than a point in time, particularly in the male, as then it encompasses the increased plasma testosterone levels and testicular size and the development of copulatory behaviour which accompany the appearance of spermatozoa, i.e. between 250 and 400–500 days of age. Moreover, in male and female marmosets there appears to be a distinction between the age at puberty (400–500 days) when gametes are produced and mating occurs and the age of sexual maturity (500–600 days) when conceptions mainly occur. Also, young females experienced more spontaneous abortions and raised fewer of their offspring than adult females. Asdell (1946) made a similar distinction between puberty and sexual maturity for rodents, sheep, pigs and other primates. There are anecdotal reports of marmosets conceiving as early as 300 days of age, but these pregnancies usually ended in abortions or the young were not reared successfully.

Fertility of the young marmosets could also be affected by the composition of the social groups. Higher percentages of offspring were raised by pairs of young males and adult females than by any other group combination (Table 2), suggesting that for rearing offspring maternal age and experience might be more important than paternal. The importance of maternal experience was again suggested by the significantly higher numbers of infant deaths among pairs of experienced adult males and young females. Ingram (1978) has also found maternal experience important in rearing young marmosets. Animals were more efficient at breeding and rearing offspring in peer groups than in pairs, and this may stem from two causes. Firstly, the peer groups introduce an element of mate selection, with competition between unrelated animals. Secondly, as the young animals are separated from their families during puberty, the peer groups may provide an adequate substitute for further socio-sexual development lacking in the pairs. Rhesus monkeys can be raised from infancy in peer groups with little apparent social deficiency (Hinde, 1974). The behaviour of common marmosets in the wild has yet to be studied, and the movement of juveniles between social groups may prove to be an equivalent socializing process to that used in our laboratory. Recent studies on the closely related tamarin monkey, *Saguinus oedipus*, show that there may be considerable interchange of older juveniles between social groups, although the adults remain in the same groups (Dawson, 1976; Warner, 1978).

In the context of a monogamous species, the role of unrelated members of peer groups in raising the young of the dominant female is puzzling, especially as the former animals were able to breed within 2 months of separation from the dominant pair. Possibly, with captive marmosets, the artificial social structure of the peer group may mimic the monogamous family group, in which newborn young are a source of great interest, with the dominant pair becoming 'parents' and the other members of the group becoming their 'juveniles'. However, the analogy between family and peer groups ends when the young of the dominant female are weaned. In the peer groups, the dominant female attacked the other females and the subordinate animals were removed, leaving the dominant pair and their offspring. In the family groups of similar size, there was either no violence following the birth of further offspring ( $n = 5$ ; D. H. Abbott, unpublished observations), or one of the older siblings attacked a younger one which had to be removed ( $n = 3$ ). As found by Rothe (1975), the parents were not involved in the expulsion of their offspring. The break-up of the peer groups might be due to the developing offspring disrupting the previous dominant–subordinate relationships. Rothe (1975) also found that the increase in aggressive behaviour of the dominant female usually led to the break-up of his artificial groups of marmosets.

Subordinate female marmosets in peer groups experienced complete suppression of fertility, because they did not appear to ovulate, but there was little evidence to suggest whether there was suppression of fertility in subordinate males, as the dominant males did not completely exclude others from mating with the dominant females. Measurement of oestrogen in urine samples collected from females in peer groups and female–female pairs indicated ovarian cyclicity only in the dominant females (Lunn, 1978). Similarly, Epplé (1967) and Rothe (1975) found that only the dominant female became pregnant in captive groups of common marmosets. However, in contrast to Rothe's (1975) findings, formerly subordinate females were able to breed successfully without being moved out of the room housing the dominant female.

In other primates the effects of dominance on female fertility are partly inhibitory, as in Gelada baboons, *Theropithecus gelada* (Dunbar & Dunbar, 1977) and rhesus monkeys, *Macaca mulatta* (Drickamer, 1974) in the wild, and in captive olive baboons, *Papio anubis* (Rowell, 1970); subordinate

female tree shrews, *Tupaia belangeri*, suffer complete suppression of fertility only with increased density of population (von Holst, cited by Epple, 1973). The mechanism(s) by which social dominance in primate societies inhibits reproduction in the female requires investigation, and the captive female marmoset may serve as a good model.

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