J. med. Primatol. 5: 266–275 (1976)

Reproductive Characteristics of Free-Ranging Panamanian Tamarins *(Saguinus oedipus geoffroyi)*[1]

GARY A. DAWSON and W. RICHARD DUKELOW

The Museum and the Department of Fisheries and Wildlife and Endocrine Research Unit, Michigan State University, East Lansing, Mich.

Key Words. Callitrichidae · *Saguinus* · Panamanian tamarin · Reproduction · Seasonality · Birth seasons

Abstract. Field observations on reproductive activity in the Panamanian tamarin *(Saguinus oedipus geoffroyi)* were made in conjunction with the examination of 131 reproductive tracts collected at regular intervals over one year. Reproductive tract characteristics were compared over seasons. Embryonic and fetal development were also assessed.

A distinct birth peak was observed from April to early June. Pregnancies in April and May point to a potential, but unrealized, birth peak in August and September. Despite the tendency toward birth peaks, reproductive activity occurred throughout the year.

Reproduction was limited to a single female per social group. The average number of infants born per female was two. Groups inhabiting lowland areas appeared to be more successful in raising young than groups inhabiting upland areas.

Introduction

Marmosets and tamarins (Callitrichidae) have become increasingly popular in recent years as animals for biomedical research. Their small size, their relative tractibility when compared to larger species, their tendency to produce twins, and, in some species, their abundance and relatively low cost are responsible for their popularity. Moreover, while other primate populations continue to decline due to overexploitation and destruction of their

[1] Supported by USPHS grant No. 1-K4-HD35, 306 and HD 07534, the Midwestern Universities Consortium for International Activities, and the Lister Hill Foundation (Gorgas Memorial Laboratory).

habitats, some callitrichid species thrive in the dense, second-growth forests which result from man's activities in the Neotropics. Thus, potentially, some callitrichid species offer at least a partial solution to the current shortage of primates for biomedical purposes.

In spite of the popularity and potential of callitrichids, their ecology, behavior, and reproductive habits have been poorly understood by investigators. Early field studies [20, 21] present evidence for pronounced reproductive seasonality in some species. Later accounts consider *Saguinus* to be nonseasonal breeders [15]. More recent works offer evidence for seasonality in reproductive effort [7, 8, 14]. The present study, which was conducted in conjunction with more extensive field studies on the behavioral ecology of *S. oedipus geoffroyi* in central Panama [2, 3] had as its objective the elucidation of the population's reproductive parameters.

Materials and Methods

Field observations of tamarin reproductive activity were made on the Pacific slope of the Panama Canal Zone from December 1972 through May 1974. In addition, 131 *S.o. geoffroyi* were collected at a rate of five animals every two weeks. Immediately after sacrifice, the animals were weighed, body measurements were taken and the reproductive tract and suprapubic gland were fixed in alcohol-formalin-acetic acid (AFA) fixative (90 parts 95% ethanol, 5 parts of 37% formalin and 5 parts glacial acetic acid) for transport to the Endocrine Research Unit at Michigan State University.

Reproductive measurements, together with body weight, body length, and the length, breadth and degree of pigmentation of the suprapubic gland were compared over three trimesters: (1) November to February, the peak breeding season ; (2) March to June, the peak season of parturition; and (3) July to October, the period of comparative reproductive quiescence. Differences among categories were determined using single classification analysis of variance with a two-sided hypothesis. Actual analysis was carried out with the Michigan State University Computer (CDC 6500).

Weights of immature individuals and uterine measures of pregnant females were excluded from this analysis.

Results

Field observations showed a distinct birth peak from late April through early June. Eighteen social groups with infants were observed during this period. Five social groups with newborn infants were seen in March, and single groups with carried young were seen in February, July and October.

Six of the seven well-developed fetuses in the collected sample dated from the months of February, March and April.

Reproductive activity was not limited to a fixed period preceding the annual birth peak. Pregnant females were found from September through May, newborn young were observed in June and July, and one collected infant was born in August. Moreover, two females collected in April and two females collected in May were in the early stages of pregnancy. These observations, together with the presence of well-developed fetuses in a female collected in September, point to the possibility of a potentially bimodal birth peak, with young being born in April and May, and in August and September. The reproductive potential evident from the April and May pregnancies is, however, rarely realized, since the sightings of infants outside the March to July season of parturition are very rare.

Some evidence exists for a postpartum estrus. Three collected females were lactating and pregnant, two of them with well-developed embryos. Also, in one social group (with one reproductive female), two sets of twins were separated by only five or six months of age. Thus the effect of lactation anestrous, if it exists at all, must be slight.

The trimestral comparison of somatic and reproductive tract measurements for mature males presented in table I revealed no differences in the size or weight of the reproductive organs. However, body weight differed markedly over trimesters ($F = 3.843$, 52 d.f., $p = 0.028$). Post-data comparison of the trimestral means for body weight using the Student-Newman-Keuls test indicated that mature males weighed significantly more during the July to October trimester than during either of the other trimesters ($p < 0.05$). The average weights of mature males did not differ between the November to February and the March to June trimesters ($p < 0.05$).

The comparison of somatic and reproductive measurements for mature females over trimesters shown in table II revealed no significant differences in reproductive tract measurements. Two measurements, body weight and the width of the suprapubic gland, did differ over trimesters ($F = 2.464$, 37 d.f., $p = 0.099$; and $F = 3.752$, 39 d.f., $p = 0.032$, respectively). The mean width of the suprapubic gland was significantly greater in the March to June trimesters ($p < 0.01$), but no significant differences were observed between the other two trimesters ($p < 0.05$). A post-data comparison of the means indicated that mature females were significantly heavier during the July to October trimester ($p < 0.05$). Weights did not differ between the other trimesters ($p < 0.05$).

Reproductive females (pregnant, lactating or post-lactating) appear to be older than nonreproductive females as demonstrated by the criteria of a higher frequency of scarring, especially on the ears and face, and the higher incidence of damaged canine teeth. The incidence of a highly developed suprapubic gland was also more prevalent in reproductive females.

The mean number of newborn infants per social group (per female) was 2.00 ± 0.40 SD (n = 26). Although social groups usually contained at least two adult females, only one mature female per group was observed to bear young. The number of reproductive females in the collected sample did not differ significantly from the expected number, based on the expectation of one reproductive female per average group size of 6.93 tamarins ($\chi^2 = 1.820$, 1 d.f., $p < 0.01$).

The mortality rate for infant tamarins is high (50% or more) during the first six months of life. Most groups are successful in raising only one of the infants. It also appears that the site of the group's home range, especially under severe climatic conditions, may affect survival. In this study, four

Table I. Somatic and reproductive tract measurements of mature male *S. o. geoffroyi*, with a comparison of measurements over trimesters[1]

	Mean	SD	n	F statistic	Significance probability of F statistic
Body weight[2]	481.58	50.04	55	3.843	0.028
Body length[3]	231.76	10.85	55	0.190	0.827
Suprapubic gland length	31.81	6.27	48	0.144	0.866
Suprapubic gland width	20.08	3.09	48	1.545	0.224
Suprapubic gland condition	2.37	0.49	46	1.107	0.340
Left testis length	11.75	1.52	54	2.248	0.116
Left testis width	7.89	1.00	54	1.222	0.303
Left testis breadth	6.16	1.23	54	0.274	0.762
Left testis weight[4]	3,174.78	1,146.61	54	0.561	0.574
Right testis length	11.83	1.82	56	0.926	0.402
Right testis width	7.74	1.38	56	0.277	0.759
Right testis breadth	6.10	1.16	56	0.016	0.984
Right testis weight	3,219.43	1,339.74	56	0.084	0.919

[1] Trimesters equal: (1) November–February, (2) March–June, and (3) July–October.
[2] Weight to nearest 0.1 g.
[3] All linear measurements in mm.
[4] Testis weights in mg.

groups inhabiting lowland areas were all successful in raising both of their twins until they were about three months of age. Two of these groups lost an infant at four months of age. The others survived until at least six months of age. In contrast, a group occupying an intermediately moist range lost its two young within two months after birth; in the seasonally dry upland habitat, two groups lost their twin infants within the first two months after birth, and two groups apparently did not produce young.

Fifteen pregnant females were recovered; the results of their examination are shown in table III. The estimated embryonic or fetal ages [12] are shown and substantiate the concept of nonseasonal breeding. The gestation length of this species has been estimated at 140 to 145 days [15].

Table II. Somatic and reproductive tract measurements of mature female *S.o. geoffroyi* with a comparison of measurements over trimesters[1]

	Mean	SD	n	F statistic	Significance probability of F statistic
Body weight[2]	502.50	54.98	40	2.464	0.099
Body length[3]	238.53	16.82	47	0.867	0.427
Suprapubic gland length	40.43	6.12	42	2.186	0.126
Suprapubic gland width	26.62	4.80	42	3.752	0.032
Suprapubic gland condition	2.67	0.48	42	0.722	0.492
Left ovary length	7.84	1.28	45	0.055	0.947
Left ovary width	5.12	0.97	45	0.902	0.411
Left ovary breadth	3.59	0.87	45	0.861	0.430
Left ovary weight[4]	855.22	453.16	45	0.779	0.465
Right ovary length	7.69	1.13	44	0.029	0.971
Right ovary width	5.14	1.16	44	0.271	0.764
Right ovary breadth	3.46	0.85	44	1.050	0.359
Right ovary weight	789.43	375.92	44	0.797	0.458
Uterus weight[5]	2,003.29	2,247.44	34	1.717	0.196
Uterus width[5]	8.80	3.13	36	1.357	0.271
Uterus depth[5]	8.02	3.54	36	0.763	0.474

[1] Trimesters equal: (1) November–February, (2) March–June, and (3) July–October.
[2] Body weight in grams, pregnant females excluded.
[3] All linear measurements in mm.
[4] Ovary weights in mg.
[5] Pregnant females excluded, weight in mg, linear measurements in mm.

Table III. Characteristics of uterine contents from pregnant females

Female	Date killed	Comments
20	April 16, 1973	twin embryos
24	May 1, 1973	no embryonic tissue present, placenta poorly fixed
25	May 1, 1973	twin embryos, developmental stage XII–XIII
119	September 27, 1973	twin fetuses; crown-rump lengths, 69.1 and 58.0 mm; weights, 15.3 and 16.3 g
130	October 23, 1973	no embryonic tissue, placenta present, some chorionic tissues
141	November 19, 1973	single embryo
160	December 17, 1973	embryonic membranes; poorly fixed
172	February 5, 1974	twin embryos, developmental stage XXII
173	February 18, 1974	single embryo, developmental stage XXI; crown-rump length 14.6 mm; weight 0.5 g
177	February 19, 1974	some chorionic tissues, no embryonic tissue
182	March 13, 1974	twin fetuses; crown-rump lengths, 37.5 and 32.8 mm; weights, 4.2 and 4.3 g
191	March 20, 1974	single fetus, with body hair, near birth
195	April 2, 1974	no embryonic tissue, placenta present
203	April 17, 1974	twin fetuses; crown-rump lengths, 55.8 and 51.6 mm; weights, 15.3 and 16.3 g
204	April 17, 1974	twin embryos, developmental stage XXI; crown-rump lengths, 14.1 and 13.5 mm; weights, 0.4 and 0.5 g

Discussion

Abundant evidence exists for a definite *S. o. geoffroyi* breeding season in central Panama. Wislocki [20, 21] found small embryos in the uteri of females in January and early February. With a gestation period of 140 to 145 days, these tamarins would be born in April, May and June. Enders [6] observed a peak season of parturition during these months, and Moynihan [14] observed that large numbers of infants appeared 'quite suddenly' in the Panama City market in May. Fleming [8] stated, on the basis of Moynihan's [14] work, that *S. o. geoffroyi* was seasonally monoestrous, with a breeding peak in January and a peak season of parturition in the early wet season when the fruits and insects eaten by tamarins are most abundant. Information gathered during this study also offers support for the existence of a birth peak. Epple [7], in a study of captive *S. o. geoffroyi*, found that births occurred in March, April, May and August. Her observations suggest that these tamarins are either seasonally polyestrous or that a postpartum estrus occurs.

She also noted an indication of postpartum estrus in two of three full-term deliveries. HAMPTON and HAMPTON [9],working with the closely related *S. o. oedipus* kept under captive conditions, observed birth peaks in spring and autumn.

With such a body of evidence pointing to a seasonal birth peak, the presence of pregnant females throughout the year, and the data indicating the potential for a second birth peak sometime in August or September, are rather surprising. The existence of the primary birth peak in March–June is easily understood since it is correlated with the appearance of insects and fruits at the beginning of the wet season. However, pregnancies leading to the birth of young at other times of the year would appear to be wasted reproductive effort, since the young would be unlikely to survive the rigors of food scarcity in the late wet and the dry season. Such pregnancies would, however, be advantageous during exceptionally favorable years and in the colonization of new habitats. The adaptive advantages of extra-birth-peak young under these circumstances may outweigh their disadvantages in seasonal habitats and habitats at carrying capacity.

The actual fate of most young which are conceived outside the November–February breeding peak leading to the March–June birth season is unknown. Their scarcity in groups observed after the birth peak implies that either very few are conceived or that those which are conceived are resorbed, aborted, or die as neonates. In light of the frequency of these extra-breeding season pregnancies seen in the collected sample, the latter possibilities are the most likely of the alternatives.

The scarcity of newborn young in August and September is also surprising when one considers the small embryos found in mature females collected during April and May. Insect foods are abundant in August and September, as are many of the smaller fruits. The failure of these pregnancies to contribute young to the population cannot be due to inadequate diet for either mother or offspring; but must rather be due to other factors, the majority of which are probably density-dependent and behavioral in nature.

The mechanism through which tamarin reproduction is attuned to the seasonally variable environment is unknown. The most common external regulators of reproduction are light, temperature and food supply; in primates changes in humidity and precipitation which presage seasonal peaks of food abundance also affect the timing of reproduction [4, 10, 13, 16, 17, 19].

Differences in photoperiod at the Panamanian latitude are slight–about 63 min between the longest and shortest days of the year. Therefore, FLEMING [8] discounts changes in the photoperiod as affecting reproduction. KOFORD

[13], in his study of exotic rhesus monkeys *(Macaca mulatta)* on Cayo Santiago Island, which lies far to the north of Panama and experiences daylight changes of about 0.5 min per day, also discounts light as a factor affecting reproduction.

Spinage [18] observed that while changes in day length at tropical latitudes might be imperceptible to mammals, the sudden shift in the timing of sunrise and sunset at the summer and winter solstices might not be. He observed that certain tropical ungulates living on the equator appear to use photoperiod in synchronizing reproductive avtivity. He hypothesized that the animals did not perceive changes in day length, which is constant to within 2 min per year, but rather the regular shifts of 25 min in sunrise and sunset time which occur at the solstices.

The sunrise-sunset shift is of greater magnitude in Panama (about 47 min over two months' time), and the breeding season of many Panamanian mammals coincides with the shift in sunrise-sunset times [8]. The peak of the effective tamarin breeding activity, based on the parturiton peak minus the 140- to 145-day gestation period, coincides with this shift. This relationship, however, may be fortuitous. Climatic changes from wet season to dry season could be the proximal cue, or reproduction might be attuned to changes in the diet which accompany this seasonal change.

Temperature may be dismissed as a factor affecting the timing of tamarin reproduction. While the mean monthly temperature does reach a low in September and October and begins to climb during the peak tamarin breeding season, the differences in mean temperature are slight and the variation among days of the month, and over years, make temperature changes a highly undependable cue.

The popularly accepted theory regarding the onset of breeding activity in central Panama is that reproductive activity is triggered by the drop in precipitation and humidity which mark the beginning of the dry season [8, 14]. For many mammals [8] the correlation between the onset of the dry season and the onset of breeding activity is a good one. This correlation does not hold, however, for this tamarin. The matings which lead to the April to early June peak do not begin with the onset of the dry season, but in the wet months of November and early December, and extend through the beginning of the dry season in late December, January and February.

Most primate species inhabiting the climatically seasonal middle American tropics show indications of seasonal breeding [11, 22]. For example, the *Saimiri*, which are small insectivore-frugivores occupying a niche which is very similar to that of *Saguinus* [5], show reproductive cyclicity accompanied by readily visible morphological changes [4]. The tamarins, in contrast, show no apparent seasonal changes in reproductive tract morphology or measurements.

The significantly greater body weights of both males and females in the third trimester (July–October) appear to be due the presence of abundant food during the first half of the trimester and in the preceding trimester. They may also reflect the maturation and growth of juveniles which entered the adult population in the first trimester as sexually mature, but smaller, adolescents. The general increase in weight is noticeable, however, even in older animals. This phenomenon appears to be strictly somatic in nature and unrelated to the 'fatted male' condition which accompanies reproduction in *Saimiri* [4].

The high rates of infant mortality in the Panamanian tamarin [2, 3, 14] might be expected, given its small size, the many predators, and an adult population which probably approaches carrying capacity. It also appears that infant mortality may vary according to habitat type. The limited data seem to indicate that groups inhabiting seasonally unsuitable upland areas are less successful in raising young than are groups whose home ranges lie in stable, lowland areas.

Acknowledgement

We acknowledge, with gratitude, the assistance of Drs. A.G. HENDRICKX, M.D. YOUNG and P. GALINDO.

References

1 BALDWIN, J.D.: Reproductive synchronization in squirrel monkeys *(Saimiri)*. Primates *11:* 317–326 (1970).

2 DAWSON, G.A.: Composition and stability of social groups of the tamarin *(Saguinus oedipus geoffroyi)* in Panama: ecological and behavioral implications. Proc. Conf. Biology and Conservation of the Callitrichidae, 1975. Smithson Instn. (in press).

3 DAWSON, G.A.: Behavioral ecology of the Panamanian tamarin *(Saguinus oedipus geoffroyi*, (Callitrichidae, primates); Ph. D. thesis, Michigan State University, East Lansing, Mich. (1976).

4 DUMOND, F.V. and HUTCHINSON, T.C.: Squirrel monkey reproduction: the 'fatted' male phenomenon and seasonal spermatogenesis. Science, N.Y. *158:* 1067–1070 (1967).

5 EISENBERG, J.F.; MUCKENHIRN, N.A., and RUDRAN, R.: The relation between ecology and social structure in primates. Science, N.Y. *176:* 863–874 (1972).

6 ENDERS, R.K.: Mammalian life histories from Barro Colorado Island. Bull. Mus. comp. Zool. Harv. *78:* 385–502 (1935).

7 EPPLE, G.: Maintenance, breeding and development of marmoset monkeys (Callitricidae) in captivity. Folia primatol. *12:* 56–76 (1970).

8 FLEMING, T.H.: The reproductive cycles of three species of opossums and other mammals in the Panama Canal zone. J. Mammal. *54:* 439–455 (1973).

9 HAMPTON, J.K. and HAMPTON, S.H.: Marmosets (Hapilidae) *(Oedipomidus oedipus):* Breeding seasons, twinning, and sex of offspring. Science, N.Y. *150:* 915–917 (1965).

10 HARRISON, R.H. and DUKELOW, W.R.: Seasonal adaptation of laboratory maintained squirrel monkeys *(Saimiri sciureus)*. J. med. Primatol. *2:* 277–283 (1973).

11 HARRISON, R.M. and WOLF, R.H.: Seasonal reproductive patterns in nonhuman primates. (In press).

12 HENDRICKX, A.G.: Embryology of the baboon (University of Chicago Press, Chicago 1971).

13 KOFORD, C.B.: Population dynamics of rhesus monkeys on Cayo Santiago; in DEVORE Primate behavior, field studies in monkeys and apes. I (Holt, Rinehart & Winston, New York 1965).

14 MOYNIHAN, M.: Some behavior patterns of platyrrhine monkeys. II. *Saguinus geoffroyi* and some other tamarins. Smithson. Contr. Zool. *18:* 1–77 (1970).

15 NAPIER, J.R. and NAPIER, P.H.: A handbook of living primates (Academic Press, New York 1967).

16 ROSENBLUM, L.A.: Some aspects of female reproductive physiology in the squirrel monkey; in ROSENBLUM and COOPER The squirrel monkey (Academic Press, New York 1968).

17 RUDRAN, R.: The reproductive cycles of two subspecies of purple-faced langurs *(Presbytis senex)* with relation to environmental factors. Folia primatol. *19:* 41–60 (1973).

18 SPINAGE, C.A.: The role of photoperiodism in the seasonal breeding of tropical African ungulates. Mammal. Rev. *3:* 71–84 (1973).

19 VANDENBERGH, J.G. and VESSEY, S.H.: Seasonal breeding of free-ranging rhesus monkeys and related ecological factors. J. Reprod. Fert. *15:* 71–79 (1968).

20 WISLOCKI, G.B.: On a series of placental stages of a platyrrhine monkey *(Ateles geoffroyi)* with some remarks upon age, sex and breeding period in Platyrrhines. Contr. Embryol. No. 133, Carnegie Inst., Washington, Publ. No. 414; pp. 173–192 (1930).

21 WISLOCKI, G.B.: Observations on twinning in marmosets. Am. J. Anat. *64:* 445–483 (1939).

22 WOLF, R.H.; HARRISON, R.M. and MARTIN, T.W.: A review of reproductive patterns in New World monkeys. Lab. Anim. Sci. *25:* 814–821 (1975).

DR. W. RICHARD DUKELOW, Endocrine Research Unit, Michigan State University, *East Lansing, MI 48824* (USA)