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## Reproduction and Aging in Marmosets and Tamarins

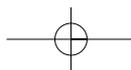
Suzette D. Tardif<sup>a</sup> · Arrilton Araujo<sup>b</sup> · M. Fatima Arruda<sup>b</sup> ·  
Jeffrey A. French<sup>c</sup> · M. Bernardete C. Sousa<sup>b</sup> ·  
M. Emilia Yamamoto<sup>b</sup>

<sup>a</sup>University of Texas Health Science Center, San Antonio, Tex., USA, <sup>b</sup>Universidade Federal do Rio Grande do Norte, Natal, RN, Brazil, <sup>c</sup>University of Nebraska at Omaha, Omaha, Nebr., USA

### Abstract

This chapter presents data on the relations between reproduction and aging in both captive and free-ranging marmosets and tamarins. The relationship is examined from two perspectives. First, the relation of age to physiological impairments in reproductive function is explored. Callitrichid females, in common with many other nonhuman primates, begin to display anovulation associated with follicular depletion at a point relatively close to the maximum life span. Unlike Old World primates, however, they continued to display significant steroidogenic activity in the ovary. There are age effects on some reproductive output variables, such as litter size and inter-birth interval, though the effects are often small. Like other mammals, male marmosets display a change in levels of androgens with age, although the magnitude of the decrease is not large and they actually mount an elevated response to GnRH challenge as they age. We also examined whether age affects either the establishment or maintenance of a breeding position, the factors most important in determining lifetime reproductive success. Infant mortality did increase with increasing parturitions, suggesting that there may have been aging or parturition effects on lactation. Generally, marmoset females were well past the age of sexual maturity at the beginning of the tenure and approaching 8–9 years at the end of it. Reproductive decline did not appear to be a gradual process, but a rather abrupt one, often causing the dismantling of the group. There are potentially interesting relations among maternal age, mass and declining reproductive performance, given the known importance of mass as a determinant of reproductive success in female callitrichids. Copyright © 2008 S. Karger AG, Basel

Marmosets and tamarins (primate family Callitrichidae) are the smallest of the anthropoid primates, ranging in adult mass from less than 150 g (pygmy marmosets) to a high of around 600 g (lion tamarins). While callitrichid primates have a life history that is slow relative to mammals of a similar size (e.g. rats who mature at 2 months and have a maximum lifespan of around 5 years), their small size means that they have a life history that is fast when compared to other primates. Marmosets and tamarins undergo puberty, as assessed by elevations in circulating or excreted gonadal steroids and pituitary





gonadotropins, at around 9–13 months of age [1–5] and have completed skeletal maturation by around 2 years of age [6]. The average lifespan of captive common marmosets is 5–7 years [7–9], whereas tamarins have a somewhat longer average life span of around 9 years [8]. The maximum lifespan of captive marmosets is around 16–17 years of age [8, 10] and around 22–25 years for tamarins [8]. Data for survival in wild populations are more difficult to acquire, but long-term studies of marked populations of lion tamarins found at least one female who died at over 16 years of age [11].

The relatively small body size of callitrichid primates and their associated fast life history makes these species of interest in the general study of aging. From a biomedical perspective, they offer the opportunity to look for age-related changes in health and disease in a variety of physiological systems and to test potential therapeutics for age-related ailments within a much shorter time frame than that offered when working with more typical Old World monkey models, which tend to mature at 3–5 years and live a maximum lifespan of 25–40 years. From an evolutionary perspective, callitrichids represent an extreme primate reproductive strategy in which the trade-offs between investment in reproduction and investment in extended survival may be significantly different from those seen in larger-bodied, longer-lived primates.

The relationship between reproduction and age can be explored in at least two different ways, both of which will be examined in this chapter. First, increasing age may result in impairments in reproductive function in the same way that increasing age is associated with impairments in other physiological systems. Reproductive senescence differs among mammalian taxonomic groups. For example, the loss of the follicular pool is the primary event shaping the end of reproductive life in female primates, whereas in rodents there is striking variety in the size of follicular pool remaining at the end of reproductive life as well as at maximum lifespan [12]. Within primates, human females are unusual in experiencing follicular depletion relatively early in the maximum lifespan, resulting in an extended period of altered hormonal environments (decreasing ovarian steroids accompanied by increasing, then declining gonadotropins) that is now believed to generate affects on disease risks [12]. With increasing numbers of older nonhuman primates available for study, it is now clear that monkeys and apes also experience follicular depletion and associated hormonal alterations (gorillas [13]; chimpanzees [14]; colobines [15]). However, the stage of life at which this occurs is generally later than that observed in humans. A better comparative understanding of reproductive senescence among mammals, including nonhuman primates, is informative to both our general understanding of aging and to producing improved models in which to study menopause.

The relationship between age and reproduction can also be examined from an evolutionary standpoint in terms of trade-offs. Physiological trade-offs may be necessary, in terms of allocation of resources to reproduction versus growth or maintenance. A number of allocation models have been proposed to define how these trade-offs may be made to optimize reproductive output [16]. Particularly for long-lived species, such as nonhuman primates, one might propose that trade-offs would be sensitive to





age. For example, the likelihood of committing resources to reproduction in marginal settings may increase with age, as the impact of retaining resources for maintenance (and, therefore, for future reproduction) is reduced. An example of such age sensitivity is found in red deer, in which the mortality rates of nursing females versus non-nursing females is higher, but only in females over 10 years of age [17].

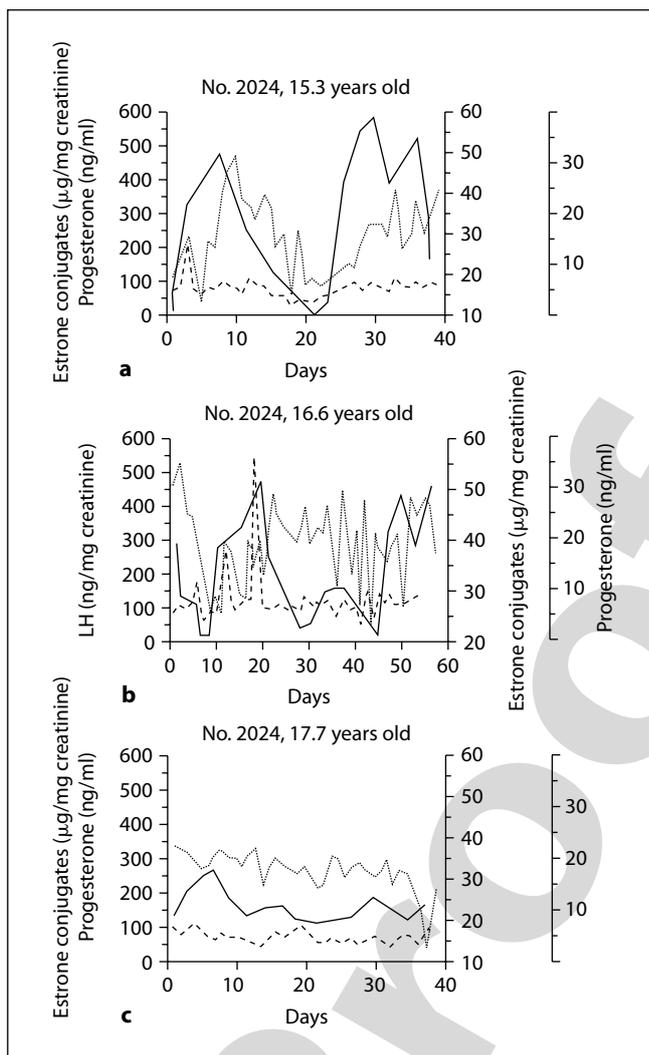
Callitrichid primates represent a particularly interesting group in which to examine the issue of age sensitivity to reproductive investment, given the unusually high variance in reproductive success among females in this taxonomic group. A number of aspects of their reproductive strategy come together to make female lifetime reproductive output much more variable in callitrichids than in other primates. Callitrichid primates are territorial and most often only one female is reproductive in a group, regardless of the number of adult females present. The suppression of reproduction in many adult females means that there may be healthy females who live their entire lifespan with minimal or no chance for reproduction – a life history finding that is unusual for mammals, including other primates [18]. At the other end of the spectrum, females who are in breeding positions may rear two offspring at a time (with twinning being the norm) and, with a postpartum ovulation occurring 10–20 days following delivery, can produce two litters per year. Therefore, a population of healthy adult females is likely to have a wide range of lifetime reproductive outputs. Given this reproductive strategy, it is of interest to determine whether age affects either the establishment or maintenance of a breeding position since these factors are likely the most important determinants of lifetime reproductive success.

This chapter is divided into sections on the relations between age and reproduction for captive and free-ranging callitrichid primates. Reflecting the availability of data, the sections concentrate most heavily on females, although data on males are also included. The specific callitrichid species discussed, reflect the availability of data on the topic of reproductive aging. The chapter includes both review of published findings as well as previously unpublished findings on captive male marmosets and on free-ranging common marmosets of both sexes.

### **Evidence of Age Effects on Female Reproduction in Captivity**

Limited studies are available on physiological aspects of reproductive aging in callitrichid primates with most work conducted on captive tamarins – saddle-backed tamarins (*Saguinus fuscicollis*) and cotton-top tamarins (*Saguinus oedipus*). Histological comparisons of the ovaries of young (2–5.4 years), middle (6.9–10.2 years) and old (12.9–15.9) tamarins revealed the expected decline in total follicular pool with age [19]. The number of large preantral follicles also decreased with age and the likelihood that these follicles would advance to the antral stage was dramatically reduced in the oldest age group, such that only 58% of oldest ovaries had at least one normal antral follicle, compared to 100% in the two younger age groups [19]. These

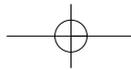




**Fig. 1.** Patterns of cyclical change in circulating progesterone and excreted estrogen conjugates and luteinizing hormone/chorionic gonadotropin (LH/CG) in one captive tamarin (*Saguinus fuscicollis*) female sampled from 15.3–17.7 years of age. Dashed line indicates urinary estrone conjugate concentration, dotted line indicates urinary LH/CG concentration, and solid line indicates plasma progesterone concentration. Reprinted from *J Reprod Fertil* 1992;94:416.

histological findings, suggesting impaired reproduction in the oldest age group, were reinforced by results from comparisons of endocrine profiles of young (3.3–5.5 years) versus old (13.1–18.7) females [20]. In young females, 8/8 cycles were ovulatory (as assessed through postovulatory increases in progesterone and urinary estrone conjugates) and 6/8 were of regular cycle length. In old females, only 6/13 cycles were ovulatory and only 3/13 were ovulatory and of regular cycle length [20]. Figure 1





illustrates the change in cycle pattern for one old female, starting at 15.3 and ending at 17.7 years of age. Old, acyclic females did not have extremely low ovarian steroids, rather their circulating and excreted steroid concentrations were similar to or higher than those observed in young, cycling females. This finding can be attributed to the continuing presence of large, steroidogenic interstitial glands in the ovary. The gland remains functional even after regular, cyclical folliculogenesis and ovulation has ceased [21]. Taken together, these results indicate that tamarins, in common with many other nonhuman primates, begin to display anovulation at or close to the maximum lifespan when compared to humans in which 50% of the maximum lifespan is post-reproductive. Unlike Old World primates, however, the tamarins continued to display steroidogenic activity in the ovary, even after regular folliculogenesis and ovulation had ceased.

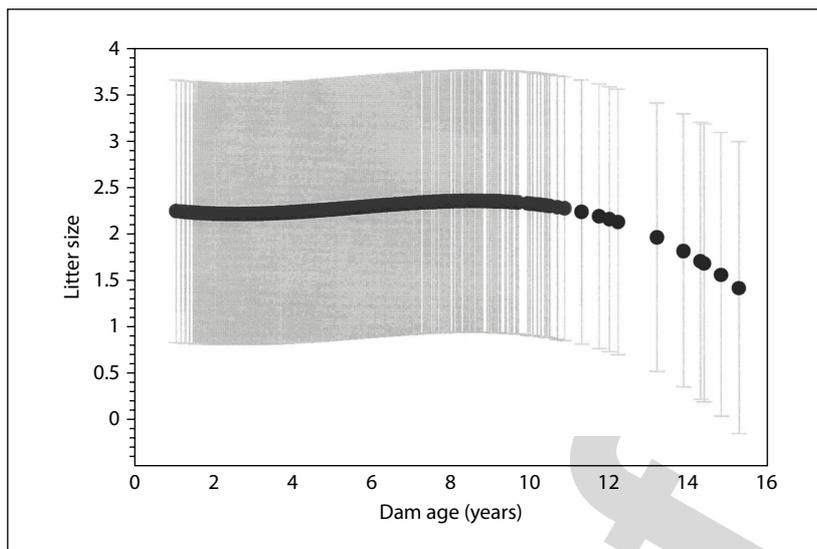
Aging effects may also be examined through comparison of reproductive output variables, such as litter size, interbirth interval (IBI), and infant survival, in dams of different ages. Some early studies reported an absence of measurable effects of maternal age on any of these variables [22, 23]. However, more recent studies suggested possible age effects on reproductive output variables, though the effects are often small. Caro et al. [24] examined reproductive records on a small number of captive common marmoset (*Callithrix jacchus*), golden lion tamarin (*Leontopithecus rosalia*) and saddleback tamarin (*Saguinus fuscicollis*) females, concluding that age-specific fertility displayed an inverted U-shaped form, with a distinctive decline in the number of females producing offspring in the later half of life. For those females who did reproduce, there was no significant relation of age to IBI. Smucny et al. [25] examined a large data base of records for captive common marmosets that included breeding records from 400 dams, to determine the relations among reproductive output, maternal age and survivorship. The survival of dams ranged from 2.0 years to 14.59 years (average = 5.74). There was a slight, but statistically significant effect of age on litter size, with decreasing litter size in dams between 12 and 15 years of age, compared to younger dams (fig. 2). IBI also appeared to increase with age, though the IBI in the oldest group was highly variable and not statistically different from the middle-aged group.

An additional variable that has been examined in one captive marmoset population is the relation of birth mass to maternal age. Older females of higher parity produced infants with significantly higher birth mass, regardless of litter size or maternal mass [26]. This finding is similar to that reported in other mammals, including humans, in which increased age or parity is associated with increased infant mass.

### **Evidence of Age Effects on Male Reproduction in Captivity**

One of the most ubiquitous effects of age on reproductive function in male mammals is the reduction in levels of testosterone across the lifespan [27]. This effect could



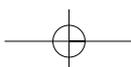


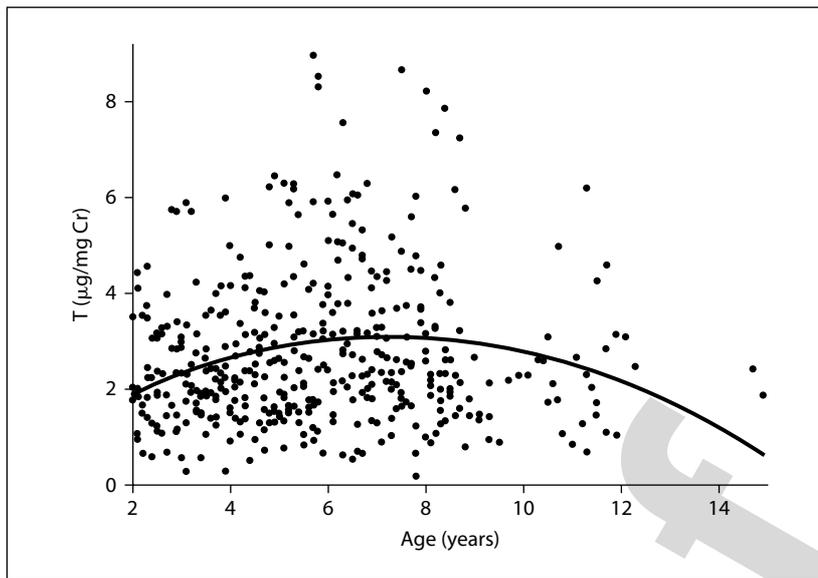
**Fig. 2.** Relation of maternal age and litter size in a large population of captive common marmosets, *Callithrix jacchus* (400 dams, >1,000 litters). Reprinted from *Am J Primatol* 2004;64:115.

potentially result from aging-related functional declines at any point in the hypothalamic-pituitary-gonadal (HPG) axis (or some combination of these elements). In human males and rodents, luteinizing hormone (LH) levels do not decline with age, but gonadotropin-releasing hormone (GnRH) pulses from hypothalamic neurons show reduced amplitude. In both humans and rodents, the most distinctive change in the HPG axis is a reduction in steroid biosynthesis of testosterone by testicular Leydig cells [see review in 28]. Since female marmosets differ from other primate species in the steroidogenic capacity of aging ovarian tissue (see above), we first assessed the impact of aging on baseline steroid concentrations in male marmosets (*Callithrix kuhlii*). Second, using an experimental challenge technique, we evaluated whether functioning in the HPG axis varied with age.

#### *Testosterone Levels over the Lifespan*

In our colony, we routinely collected first-void urine samples from all animals at least twice each week, and these samples were processed for urinary testosterone (T) levels using methods described in Nunes et al. [29]. Urinary T levels accurately reflect circulating concentrations [30]. We accessed archived samples for 15 males, and calculated monthly averages for each male. All males contributed samples beginning at two years of age, and continuing through their tenure in our colony. Two males contributed samples beyond 14 years of age. The data, shown in figure 3, reveal that androgen levels, both within and among males, are highly variable. However, a polynomial curve-fitting exercise reveals an age-related pattern within this variability. Urinary



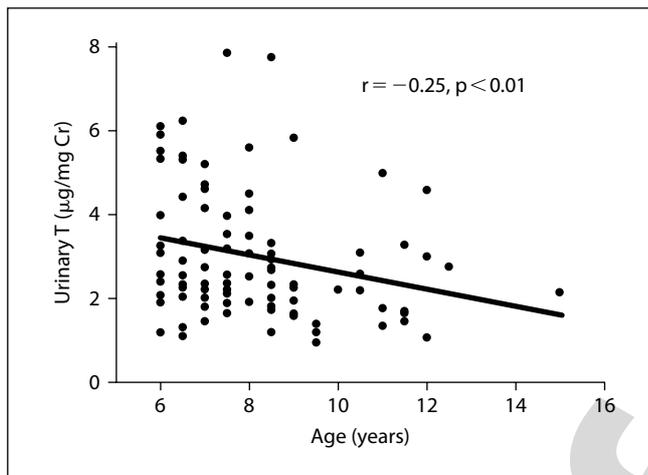


**Fig. 3.** Changes in urinary testosterone (T) concentrations over the lifespan in captive male marmosets, *Callithrix kuhlii*. Curved line represents the best-fitting line derived from polynomial regression.

T levels in marmosets rose throughout adulthood until approximately 7.5 years of age, at which point T levels began dropping. A more detailed analysis of 6-month averages of urinary T revealed a significant decline from 6 through 15 years of age (fig. 4). While the correlation between age and urinary T was significant, age accounted for only a small proportion of variance in urinary T among males ( $r^2 = 0.0625$ ). Other sources of variation may include stable individual differences among males [31], presence of young dependent offspring [32], and differences in group demography, particularly the presence or absence of reproductive females [33]. Thus, like other mammals, male marmosets display a change in levels of androgens with age, although the magnitude of the decrease is not large.

#### *GnRH Challenge*

The dynamics of HPG function in aging males marmosets was evaluated by challenging male marmosets with synthetic GnRH, and assessing Leydig cell function directly, by measuring plasma T, and pituitary gonadotrope function indirectly, given that any increased T production must be mediated via elevated pituitary-derived LH secretion. The data reported here were published previously in aggregate [30], but for the purposes of this chapter we have reanalyzed the data set from the perspective of aging. Twelve male marmosets were tested, 8 of which received GnRH (2 µg i.v.), and 4 of which received vehicle control treatment. A baseline plasma sample was collected prior to treatment, and at 45–60 min following treatment. Baseline samples for all

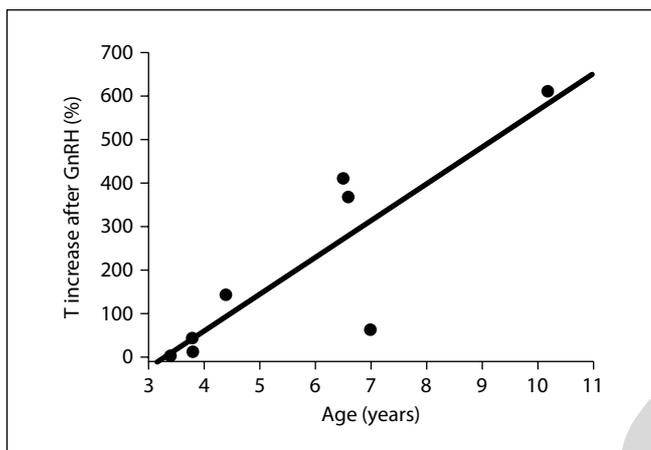


**Fig. 4.** Changes in urinary testosterone (T) concentrations from six to 15 years of age in captive male marmosets, *Callithrix kuhlii*. Data points represent 6-month averages.

males revealed a weak but negative relationship between age (range 3.5–10.5 years) and plasma T ( $r = -0.41$ ,  $p = 0.18$ ). All males responded to GnRH treatment with elevated circulating T concentrations [30], but the magnitude of increase in circulating T was strongly predicted by male age. Older males showed dramatically greater changes in circulating T than younger males (fig. 5); three of the four oldest males exhibited four- to sixfold increases in circulating T in response to GnRH challenge, while the youngest males had dampened responses to the challenge. Similar patterns were noted for levels of circulating estradiol in males: older males tended to have lower circulating levels of estradiol, but older males showed proportionately greater increases in circulating estradiol following the GnRH challenge. The findings suggest that in aging male marmosets, pituitary gonadotrophs maintain their capacity to respond to GnRH stimulation, and that Leydig cells in aging males retain their capacity to synthesize and release androgens when stimulated by LH. Given the magnitude of change in circulating T and estradiol, these results also suggest that the HPG axis in older male marmosets becomes hyperresponsive to GnRH stimulation.

#### Evidence of Age Effects on Reproduction in the Wild

We report here on reproduction and aging in a free-ranging population of common marmosets, comparing results to published findings on other callitrichid species. The marmoset population was followed for 10 (1991–2001) years in a field site in Northeastern Brazil ( $5^{\circ}47'42''\text{S}$  e  $35^{\circ}12'34''\text{W}$ ). Group composition and size are



**Fig. 5.** Relationship between age and the proportionate change in plasma testosterone (T) following GnRH challenge in captive male marmosets, *Callithrix kuhlii*. Values represent (post-treatment T/baseline T)  $\times 100$ .

**Table 1.** Number of individuals by sex that died in each age class compared to those born (infant), and to those that reached the age class (juvenile and subadult), number of individuals that reached adult age, and percentage survival in each age class in 9 free-ranging groups of common marmosets, *Callithrix jacchus*

	Infant	Juvenile	Subadult	Adult
Females	0/44	7/44	3/37	34
Males	2/52	8/52	2/46	44
Unknown sex	50/58	8/8	–	–
Total	52/156	23/104	5/83	78
% of survival	66.7	77.9	94.0	–

described elsewhere [34–36]. During the monitoring of nine free-ranging groups of common marmosets we were able to record data from 209 individuals. From this total, 55 were already in the social groups and we could only estimate adult age using body mass, metric measurements and dental wear analysis [37]. Table 1 shows the distribution by sex and age classes of the 209 animals relative to mortality. These data suggest that early life mortality is relatively high and is similar for males and females, resulting in similar percentage of adult males and females in the population. Also, that mortality decreases as individuals get older, reaching as high as 94% for subadults.

Age is an especially difficult variable to investigate in wild primates, including callitrichids. Even in long term studies, the extended life span of primates when

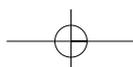


compared to nonprimate mammals frustrates attempts to determine the exact ages for most individuals, except the younger ones. In our study, we used two types of morphological data, body and dental conditions, as age indicators. Both were measured cross-sectionally and longitudinally as these variables change over time for specific individuals.

How does the aging process affect reproduction in free-ranging females? To answer this question, we attempted to map the reproductive life of females in the wild. The first point in the timeline is age at first reproduction. In captivity, females may conceive as early as one year of age, when they are sexually mature, and recommendations of initiating breeding at 18 months of age are common [9]. In the wild, however, there are many constraints on breeding, and marmoset females, although able to conceive, may not find a suitable partner, find a breeding vacancy or overcome competition with other breeding females [36, 38–39]. Accordingly, we found that first parturition occurred at a much later age in wild females. Three females, monitored from birth, gave birth at 29, 31 and 35 months. All three sets of offspring were lost, consisting in failed attempts to breed [36]. Data on body mass hinted that at least two of those females had been pregnant before and that those pregnancies did not come to term. Another subordinate female, the sibling of one of those cited above, exhibited the mass indicative of a pregnancy (441 g), close to delivering, when she was 26 months old. Four other females were adults when monitoring of their groups began. They too experienced unsuccessful breeding attempts (pregnancies to term but with death of the infants right after birth) 29, 37, 40 and 40 months after the group had been identified. Taken together these observations strongly suggest that females in the wild experience a much later age for first parturition in comparison with captive females. These findings are similar to those reported for golden lion tamarins, with an average age of first reproduction of 3.6 years, but a range of 2–6 years [11]. Goldizen and Terborgh [40] reported that the median age at which free-ranging saddleback tamarin females had their first offspring was 3 years, but with a range of 2–4.5 years.

In summary, the beginning of reproductive tenure is a later event in the life of a wild female than in a captive female. Exact ages are not available, but data on the interval between leaving the natal group and occupying a breeding slot indicated that these slots were rare and difficult to obtain. We have data from the site in Brazil on four subordinate common marmoset females that were first identified and marked as adults (table 2). They later left their group and migrated to another, where they occupied the breeding position. Intervals between leaving the group and beginning of tenure averaged 29.6 months and varied between 6 and 44 months. The notable short interval was the result of the sudden death of a breeding female followed by the immediate return of a previously subordinate female (who had only recently left the group) who took on the breeding position. These data are in agreement with those reported for age of first parturition and support the same conclusions.

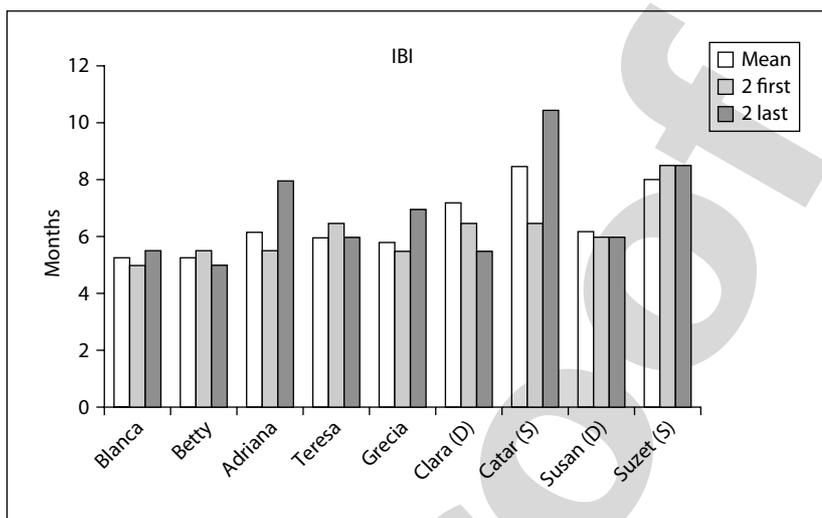
The potential effects of age on reproductive outcomes were analyzed by comparing individual profiles. We selected females that had bred at least four times in the same





**Table 2.** Time interval between leaving the group and obtaining a breeding slot in free-ranging female common marmosets, *Callithrix jacchus*

Female	Date of leaving	Date of breeding slot	Interval months
Betty	03/1992	07/1994	28
Adriana	01/1994	05/1997	40
Barbie	11/1992	07/1996	44
Paloma	08/1997	02/1999	06
Mean time			29.5

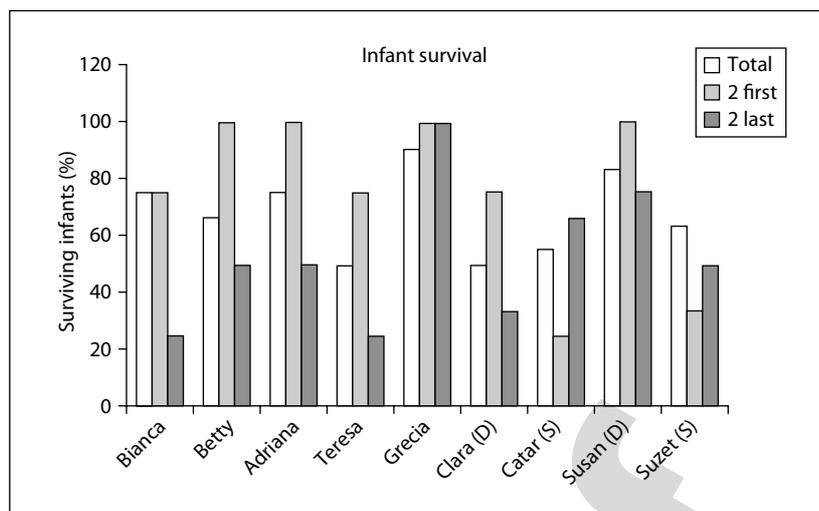


**Fig. 6.** Mean overall IBI (white columns), mean of the first two IBIs (light-gray columns), and the last two IBIs, from 5 monogamous and 4 polygynous free-ranging common marmoset females, *Callithrix jacchus*. D indicates dominant and S secondary breeder in polygynous groups.

group and determined both the IBI and the percentage of infant survival during their tenure. Five of these females were the only breeders in their group and four others were either the dominant or the subordinate breeding female in two polygynous groups. The monogamous females had 8, 4, 7, 4 and 12 parturitions, the dominant polygynous females had 6 and 7 parturitions and subordinate polygynous females had 5 and 6 during the period their group was monitored. Tenure for these females varied from 19 to 68 months, averaging 42 months ( $\pm 15.6$  SD). Surprisingly, these values did not differ dramatically from the average and maximum reproductive life spans for captive marmosets [25].

Figure 6 presents the mean IBI for all births during those nine females' tenures, as well as the mean of the first two and last two IBIs of their tenure. If aging was an

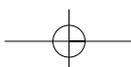


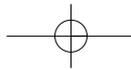


**Fig. 7.** Percentage of infant survival for 5 monogamous and 4 polygynous free-ranging common marmoset females, *Callithrix jacchus*. White columns = All parturitions; light-gray columns = first two parturitions; dark-gray columns = last two parturitions. D indicates the dominant and S the secondary breeder in polygynous group.

important influence in their reproduction, we would expect that the mean of the last two IBIs would be higher than both the general mean and the mean of first two IBIs. This relationship was confirmed for only three of the females: Adriana, Grecia and Catarina – this last female a secondary breeder in Clara's group. Catarina's mean IBI was the highest of all females, and it was possible that the high IBI was a consequence of competition with Clara rather than aging. Adriana and Grecia, the two monogamous females that presented a high IBI for their last two parturitions both had long tenures (44 and 68 months, respectively), but the increase in that mean was the result of one long IBI only. Noteworthy, on the other hand, was the small variation in the IBI of most of the females. The mean IBI for all monogamous females was 5.7 months ( $\pm 1.2$  SD) and 7.4 months for polygynous females ( $\pm 2.8$  SD).

Figure 7 presents the percentage of infant survival for the nine females, during the entire tenure, and for the first two and the last two parturitions monitored. In six of the seven primary breeders (either monogamous or dominant polygynous females), percentage of infant survival for the last two parturitions was decreased. The only female that did not show this effect was Grecia, the female with the longest tenure (68 months). The two secondary breeders both displayed the opposite pattern, with increased infant survival in the later litters. Perhaps this outcome was related to changes in the competitive environment as the primary breeder aged. As infant mortality increased with increasing parturitions, infant deaths/disappearances were also timed differently (table 3). By the last parturition, over 35% of infants were dead or





**Table 3.** Relation of parturition number to timing of infant death or disappearance in free-ranging common marmosets, *Callithrix jacchus*

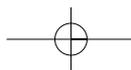
Parturition	% of infants dead/disappeared during			% alive at 10 months
	0–2 months	2–5 months	5–10 months	
First	0	0	0	100
Second	0	30	0	70
Next to last	0	33.3	33.3	33.3
Last	35.7	28.6	28.6	7.1

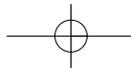
disappeared during the lactation period (0–2 months), whereas no infants died during that period in earlier parturitions, suggesting that there may have been aging or parturition effects on lactation.

Although we did not have the real age of breeding females when they ended their tenure, other data suggested that they probably were old and at the limit of their reproductive capacity. Data so far indicate that females started their breeding attempts around two to two and a half years. The same amount of time, on average, seemed to be necessary to find a breeding slot, and tenures, once acquired, were mostly long lasting [39]. So, a female would be at least 4.5 to 5 years old at the beginning of the tenure and approaching 8–9 years at the end of it. This was not, as far as we were able to see, a gradual process, but a rather abrupt one, often causing the dismantling of the group, and probably indicating that the female was not able to maintain either behavioral dominance over the group and/or her breeding activity.

Bales et al. [11] reported no evidence for age-related decline in fertility in wild golden lion tamarins, as assessed by number of offspring born and reared per year. They reported an average last age of reproduction of 6.1 years, with a maximum of 16.1 years. These figures closely reflected the average and maximum life spans, further supporting the finding of an absence of measurable aging effect on this reproductive parameter, in contrast to the findings reported by Caro et al. [27] for captive lion tamarins. However, potential age effects in free-ranging lion tamarins may be masked by the over-riding effect of maternal mass and the relationship between maternal mass and age (see 'Evidence for Trade-offs between Reproduction, Morbidity and Mortality').

If age effects are difficult to investigate in wild females it becomes much more difficult in males, which do not show considerable physiological modification in mass or morphology during reproductive aging. For free-ranging common marmosets, in the absence of genetic tools, social and affiliative interactions between males and breeding females are used to identify the breeding male [34, 41]. Systematic studies have not been carried out to investigate if males compete for breeding slots. In callitrichids, males living in the same group show low agonism (*C. jacchus* [42]; *C. flaviceps* [43];





**Table 4.** Immigration episodes of females into social groups and the number and age of adult males in each group at the time of female arrival, in free-ranging common marmosets, *Callithrix jacchus*

Group	Age of immigrating female, months	Number of males in group (ID and age in months)	Breeding male
Belém	>24	2 (Br= 41; Bj=26)	Bj
Chuí	>58	4 (Ch>58; Cz=41; Cv=18; Cn=18)	Cz
Plantação	>24	7(St >58; Sk=35; Sd=23; su=23; Sz=19)	Sk

*S. mistax* [44]) and no overt aggression between father and sons was recorded in family groups in captivity [45].

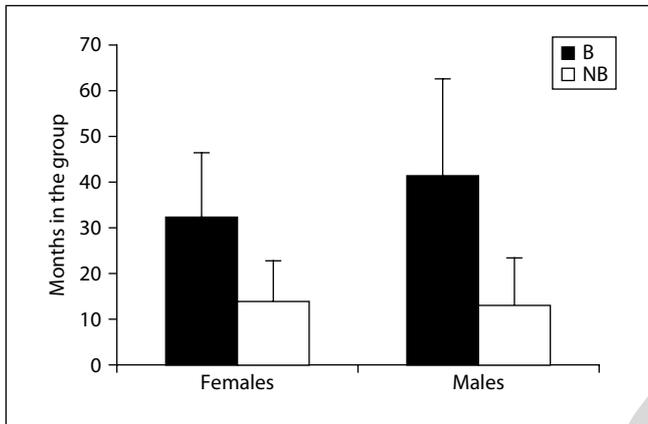
During the long-term monitoring of nine groups of common marmosets we recorded three episodes of immigration of adult females following the disappearance or death of resident breeding females. In all situations, more than one adult male was present, offering the opportunity to examine the relation of male age to reproductive access to a newly immigrated reproductive female. Table 4 provides the ages of all adult males in each group and the identity of the male observed engaging in sexual interactions with the breeding female. Age of males seems to be critical, and in this small sample, females consistently chose mature, but not the oldest, resident males with which to mate.

In order to determine whether age likely had a different effect on reproductive tenure in males than in females, we analyzed the data regarding tenure in breeding position. Differences between breeding males and females were not found ( $t$  test = 0.183). The long duration in months that breeding common marmoset males and females remained in the group highlights the importance of breeding position in maintaining group membership. This observation was supported by a comparison of the long tenure in groups for breeding versus short tenure for non-breeding animals of either sex (fig. 8). No emigration episodes were witnessed for breeding males or females (fig. 9).

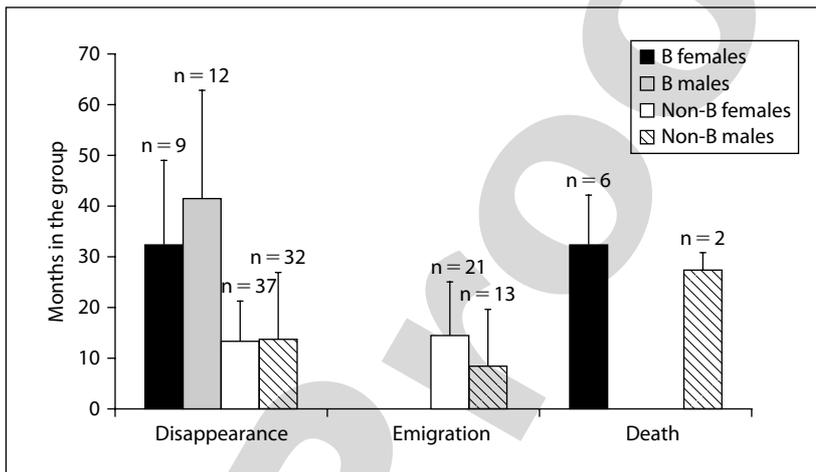
#### **Evidence for Trade-Offs between Reproduction, Mordibity and Mortality**

Two findings suggest that exploration of the timing of marmoset and tamarin reproduction, as it relates to physiological trade-offs, are worth further examination. First, in a captive setting, in which causes of death associated with predation and dispersal are eliminated, female marmosets had lower survival than did males (fig. 10). This is a finding similar to that reported for other small-bodied New World primates in which males participate heavily in infant care [46]. Allman et al. [46] interpreted these findings as reflecting the importance of males in infant care. However, upon examination of causes of death in those subjects represented in figure 7, we propose that the difference was



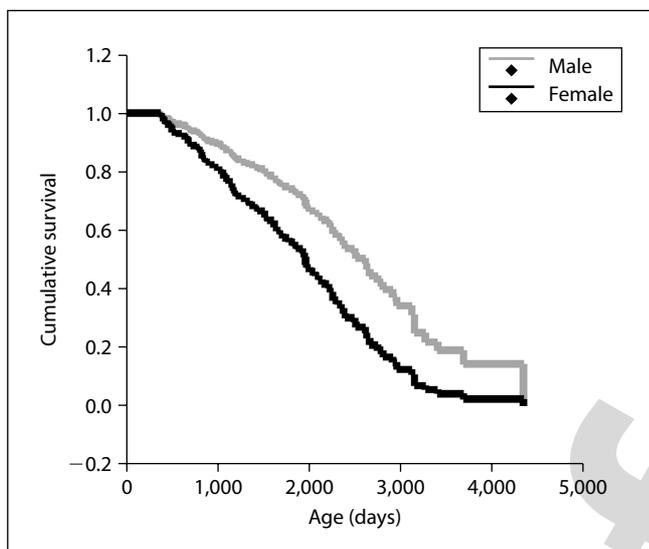


**Fig. 8.** Mean number of months that breeding and nonbreeding free-ranging male and female common marmosets, *Callithrix jacchus*, remained in their natal groups before emigration, disappearance or death. Differences between breeding males and females were not found ( $t$  test = 0.183).



**Fig. 9.** Number of months that breeding and nonbreeding free-ranging male and female common marmosets, *Callithrix jacchus*, remained in the social group, prior to disappearance, emigration or death.

caused by an increased risk of death in females related to the costs of reproduction. Studies of captive common marmosets, in this same population, have found that small-bodied females who reared twin offspring were more likely to be ill and less likely to be fertile in the following year than small females who reared singletons or large females rearing either litter size [47]. We, therefore, contend that in a captive population in which a broad array of females are offered the opportunity to reproduce, there was



**Fig. 10.** Postnatal survivorship in male versus female captive common marmosets, *Callithrix jacchus* (colony of the Southwest National Primate Research Center).

reproduction-exacerbated morbidity and mortality and these exacerbations ~~was~~ worst in small females.

The data presented in this chapter on free-ranging common marmosets suggested that females near the end of their reproductive life may not be able to support as many infants surviving to weaning as they did in the early parts of their reproductive tenure. Bales et al. [11] explored whether current reproductive success negatively impacted future reproduction in wild golden lion tamarins finding no evidence of such an effect. However, they did find a strong relation between maternal body size and reproductive success, as measured by number of offspring produced per year. It is possible that relatively small females in poor condition, of the type that would have experienced reduced fertility in a captive setting, would simply forgo reproduction in a feral setting or be unable to retain a breeding position.

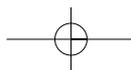
Age may be related to reproduction through its effects on female body mass, as body mass is tied to both age and reproductive outcome in callitrichid primates. Ovulation number and litter size have been shown to be determined by maternal body size [48] and females who lost mass during pregnancy as a result of nutritional restriction aborted if restrictions were at mid-term, and they experienced more frequent pre-term deliveries if restrictions were at late-term [49]. Maternal body size was also related to infant growth as supported through lactation [47]. Bales et al. [11] found maternal body mass to be the single most important variable in determining reproductive output in free-ranging golden lion tamarins.



An inverted U-shaped relationship between age and body mass has been reported in captive common marmosets [50] and wild golden lion tamarins [11]. In lion tamarins, females that were at the younger and the older age range tended to have smaller litter sizes and rarely had two litters a year, compared to females in middle-age [Bales, pers. commun.]; however, this effect is swamped in analyses by the relatively larger effect of body mass. It is likely that the lower mass of young females did not reflect reproductive costs given that these females were most likely gaining mass toward their peak mid-age mass values. However, older females were losing mass compared to their mid-age peak and this loss of mass might be either a cause or an effect of reproduction. Therefore, in considering the extremely competitive environment in which free-ranging marmoset and tamarin females attempt to reproduce, there may be adaptive advantage to forgoing reproductive attempts or minimally investing in a given attempt (through smaller litter size or reduced lactation output) while young and small, putting more investment into amassing more maternal body mass. Old females, however, might be expected to invest at a rate that would perhaps result in mass loss, if they were nearing the end of their life span. Additional longitudinal data on the relations among age, mass and reproductive output in free-ranging populations, along with data on experimental manipulation of energy availability in captive mothers of different ages would be necessary in order to test these hypotheses.

### Conclusions and Future Directions

The relatively small body size of callitrichid primates and their associated fast life history makes these species of interest in the general study of aging. In terms of female reproductive physiology, marmosets and tamarins are similar to many other nonhuman primates since they begin to display anovulation associated with follicular depletion at a point relatively close to the maximum life span. Unlike Old World primates, however, they continue to exhibit significant steroidogenic activity in the ovary, even after regular folliculogenesis and ovulation have ceased, due to the presence of a persistent steroidogenic interstitial gland. Therefore, while potentially valuable for studying other systems, the value of marmosets as a human menopause model is somewhat limited. Some studies find no age effects on reproductive output variables in captive callitrichids while other studies find limited effects, such as a slight, but statistically significant effect of age on litter size, with decreasing litter size in dams between 12 and 15 years of age. One consistent effect in captive marmosets is production of higher birth mass infants by older, higher parity females, regardless of litter size. Like other mammals, male marmosets displayed a change in levels of androgens with age, although the magnitude of the decrease is not large. The findings suggest that in captive, aging male marmosets, pituitary gonadotropes maintain their capacity to respond to GnRH stimulation; that Leydig cells retain their capacity to synthesize and release androgens when stimulated by LH; and that the HPG axis becomes hyperresponsive to GnRH stimulation.





Callitrichid primates represent a particularly interesting group in which to examine the issue of age sensitivity of reproductive investment in free-ranging animals, given the unusually high variance in reproductive success among females in this taxonomic group. Given this unusual reproductive strategy, it is of interest to determine whether age affects either the establishment or maintenance of a breeding position, factors that are likely the most important determinants of lifetime reproductive success. Females in the wild experience a later age for first parturition in comparison with captive females. Some reproductive output variables, such as IBI, appear to be not affected by age. Analysis of data on wild golden lion tamarins found no effect of age on infant survival. However, in wild common marmosets, over 35% of infants were dead or disappeared during the females' final lactation periods, whereas no infants died during that period in earlier parturitions, suggesting that there may have been aging or parturition effects on lactation. These variable findings on the relation between age and reproduction may be associated with the interactions among age, body mass and reproduction. Female body mass is strongly related to reproductive variables in callitrichid primates and aging is associated with decline in body mass; the extremely strong effect of mass may well mask age effects except in very large samples. Therefore, in considering the extremely competitive environment in which free-ranging marmoset and tamarin females attempt to reproduce, we hypothesize that there may be adaptive advantage to forgoing reproductive attempts or minimally investing in a given attempt (through smaller litter size or reduced lactation output) while young and small, putting more investment into amassing more maternal body mass. Old females, however, might be expected to invest at a rate that would perhaps result in mass loss, if they were nearing the end of their life span.

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Suzette D. Tardif

Barshop Institute for Longevity and Aging Studies, University of Texas Health Science Center  
15355 Lambda Drive, STCBM Bldg, Room 2.200.04  
San Antonio, TX 78245 (USA)  
Tel. +1 210 562 5033, Fax +1 210 562 5034, E-Mail tardif@uthscsa.edu