Articles

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LONG-TERM DATA ON REPRODUCTION, SEASONALITY AND LONGEVITY OF A CAPTIVE POPULATION OF BLACK LION TAMARINS (*LEONTOPITHECUS CHRYSOPYGUS*) FOR *EX SITU* CONSERVATION

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Abstract

This study compiles historical population data on the black lion tamarin population kept in captivity at the São Paulo Zoological Park Foundation (FPZSP), Brazil, from the first entry record in 1986 until December 2020. It presents data on sexual maturity, gestation, fecundity, births, sex ratio and life span for 141 animals kept during this time period. The first registered birth occurred in 1987 and since then another 98 live births have occurred, making this institution an international reference for black lion tamarin species management. Management techniques have continued to improve, focusing on life expectancy of the captive population, demographic growth, maintenance of genetic variability, and the *ex situ* conservation of this endangered species. Historical analyses show a unimodal pattern of birth seasonality in this captive population, with an average of two offspring per pregnancy and a survival rate of 1.4 offspring per pregnancy. Although the overall average was one pregnancy per year, 31% of breeding females had more than one annually. Mean age at sexual maturity for females was 39 months with a minimum of 25 months, while males matured at a mean of 68 months with a minimum of 38 months. The oldest reproducing female was 13.5 years old, and the oldest male was 13.1. The longest-living individuals were a 21.8-year-old female and a 19.5-year-old male. Of the 133 animals born, 69.9% survived their first month of life. Among these, the sex ratio was 0.633 males to 0.367 females. This compilation of information on the reproductive biology of captive black lion tamarins contributes toward integrated conservation actions for this endangered primate.

Keywords: birth seasonality, Callitrichidae, gestation, maturity, Platyrrhini

Resumo

Este estudo compila dados populacionais históricos da população de mico-leão-preto mantida sob cuidados humanos na Fundação Parque Zoológico de São Paulo (FPZSP), Brasil, desde o primeiro registro de entrada em 1986 até dezembro de 2020. Apresenta dados sobre maturidade sexual, gestação, fecundidade, nascimento, razão sexual e longevidade para os 141 animais mantidos durante esse período. O primeiro nascimento registrado ocorreu em 1987 e, desde então, foram 98 animais nascidos vivos, tornando a instituição referência internacional no manejo da espécie. Ao longo do tempo, as técnicas de manejo foram aprimoradas visando o crescimento demográfico, manutenção da diversidade genética e conservação *ex situ* desta espécie ameaçada de extinção. A análise histórica demonstrou sazonalidade nos nascimentos com padrão unimodal e média de dois filhotes por gestação, com uma taxa de sobrevivência de 1,4 filhotes por gestação. Apesar da média global de uma gestação por ano, 31% das fêmeas reprodutoras registraram mais de uma gestação por ano. A maturidade sexual média foi de 39 meses para as fêmeas, com um mínimo de 25 meses, enquanto os machos atingiram a maturidade em média aos 68 meses, com um mínimo de 38 meses. A fêmea reprodutora mais velha tinha 13,5 anos de idade e o macho mais velho 13,1. Os indivíduos mais lonjevos foram uma fêmea de 21,8 anos e um macho de 19,5 anos. Dos 133 animais nascidos, 69,9% sobreviveram ao primeiro mês de vida e a proporção foi de 0,633 machos para 0,367 fêmeas. Este compilado de informações sobre a biologia reprodutiva de micos-leões-pretos sob cuidados humanos visa contribuir com as ações de conservação integrada desta espécie ameaçada de extinção.

Palavras-chave: Callitrichidae, gestação, maturidade, Platyrrhini, sazonalidade de nascimento

Introduction

The black lion tamarin (*Leontopithecus chrysopygus*) is a platyrrhine primate endemic to the Atlantic Forest of the interior of the state of São Paulo, Brazil, and is currently categorized as Endangered by the International Union for Conservation of Nature (IUCN) (Rezende et al., 2020). The species is threatened mainly due to habitat loss and fragmentation (Passos et al., 2018). The population in the wild is estimated to be around 1,600 individuals distributed among 15 localities, with only one of these populations predicted to be viable for the medium to long-term (Rezende et al., 2020).

This species was considered to be extinct in the wild for 65 years and was only rediscovered in 1970 (Coimbra-Filho, 1976). After its rediscovery, seven individuals were captured in 1973 at the Morro do Diabo State Park in São Paulo and taken to begin the first breeding colony maintained at the Banco Biológico of Tijuca, an institution currently known as the Rio de Janeiro Primatology Center (CPRJ). At CPRJ, the captive population grew slowly, from the seven animals captured in 1973 to a population of 26 in 1984 (Wormell, 2020). In 1985, eight groups of the species were captured in the Morro do Diabo region due to the imminent flooding of 3,000 ha for the construction of a hydroelectric power plant. These animals were sent to different sites, including the São Paulo Zoological Park Foundation (FPZSP) that received, in 1986, their first individuals of the species: six males and eight females.

With a captive population increase through successful breeding, individuals of the species were distributed to zoos around the world according to studbook keeper recommendations, reaching the maximum population size in 1999, when there were 112 captive animals in 11 institutions on record. However, as years went by, reproductive success declined, mainly due to the low number of founders in the captive population and due to the use of contraceptive implants in some of the institutions (Wormell and Price, 2001). Since then, the global population has declined considerably, with the most recent official census (April 2023) reporting only 84 captive animals in eight institutions (Wormell, 2023).

Studies conducted with the species in the wild generated information on ecology (e.g. Keuroghlian and Passos, 2001; Rylands, et al., 2002; Garbino et al., 2020; Kaisin et al., 2023), genetics (e.g. Perez-Sweeney et al., 2005; Caldano, 2014), taxonomy (e.g. Garbino et al., 2016), conservation (e.g. Culot et al., 2015; Rezende et al., 2020) and population management (e.g. Rezende, 2014). Captive populations, on the other hand, have led to studies in the areas of ethology (e.g. Feistner and Price, 2000; Monticelli and Morais, 2015; Oliveira, 2016; Santana, 2020), physiology (Bertoli et al., 2019), microbiology (e.g. Fatoretto et al., 2022), and genetics (e.g. Ayala-Burbano et al., 2017, 2020). *Ex situ* breeding programs have been identified as critical components for lion tamarin (*Leontopithecus* spp.) conservation actions (Seal et al., 1991) and several studies have addressed important aspects of reproductive biology of tamarins in captivity (French et al., 1996; Wormell and Price, 2001; McCoy et al., 2019). These studies have compiled information from two of the three largest species populations throughout their *ex situ* maintenance history, with data from 19 years of management at CPRJ (French et al., 1996) and 10 years at the Jersey Zoo (Wormell & Price, 2001).

The data presented here compiles information on the 35-year history of the black lion tamarin population at FPZSP, with a focus on their reproductive biology. These are important records of the current largest *ex situ* population of the species and will contribute to guiding integrated management and conservation of this endangered primate.

Methods

We compiled and analyzed the information contained in the biological data sheets of each individual kept in captivity at the FPZSP. We analyzed the following information: reproductive performance (pregnancy per year), age at first and last reproduction, origin of the animals, number of pregnancies, size and sex ratio of litters, interval between pregnancies, percentage of premature/stillborn infants, rejection of infants by mother, life span, and other related information. Sexual maturity was only considered for animals with known birth age and pairing, as it was evaluated by the reproductive outcome. A Mann-Whitney non-parametric test was used to evaluate birth seasonality.

Results

Population and sexual maturity

Through December 2020, the FPZSP had kept 141 black lion tamarins, of which 86 were males and 55 females. With the inclusion of the 35 premature/stillborn specimens, this number reached 176 individuals that have been integrated into the data analysis. The species first reproduced at this institution in 1987; the parents were wild individuals that were incorporated into the captive population in 1986. Of the 141 animals, 98 were born at the Foundation, 21 entered with the aim of genetic management based on the studbook's recommendations, and 22 were saved by environmental agencies due to anthropic impacts such as hunting and capture for illegal captivity.

The animals left the institution through various means: 80 individuals died, 28 left through genetic management practices between institutions with the aim of forming new unrelated pairs, and 33 were still alive in December 2020. Of the 35 premature/dead offspring of undetermined sex, 14 were stillborn and 21 were premature.

Only 19 of the 55 females kept in captivity produced offspring. Among the seven reproductive females of known age, the youngest to reproduce gave birth at 25 months (mean 39 months; n = 7). The male that reproduced the earliest became a father at 38 months old (mean 68 months; n = 9).

Gestation, litter size and life span
Of the 141 animals, only 20 males and 19 females reproduced, representing 27.6% (n =39) of the population, considering only individuals that survived beyond one month of age. Throughout this period, the 19 breeding females were responsible for 66 pregnancies that included live, premature and stillborn offspring. These pregnancies resulted in the birth of 133 offspring. Overall, once live offspring survived one month of life, the parenting success rate was 100% (n = 93) (Table 1).

Of the 19 females that reproduced, most had one pregnancy per year, but six of these females (31%) completed two pregnancies within a year on at least one occasion during their reproductive life. Of these six females, four showed biannual (i.e. two pregnancies per year) gestation on only one occasion and two displayed repeated biannual gestation in three different years. In addition, one of these females stood out with three pregnancies in the same year (March 2018: three well-formed fetuses aborted, August 2018: two healthy newborns, and December 2018: one healthy newborn).

For females with more than one pregnancy per year, the interval between parturitions ranged from four to 10 months. The most prolific female had eight pregnancies over 44 months (an average of one gestation every 5.5 months) that culminated in the births of 18 total offspring. Another female had eight pregnancies over a period of 52 months (an average of one gestation every 6.5 months) which culminated in the birth of 17 total offspring. The oldest individuals to produce live and healthy offspring were a female aged 13 years and 5 months and a male aged 13 years and 11 months.

The most common litter size was two infants, followed by pregnancies of one and three infants (Table 2).

Of the animals that were born and died at the FPZSP during the reported period, the longest-living female was 21 years and 8 months, and the longest-living male was 19 years and 5 months.

Birth seasonality and sex ratio
Births occurred in all months and seasons of the year, except July, a period characterized by lower temperature and humidity. However, September and October were the peak months for parturitions under captive conditions (Figure 1). Seasonality was significant (U = 3.5; p = 0.02; N = 66) with births more common during the spring/summer period (September-February). Among the 98 sexed animals born, the ratio was 0.633 males to 0.367 females.

Table 1. Premature and stillbirths, rejections, and infant survival at FPZSP, São Paulo, Brazil, as compared to data from Jersey Zoo (Wormell and Price, 2021). *These two rejected offspring were from the same mother during two different litters of three infants.

	Nº of infants Born (M. F. ?)	Nº of premature/stillbirths	Nº of live-born infants rejected	Nº of non-rejected infants dying at <1 month	Nº of infants surviving to >1 month
Wormell and Price, 2001	57 (18.19.20)	18 (31.6%)	0 (0%)	6 (15.4 %)	32 (56.1%)
This study	133 (62.36.35)	35 (26.3%)	*2 (1.5%)	3 (2.2%)	93 (69.9%)

Table 2. Comparison of black lion tamarins' litter sizes over 35 years of maintenance at FPZSP, São Paulo, Brazil to other studies of black lion tamarins by the Jersey Zoo (Wormell and and Price, 2001) and WAZA (McCoy, 2019).

			Frequency of each litter size			Mean litter size	
	Nº of breeding females	Total litters	1	2	3	At birth	Surviving to >1 month
Wormell and Price, 2001	3	31	6 (19.4%)	24 (77.4%)	1 (3.2%)	1.84	1.03
McCoy, 2019	-	275	94 (34.2%)	158 (57.45%)	23 (8.35%)	-	-
This study	19	66	19 (28.7%)	39 (59%)	8 (12.1%)	2	1.4

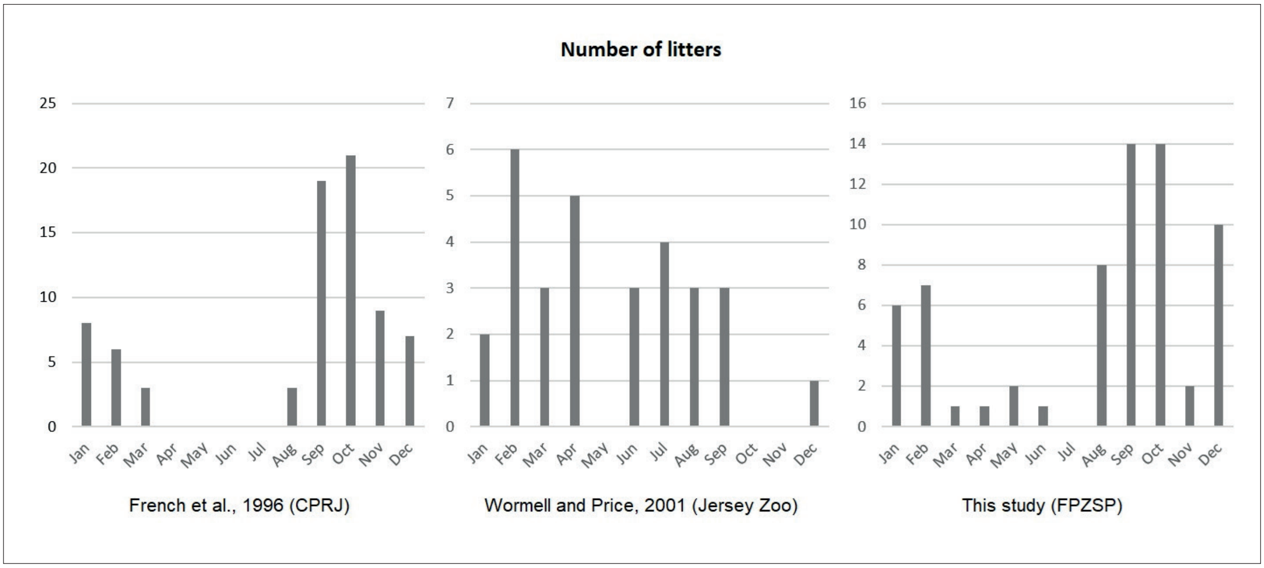

Figure 1. Seasonal distribution of black lion tamarin births kept at FPZSP over 35 years of maintenance at FPZSP, São Paulo, Brazil, compared to birth seasonality at CPRJ in Rio de Janeiro, Brazil, and Jersey Zoo in the British Isles.

Discussion

Historical data shows that this captive black lion tamarin population exhibits a unimodal birth seasonality, with an average of two offspring per pregnancy and a survival rate of 1.4 offspring per pregnancy. While the average is one pregnancy per year, 31% of females had multiple pregnancies annually. On average females reached sexual maturity at 39 months, and males at 68 months. The oldest reproducing female was 13.5 years, and the oldest male was 13.1 years. The longest-lived individuals were 21.8 years (female) and 19.5 years (male). Of 133 births, 69.9% survived the first month, with a sex ratio of 0.633 males to 0.367 females.

The female that reproduced earliest in FPZSP was 25 months old and the male was 38 months old. This age is higher than that reported in other studies on *Leontopithecus* regarding the onset of reproduction in both captivity and the wild.. In order to interpret these data, it is important to note that in captivity, the minimum age for reproduction may be directly related to management decisions and not necessarily to biological aspects. The onset of reproduction among Callitrichidae species is variable and highly controlled by their social environment (Dettling and Pryce, 1999). In captivity, *Callithrix jacchus* can breed as young as 13 months of age (Jaquish et al., 1991), whereas for lion tamarin species reports are as early as 18 months (Sussman and Kinzey, 1984; Baker et al., 2002). In the wild, the onset of sexual activity for black lion tamarins has also been reported from 18 months of age (Valladares-Padua, 1993). In addition, studies indicate that the sexual maturity of females of the genus *Leontopithecus* usually occurs within a family group (Dettling and Pryce, 1999; De Vleeschouwer et al., 2001). However, a study of *L. rosalia* in the wild reported a greater occurrence of reproductive activity in young and subordinate females residing in groups with at least one unrelated male compared to females residing in groups with only related individuals. Reproductive activity was also found in young and subordinate females of groups where there was a change in the social status of the dominant female (French et al., 2003). These studies suggest that the social structure of the group and the presence of unrelated individuals affect the reproduction of subordinate females. However, considering the restricted environment of captivity and the aggressiveness typically exhibited toward new unrelated individuals by cohesive family groups, maintaining such an individual safely would be difficult. Given the complexity of this social and reproductive context, Callitrichidae populations kept in captivity under conservation breeding programs must be rigorously studied in order to obtain the best management strategies.

Of the 141 studied animals, only 27.6% (n =39) reproduced, ranging from one to three pregnancies per year. In the wild, *Leontopithecus* species typically exhibit one gestation per year (French et al., 2002). Despite the modal pattern of one pregnancy per year per female, French et al. (1996) reported that 19.7% of *Leontopithecus* females kept in captivity had more than one pregnancy per year on at least one occasion throughout their reproductive life. For wild golden lion tamarins, only 14.9% of breeding females had more than one reproduction per year (Kleiman et al., 1982; Dietz et al., 1994) whereas there is only one reported occurrence of biannual gestation for wild black lion tamarins (Caldano, 2014). The fact that 31% of breeding females kept at the FPZSP have more than one gestation per year may be related to the constant supply of higher energy food. Indeed, food availability is an important determinant of annual reproductive cycles as shown in other Callitrichidae species (Goldizen et al., 1988). Tardif et al. (2002) observed the higher levels of reproduction of *Callithrix jacchus* in captivity were related to excessive energy reserves due to an adapted diet, which affected the mothers' ovulation dynamics. In ex situ conservation programs for endangered species, dietary variation throughout the year can be a valuable tool for stimulating reproduction, as demographic growth is essential for establishing an insurance population.

In wild populations of the genus *Leontopithecus*, average fecundity of two offspring per litter has been reported (Moro-Rios et al., 2009). However, litters of three can exist even if they tend to be uncommon in the wild (Digby et al., 2011). The litter sizes found in this study indicate a higher proportion of litters with three offspring at the FPZSP when compared to the Jersey Zoo and wild populations. This could be associated with a potentially higher energy intake from the diet offered at the FPZSP (Goldizen et al., 1988; Tardif et al., 2002). In this context, we would expect the FPZSP population to have a lower proportion of litters with only one offspring for the same reasons related to the idea of excess energy. However, the difference in the recorded values could also possibly be related to other factors, such as the origin of the breeding animals for each litter. McCoy et al. (2019) reported that offspring of different Callitrichidae species, when originating from single litters, produced more offspring in captive populations than offspring originating from litters with multiples.

Maximum life expectancy of the black lion tamarin in the natural environment is still unknown (Passos et al., 2018). However, with the limited captive information we have, the maximum life expectancy at the Rio de Janeiro Primatology Center is 17.11 years, compared to 31.7 years for a golden lion tamarin kept at the Houston Zoo, and 21 years for a golden-headed lion tamarin kept at the Palmyre Zoo (Weigl, 2005). The 21.8-year-old female at FPZSP represents the oldest captive individual of the species recorded to date, compatible with the observed maximum age for the congener golden-headed lion tamarin.

Life expectancy of animals in the wild and in captivity may be affected by different factors. In natural environments, age-related vulnerability may increase the chance of predation or limit access to resources. Under human care, these factors are better regulated, with consistent food resources, yet animals are not free from infectious diseases or stresses potentially generated by captivity (Ricklefs and Scheuerlein, 2001). Studies on the causes of death in the *Leontopithecus* genus can provide valuable insights into how to maintain healthy, sustainable populations in *ex situ* environments, as well as to understand the connection between reproductive history and life expectancy. Ricklefs and Cadena (2007) examined the link between life expectancy and reproductive investment in several callitrichid species in captivity, including *L. rosalia*. Their findings revealed no negative correlation between fecundity and age at death, a relationship often assumed for natural populations with limited resources.

In the FPZSP, births occurred in all months except July. Births showed a unimodal distribution across the year with a peak in September to October. The peak of births in the FPZSP corresponds to the beginning of a period of increased rainfall and temperatures in São Paulo state, which is also observed in other Atlantic Forest regions of southeastern Brazil, matching the timing of the reproductive peak of other *Leontopithecus* species in the wild (Dietz et al., 1994).

A marked reproductive seasonality has been reported for captive *Leontopithecus chrysopygus,* with births distributed bimodally, with a primary peak in October and a secondary peak in January to February (French et al., 1996). When under the same management conditions, *L. chrysomelas* and *L. rosalia* showed a unimodal pattern, with peak births in September and October, respectively (French et al., 1996). This similarity in the reproductive timing of captive and wild populations of *Leontopithecus* has been related to environmental factors, such as photoperiod, temperature, and rainfall (Dietz et al., 1994, French et al. 1996). This argument may be linked to the changes in birth timing observed in Wormell and Price's (2001) study, as well as differences noted between *L. rosalia* populations in the northern and southern hemispheres (Kleiman et al., 1982). Since the black lion tamarin population at FPZSP is housed outdoors in varying climatic conditions, it is believed that environmental factors significantly influence the observed seasonality.

At FPZSP, the sex ratio for black lion tamarins exhibited the highest birth bias found to date for Callitrichidae species, with more males being born, corroborating the findings of French et al. (1996) during the initial population analyses of black lion tamarins born in captivity. Disparity in the birth sex ratio is not a new finding for mammals (Faust and Thompson, 2000; Thogerson et al., 2013) and has already been reported for other Callitrichidae species: *Oedipomidas oedipus* (Snowdon et al., 1985; Baker and Woods, 1992; Price and McGrew, 1990; Johnson et al., 1991; Boulton and Fletcher, 2015); *Tamarinus imperator* (Baker and Woods, 1992); *Callithrix jacchus* (Poole and Evans, 1982; Box and Hubrecht, 1987; Rothe et al., 1992); *Leontopithecus rosalia* (Rapaport et al., 2013) and *Cebuella pygmaea* (Ziegler et al., 1990). This male-biased birth ratio observed at FPZSP may reflect an evolutionary tendency in this species toward a non-equal sex ratio, differing from other small platyrrhines which have ratios of up to 0.5, as is the case for some species in the genus *Callithrix* (McCoy et al., 2019).

The disparity in the sex ratio of the *ex situ* population of black lion tamarins hypothetically may be related to the presence of inbreeding. In an analysis of the international studbook (Wormell, 2020) it is possible to notice that despite a slight trend toward male births since the beginning of the captive population, the disparity in the sex ratio at birth increased from 2010 to the present. Simultaneously, there has been a gradual increase in the average inbreeding coefficient and a decrease in genetic diversity. Consequently, the unequal male-biased sex ratio may be a consequence, or an aggravation, of the rise in the inbreeding coefficient and loss of genetic diversity. However, in the evaluation of two prolific couples kept at the FPZSP, we found two distinct situations. A pair that included a female born in the wild (WB) and a male born in captivity (CB, son of WB) was responsible for nine pregnancies and 19 offspring with a sex ratio of 0.474 males to 0.526 females, close to an equal distribution of 0.5. The second pair included a WB male with a CB female (of WB lineage) with no history of inbred reproduction; for this pair eight pregnancies occurred that gave rise to 17 offspring at a ratio of 0.765 males to 0.235 females. This WB male came from the Morro do Diabo State Park, where we infer that individuals have greater genetic diversity due to a population size estimated at 1,200 individuals (Paranhos, 2006). This is the largest known species population and is considered to be the only viable long-term population due to demographic and genetic factors (Holst et al., 2006).

Another approach worth discussing is that of Silk and Brown (2008), who argued that social and environmental dynamics can influence the reproductive decisions of primates. They suggested that the sex ratio may serve as an adaptive response to these conditions. In contexts where resources are abundant, it may be more advantageous to have males, as they can compete for females and contribute to reproduction. Conversely, in environments where competition for resources is intense, it may be more beneficial for females to have daughters, who can gain from maternal support and social networks. Given that *ex situ* resources are plentiful and do not require competition, the observed sex allocation, which is biased towards males, is consistent with this hypothesis.

Regardless, in captive populations, the disparity in sex ratio can hinder *ex situ* conservation actions by reducing the possibilities of forming new pairs and, consequently, slowing demographic increase and the maintenance of genetic variability in the population. Generally, breeding pairs are kept together as long as there is success in generating new individuals. Sometimes, this is the only viable strategy. However, it can lead to a greater genetic representativeness of only a small portion of the available animals due to the smaller effective population size. This factor associated with the existence of animals that do not initiate reproductive activities, something also observed in the black lion tamarin population of Jersey Zoo (Wormell and Price, 2001), leads to the stagnation or even decrease in population over years. In the case of the FPZSP, the effective size of the historical population was 28.3% and by December 2020, it was only 12.1%. A strategy to obtain greater reproductive success is related to the development of assisted reproduction techniques from the collection of semen of non-breeding males, especially potential founders. Actions of this type are still scarce and are based on previous studies with the golden-headed lion tamarin (*Leontopithecus chrysomelas*) (Arakaki, 2017, 2019).

The endangered black lion tamarin has few animals and institutions included in *ex situ* conservation programs, and since there are few actively reproducing pairs, the constant updating of population information is of paramount importance for the optimization of *ex situ* maintenance protocols with a focus on integrated conservation of the species.

Conclusions

Our long-term data on birth seasonality, as well as on age at sexual maturity, can help institutions in the elaboration of *ex situ* management strategies for *Leontopithecus chrysopygus*, especially regarding the best timing to separate individuals born in a given family group and how to approach new pairings with a focus on reproduction. Similarly, the evidence found in this study for viable reproduction in older individuals can assist in decision making for pairing recommendations with a focus on reproduction and increasing *ex situ* populations.

We observed a significant sex skew towards males in the proportion of *Leontopithecus chrysopygus* births. We believe that, similar to other Callitrichidae species, this male-biased sex ratio at birth may be related to sex allocation strategies rather than being a consequence of an increased inbreeding coefficient or a loss of genetic diversity in the *ex situ* population. This could be a potential focus for future studies aimed at understanding the sex allocation dynamics of the species.

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