

## RESEARCH ARTICLE

# Characteristics of Reproductive Biology and Proximate Factors Regulating Seasonal Breeding in Captive Golden-Headed Lion Tamarins (*Leontopithecus chrysomelas*)

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Reproduction is highly demanding in terms of energy expenditure, and the costs and benefits associated with postponing or investing in a reproductive effort are crucial determinants of an individual's fitness. Understanding the reproductive potential of a species under varying ecological conditions offers important insights into the dynamics of its social system. This study provides the first detailed analysis of the reproductive potential of wild- and captive-born golden-headed lion tamarins (*Leontopithecus chrysomelas*) under captive conditions, based on studbook data compiled during 1984–2000. Litters produced by wild-born females breeding in captivity are similar in size to litters observed in the wild, but smaller than litters of captive-born females. The more stringent ecological conditions experienced by wild-born females during maturation may result in a lifelong effect on litter size. However, interbirth intervals are shorter for wild-born than captive-born females. The relatively smaller burden of infant care that results from having smaller litters may allow wild-born females to sustain the next pregnancy sooner. Reproduction in the Brazilian captive population is highly seasonal for both wild-born females and females born in captivity in Brazil. Changes in photoperiod over a year provide a proximate explanation for changes in the proportion of conceptions and births per month. Outside Brazil, breeding occurs year-round, and no clear birth peak is apparent. Information from field reports that could be used to relate this finding to ecological factors, such as resource availability, is unavailable. *Am. J. Primatol.* 60:123–137, 2003. © 2003 Wiley-Liss, Inc.

**Key words:** callitrichids; lion tamarins; seasonality; reproductive biology

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## INTRODUCTION

Reproduction is a highly demanding activity in terms of energy expenditure. Ecological conditions, such as climate, or seasonal shortages in food availability may severely limit an individual's opportunities for reproduction, even if a suitable mate is present and social conditions would allow reproduction to occur. When ecological conditions are unfavorable, postponing reproductive efforts to times when conditions are more optimal will increase the offspring's chances of survival while not adversely affecting the parent's overall fitness [Crews, 1987; Lindburg, 1987; Bronson, 1989]. On a proximate level, external cues such as changes in photoperiod, environmental temperature, precipitation, or food availability may be used to anticipate the most optimal period for reproducing [Bronson, 1989, 1995; Crews, 1987; Lindburg, 1987].

Social groups of callitrichids (Callitrichidae; marmosets and tamarins) generally consist of one reproducing pair and a varying number of other group members (frequently the offspring of previous generations) [Rothe & Darms, 1993; French, 1997]. All group members provide infant care. Seasonality of breeding has been described for both wild [e.g., Goldizen et al., 1988; Stevenson & Rylands, 1988; Soini, 1988; Dietz et al., 1994] and captive [e.g., Brand, 1980; French et al., 1996; Sousa et al., 1999] populations of callitrichids.

Golden-headed lion tamarins (*L. chrysomelas*) are listed as endangered [Hilton-Taylor, 2000]. A conservation breeding program was set up in the early 1980s to reclaim illegally exported animals and develop a secure captive gene bank [Kleiman & Mallinson, 1998]. Management of animals kept in captivity involves the compilation of a studbook, which contains information on several aspects of reproductive biology (e.g., litter sizes, timing of births, and interbirth intervals). Analysis of such data provides insight into the reproductive potential of a species, and offers the opportunity to investigate differences among individuals and compare findings with results obtained from field studies. Such analyses have already been presented for golden lion tamarins (*L. rosalia*) [Kleiman, 1977; Kleiman et al., 1982]. French et al. [1996] provided an overview of reproductive performance in the genus *Leontopithecus*, and compared *L. chrysomelas*, *L. rosalia*, and *L. chrysopygus*, using data from the Centro de Primatologia do Rio de Janeiro (CPRJ). They examined seasonality of breeding in a captive population in which proximate factors (e.g., temperature, rainfall, and photoperiod) that can affect seasonal breeding were similar for all of the animals (the CPRJ lies within the original distribution area of *L. rosalia*, but not those of *L. chrysomelas* and *L. chrysopygus*). They concluded that *Leontopithecus* has a distinct birth peak in captivity, but did not identify the underlying proximate factors.

The current work presents detailed information on the reproductive biology of golden-headed lion tamarins (including litter sizes, interbirth intervals, and seasonality of breeding) for the entire captive population, and investigates differences between animals inhabiting the Northern and Southern Hemispheres. In addition, the proximate factors that regulate seasonal breeding in this species are investigated by studying the distribution of conceptions and births in regions with different climates and latitudes. Populations distributed over a wide range of latitudes may exhibit a gradient in the timing of reproduction corresponding to latitudinal differences in photoperiod [Lindburg, 1987]. Furthermore, we investigate differences in reproductive potential between wild-born and captive-born animals. We examine the degree to which the original, rather than the current, living conditions of an individual determine its potential reproductive

output. One can assume resources and environmental conditions in general to be more predictable and less limiting in captivity than in the wild. If current living conditions determine an animal's reproductive output, we expect wild- and captive-born females to have a similar reproductive output in captivity, which should be higher than the one realized in the wild. Alternatively, if the environment in which an animal matures has an impact on its later reproductive potential, wild-born animals should have a different reproductive output than captive-born animals. Prior to parturition, variation in individual reproductive output can be a result of variation in litter size and/or interbirth interval.

## METHODS

### Data Set

We used studbook information on litters registered as born in captivity during the period of 1984–2000. This information is updated annually through questionnaires sent to all institutions holding golden-headed lion tamarins that are listed in the International Studbook [Leus & De Vleeschouwer, 2001]. The respondents included three Asian, 24 European, 17 North American, and 11 Brazilian institutions. Animals were classified as “wild-born” if they were imported from Brazil into the captive population. Animals born in zoological institutions were classified as “captive-born.” Litters with unknown birth dates, or for which the identity and/or origin of one or both parents were unknown, were excluded. We also excluded litters born to females after the female had been treated with melengestrol-acetate implants, since litter size appears to be affected by the use of this type of contraception [De Vleeschouwer et al., 2000a]. The final data set consisted of 734 litters, born to 185 females (58 wild-born and 127 captive-born).

The European, Asian, and North American populations were analyzed as one population located in the Northern Hemisphere, and are hereafter referred to as the “Northern population,” as opposed to the Brazilian (captive) population. All institutions in Asia housing golden-headed lion tamarins were located in the Northern Hemisphere.

### Calculation of Interbirth Intervals

We calculated interbirth intervals for all females that had at least two consecutive litters with the same male. Females in captivity may be placed with another male at some point in time, for management or genetic reasons. While they may breed successfully when introduced to their new mate, the process of pair formation and possible stress associated with the new social situation may delay conception and result in a longer interbirth interval than if they had stayed with their former mate continuously. Thus, excluding these interbirth intervals resulted in a more reliable data set. The mean duration of gestation in this species is 125 days [De Vleeschouwer et al., 2000b]. Interbirth intervals shorter than 125 days that resulted in stillborn infants were excluded from the analysis. Likewise, we excluded intervals for which it was unclear whether the female and male had been housed together continuously without some form of birth control. After excluding unreliable data, 65% (476 of the original 734 litters) of the original data set was available for analysis.

Since ovulation and conception per se were not measured directly in this study (e.g., through analysis of hormones), conceptions *not* leading to term pregnancies may have gone unnoticed. Thus, a given interbirth interval may have

resulted from a successful conception leading to a term pregnancy, or alternatively, included one or more successful conceptions followed by an abortion or resorption of the embryo.

### **Classification of Institutions Based on Housing Conditions**

Along with the annual questionnaire in 1997, we asked institutions for information regarding housing conditions (including the existence and accessibility of outdoor facilities, the presence of natural and artificial light in indoor rooms) and changes over the years. We considered animals to be subject to changing climatic conditions if they had year-round or nearly year-round (i.e., animals were confined indoors for <20 days per year) access to outdoor cages. Light conditions were determined based on the following criteria:

1. Light N: Institutions that had outdoor and indoor cages with natural light available. Institutions that used additional artificial light during a period that did not extend beyond the hours when natural light was available were also included in this category.
2. Light N+A: Institutions that had outdoor and indoor cages with natural light available, and that used additional artificial light during a period that extended beyond the hours when natural light was available.
3. Light A: Institutions that had only artificial light available.

### **Climatic Data and Photoperiod**

Data on mean monthly temperatures and amounts of precipitation averaged over the period of 1961–1990 for every location where births occurred were obtained from the Royal Meteorological Institute of Belgium. Dr. E. Price provided similar data covering the years 1978–1998 for Jersey (Channel Islands, UK). Average monthly photoperiods were calculated based on hours of sunrise and sunset as obtained from the U.S. Naval Observatory site ([http://aa.usno.navy.mil/data/docs/RS\\_OneYear.html](http://aa.usno.navy.mil/data/docs/RS_OneYear.html)). Average monthly photoperiods may differ slightly between years. This difference is on the order of a few minutes for 1 or more months (<5 min (our own calculations)). Since we wanted to determine the general relationship between photoperiod and the timing of conceptions and births over an extended period of time, rather than during a particular year, and because calculating and averaging monthly photoperiods for every location over 1961–1990 would have been very time-consuming, we used average monthly photoperiods calculated for each location separately for a randomly chosen year (i.e., 1975).

### **Statistical Analysis**

We used analysis of variance (ANOVA; Proc MIXED in SAS®) to investigate differences in mean litter sizes and interbirth intervals between captive- and wild-born females, and between the Northern and Brazilian populations. In all analyses, female ID was included as a random effect in order to avoid pseudoreplication. Data on interbirth intervals were log-transformed to meet the requirements for parametric testing. To control for effects of litter size on interbirth interval, current litter size (defined as the number of infants born in the litter for which the interbirth interval was calculated), and previous litter size (defined as the number of infants in the litter born prior to the litter for which the interbirth interval was calculated), were included as covariates. Additionally, in

order to exclude biases due to underrecording of very long interbirth intervals, we performed a robust analysis deleting the two shortest and two longest interbirth intervals in each group. Denominator degrees of freedom were estimated using the Satterthwaite method.

The date of conception for a given litter was calculated by subtracting 125 days from the date of birth [De Vleeschouwer et al., 2000b]. We used conception and birth dates of litters as the basis for investigating the proximate factors regulating seasonal breeding. Note that since ovulation and conception were not measured directly, only successful conceptions leading to term pregnancies were included in this analysis. Only locations for which the number of litters was at least 10 were included. For each location we determined the number of litters conceived and delivered in a given month and divided this by the total number of litters for that location, thereby obtaining monthly proportions of the total number of conceptions and births for a given location. Analyses were restricted to those institutions that housed their animals subject to changing climatic conditions, and for which light conditions were either N or N+A. An ANOVA, stratified for “population” (Brazilian vs. Northern), was used to compare the proportion of conceptions and births per month between different light regimes. It revealed no significant difference between institutions with light conditions N and those with light conditions N+A. We therefore grouped both categories. The calculated proportions were then used as dependent variables in an analysis of covariance (ANCOVA; Proc GLM in SAS®) with mean monthly temperature, mean monthly amount of precipitation, and mean monthly photoperiod as independent variables, and stratified for “female origin” and “population.” Birth dates for litters from the same females were considered as independent data points. For female origin, we defined three categories:

1. Wild-born females.
2. Females born in captivity in Brazil. These females had been born in two Brazilian institutions with very similar latitudes (Centro de Primatologia do Rio de Janeiro: 22°53'S and Parque Zoológico de São Paulo: 23°33'S), and had all been housed with permanent access to outdoor cages during their development into adulthood. Note that these latitudes are outside the geographical distribution area of wild golden-headed lion tamarins (14–16°S [Coimbra-Filho & Mittermeier, 1973; Pinto & Rylands, 1997]).
3. Females born in captivity in the Northern population. Most of these females were transferred before they were put into a breeding situation. They came from different original locations and had been subjected to different photoperiodic regimes and climatic conditions during their development, or had not had access to outdoor cages.

Table I summarizes information on the institutions included in the analyses.

## RESULTS

### Litter Size

Table II lists details on litter sizes for captive- and wild-born females breeding in captivity in the Northern and Brazilian populations. Litter size is significantly affected by female origin, but not by the population in which breeding occurs (ANOVA: female origin \* population:  $F_{1,137} = 0.00$ , NS; population:  $F_{1,137} = 0.08$ , NS; female origin:  $F_{1,137} = 4.56$ ,  $P < 0.05$ ). Captive-born females have higher mean litter sizes, because they produce a higher proportion of twin litters and have triplets more frequently than do wild-born females (Table II).

**TABLE I. Light Conditions and Number of Litters per Category of Females in Institutions Included in the Analysis on Proximate Factors Regulating Seasonal Breeding**

Institution	Light	Number of litters		
		Captive-born, North	Captive-born, Brazil	Wild-born
Northern population				
Apenheul Primate Park (NL)	N+A	–	11	–
Belfast Zoological Gardens (E)	N	13	–	–
Hong Kong Zoological Gardens	N	16	–	–
Jersey Zoo (UK)	N+A	–	41	–
La Palmyre Zoo (FR)	N+A	32	–	–
Lisbon Zoo (P)	N	11	–	–
Brazilian population				
Centro de Primatologia do Rio de Janeiro	N	–	} 59	} 35
Rio de Janeiro Zoo	N	–		
Parque Zoológico de São Paulo	N	–	28	37

**TABLE II. Number of Litters for Each Litter Size, and Mean Litter Sizes for Captive-Born and Wild-Born Females Breeding in Captivity in the Northern and Brazilian Population**

	Captive-born females	Wild-born females
Northern population		
Number of litters:	368	115
Singletons	119 (32.3%)	52 (45.2%)
Twins	236 (64.1%)	63 (54.8%)
Triplets	13 (3.5%)	–
Mean litter size $\pm$ S.E.	1.71 $\pm$ 0.03	1.55 $\pm$ 0.04
Brazilian population		
Number of litters:	112	139
Singletons	31 (30.6%)	59 (42.4%)
Twins	81 (66.5%)	79 (56.8%)
Triplets	–	1 (0.7%)
Mean litter size $\pm$ S.E.	1.72 $\pm$ 0.04	1.58 $\pm$ 0.04
Overall	1.71 $\pm$ 0.02	1.57 $\pm$ 0.03

### Interbirth Intervals

An ANOVA with current litter size, previous litter size, female origin, and population as independent covariates revealed an interaction effect of current litter size and previous litter size (ANOVA:  $F_{4,425} = 4.95$ ,  $P < 0.001$ ) on the length of the interbirth interval. All other interaction effects were nonsignificant. Significant effects also existed for current litter size ( $F_{2,432} = 5.69$ ,  $P < 0.005$ ), previous litter size ( $F_{2,432} = 3.38$ ,  $P < 0.05$ ), female origin ( $F_{1,107} = 4.38$ ,  $P < 0.05$ ), and population ( $F_{1,107} = 25.74$ ,  $P < 0.0001$ ) separately. Table III lists details on interbirth intervals depending on current and previous litter sizes. These values



TABLE III. Mean, Range, and Median Interbirth Intervals Depending on the Size of the Current and the Previous Litter

Current litter size	Previous litter size		
	Singleton	Twin	Triplet
Singleton			
Mean ± S.E.	192.7 ± 7.9 (n=80)	202.5 ± 13.2 (n=70)	547.0 ± 39.0 (n=2)
Range	129-404	128-826	508-586
Median	162.5	153.5	547
Twin			
Mean ± S.E.	193.0 ± 8.1 (n=78)	210.7 ± 6.1 (n=211)	160.6 ± 14.8 (n=5)
Range	129-386	129-669	132-213
Median	158	175	162
Triplet			
Mean ± S.E.	173.0 ± 11.0 (n=2)	195.4 ± 10.6 (n=5)	200.3 ± 39.9 (n=3)
Range	162-184	155-214	149-279
Median	173	200	173

suggest that the effects of current and previous litter sizes are due mainly to births of triplets, for which the sample size is very small. An ANOVA on a reduced data set excluding data from triplets revealed no interaction effects, and significant main effects for female origin and population only (female origin:  $F_{1,105} = 4.26$ ,  $P < 0.05$ ; population;  $F_{1,105} = 25.34$ ,  $P < 0.0001$ ; current litter size:  $F_{1,421} = 0.20$ , NS; previous litter size;  $F_{1,423} = 0.27$ , NS). Table IV lists values of interbirth intervals for captive- and wild-born females breeding in the Northern and Brazilian populations, based on data from singletons and twins only ( $n = 439$ ). Interbirth intervals are shorter in the Northern population, for both captive- and wild-born females. Within both populations, captive-born females produce litters at longer intervals compared to wild-born females.

Median values of interbirth intervals for the different categories of females are given in Table IV. The mean duration of gestation is 125 days, and the first ovulation occurs on average 17 days postpartum [De Vleeschouwer et al., 2000b; French et al., 2002]. Thus, litters born after an interbirth interval of  $< 142$  days are the result of females successfully conceiving at the first ovulation postpartum. Further, the average length of an ovarian cycle is 21 days [De Vleeschouwer et al., 2000b]. Thus, the median value for an interbirth interval of 136 days for wild-born females breeding in the Northern population indicates that half of the litters result from successful conceptions at the first ovulation postpartum. For captive-born females breeding in the Northern population, the median value is 158 days, indicating that successful conception occurs by the second ovulation postpartum in half of the litters (assuming that postpartum ovulation took place within the average time interval, but conception was not successful). Median values for captive- and wild-born females breeding in Brazil are considerably longer (226-270 days), indicating that after parturition these females go through a period of at least 3 months before successfully conceiving again.

### Proximate Factors Regulating Seasonal Breeding

Figure 1 illustrates the distribution of the number of successful conceptions and births resulting from term pregnancies over the year for the different

**TABLE IV. Mean, Range, and Median Interbirth Intervals for Captive-Born and Wild-Born Females Breeding in the Northern and Brazilian Captive Population**

	Captive-born females	Wild-born females	All females
Northern population			
Mean $\pm$ S.E.	196.6 $\pm$ 5.8 (n=237)	164.4 $\pm$ 5.3 (n=89)	187.8 $\pm$ 4.5 (n=326)
Range	129–826	129–364	
Median	158	136	153
Brazilian population			
Mean $\pm$ S.E.	257.8 $\pm$ 12.6 (n=57)	235.2 $\pm$ 11.0 (n=56)	246.6 $\pm$ 8.4 (n=113)
Range	128–424	131–409	
Median	270	226	243
Mean $\pm$ S.E.	208.5 $\pm$ 5.4 (n=294)	191.8 $\pm$ 6.1 (n=145)	
Median	172.5	156	

categories of females and the populations in which they breed. For wild- and captive-born females breeding in Brazil, the observed distribution of conceptions and births is significantly different from random (conceptions: wild-born females:  $\chi^2_{11} = 33.33$ ,  $P < 0.0005$ ; births: wild-born females:  $\chi^2_{11} = 35$ ,  $P < 0.0005$ ; conceptions: captive-born females:  $\chi^2_{11} = 86.66$ ,  $P < 0.00001$ ; births: captive-born females:  $\chi^2_{11} = 86.66$ ,  $P < 0.00001$ ). A distinct birth peak emerges in September–October due to a concentration of conceptions in May–June. Overall, the breeding season in the Brazilian population extends from July to March.

For females breeding in the Northern population, the distribution of conceptions and births over the year is not different from random, both for females born in captivity in Brazil and for those born in the north.

Table V summarizes the results of the regression analyses investigating the effects of precipitation, temperature, and photoperiod on the monthly distribution of conceptions and births. For wild-born females (all of which were housed in Brazil (Table I)), analyses indicate a significant relationship between the monthly proportion of conceptions and the independent variables of temperature, precipitation, and photoperiod, which explains 33% of the variability in the monthly proportion of conceptions ( $R^2 = 0.33$ ). However, except for the intercept, none of the partial correlation coefficients  $\beta$  are significant. There is also a significant relationship between the monthly proportion of births and the independent variables, which explains 33% of the variability ( $R^2 = 0.33$ ). Partial correlation coefficients point to a significant positive effect of photoperiod, with the proportion of births increasing as photoperiod increases (Fig. 2). The resulting regression equation is  $y = -0.49 + 0.057 * x$ .

For captive-born females, the results differ depending on whether the females are born in the Brazilian or the Northern population, and in which population they are breeding. For females born and breeding in captivity in Brazil, there is a significant linear relationship between the independent variables and monthly proportion of conceptions, which explains 45% of the variability ( $R^2 = 0.45$ ). For births, there is a nonsignificant trend ( $R^2 = 0.26$ ). There is a significant negative effect of photoperiod on the monthly proportion of conceptions, with more conceptions occurring as photoperiod is decreasing (regression equation  $y = 0.85 - 0.062 * x$ ; Fig. 2). Conversely, the monthly



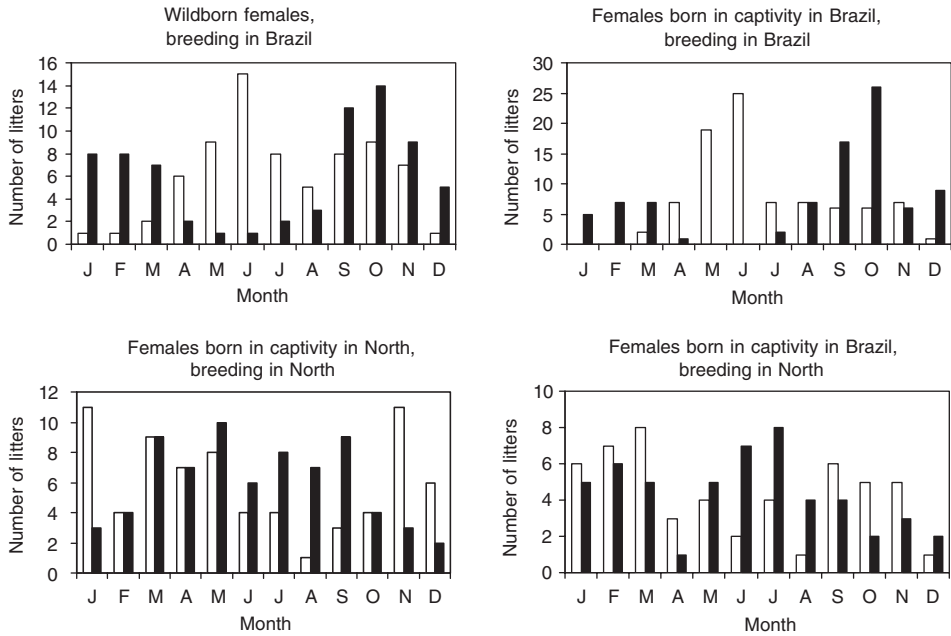


Fig. 1. Distribution of conceptions and births over months for captive-born females reproducing in the Northern and Brazilian populations, and wild-born females reproducing in the Brazilian population. Data for wild-born females reproducing in the Northern population were not available. White bars indicate conceptions; black bars indicate births.

proportion of births increases as photoperiod increases (regression equation  $y = -0.55 + 0.072 * x$ ).

For captive-born females born in the Brazilian population but breeding in the Northern population, there is no linear relationship between the independent variables and the monthly proportion of conceptions or births. The same is true for captive-born females born and breeding in the Northern population.

## DISCUSSION

Given that reproduction is highly demanding in terms of energy costs, a female's ability to increase her reproductive output (by producing larger litters or more litters per year) is probably largely dependent on the amount and nutritional value of the available food resources. Callitrichids have about the highest reproductive potential of all primates [Tardif et al., 1993] and are considered to have been evolutionarily selected for potential variation in reproductive output in relation to resource availability [Tardif & Jaquish, 1997]. Under captive conditions, food availability is not restricted, and females are expected to increase their reproductive rate in response to these less stringent conditions. In the wild, golden-headed lion tamarins usually produce only one litter per year, and mean litter size is 1.54 infants per litter [Dietz et al., 1996; Dietz, 1997]. However, actual litter size at birth may be somewhat higher, since infants are hard to see during the first week of life [Dietz et al., 1996]. The present study has demonstrated that females of this species do reproduce at a higher rate under captive conditions, but only if they were also born in captivity. More particularly, captive-born females have higher mean litter sizes (1.72 infants per

**TABLE V. Results of the Regression Analyses on Proximate Factors Determining the Distribution of Conceptions and Births in Captive-Born and Wild-Born Females Breeding in the Northern and Brazilian Captive population**

	Conceptions	Births
Wild-born females breeding in Brazil	$R^2=0.33$ , $n=24$ , $P<0.05$ Intercept: $\beta=0.57$ , $P<0.05$ ; Temperature: $\beta=-0.003$ , $P=0.53$ ; Precipitation: $\beta=-0.00002$ , $P=0.95$ ; Photoperiod: $\beta=-0.034$ , $P=0.13$	$R^2=0.33$ , $n=24$ , $P<0.05$ Intercept: $\beta=-0.49$ , $P<0.05$ ; Temperature: $\beta=-0.004$ , NS; Precipitation: $\beta=-0.0003$ , NS; Photoperiod: $\beta=0.057$ , $P<0.05$
Captive-born females born and breeding in Brazil	$R^2=0.45$ , $n=24$ , $P<0.01$ Intercept: $\beta=0.85$ , $P<0.005$ ; Temperature: $\beta=-0.001$ , NS; Precipitation: $\beta=0.0001$ , NS; Photoperiod: $\beta=-0.062$ , $P<0.05$	$R^2=0.26$ , $n=24$ , $P<0.1$ Intercept: $\beta=-0.55$ , $P=0.054$ ; Temperature: $\beta=-0.01$ , NS; Precipitation: $\beta=-0.001$ , NS; Photoperiod: $\beta=0.072$ , $P<0.05$ .
Captive-born females born in Brazil but breeding in the Northern population	$R^2=0.23$ , $n=24$ , ns	$R^2=0.24$ , $n=24$ , ns
Captive-born females born and breeding in the Northern population	$R^2=0.06$ , $n=48$	$R^2=0.08$ , $n=24$ , ns

litter) than either females breeding in the wild (1.54 infants per litter [Dietz et al., 1996] or wild-born females breeding in captivity (1.58 infants per litter (this study)).

Ovulation rate and litter-size reduction during pregnancy determine litter size at birth, and both are influenced by a female's nutritional status [Tardif & Jaquish, 1994, 1997]. Female body mass has been shown to influence the number of live births in golden lion tamarins, with heavier females having larger litters [Bales et al., 2001]. In the current study we were not able to assess the nutritional status of captive- and wild-born females, and possible differences in the quality of nutrition and other management practices between institutions. It is important to investigate those effects in further studies. Nevertheless, it seems unlikely that differences in nutritional status and/or management alone could fully explain the observed differences in litter size between wild- and captive-born females, since many of these females were housed in the same institutions and presumably were subject to the same nutritional regimes. An alternative explanation may be found in the different conditions experienced by wild- and captive-born females during their development. Wild-born females breeding in captivity have a mean litter

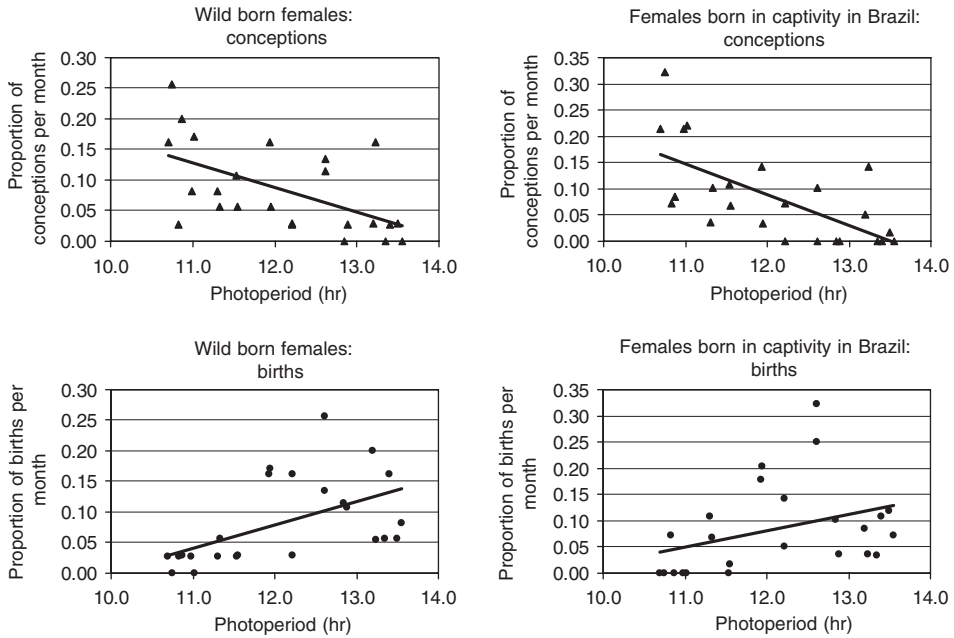


Fig. 2. Relationship between the monthly proportion of conceptions and mean monthly photoperiod for wild- and captive-born females reproducing in the Brazilian population. Regression equations are given in the text.

size of 1.58, which is virtually identical to the mean litter size of 1.54 observed in wild groups [Dietz et al., 1996]. Wild-born animals brought into captive conditions have grown up partly or entirely in the wild, where food supply is probably more restricted than in captivity. These animals often had been confiscated from illegal shipments and had lived under very poor conditions before they were transferred to official institutions. Tardif and Jaquish [1997] found a relationship between body weight and the number of ova in female *Callithrix jacchus*: heavier females produce more ova and larger litters than females that weigh less. High-calorie or high-protein diets also result in larger litters in *C. jacchus* [Tardif & Jaquish, 1994] and *Saguinus oedipus* [Kirkwood, 1983] compared to regular diets. The present study indicates that apart from the current condition of the female, the energy conditions of the environment in which she developed are another factor that determines her later reproductive output. Captive-born golden-headed lion tamarin females have on average a higher body weight than wild-born females, even if both have been fed the same diet (Van Elsacker, unpublished data). Wild-born females appear to be limited in their ability to use the extra available energy for improving their own condition and reproductive output, likely due to the harsher conditions experienced during their youth.

Similar findings of a higher litter size in captive-born females have been reported only for *C. jacchus* [Stevenson & Sutcliffe, 1978]. While some studies report that mean litter size increases with the age of the colony (*L. rosalia* [Kleiman et al., 1982], *C. jacchus* [Poole & Evans, 1982; Box & Hubrecht, 1987], and *Saguinus oedipus* [Kirkwood et al., 1983]), it is unclear whether this is due to a proportionally higher number of captive-born females breeding or by females producing larger litters later in their reproductive life.

Wild-born females produce smaller litters, but have shorter interbirth intervals than captive-born females. Given enough time, wild-born females breeding in the Northern population might thus achieve a higher lifetime reproductive output than captive-born females (wild-born: 1.57 infants/164.4 days or 3.49 infants/year; captive-born: 1.71/196.6 or 3.17 infants/year). For females breeding in Brazil, both effects cancel each other out (wild-born: 1.57/235.2 or 2.44 infants/year; captive-born: 1.71/257.8 or 2.42 infants/year). This calculation of reproductive *output* only takes into account the number of infants born over a time span of 1 year. In order to say whether this also results in a higher reproductive *success* rate for wild-born females, one needs to look at factors influencing infant mortality and investigate how these influence the eventual number of infants reaching reproductive maturity. We are currently investigating this issue.

Based on the median interbirth intervals, it appears that wild-born females frequently conceive at the first ovulation postpartum, whereas relatively more captive-born females conceive at the second ovulation postpartum only (this study). This result should be interpreted with caution, since ovulation per se was not measured in the current study, and thus longer interbirth intervals may have included instances of earlier conceptions leading to abortion or embryonic resorption. Wild-born females may also experience their first postpartum ovulation sooner than captive-born females. Endocrine data collected from captive-born females at the Antwerp colony indicate that the first postpartum ovulation occurs at 17 days [De Vleeschouwer et al., 2000b; French et al., 2002]. In order to verify whether wild-born females indeed conceive sooner than captive-born females, data on the timing of the first ovulation postpartum in wild-born females, and direct monitoring of ovulation and conception in both wild- and captive-born females is necessary. Tardif et al. [2001] observed that small female common marmosets (*C. jacchus*) rearing singletons were equally likely to conceive in the next year as large females, but small females rearing twins were less likely to conceive than large females rearing twins. It might be that the relatively smaller energy burden of infant care for wild-born females (given an overall lower mean litter size for this group) allows them to sustain the next pregnancy sooner than captive-born females. However, this needs to be evaluated taking into account potential differences in carrying effort and female nutritional status between wild- and captive-born females.

Females in the Northern population reproduce faster than females in Brazil, as evidenced by their shorter interbirth intervals. They also reproduce faster than wild females, for which one litter per year is the norm [Dietz et al., 1996; Bach et al., 2001]. Consequently, births in the Northern population are spread out over an extended period, without a clear birth peak. In contrast, females housed in Brazil regularly go several months before conceiving the next litter. Moreover, there is a clear birth peak in September and October in Brazil, for both captive- and wild-born females. French et al. [1996] also reported a clear birth peak in September and October for golden, golden-headed, and black lion tamarins housed at Centro de Primatologia do Rio de Janeiro (also included in this study); however, they did not differentiate between captive- and wild-born females. Kleiman et al. [1982] noted seasonal breeding in captive *L. rosalia*, housed in the Northern hemisphere, with births being concentrated in March–September. Wild golden lion tamarins also show a birth peak, corresponding to the start of the rainy season [Dietz et al., 1994]. Thus, birth peaks appear to be typical of the genus *Leontopithecus*, and, at least for wild golden lion tamarins, this results in offspring benefiting from increased food abundance at the time of weaning [Dietz

et al., 1994]. In *Saguinus fuscicollis*, births are also timed such that lactation and weaning occur when food is most abundant [Goldizen et al., 1988]. The original geographical distribution area of golden-headed lion tamarins (14–16°S) lies closer to the equator than the latitudes of the institutions where golden-headed lion tamarins in Brazil bred in captivity (22–23°S). The climate within this distribution area varies geographically. In the eastern part, there is no clear dry season, and temperature and precipitation vary little year-round. The western part of the species' distribution, however, has a distinct dry season of 3–4 months [Pinto & Rylands, 1997; Coimbra-Filho & Mittermeier, 1973]. Information on seasonal changes in food abundance is as yet unavailable, as is information on seasonality of breeding in wild golden-headed lion tamarins. It would be interesting to see whether this species also breeds seasonally in its natural habitat, and whether this is correlated with seasonal and geographical changes in climate and food abundance.

On a proximate level, photoperiod was the most important factor associated with the onset of reproduction in females housed in Brazil. Most conceptions took place during the months of May–June, which corresponds to the winter solstice (21 June) in the Southern Hemisphere. Also, even if the ultimate reason for seasonal breeding (likely changes in food abundance) is no longer present (as in captivity), breeding is still seasonal. It appears that both the climate under which the animals develop and the climate under which they are currently housed influences their reproduction. On the other hand, despite the more profound differences in length of photoperiod, breeding in the Northern population is not seasonal and is not influenced by any changes in this parameter. This is true both for females raised in outdoor enclosures in Brazil and for females raised under various regimes in the Northern population. Thus, at least for females raised in Brazil under conditions that would promote sensitivity to photoperiod, the climate experienced during their development no longer seems to influence their later pattern of breeding. The data on females born in captivity in the North are hard to interpret, since these females were raised under various conditions (sometimes without natural light available). Unfortunately, we did not have data on breeding by females born in captivity in the Northern population and breeding in Brazil, or wild-born females breeding in the Northern population. Such information would be valuable for further clarifying the impact of current and past climatic influences on reproduction. Also lacking in this study were data regarding the quality of nutrition and nutritional status of individual females, and differences in management practices among the different institutions, which could be important factors in explaining some of the differences between the two populations.

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