Sources of Variability in Numbers of Live Births in Wild Golden Lion Tamarins (*Leontopithecus rosalia*)

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We examined the effects of several variables on the number of live births in multiparous females in a wild population of golden lion tamarins (*Leontopithecus rosalia*). Independent variables included the number of infants born to a female the previous breeding season, the number of infants weaned the previous breeding season, the female's age and body mass, the number of adult males and helpers in the group, and the inbreeding coefficient of the offspring. We also tested the hypothesis that trapping and chemical immobilization during pregnancy affected the number of live births. Female body mass was the only statistically significant predictor of the number of live-born infants in the current season when both first and second peaks were included. Characteristics that predicted higher numbers of infants in the first peak of a season were the number of infants born the previous season and the body mass of the female. The greater the number of infants born the previous season, the greater the number of infants born in the first peak of the current season. Factors positively correlated with the number of live births in the second peak within a season included the number of infants born the previous season, as well as the number of available helpers. Due to sample size constraints, the analysis of litters in the second peak did not include body mass of the female as a variable. Inbreeding and handling did not affect the number of live births. We found no evidence that current reproduction negatively impacts future reproduction in this species. We also found no evidence for an age-related reduction in fertility. Am. J. Primatol. 54:211–221, 2001.   © 2001 Wiley-Liss, Inc.

INTRODUCTION

There has been extensive study of the maternal characteristics that affect postnatal infant survival in callitrichid primates [Tardif et al., 1986; Pryce et al., 1988, 1993, 1995; Baker & Woods, 1992; French et al., 1996]. Variables that might

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affect the likelihood of conception or successful gestation, and therefore the number of infants born, have received less attention, particularly in wild populations.

Golden lion tamarins (*Leontopithecus rosalia*) are members of the family Callitrichidae, which consists of marmosets, tamarins, and lion tamarins [Mittermeier et al., 1988]. Most golden lion tamarins in Poço das Antas Reserve, the largest remaining wild population, live in reproductive groups that range from two to 14 individuals, with a historical mean group size of 5.6 individuals [Dietz & Baker, 1993] (Baker and Dietz, unpublished data). Mean age at first reproduction is 3.6 yr; reproduction continues until death (Table I).

In Poço das Antas Reserve, golden lion tamarin reproduction is restricted to August through February, with the major birth peak in October–November and a smaller peak in February [Dietz et al., 1994]. Because of a fertile post-partum estrus, females in breeding groups have the potential to produce zero, one, or two litters per August–February birth season [Dietz et al., 1994]. The mean birth dates for first litters and for only litters are in November, and it is rare for an only litter to be born past December [Dietz et al., 1994]. The mean birth date for a second litter is February 11 [Dietz et al., 1994]. Litters may contain one to three infants, with the modal litter size being twins. For females producing two litters within a season, litter size and infant mortality do not differ between first and second litters [Dietz et al., 1994]. Factors that influence the number of infants born per reproductive attempt have not been studied in any callitrichid population.

Many variables may affect the number of live births to a female. One factor that may influence failure of a conception/pregnancy is significant investment in reproduction in the previous season [Altmann et al., 1978]. Production of offspring in one season may reduce a female's energy reserves to the extent that her reproduction in the following season is compromised. The concept of "trade-offs" between current and future reproduction is well established [Stearns, 1992], and has been demonstrated in natural and manipulated populations of various species, including red deer (*Cervus elaphus*), collared and pied flycatchers (*Ficedula albicollis*, *F. hypoleuca*) and great tits (*Parus major*) [Clutton-Brock et al., 1983; Gustafsson & Pärt, 1990; Slagsvold, 1984] (but see Pettifor et al. [1988]). Data from studies of captive marmosets (*Callithrix jacchus* [Sousa et al., 1999]) and lion tamarins (*Leontopithecus* sp. [French et al., 1996]) do not support the existence of such trade-offs for callitrichids. However, greater energy constraints would be predicted for wild females than for captive females fed ad libitum. A female's body mass, therefore, may be particularly important in the wild.

Body mass in captive callitrichids has been shown to influence number of eggs ovulated [Tardif & Jaquish, 1997] and the likelihood of fetal loss during gestation [Tardif & Jaquish, 1997]. Only indirect data on the effects of female body mass on reproduction are available from the wild. Female golden lion tamarins do not lose body mass during lactation [Dietz et al., 1994], nor does a greater average number of helpers lengthen female reproductive tenure [Bales et al., 2000].

TABLE I. Summary Statistics on Females in Poço das Antas Population*

	Average	Range
Number of breeding seasons in study per female	3.8 seasons	½ season – 13.5 seasons
Age at first reproduction	3.6 years	2 years – 6 years
Age at last reproduction	6.1 years	3 years – 16.1 years

*n = 43 females; total number of breeding seasons = 162.5; females with body mass data, n = 24.

Although participation in infant-carrying by other group members might be predicted to relieve females from the energy burden of carrying infants (at a time when they may be pregnant with their next litter), the extent to which helpers actually provide relief to females is unclear. In a review of the effects of helpers on parental transport of infants in callitrichid species [Bales et al., 2000], only 23% of studies showed a helper-related reduction in maternal infant transport. However, effects may vary depending on the sex and social status of the helper. For example, adult males may be more effective than immature offspring at reducing the female's transport burden [Heymann & Soini, 1999; Bales et al., 2000].

Both female body mass and fertility may decline with age. Reproductive senescence in nonhuman primates is a controversial topic [Lancaster & King, 1985; Pavelka & Fedigan, 1991; Tardif & Ziegler, 1992; Paul et al., 1993; Caro et al., 1995]. It has been proposed that reproductive senescence is an adaptive trait in wild females. If the death of the mother when the offspring are very young would compromise the survival of these offspring, an older mother might be better off continuing to invest in older offspring rather than continuing to reproduce [Rhine et al., 1980, reviewed in Paul et al., 1993]. It has also been suggested that predation and other factors prevent most nonhuman primate females from reaching the age at which senescence would occur in nature [Jolly, 1985]. Age-related changes may also affect fertility without a complete cessation in reproduction. Age-related effects have been observed in captive callitrichids, with decreasing numbers of primary follicles, irregular hormonal cycles, and even apparent cessation of ovulation in old females [Tardif, 1985; Tardif & Ziegler, 1992].

In addition to age, body mass, and number of helpers, inbreeding depression is another potential factor influencing conception and pregnancy success. Small populations are likely to exhibit elevated levels of inbreeding, and high inbreeding levels may contribute to reproductive failure through infant mortality [Ralls & Ballou, 1982]. Indeed, inbreeding and inbreeding depression have been observed in this population of golden lion tamarins [Dietz et al., 2000]. Infants believed to be inbred died at a rate approximately three times higher than non-inbred infants, with the effects being most acute during the first 6 months of life [Dietz et al., 2000].

An additional source of variation in numbers of live births may be physical manipulation of females by researchers. Handling during pregnancy for marking, collection of blood, or to affix radiocollars could increase the likelihood of pregnancy loss. Captive callitrichids exhibit relatively high levels of prenatal pregnancy loss, perhaps due to handling stress [Heger et al., 1988]. In this analysis, we use data from a long-term field project on golden lion tamarins to examine the effects of age, body mass, previous reproduction, group size and composition, inbreeding, and handling on the number of live births to multiparous females.

METHODS
Subjects

This study was conducted in Poço das Antas Biological Reserve, Rio de Janeiro State, Brazil, which contains approximately 250–350 golden lion tamarins [Ballou et al., 1998]. The groups in the study population are native and unmanipulated, except for semiannual trapping, and have been under continuous study since 1983. All individuals are marked and habituated to human observers. At least one animal in each group and some animals of dispersing age are radiocollared to facilitate location [Dietz & Baker, 1993; Baker et al., 1993].

The dates and circumstances of all births, deaths, emigrations, and immigrations are recorded. Only births that are live, and in which the offspring survive until the first postnatal contact with the group, are detectable. We recorded the number of infants born per each reproductive attempt. The first reproductive attempt was eliminated from the data set because it was by definition successful, and previous pregnancy loss in primiparous females was not detectable.

We refer to the August–February time period, in which a female may have two litters, as a birth "season." We refer to litters born from August to December as being in the "first peak," whereas litters born in January and February will be referred to as in the "second peak." Each female therefore has two "reproductive attempts" in one birth season.

Our analysis included data on 43 tamarin females that were potentially reproductive, for a total of 162.5 female-seasons (Table I). Lone or nonterritorial individuals do not reproduce in this population [Baker et al., 1993, Baker & Dietz, 1996)]; therefore, females not in an established territorial group were eliminated from the data set. We included all females with known birth dates or whose age could be estimated to within a year. Age estimates were based on body mass, the eruption of permanent teeth, and tooth wear.

Inbreeding

Paternity was attributed to the dominant male in the group [Baker et al., 1993], or to the eldest male if dominance relationships were unknown. If no unrelated males were present in the group at the time of conception, paternity was attributed to the female's own (putative) father (if present), brother, or son. We cannot be certain extra-group copulations (EGCs) did not take place in these cases. Both incestuous copulations and EGCs have been observed in this population (Baker and Dietz, unpublished data). Infants conceived as a result of an EGC would have lower inbreeding coefficients than those that were assigned. In this analysis inbreeding would probably be overestimated. Cases of more distant inbreeding (at the level of cousins, second cousins, etc.) could be more reliably assigned. A separate analysis was carried out using just these cases. In this second analysis some cases of high inbreeding were probably excluded.

For seasons in which a female did not produce detected infants, the "conception date" was calculated as 132 days [Kleiman, 1977] before the mean birth date for the population for that peak (October/November or February [Dietz et al., 1994]). Paternity of the "potential" infants was attributed according to the group composition at that time.

Effects of Handling

Researchers attempted to live-trap and examine under anesthesia all of the animals in the study population at intervals of approximately 6 months. However, due to a variety of reasons, the interval between trapping events might exceed 1 year for any particular animal. A potential information bias existed in our evaluation of the effects of biomedical examination on pregnancy outcomes. Females examined more often were typically those from groups under more frequent observation, and thus were also likely to have their infants detected sooner post partum than were females in groups handled less often. Thus, we were more likely to miss live-born infants that died perinatally for females that were observed and handled less frequently. In order to control for this potential bias, we performed a within-female comparison, using a paired Wilcoxon signed-rank test.

We compared the number of infants resulting from a reproductive attempt during which a female was handled with the number from a reproductive attempt during which she was not handled. We minimized age and seasonal effects by choosing pregnancies for this analysis from adjacent seasons and only from the first birth peak. If there was more than one potential pair of pregnancies for a female, one was chosen randomly.

Female Body Mass

Female body mass may affect the number of live births; however, we encountered several problems when including body mass in our analysis. For each birth, female body mass had to be measured shortly before conception, or in early pregnancy before significant gain from the fetuses [Dietz et al., 1994, Tardif & Jaquish, 1997]. The relative scarcity of these data greatly reduced our overall sample size, and the data were insufficient to include female body mass in the model for litters in the second peak.

Body mass data were included for all seasons in which a female had been handled in May or afterward (for litters from the first peak), or in September or afterward (for litters from the second peak), and was nonpregnant or in early pregnancy at the time of examination (as determined by palpation during handling, and retroactively by birth date of infants). Body mass in early pregnancy (the first 6 weeks of gestation) was assumed to be reflective of the nonpregnant body mass of the female. We tested this assumption by comparing body masses of nonpregnant females with those in early pregnancy and by charting body mass throughout pregnancy for 14 females.

Statistical Analysis

The data were analyzed using generalized linear mixed models, with the female's identity included as a random effect. Generalized linear models provide for the inclusion of random effects, such as individual animal identities, addressing the problem of pseudo-replication by accounting for correlations within the data [Diggle et al., 1999]. For any analysis in which female identity had a covariance parameter other than zero, the data set was reduced to one entry per female. If the covariance parameter of female identity was zero, each reproductive attempt by the female was included as an independent observation. Models were selected by backward selection procedures and final models contained only significant variables ($P < 0.05$). The significance of each coefficient in the model was therefore determined based on an analysis of variance, with F values reported only for those coefficients that were significant. Computer analysis was carried out using the GLIMMIX macro [Littell et al., 1996] in SAS 6.12 (SAS Institute, Cary, NC), using Poisson error terms. The use of stepwise selection methods for observational data is controversial [James & McCulloch, 1990]; in general, all-possible-regressions methods are preferred [Kleinbaum et al., 1988]. As an all-possible-regressions procedure is not available for this macro, the backward selection method was the most methodologically feasible model selection procedure. However, because of the large number of tests done during such a procedure, replication of the model is advisable when additional data become available.

To account for the fact that the effects of age are often nonlinear, age was divided into four categories (under 4 yr, 4–8 yr, 8–12 yr, and above 12 yr). These age classes were chosen because they corresponded to the tooth wear categories

used for age estimations. The female's identity and her age were computed as class effects. The independent variables in the models are detailed in Table II.

RESULTS

We verified the assumption that body mass of nonpregnant females was not significantly different from that of those in early pregnancy (nonpregnant body mass: n = 18; mean = 591.8 g, SE = ±10.3 g; early pregnant body mass: n = 21; mean = 577.1 g, SE = ±6.7 g; two-sample t-test, t_{37} = −1.23, P = 0.23). In addition, in 14 pregnancies for which repeated body masses during a single pregnancy were available, almost all gain occurred during the second half of pregnancy (Fig. 1).

When considering both first and second peaks together, the only variable to exert a significant effect was maternal body mass (Table II). Greater pre- or early pregnancy body mass was significantly associated with a greater number of live births (Fig. 2). Number of infants born the previous season, number of infants weaned the previous season, age of the mother, number of males in the group, number of helpers, and inbreeding coefficient were not significant predictors of number of live births. A separate analysis, which considered only the more distant (and probably more reliable estimates of) levels of inbreeding, also failed to find a significant effect of inbreeding on number of live births.

For litters from the first birth peak only, the significant variables included the number of infants born the previous season and body mass of the female. Females that gave birth to more infants the previous season gave birth to more infants in the first peak of the current season (Table III).

For litters from the second birth peak only, the two variables found to affect the number of live births were the number of infants born the previous season and the number of helpers in the group. Females with more helpers gave birth to more infants in the second peak: litters with zero infants (n = 99), mean helpers = 2.26 (SE = ±0.10); litters with one infant (n = 2), mean helpers = 2.5 (SE = ±0.50); litters with two infants (n = 34), mean helpers = 3.06 (SE = ±0.19); and litters with three infants (n = 1), mean helpers = 3.0 (SE = 0). Females that had more infants in the previous season gave birth to more infants in the second peak: litters with zero infants, mean previous infants = 1.11 (SE = ±0.12); litters

TABLE II. Independent Variables Included in Mixed Models and Final Model Statistics*

Final model	n	Partial corr.	Effect estimate	F-value	P-value
First and second peaks combined[a]					
Female body mass (g)	24	r = 0.53	0.0165	$F_{1,22}$ = 7.42	0.0124
First peak only					
Female body mass (g)	18	r = 0.58	0.0121	$F_{1,15}$ = 8.48	0.0178
Infants born previous season	18	r = 0.76	0.4068	$F_{1,15}$ = 5.98	0.0273
Second peak only[a]					
Number of helpers	136	r = 0.31	0.1249	$F_{1,133}$ = 9.30	0.0028
Infants born previous season	136	r = 0.37	0.0962	$F_{1,133}$ = 16.7	< 0.0001

*Independent variables: maternal body mass; number of infants born previous season; number of infants weaned previous season; maternal age; inbreeding coefficient of offspring; number of adult males in group; number of helpers in group; random variable, maternal identity.
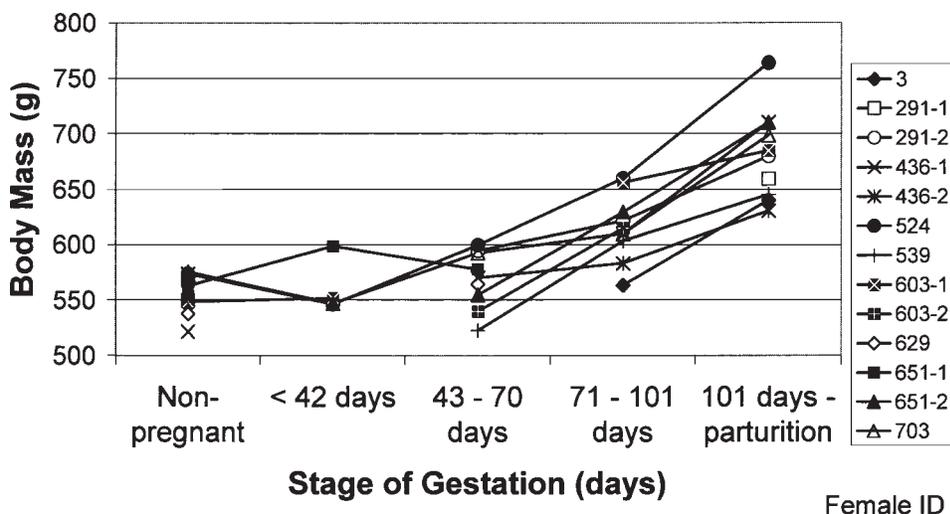[a]Maternal body mass was not included in the analysis of litters in the second peak.

Fig. 1. Body masses of females collected at different stages of pregnancy (n = 10 females, 14 pregnancies).

with one infant, mean previous infants = 2.0 (SE = 0); litters with two infants, mean previous infants = 2.26 (SE = ±0.23); and litters with three infants, mean previous infants = 4.0 (SE = 0).

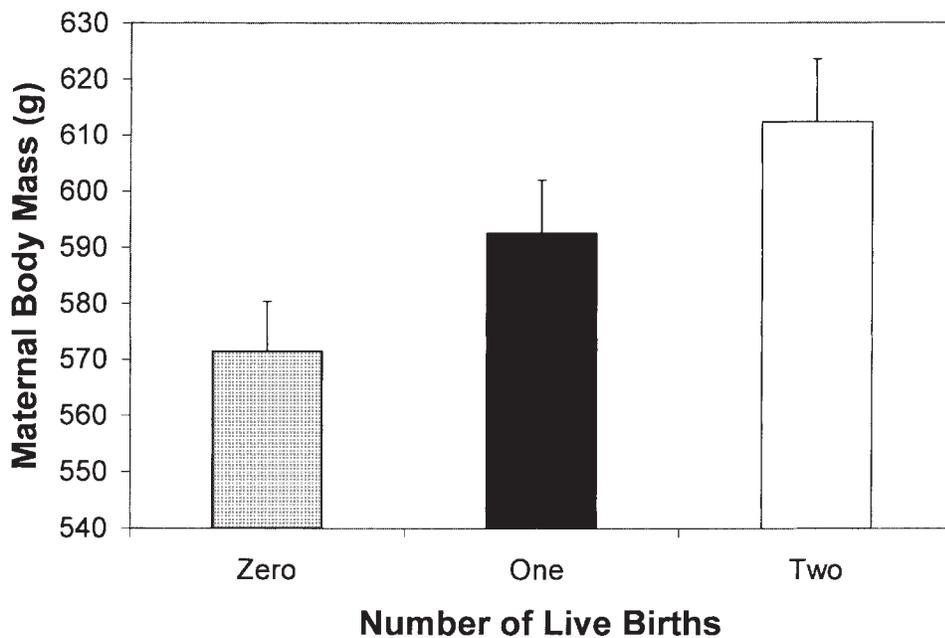We found no significant difference in the number of live infants born to fe-

Fig. 2. Average number of live-born infants in relation to female body mass, first and second peaks combined (litters with zero infants (n = 13), mean body mass = 571.5 g (SE = ± 8.9 g); litters with one infant (n = 2), mean body mass = 592.5 g (SE = ± 9.5 g); and litters with two infants (n = 9), mean body mass = 612.4 g (SE = ± 11.2 g)).

TABLE III. Relationship of Number of Live-Born Infants in the Current Season (First Peak) to Number of Infants Born in the Previous Season and Maternal Body Mass

Number of infants born in current season, first peak	Mean non-pregnant maternal body mass (g) (SEM ± S.E.)	Mean total number of infants born in previous season (SEM ± S.E.)
Zero (n = 8)	560.12 ± 12.7	0.25 ± 0.25
One (n = 2)	592.50 ± 9.5	1.50 ± 0.50
Two (n = 8)	614.25 ± 12.11	2.25 ± 0.41

males from pregnancies in which they had been handled and in pregnancies in which they had not been handled (n = 29, S = 14.0, NS). Females handled during pregnancy gave birth to a mean of 1.24 infants (SE = ± 0.15 infants), while the same females gave birth to a mean of 1.24 infants (SE = ± 0.16 infants) following pregnancies during which they were not handled.

DISCUSSION

We found no evidence that high reproductive investment in one breeding season led to reduced reproductive success in the following season. In fact, the greater the number of offspring produced and weaned in the previous season, the more offspring the female produced in the next season. There is thus no evidence for a trade-off in current and future reproduction. Indeed, it appears that females may have individual histories of either high or low breeding success. Similar results were found for pied flycatchers (*Ficedula hypoleuca* [Harvey et al., 1985]), in which females that bred in their first and second years were more likely to survive and breed for a third year. In addition, female flycatchers that had bred before had larger clutches.

Individual histories of either high or low breeding success may be determined by the body mass of the female, which was the only significant predictor of number of live births when considering both first and second peaks. This analysis parallels previous findings of captive studies that litter size in callitrichids is adjusted prenatally according to the body mass of the mother [Tardif & Jaquish, 1997]. In addition, it provides a possible explanation for the observed lack of effect of lactation on body mass in golden lion tamarin females [Dietz et al., 1994]. If litter size has already been adjusted downward in females at low body mass, lactation would presumably become less of a burden for females in poor condition. A female's body mass may be influenced by many factors, including heredity and availability of resources. It is possible that the effect of helpers, which was significant in the analysis of litters in the second peak (in which body mass was not included due to sample size constraints) is mediated through its effects on maternal body mass. That is, mothers with more helpers may carry less and be in better condition for the next reproductive attempt.

We found no evidence for an age-related decline in fertility, in that age was not significant in any of the final models. Age effects may therefore be mediated through body mass; in fact, body mass in females in this population does change in a U-shaped relationship with age (Dietz, Baker, and Bales, unpublished data). One adaptive explanation for an age-related decline or cessation of fertility focuses on the fact that the death of a mother compromises the survival of very young dependent offspring. Following this argument, a very old female, rather than give birth at such an advanced age that she is likely to die before her infant

is independent, should instead invest in older offspring or grand-offspring [Rhine et al., 1980, reviewed in Paul et al., 1993]. However, in the callitrichid cooperative breeding system, other group members may reduce mortality of orphaned offspring. In this population we observed infants as young as 5 weeks of age survive the death of their mother, probably due to care from other group members (Bales, Baker, and Dietz, unpublished data). This age is several weeks before normal weaning but after the advent of solid food intake and food sharing by adults [Baker, 1991]. Infant care patterns may reduce the impact of maternal mortality on infant survival, and thus explain the apparent lack of reproductive senescence in wild golden lion tamarins, as well as in other callitrichids.

We also found no evidence that handling and chemical immobilization during gestation reduced pregnancy success. Handling of animals during the mating season or while they are pregnant has been shown to affect reproductive success in various mammals (red deer (*Cervus elaphus*) [Audigé et al., 1999]; mountain goats (*Oreamnos americanus*) [Côté et al., 1998]). In contrast, there was no effect of animal handling on prenatal loss in several primate species (rhesus (*Macaca mulatta*), cynomolgus (*Macaca fascicularis*), and bonnet macaques (*Macaca radiata*) [Hendrie et al., 1996]). It is likely that taxonomic groups have differing levels of vulnerability to handling-related pregnancy loss, which has important implications from an animal welfare and conservation perspective.

The inbreeding coefficient of observed or potential offspring was not a significant predictor of the number of live offspring actually produced. Neither did we find a significant relationship between the inbreeding coefficient and number of live births when we considered only offspring with lower, and probably more reliable, inbreeding coefficients. However, our knowledge of paternity is not complete, and this and other sources of incomplete knowledge of genealogies may have led to under- or overestimations of inbreeding coefficients in some cases. Although pregnancy loss may not be exacerbated by inbreeding, other analyses performed on this population show that inbred infants have lower postnatal survivorship [Dietz et al., 2000].

The number of live births per female is one measure of reproductive success in wild populations of primates. The number of infants that survive to weaning and reproductive age, as well as the number of infants that eventually reproduce themselves, are additional measures [Rhine, 1997]. It is possible that each of these measures of reproductive success is affected by a different suite of ecological and genetic factors (for instance, as shown in this study and in Dietz et al. [2000], inbreeding appears to affect postnatal but not prenatal survivorship). Further investigation of the variables influencing these measures will aid in our understanding of the basic biology of primate species, as well as in their conservation.

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