

THE CHALLENGE HYPOTHESIS: FECAL CORTISOL LEVELS IN MALE RED-
BELLIED LEMURS DURING THE REPRODUCTIVE SEASON

By

LILLIAN ANNA STOLAR

A Thesis Submitted to The Honors College

In Partial Fulfillment of the Bachelors degree
With Honors in

Anthropology

THE UNIVERSITY OF ARIZONA

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Approved by: 

Dr. Stacey Tecot
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Abstract:

In red-bellied lemurs (*Eulemur rubriventer*), a pair-bonded, monogamous species with paternal care, male fecal cortisol levels fluctuate over the reproductive season. The Challenge Hypothesis suggests a relationship between mating and infant care systems and hormone levels. During mating, fecal cortisol levels should be low due to little male-male mate competition. During gestation, males and females should have correlated hormonal responses if males prepare for infant care during their mate's pregnancy. Throughout infant growth, male fecal cortisol levels should elevate because paternal care is present. Red-bellied lemur male fecal cortisol levels were compared across reproductive seasons, and with their mate's fecal cortisol levels. Fecal cortisol levels were low during the mating season, higher during gestation, and highest around birth. During gestation, fecal cortisol levels were lower in males than females, and male fecal cortisol levels elevated about one to two weeks after their mate's. These results support predictions based on the Challenge Hypothesis, and suggest a paternal hormonal profile in this species.

Introduction:

The Challenge Hypothesis, proposed by Wingfield et al. (1990), suggests that there is a relationship between hormone levels and mating and infant care systems. Both testosterone and cortisol are important throughout the reproductive season and do change within individuals during mating and birthing seasons in many different species (Wingfield et al. 1990; Cavigelli 1999; Strier et al. 2003; Wynne-Edwards and Timonin 2007; Ostner et al. 2008). The driving force behind these hormonal changes may be the different mating and infant care systems of the species. Thus, hormone levels should change within individuals of a species based on the species' mating and infant rearing systems. For example, monogamous species would differ from polygynous species because of their differences in levels of male-male mate competition (accompanied by aggression) and, in some cases, male care of infants (Wingfield et al. 1990).

Testosterone, a hormone associated with aggression, is important to reproduction (Wingfield et al. 1990). Because birds have diverse mating and parenting strategies and are well studied, they are ideal to use for understanding how hormones relate to reproduction. During the mating season, in species that mate polygynously, males tend to show an increase in testosterone levels. High testosterone levels are commonly seen in species with high levels of male-male aggression during the mating season (Wingfield et al. 1990; Ostner et al. 2008). Although this increase is expected in male groups where aggression is high, monogamous birds with low levels of mate competition have low testosterone levels (Wingfield et al. 1990).

In many species, testosterone tends to decrease around infant birth in males who provide paternal care, suggesting that lower levels of aggression help facilitate infant care (birds, Wingfield et al. 1990; rodents, Wynne Edwards and Timonin 2007; lemurs, Ostner et al. 2008; humans, Gettler et al. 2011). In birds that provide paternal care, such as western gulls and some

songbirds, testosterone levels are significantly lower around infant birth than during other parts of their reproductive season (Wingfield et al. 1990). In rodents and common marmosets (*Callithrix jacchus*), low testosterone is usually seen with high levels of paternal care (Wynne-Edwards and Timonin 2007; Prudom et al. 2008). In humans, low testosterone is even prevalent among expecting males as compared to non-expectant males (Wynne-Edwards 2001; Gettler et al. 2011). In contrast, testosterone levels remain high in species without paternal care in birds, such as turkeys (*Meleagris*), as well as in some primates, such as lemurs (*Lemuroidea*) (Wingfield et al. 1990; Ostner et al. 2008). Turkeys and red-fronted brown lemurs show no paternal care and have high levels of testosterone throughout their reproductive season, including when infants are born (Wingfield et al. 1990; Ostner et al. 2008; Tecot et al. 2015). While testosterone is important to males during the reproductive season, it is not the only hormone related to reproductive behaviors; cortisol is a hormone associated with behavioral changes during the mating, gestation, and birthing periods.

Cortisol is a hormone used to regulate stress (Selye 1973). When high levels of cortisol are present in an individual, it is often interpreted as a response to a stressor, such as predators, weather changes, or other environmental perturbations (Pride 2005; Tecot 2013). However, this is not true during the reproductive season. While a female is pregnant, cortisol levels increase as circulating levels of ovarian hormones increase (Setchell et al. 2008). This means that cortisol is not only related to avoiding stress, but also to reproduction. Cortisol is also related nurturing behavior in humans (Berg and Wynne-Edwards 2002). Similar to testosterone, elevated cortisol is related to aggression and dominance (Cavigelli 1999; Bercovitch and Ziegler 2002). Cortisol has been investigated in tests of the Challenge Hypothesis, because of its link to aggression,

dominance, and reproduction (Cavegelli 1999; Bercovitch and Ziegler 2002; Setchell et al. 2008).

Because cortisol is associated with aggression and competition, it is expected to vary with levels of mate competition. Indeed, male muriqui monkeys who show little male-male aggression have low cortisol levels during the mating season (Strier et al. 2003). In contrast, species such as Verreaux's sifaka (*Propithecus verreauxi*) and red-fronted brown lemurs (Fichtel et al. 2007; Ostner et al. 2008), where males have high levels of aggression and mate competition, have elevated cortisol levels during the mating season. Females may have high cortisol levels during the mating season as well. This pattern may be due to the potential stress of finding a mate, or preparation for pregnancy (Strier et al. 2003; Carnegie et al. 2011). Low cortisol levels may be seen in females that are monogamous, or that compete little for a mate.

Throughout gestation, cortisol levels remain at baseline levels in species with little or no paternal care, but fluctuate in males that provide paternal care (Reburn and Wynne-Edwards 1999; Ziegler et al 2004; Fichtel et al. 2007; Ostner et al. 2008). It is hypothesized that gestational elevations in males help prepare them for infant care once the infant is born (Wynne-Edwards and Timonin 2007), however this has not been extensively tested. In females, cortisol levels during gestation gradually increase as her fetus develops, with a significant mid-gestation elevation when the transitional zone of the fetal adrenal glands forms (Umezaki et al. 2001).

Around and after infant birth males that provide paternal care show an increase in cortisol levels, as observed in paternal male rodents (Wynne-Edwards and Timonin 2007). Verreaux's sifaka males, which have little paternal care, show little change in cortisol level around infant birth (Fichtel et al. 2007). Although the reason for high cortisol levels in males around infant birth is unknown, it is hypothesized that high cortisol levels may result from the stress of having

an infant, the novelty of having an infant, having to nurture an infant, resource scarcity, and/or the potential of infanticide (Berg and Wynne-Edwards 2002; Tecot 2008; Brockman et al. 2009; Tecot 2013). Most females also show an increase in cortisol levels around birth as a response to the birthing process (Strier et al. 2003; Setchell et al. 2008).

Because of the possible correlation between cortisol and male-male mate aggression and infant care, changes in fecal cortisol levels are likely related to mating and infant care systems, as proposed for testosterone according to the Challenge Hypothesis. Support for the Challenge Hypothesis was found in the red-fronted brown lemur, which mates polygynandrously and lacks paternal care (Ostner et al. 2008). A species that is monogamous with paternal care and has little male-male aggression for mates would give new insights into understanding whether the Challenge Hypothesis can accommodate cortisol as well as testosterone changes, because tests of this hypothesis in primates have focused on species with mate competition who lack paternal care.

Red-bellied lemurs (*Eulemur rubriventer*) are an ideal species to test the Challenge Hypothesis because males have little aggression during the mating season, males and females are pair-bonded and monogamous, and males help take care of infants (Merenlender 1993; Overdorff and Tecot 2006; Tecot et al. 2015). A female and male pair lives together in close proximity for multiple years, throughout the reproductive season, including the mating period (Tecot et al. 2015).

We expect that fecal cortisol levels will vary over three reproductive stages: mating, gestation, and infant dependence/development. During the mating season, fecal cortisol levels should be relatively low in both males and females due to low levels of male-male aggression. Throughout gestation, fecal cortisol levels in red-bellied lemurs should fluctuate with the highest

levels around mid-gestation and conception (weeks 9 and 18) (Ziegler et al. 2004). Females should have increasingly elevated fecal cortisol levels during this time and it is expected that males' fecal cortisol levels will rise and fall with the female's fecal cortisol levels (although the male's fecal cortisol level elevations should occur approximately one or two weeks after the female's). After birth and during infant growth, we expect fecal cortisol levels to be highest in both males and females (around weeks 20-23).

Methods:

Research Sites

Data were collected on red-bellied lemurs (*Eulemer rubriventer*) in two different sites in Madagascar. The two sites, Talatakely and Vatoharanana, were located within Ranomafana National Park (Tecot 2008) (Figure 1). The whole park is 416 km² or 41,500 hectares (Tecot 2008). Ranomafana National Park is a montane rain forest, so it is characterized by dense forest and heavy rainfall during the wet season (Tecot 2008). While the wet season is from January to March, the dry season is June to October (Dunham et al. 2011). A study spanning 1965 to 2006 recorded an average of 508 mm of rain during the wet season, but an average of only 143 mm of rain during the dry season (Dunham et al. 2011).

Subjects

Red-bellied lemurs are prevalent within the Ranomafana National Park, with this park hosting at least 31 groups in two of its several sites (13.96 individuals per km² in Vatoharanana and 8.17 individuals per km² in Talatakely); this is the largest population of wild red-bellied lemurs in the world (Tecot 2008; Herrera et al. 2011). The mating season for these lemurs begins in May and infant birth is typically between August to October, although there have been births observed in eight different months (Tecot 2010). Data for this study were collected from five

different pair-bonded groups from June 2003 through March 2005 (Tecot 2008, 2013).

Individuals were identified by distinct, individual markings (Tecot 2008). Some individuals also had been tagged with colored collars (see Tecot 2008).

Data from pair-bonded groups containing at least one adult male, one adult female, and an infant (after infant birth) were used in this study ($n = 5$ groups). During the study, each group had at least one infant, and one group had two infants, resulting in six reproductive periods analyzed (Table 1).

Hormone Collection and Analysis

Fecal cortisol data were collected from each site and each individual between September 2003 and March 2005 (19 months). Fresh fecal samples were opportunistically collected before noon every day to control for any circadian effect on hormone excretion. Samples were placed in aluminum foil and labeled with the individual, time, date, and location, and then desiccated by a fire or in a drying oven to preserve steroids (Tecot 2013). One or two samples were obtained for most individuals each week. S. Tecot conducted extractions and assays of 925 samples at the Wisconsin National Primate Research Center (Tecot 2008). Specific details on how the fecal samples were processed and how hormones were extracted are available in Tecot (2008, 2013). Fecal cortisol levels are expressed as ng/g of feces in a subset of 330 samples that were collected during the mating, gestation, and infant growth periods (see below).

Data Analysis

When there was more than one fecal sample per individual per week, fecal cortisol values were averaged. Birth dates for each infant were determined based upon the first sighting of the infant, the last day the group was observed without an infant, and the infant's body size. Conception dates were estimated by subtracting 126 days from the infant's estimated birth date.

Fecal cortisol levels for each individual were compiled for each reproductive week, spanning three weeks before conception (week 0) through five weeks after birth. Data were further compiled into reproductive stages: mating (weeks -3 to 0), gestation (weeks 1-16), and infant growth (weeks 17-23). Data were not available in some weeks for some individuals, but all individuals had at least one weekly value for each reproductive stage. Within each reproductive stage the weekly values were averaged for each individual.

Data were analyzed in SPSS Statistics, version 20. Data were tested for normality using a Kolmogorov-Smirnov test, and were found to be normal. A repeated measures general linear model was performed with the independent variables sex and period, and fecal cortisol as dependent variables (female fecal cortisol during mating, gestation, and infant development periods, and male fecal cortisol during mating, gestation, and infant development periods). The first period where the concentration of fecal cortisol increased by 2 SD or more from the mean of the previous week's sample was used to determine when gestational fecal cortisol levels rose significantly for the first time in males and in females, after Ziegler et al. (2004).

G*Power 3.1 was used to determine if the sample size was large enough to find a significant relationship. Effect size was found through using partial eta squared values (found using SPSS Statistics v. 22). The probability error was set to a value of 0.05. The power value was placed at 0.9 because 0.9 is equal to 1 minus beta (probability of a type II error). The power value 0.9 gives the minimum number of groups needed to reach significance. The number of groups was set at 1 and number of measurements 2, because both sex and reproductive period were measured. G*Power 3.1 found that a sample size of at least 18 groups (each consisting of a male and a female pair) was necessary to reach significance. Therefore, the statistical analyses presented here will be used to observe trends in the data.

Table 1. Group composition and data collection during reproductive months.

Group	Number of Males (ID)	Number of Females (ID)	Data Collection	Birth Date of Infant	Number of Fecal Samples, males	Number of Fecal Samples, females
A (1)	1 (GG)	1 (TRI)	11/2003-05/2004	03/23/2004	17	22
A (2) ¹	1 (GG)	1 (TRI)	05/2004-12/2004	11/02/2004	27	28
C	1 (PY)	1 (FNC)	04/2004-10/2004	09/14/2004	34	31
1	1 (PO)	1 (RR)	04/2004-10/2004	09/07/2004	31	21
2	1 (BO)	1 (RADIO)	03/2004-10/2004	08/31/2004	37	38
3	1 (BR)	1 (FATTY)	03/2004-09/2004	08/25/2004	21	23
Totals:					167	163

¹The adult female in Group A had two infants during the study due to out-of-season breeding.

Results

As predicted, individual fecal cortisol levels changed throughout the reproductive season, in all groups (Figure 1). Males and females did not differ statistically in their mean fecal cortisol levels across reproductive periods ($F(2,10)=2.687$; $p>0.05$; Figure 2). Fecal cortisol levels increased throughout the reproductive season in both males and females (Figure 2). This rise showed the lowest levels around the mating period, higher levels around gestation, and the highest levels at and around the infant growth period (Figure 2).

During the 3 weeks encompassing the mating period (weeks -3 to -1), there was little fluctuation or increase in fecal cortisol levels, as predicted (Figures 1 and 2). There was a spike in fecal cortisol levels around mid-gestation (week 9), and fecal cortisol levels continued to rise and fall throughout gestation in both males and females, with a final peak around infant birth (week 18) (Figure 1). Throughout gestation, male fecal cortisol levels elevated 2SD above the

mean 1 week after the female's fecal cortisol levels (Figure 1 and Table 2). However, mean fecal cortisol levels differed between males and females the most during the gestation period.

Finally, fecal cortisol levels were highest in both males and females during the infant growth period (Figures 1 and 2). Male and female mean fecal cortisol levels differed the least at this time, compared with the other periods analyzed, as predicted (Figure 2). Out of the three reproductive periods, the infant growth period (which included birth and lactation) had the highest mean fecal cortisol levels for males and females.

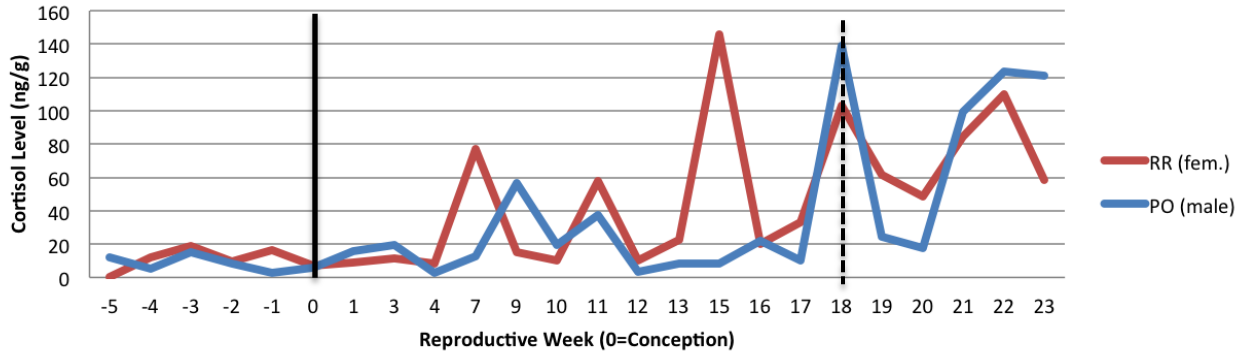


Figure 1. Representative male and female fecal cortisol levels during reproductive weeks -5 to 23. The vertical line indicates week 0 (conception); the dashed black line indicates week 18 (infant birth)

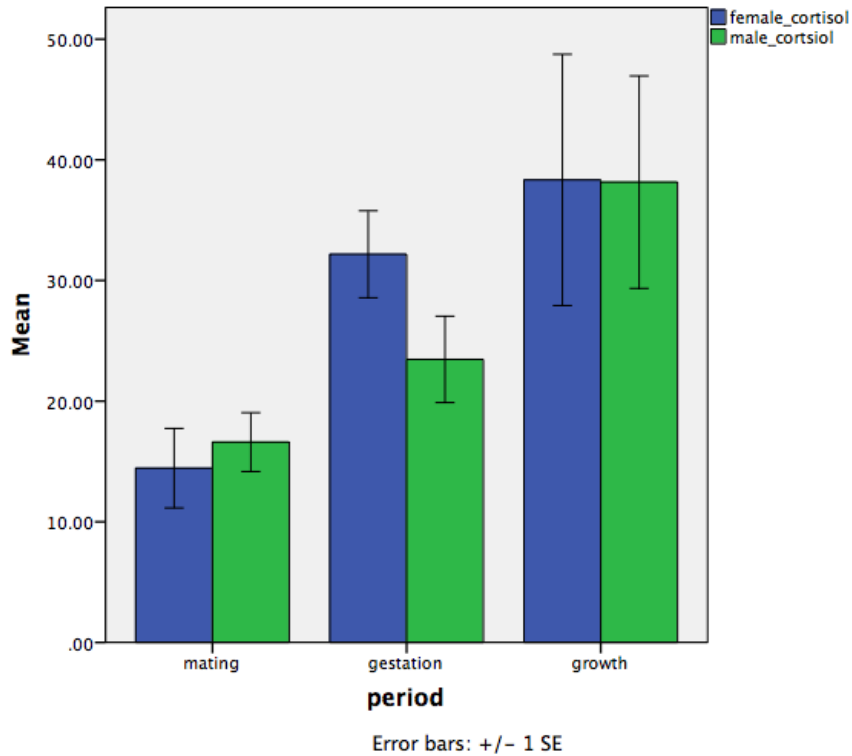


Figure 2. Mean fecal cortisol levels for males and females during the three reproductive periods (with standard error bars +/- 1)

Table 2. Weekly fecal cortisol increase in males and females (* marks weeks with an increase of 2 standard deviations or more from the mean of the previous weeks)

Reproductive Week							
Mean Fecal Cortisol	4	5	6	7	8	9	10
Female	17.96	50.17*	19.94	30.74*	15.90	48.56*	25.05
Male	8.58	18.73	23.58*	16.64	48.05*	31.02	26.16

Discussion:

Our study showed that male red-bellied lemurs have an overall increase in fecal cortisol levels throughout reproduction. We compared fecal cortisol levels of males and females and

found that male and female fecal cortisol levels did not differ substantially during the mating, gestation, or infant birth periods. Fecal cortisol levels in both sexes increased from the mating period through the infant development period. As predicted, hormone levels remained low during the mating period, and high during the infant care period. This overall increase in fecal cortisol over reproduction, and patterns of fecal cortisol elevation during gestation, indicate that males undergo hormonal changes despite not being pregnant. This pattern contrasts with the red-fronted brown lemur, wherein fecal cortisol levels were elevated in males during the mating and birth periods, but low during gestation and infant development (Ostner et al. 2008). Together, results from these two studies are consistent with the Challenge Hypothesis (Wingfield et al. 1990).

Fecal cortisol levels were lowest during the mating season compared to any other reproductive period in both males and females. Low fecal cortisol levels during the mating season are most likely because red-bellied lemurs have low levels of male-male aggression in general, including during the mating season (Merenlender 1993; Cavegelli 1999; Bercovitch and Ziegler 2002; Overdorff and Tecot 2006; Setchell et al. 2008; Tecot 2008). Since red-bellied lemurs are pair-bonded and monogamous (Tecot et al. 2015), there is hypothetically little to no need for males to compete with one another for females (Overdorff and Tecot 2006; Tecot 2008). In male red-fronted brown lemurs, male-male aggression is high during the mating season (Ostner et al. 2008). These high levels of aggression can help explain elevated fecal cortisol levels during that period (Cavegelli 1999; Bercovitch and Ziegler 2002; Ostner et al. 2008; Setchell et al. 2008). Red-bellied lemur males and females can remain in pairs for several years (Tecot et al. 2015). Since red-bellied lemur males do not have to find and compete for a mate

every year, they show no signs of aggression (Tecot 2008), and have reduced fecal cortisol levels during the mating season, as predicted.

Throughout gestation, mean fecal cortisol levels were higher than during the mating period in both males and females. As expected, females had an increase in fecal cortisol levels during gestation with peaks around mid-gestation (weeks 8-9) and just before birth (week 17). These peaks in female fecal cortisol levels are likely due to pregnancy (Ziegler et al. 2004), but the increase in fecal cortisol in males during gestation is not yet fully understood. In primate species with paternal care, male fecal cortisol levels tend to fluctuate with the female's gestational fecal cortisol levels, with about a one-week delay (Table 2) (Humans: Berg and Wynne-Edwards 2002; tamarins: Ziegler et al. 2004; Humans: Wynne-Edwards and Timonin 2007). Similar changes in fecal cortisol levels were observed in red-bellied lemur males (Figure 1). Paternal behavior in red-bellied lemurs varies; some males provide care and some do not (Tecot et al. 2012, 2013). Future research should compare these males to determine whether fecal cortisol fluctuations during a mate's pregnancy are associated with individual paternal behavior. At least one closely related species that does not provide paternal care, such as the red-fronted brown lemur, does not have elevated fecal cortisol levels during gestation (Ostner et al. 2008).

The highest mean fecal cortisol levels in males and females were during the infant growth period. Male and female fecal cortisol levels were also the most similar during this time. Although our prediction was supported, it was surprising how similar fecal cortisol levels were in the males and females. Fecal cortisol levels might be similar because the infant growth period in this study included infant birth and infant care. Elevated fecal cortisol levels in mothers may result from the energy expended on birth, lactation, and infant care (Strier et al. 2003; Ziegler et

al. 2004; Carnegie et al. 2011). Similarly, caring for the infant might have increased the energetic contribution of the father, which may be reflected in elevated fecal cortisol levels. This trend was not seen in red-fronted brown lemurs (Ostner et al. 2008). In this species, males did have high fecal cortisol levels at birth, but levels quickly dropped during the female's lactation period and remained low (Ostner et al. 2008). Other differences between these species may be responsible for these different results. For example, variable environmental stressors such as food availability or amount of rainfall could yield different results for these two species. However, other species with paternal care also have elevated fecal cortisol levels during infant growth (Campbell's dwarf hamster (*Phodopus campbelli*), Reburn and Wynne-Edwards 1999; black tufted-ear marmosets (*Callithrix kuhlii*), Nunes et al. 2001; humans, Gettler et al. 2011). Furthermore, species lacking paternal care do not have elevated fecal cortisol levels during infant growth (Verreaux's sifaka, Fichtel et al. 2007; red-fronted brown lemur, Ostner et al. 2008). I am not aware of any studies showing species without paternal care with elevated fecal cortisol levels after infant birth. Elevated fecal cortisol levels after/during infant development in a species that does not provide paternal care may be related to infanticide, nurturing, resource scarcity, or the novelty of an infant (Tecot 2008, Brockman et al. 2009, Tecot 2013).

Although the data provided on red-bellied lemurs suggests support for the Challenge Hypothesis, further study is required. While much research has focused on testing the Challenge Hypothesis in primate species with high levels of male mate competition (Strier et al. 1999; Lynch et al. 2002; Fichtel et al. 2007; Behie et al. 2010), few primate studies have focused on species with low or no competition between males for mates (Strier et al. 2003). Of those, only red-bellied lemurs are monogamous and pair-bonded, and have paternal care. A variety of

primate species with different mating and infant care systems must be studied in order to understand how the Challenge Hypothesis applies to primate species.

More data on red-bellied lemurs should be collected to increase the sample size of this study and allow for better statistical analysis and interpretation. For example, gestational fecal cortisol levels were similar in males and females and males appeared to respond to hormonal changes in females. However, male and female fecal cortisol levels were less similar during this period compared with other periods, and would likely differ significantly with sufficient power to detect a difference. This study did not have enough power to find any statistically significant differences between male and female fecal cortisol levels during the reproductive season, though fecal cortisol profiles from mating through infant development appeared to have consistent trends. A study incorporating data from at least 18 study groups would allow us to determine if the sexes significantly differed from one another, and if male fecal cortisol levels significantly changed across seasons. Nevertheless, increasing the sample size can be very difficult. Red-bellied lemurs only live in Madagascar and are difficult to find and observe due to small group sizes and an arboreal lifestyle. Furthermore, intensive and frequent study of each group is required in order to construct hormonal profiles, making it difficult to study more groups.

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