



It's All in the Timing: Birth Seasonality and Infant Survival in *Eulemur rubriventer*

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Abstract Highly seasonal breeding has been considered one of the keys to understanding Malagasy primate socioecology. Strict seasonal breeding may be particularly critical for Malagasy primates because they live in such energetically challenging seasonal environments. Lemurs also live in highly unpredictable environments, and there is growing evidence that reproductive timing may be mediated by additional factors, suggesting that more relaxed breeding seasonality is adaptive in some cases. I tested the adaptive breadth of the birth peak in *Eulemur rubriventer*, which breed in several different months. I describe reproduction in the species by determining the timing and extent of the birth season (period in which all births occur) and birth peak (period in which the majority of births occur); test whether relaxed reproductive seasonality might increase reproductive success by comparing infant mortality within and outside the birth peak; and model the extent to which fruit availability has an influence on the timing of reproduction. I collected birth data on 5 groups in 2003–2005, which I combined with demographic data that

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D. Overdorff collected from 5 focal groups and additional censused groups between 1988 and 1996. Thirty births occurred in 8 different months. Births were significantly seasonal, with a unimodal birth peak in late August/September/October, and a mean birth date of October 11. Twenty-three births (76.7%) occurred within 54 d (14.79%) of the year. No births occurred May–July, indicating that conceptions did not occur from late December through late February, and cycling (estimated using gestation length) did not occur until *ca.* 101 d after the austral summer solstice (December 21). Of 22 infants followed regularly, 18 were born in the birth peak, of which 2 died (11%). All 4 infants born out of season died. Based on fruit availability, I calculated a Theoretical Overlap index (T), which indicated a 3-mo window with optimal food conditions for reproduction. This window corresponded to the timing and breadth of the birth peak in *Eulemur rubriventer*. These results indicate that a breeding season >3 mo within a given year is not adaptive in the species, likely due in large part to the availability of fruit during key reproductive stages, particularly before breeding.

Keywords *Eulemur rubriventer* · infant mortality · relaxed breeding · reproductive strategies · seasonal reproduction

Introduction

Timing reproductive events with dynamic ecological processes such as temperature, rainfall, and food production is widespread among mammals (Bronson and Heideman, 1994). Reproductive seasonality occurs when an environment is predictably seasonal from year to year, and when individuals can maximize fitness by timing a critical reproductive stage with optimal conditions (Negus and Berger, 1972). Some species living in highly seasonal and predictable environments do not need to maintain high energy levels to conceive (income breeders: Brockman and van Schaik, 2005; Drent and Daan, 1980); mating is signaled by cues such as photoperiod (Sadlier, 1972) that can reliably indicate when seasonal changes in food availability or climate will occur, and breeding synchrony may result from maximizing food quality and availability during times of high energetic need, such as peak lactation and weaning (Altmann, 1980; Clutton-Brock *et al.*, 1989; Jolly, 1984; Lee, 1996; van Schaik and van Noordwijk, 1985). However, in less predictable environments, where species may not be able to anticipate when or where food might be abundant, greater variation in when species breed may be expected, the extent of which can depend upon the female's energetic condition (Lichtenbelt, 1993). These species (capital breeders: Brockman and van Schaik, 2005; Drent and Daan, 1980) can take advantage of food abundant periods by storing nutrients and only breeding once they reach high enough stores for successful reproduction. Energetic stress can suppress reproduction to conserve reproductive effort when the environment is unfavorable (Wasser, 1996), and conversely energetic surplus may support reproduction outside of the typical mating season (Brockman and van Schaik, 2005), such as in female Hanuman langurs (*Presbytis entellus*) that breed year-round where food is provisioned and readily accessible (Harley, 1988). Only those in good condition conceive where food availability is seasonal (Koenig *et al.*, 1997).

Most mammalian species fall somewhere in the middle of this "income" vs. "capital" breeding dichotomy (Negus and Berger, 1972), whereby they respond to endogenous and exogenous cues, resulting in conception windows intermediate in duration between those in strict income and capital breeders (Brockman and van Schaik, 2005). Recent research has shown that primates are no exception. For instance, though *Propithecus verreauxi* are highly seasonal breeders and respond to photoperiodic change (Brockman and van Schaik, 2005), they also seasonally gain weight and mate during high and declining food availability. Further, higher mating season body masses increase the likelihood that a female will successfully bear and raise offspring (Lewis and Kappeler, 2005). Species that respond to both endogenous and exogenous cues for mating have been termed Relaxed Income breeders (Brockman and van Schaik, 2005).

Breeding in Energetically Poor Environments

Highly seasonal breeding may be particularly critical for Malagasy primates because they live in energetically challenging seasonal environments with longer periods of fruit scarcity (Wright, 1999; Wright *et al.*, 2005), poorer soils, slower tree growth, and smaller tree crowns (Balko and Underwood, 2005; Ganzhorn *et al.* 1999a, b; Hemingway, 1995; Morland, 1991; Overdorff, 1993a, b, 1996a, b). Fruit availability may coincide with that of flowers and leaves, leaving little compensation for fruit scarcity during the long lean season (Bollen and Donati, 2005).

Though seasonal breeding occurs in other primates (DiBitetti and Janson, 2000), Janson and Verdolin (2005) conducted a meta-analysis of primate species reproduction and reported significantly greater seasonal breeding in lemurs. Lemurs have 1 birth season per year in which they are mono-estrous and occasionally polyestrous (maximum 3 cycles per season), and have short individual estrus periods (12–48 h in most lemurs) compared with haplorrhines (Bogart *et al.*, 1977; Brockman and van Schaik, 2005; Brockman *et al.*, 1995; Curtis *et al.*, 2000; Evans and Goy, 1968; Jolly, 1966; Kappeler, 1987; Petter-Rousseaux, 1980; Pochron *et al.*, 2004). Lemurs are particularly tightly entrained to photoperiodic cues, wherein changes in day length regulate mating (Pereira, 1993; Rasmussen, 1985; van Horn, 1975), either inhibiting or signaling reproduction, even in the absence of changes in temperature or diet. Though minor compared with nontropical regions, changes in day length can cue reproductive preparation in lemurs, *e.g.*, testis size increase, vaginal opening, or behavioral change, which lasts 2–3 mo and culminates in female cycling (Rasmussen, 1985; van Horn, 1975, 1980). In captive ring-tailed lemurs (*Lemur catta*), long days initiated this quiescent period, which continued as day length decreased and lasted *ca.* 105 d (van Horn, 1975). Breeding is highly synchronized within lemur species, resulting in a narrow birth season ("discrete period...to which all births are confined", Lancaster and Lee, 1965, p. 488) of *ca.* 2 wk (Jolly, 1967; Pereira, 1991; Rasmussen, 1985; Sauther, 1998), and a birth peak ("the period...in which a high proportion of births but not all births are concentrated", Lancaster and Lee, 1965, p.488) that approximates the birth season.

Though varying degrees of ecological seasonality are present throughout Madagascar (Dewar and Richard, 2007), island-wide interspecific synchronized weaning in larger-bodied lemurs suggests that seasonal breeding may result from

selection for food abundance during mid- to late lactation and weaning, when energetic demands on mothers and infants are highest (Jolly, 1984; Wright, 1999). In seasonally dry forests in western Madagascar, ring-tailed lemurs (Beza Mahafaly Special Reserve, Sauther, 1993) and Verreaux's sifaka (*Propithecus verreauxi verreauxi*, Kirindy forest, Lewis and Kappeler, 2005) weaned infants during food abundance, between December and March. Similarly, in Ranomafana National Park, an eastern tropical rain forest with less seasonality in climate, but with highly seasonal phenology (Wright *et al.*, 2005), ≥9 species weaned infants during food abundance between December and March (weaning time in the 3 remaining identified species in Ranomafana National Park remains unknown, Wright, 1999), regardless of differences in reproductive schedules, *e.g.*, conception and birth dates, gestation lengths. Higher infant mortality during lactation in dry years when food is less abundant demonstrates the importance of such timing (*Lemur catta*: Gould *et al.*, 1999; aged *Propithecus edwardsi*: King *et al.*, 2005). By extension, if births occur outside of the typical birth peak, late lactation/weaning may be more likely to coincide with food scarcity, unless a shifting birth period occurs in tandem with shifting food availability, resulting in higher infant mortality.

Breeding in Energetically Unpredictable Environments

Though it has been widely suggested that Madagascar's highly seasonal environment selected for highly seasonal breeding (Jolly, 1984; Young *et al.*, 1990), irregular phenological cycles call into question how much of a driving force ecological seasonality is for lemur breeding (Overdorff, 1991). For instance, in Madagascar the timing and amount of rainfall is highly variable interannually (Dewar and Richard, 2007), yielding irregular and asynchronous phenological cycles with long periodicity, particularly in the eastern rain forests (Bollen and Donati, 2005; Wright, 1999; Wright *et al.*, 2005). Unreliable periods of potential energetic intake and storage may present seasonally breeding fauna in these habitats with a strikingly challenging environment within which to find food, reproduce, and survive. Lemurs living in habitats where the period of peak food availability varies year to year may be under particularly high selective pressure on the timing of lactation and weaning. Infant mortality was higher in red-fronted lemurs (*Eulemur fulvus rufus*) when resource availability peaked during late gestation and early lactation rather than later, during mid-lactation and weaning (Overdorff *et al.*, 1999). These results imply a risk of high infant mortality with slight interannual changes in the timing of plant phenophase. However, seasonal breeding can be more relaxed in lemurs. Several researchers have reported birth peaks as long as 3 mo (Budnitz and Dainis, 1975; Jolly *et al.*, 2002), and supra-annual aseasonal breeding where births occur in several different months from year to year (Brockman and van Schaik, 2005; Mutschler, 1999; Whitten and Brockman, 2001). In seasonal yet interannually unpredictable environments, some relaxation of breeding seasonality may confer an advantage.

The argument for an ecological influence on island-wide seasonal breeding in lemurs living in variable climates would be bolstered by more data on the relationships between breeding seasonality, phenological cycling, and diet (Richard and Dewar, 1991). Specifically, “(t)he case for breeding seasonality being

ecologically determined would be greatly strengthened... if it could be shown that survival is lower among infants born early or late in the birth season" (Richard and Dewar, 1991, p. 166). Because relaxed seasonal breeding is a rare occurrence in lemurs, the impact of such timing on lemur infant survival, or the adaptive breadth of the birth season, remains unexplored.

Red-bellied lemurs (*Eulemur rubriventer*) are a good model to examine the selective pressures acting on seasonal breeding because they have a seasonal diet, composed largely of ripe fruit, and appear to be seasonal breeders with occasional relaxed seasonality in the timing of births (Durham, 2002; Overdorff, 1996a, b; Overdorff and Tecot, 2006; Tecot, 2008), but with perhaps the least flexible social system. They are monogamous (Merenlender, 1993) and live in small family groups consisting of 1 pair-bonded adult female and male and their offspring. One female breeds per group, although offspring may be of reproductive age (Merenlender, 1993; Duke Lemur Center records), and adults weigh *ca.* 1.55–2.21 kg (Glander *et al.*, 1992; Terranova and Coffman, 1997; Tecot *unpub. data*). Though no detailed analysis of reproductive timing in wild *Eulemur rubriventer* has occurred, it has been reported that this species typically enters estrus in May/June, with a gestation length of *ca.* 126 d (Duke Lemur Center records) that coincides with the austral winter, and gives birth in September/October (Overdorff, 1991; Overdorff and Tecot, 2006; Tecot, 2008). Age at weaning is estimated at 110–135 d (Overdorff, 1996b *unpub. data*). Observations since 2000 indicate that *Eulemur rubriventer* in Ranomafana National Park have a 2-yr interbirth interval (Tecot *pers. obs.*; cf. Overdorff, 1991), with occasional twinning (1 pair in 5.6 births; Tecot and Overdorff, 2005). Infant mortality has been estimated to reach 50% (Overdorff, 1991).

My overall aim is to describe reproduction in *Eulemur rubriventer*, investigate seasonality of reproduction, and test the optimality of the birth season. I then attempt to model the extent to which food production has an influence on the timing of reproduction and survival of infants in this species. If *Eulemur rubriventer* respond to exogenous cues, then I predict that they will breed seasonally, with a distribution of births that differs significantly from a uniform distribution (Janson and Verdolin, 2005), a narrow birth peak occurring in September and October of each year (Overdorff, 1991), and a 105-d period of reproductive inactivity following the longest day, austral summer solstice (van Horn, 1975, 1980), and resulting in no births in May, June, or July. If *Eulemur rubriventer* respond to endogenous cues, births will regularly occur outside of the birth peak, as observed previously (Durham, 2002; Tecot *pers. obs.*). If relaxed breeding seasonality is an adaptive strategy enabling *Eulemur rubriventer* to respond adaptively to a stochastic environment (Durham, 2002), then the timing of births from year to year will not influence infant survival, and infants born outside the birth peak will be as likely to survive as those born within the birth peak. However, if births outside of the birth peak are disadvantageous, because critical time periods for reproduction or infant development are not met with food abundance, then infants born outside the birth peak will be less likely to survive than those born within the birth peak. Finally, if the availability of food influences the timing of reproduction and the survival of infants, then I predict that reproduction occurs most often when there is maximal overlap between fruit abundance and all reproductive stages combined.

Methods

Sites

I collected data in Ranomafana National Park (RNP), which consists of 43,500 ha of evergreen rain forest in southeast Madagascar ($21^{\circ}02' - 21^{\circ}25'S$ and $47^{\circ}18' - 47^{\circ}37'E$; Wright, 1997). RNP is 600–1513 m in elevation, and is highly seasonal with distinct wet and cool/dry seasons (Jury, 2003), and an average of 3090 mm of rain per year (Overdorff, 1996b; Tecot, 2008; Wright *et al.*, 2008). RNP has large seasonal peaks and prolonged troughs in food availability, particularly fruit (Hemingway, 1995; Overdorff, 1993a, 1996a, b; Overdorff and Strait, 1998; Tecot, 2008; Wright *et al.*, 2005), the main resource exploited by *Eulemur rubriventer* (Durham, 2003; Overdorff, 1993a,b; Tecot, 2008). Across years, annual rainfall totals (range 1500 mm–4000 mm per year), phenological patterns, and the lengths of wet and dry seasons vary to a great extent (Wright *et al.*, 2005). The predictability of fruits, flowers, and new leaves can vary dramatically as they are linked with rainfall in some years (Grassi, 2001; Hemingway, 1996), but not consistently (Hemingway, 1998; Overdorff and Wright *unpub. manuscript*), nor in all sites (Tecot, 2008). Study groups were located in 2 adjacent rain forest sites within RNP: Vatoharanana (primary forest) and Talatakely (selectively logged forest). Talatakely has a less continuous tree canopy, lower tree species diversity and density, and trees smaller in diameter at breast height, height, and crown volume compared with Vatoharanana (Tecot, 2008).

Subjects

D. Overdorff studied 5 habituated *Eulemur rubriventer* groups ($n=12$ individuals) between 1988 and 1990 in Vatoharanana. She conducted censuses on the entire Vatoharanana population ($n=12$ groups) regularly through 1996 (Overdorff, 1991, *pers. comm.*). In addition, my research assistants and I studied 5 red-bellied lemur groups for 19 mo between 2003 and 2005 in Vatoharanana (2 groups) and Talatakely (3 groups). Each group contained 2–5 individuals, consisting of 1 adult breeding pair and their offspring (Overdorff and Tecot, 2006). At least 1 adult in each habituated group in both studies wore a colored collar for identification of the group. We distinguished individuals within the group by individual markings, body sizes, and sexual dichromatism.

Data Collection

Overdorff followed each of her focal groups for 4 continuous days twice per month on average, and I followed each of my focal groups 1–3 d/wk. We recorded all occurrences of births and disappearances/deaths in our focal groups (Altmann, 1974).

During monthly censuses, Overdorff recorded the number, age, and sex of individuals using methods in Johnson and Overdorff (1999) for *Eulemur fulvus rufus*. Because *Eulemur rubriventer* lives in small family groups, Overdorff was able to identify mothers and infants from week to week, and to determine the approximate age and date of disappearance/death of infants.

Groups were sometimes not observed more than once per month, resulting in a large number of birthdates that were not known precisely, which introduced 2 potential issues: 1) measures of central tendency (mean, median, mode) are similar; and 2) more births than were recorded may have occurred if they resulted in very early death. The fact that *Eulemur rubriventer* live in small family groups with 1 breeding female and Overdorff recorded births in each group during the years in question, with the exception of 1 group (group I) in 1989, indicates that she likely observed all births in each group each year, partially resolving issue 2. However, the loss of infants before observed births cannot be ruled out.

To determine abundant and scarce fruit seasons, I analyzed the monthly presence of fruit observed on all trees present in 3 botanical plots (100 m × 10 m, 5 m × 50 m, 10 m × 25 m) randomly distributed in home ranges of *Eulemur rubriventer* in Vatoharanana, between January and December, 2004. These plots contained 422 plants from 76 species and 33 families exploited by *Eulemur rubriventer* (Tecot, 2008).

Data Analysis

I used circular statistics to assess the seasonality of reproduction (Batschelet, 1981). I transformed birth dates to a number out of a 365-d year with January 1 as d 1 for analysis. When births were not known to the exact date, I used the mean day within the range of potential birth dates as an estimate of birth date. I then used month as the unit of analysis, where the day number assigned to each birth in a month was equal to the median of birth dates for the month in which it occurred. Days corresponded to points on a circle with a radius of 1, and d 1 equal to 0°. Unlike linear statistics, this method corrects for the influence of the position of the starting date, e.g., December 31 (d 365) and January 1 (d 1) are as similar to each other as June 30 (d 181) and July 1 (d 182). I calculated the vector length r as a measure of dispersion and corrected for small sample size using Batschelet's correction (Batschelet, 1981). r is equal to the sum of the x - and y -axis components of each vector for each birth date. I used the mean vector length (the angle of the sum of vectors of the birth date data points) as a measure of the birth season, ranging from 0 (uniform) to 1 (clumped), and used the Rayleigh test (z) to determine whether the data departed from a random distribution (Batschelet, 1981). I analyzed the birth peak by month, and defined it as the period of consecutive months in which the majority of births (>51%) occurred (Lancaster and Lee, 1965). If the removal of any consecutive month did not reduce the percentage of births in the peak to <51%, it was not considered part of the birth peak. I also qualitatively assessed the timing of births by day within each year, because monthly analyses ignore the proximity of days in consecutive months.

To determine the number of days of reproductive inactivity in relation to the longest day of the year, I estimated conception dates by subtracting 126 d (gestation length) from birthdates, and I calculated the latency period between the austral summer solstice and mean estimated peak conception dates and subtracted 1 cycle length. In Madagascar, the austral summer solstice (longest day) in 2004 occurred on December 21. I used estimated conception dates from 2004 because birth dates in that year were the most precise (no births occurred in 2003 or 2005), and a cycle length of 30.5 d: the mean of that reported for *Eulemur mongoz*, 31 d (Perry *et al.*, 1992) and *E. fulvus*, 30 d (Boskoff, 1978).

I calculated the proportion of all births observed each month, and used the proportion of births inside and outside the birth peak to determine the frequency with which out-of-peak breeding occurred. Because we did not know the fates of all 30 infants born during this study (total infants), I used a subset of 22 infants (followed infants) to investigate infant mortality. Because of the small sample sizes, I used Fisher's exact probability test to determine whether infant mortality significantly differed across birth peak and nonbirth peak periods, and the relative impact of out-of-peak season breeding on survivorship.

I determined periods of fruit scarcity and abundance using the proportion of exploited trees bearing fruit each month. The mean monthly percentage of trees with fruit present was 5.7% (range 1.02–14.62%). Thus, the abundant period was when fruit was present on $\geq 5.7\%$ of trees and the scarce period was when fruit was present on $\leq 3.01\%$ of trees. January–June were abundant; July–December were scarce.

To model the relationship between reproduction and resource availability, I calculated a Theoretical Overlap index (T). T is equal to the percentage of fruit-abundant months contained within each stage of 1 reproductive year, totaled throughout 1 yr of reproductive cycling, such that:

$$T = \sum_{i=1}^4 (n_i/N_i)/4$$

where n =the number of months in which fruit was abundant in each i th stage, and N =the total number of months in each i th stage. T yields a number between 0 and 4, which is divided by 4 and expresses the proportion of the highest maximum possible. Stages are 1) prebreeding (2 mo); 2) gestation (4 mo); 3) lactation (4 mo); and 4) infant independence (2 mo). I calculated T 12 times by serially shifting the start month of stage 1 by 1 mo. Significance for all tests was set at $p < 0.05$.

Results

Thirty births occurred in 8 different months (Fig. 1), and births were not evenly distributed throughout the year. The corrected r for *Eulemur rubriventer* was 0.87 ($p < 0.001$), indicating a significantly seasonal distribution. Twenty-one births (70%) were concentrated in September ($n_{\text{births}}=8$) and October ($n_{\text{births}}=13$) (Supplement Table I) and the mean birth date was d 284 (October 11).

Depicting birth dates by year (Fig. 2), births largely clustered between d 250 and 300 (September 6–October 20) on a 365-d scale (January 1=d 1). Yearly results indicate that when researchers observed groups more frequently, births clustered more tightly, and suggest that in other years the spread of births within the birth peak may be overestimated and births may have begun slightly earlier. For instance, both August births occurred in the last week of the month in 2004, when 1 birth occurred each week beginning August 25 and ending September 14 (1 birth occurred November 2004). Thus, the data clearly indicate a single birth peak spanning late August through October (d 238–292), and 76.7% of all births occurred on 14.8% of days of the year.

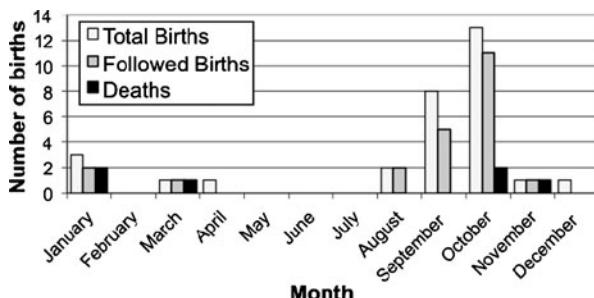


Fig. 1 Total number of births each month observed during censuses and group studies, 1988–1996 and 2003–2005 (total infants, white bars, $n=30$). The number of births observed each month from focal groups in which the fates of infants are known (followed infants, gray bars, $n=22$), and the number of followed infants born in each month that died within 12 mo (black bars).

Seven births (23%) occurred outside the birth peak (Supplement Table I). Births occurred in all months except February and May–July; thus conceptions occurred in all months except October and January through March. Mean latency between the austral summer solstice and estimated birth peak conceptions was $132 \text{ d} \pm 8.66$ ($n=4$). The mean latency period between the austral summer solstice and estimated cycling was $101 \text{ d} \pm 9$ ($n=4$) (Table I).

Infant mortality significantly differed according to whether infants were born within the birth peak (August/September/October) or not (2-tailed Fisher's exact probability test $p=0.002$). 100% of followed infants born outside the birth peak ($n_{\text{infants}}=4$) died within 3 mo (Supplement Table I). In contrast, 11% of followed infants born within the birth peak ($n_{\text{infants}}=18$) died within their first year (Fig. 1), only 1 of which (5%) died within 3 mo (from injuries sustained on a fall).

Monthly theoretical overlap indices (T) indicated that fruit abundance is maximized throughout reproduction when the prebreeding stage is initiated in

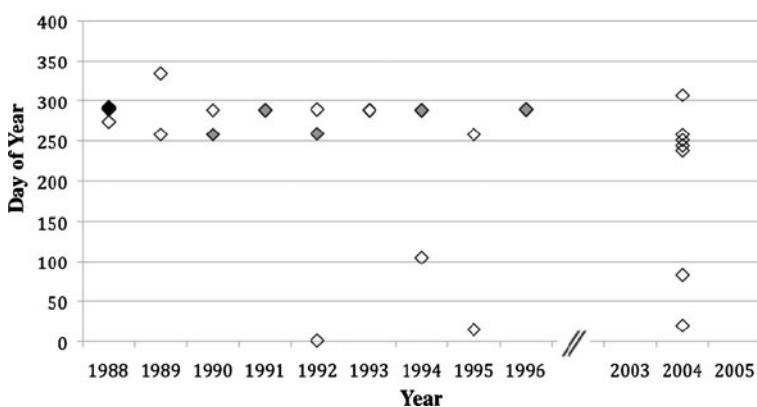


Fig. 2 Annual spread of total infant births ($n=30$) throughout a 365-d year, beginning 1988 and ending 2005. January 1 is d 1 for graphical representation. The line break on the x -axis indicates a break in data collection (1997–2002 inclusive); no births occurred in focal groups in 2003 and 2005. Black solid diamonds indicate overlap of 3 births; gray diamonds indicate overlap of 2 births; open diamonds indicate a single birth.

Table 1 Latency period between the summer solstice (signaling the start of declining day length) and resumption of cycling

Birth date ^a	Estimated conception date ^b	Latency to conception (in days) ^c	Latency to cycling (in days) ^c
August 25, 2004	April 21, 2004	122	91.5
August 31, 2004	April 27, 2004	128	97.5
September 7, 2004	May 4, 2004	135	104.5
September 14, 2004	May 11, 2004	142	111.5
	Mean	132±8.66	101±9

Four in-season births recorded in 2004 are used to demonstrate the latency period between the summer solstice (signaling the start of declining day length) and resumption of cycling. No births have ever been recorded between May through July (estimated mating late December–late February)

^a All births considered in season in 2004

^b Conception date estimated by subtracting 126 d from birth date, based on Duke Lemur Center records

^c Based on summer solstice on December 21, 2004

March, April, or May, giving the lemurs a 3-mo window in which to breed with maximal overlap with fruit within each stage combined (Fig. 3). When prebreeding occurs in March and April, births occur in September and October, respectively. Therefore, *Eulemur rubriventer* adopt the most optimal strategy when breeding in peak season, by timing both prebreeding and infant independence stages to coincide with fruit abundance (Supplement Table II, Fig. 4). If breeding occurs out of peak season, other stages may be met with a high proportion of fruit abundance, but relative overlap with fruit abundance during prebreeding and/or infant independence stages is low or nonexistent, and the whole of reproduction is not maximized.

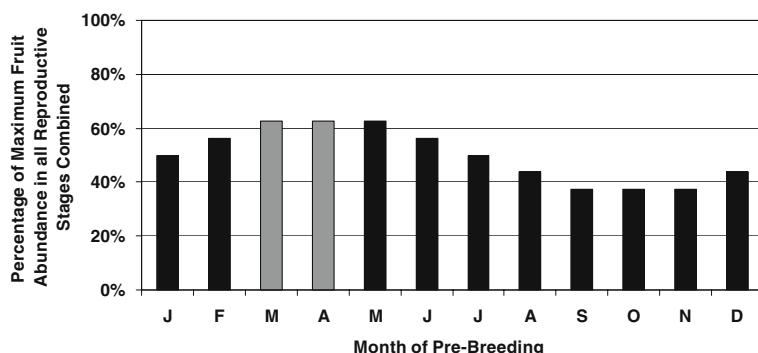


Fig. 3 Moving theoretical overlap of fruit abundance throughout a 12-mo reproductive cycle. Bars represent the percentage of fruit abundant months out of the total number of months in each reproductive stage, combined across all stages. Each month on the x-axis represents the theoretical starting point, or the first month of prebreeding. In order, stages are prebreeding (2 mo), gestation (4 mo), lactation (4 mo), and infant independence (2 mo). Gray bars represent modal prebreeding period of the focal groups.

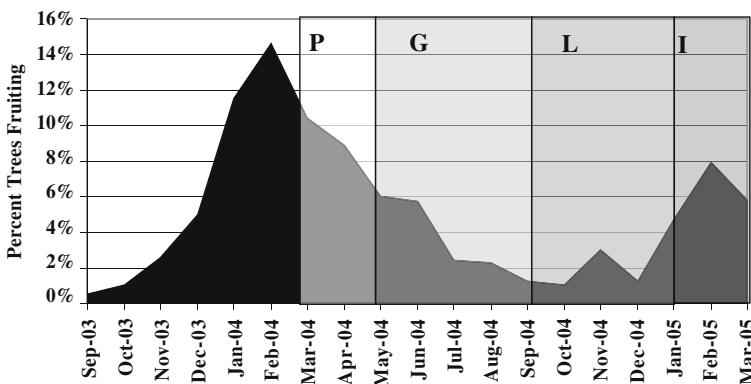


Fig. 4 Timing of seasonal births in relation to fruit availability. I collected all data between September, 2003 and March, 2005. Fruit availability is based on the presence of exploited plant species in botanical plots in Vatoharanana. Reproductive stages are based on the timing of seasonal births in *Eulemur rubriventer*. P=prebreeding; G=gestation; L=lactation; I=infant independence. I used phenological data collected between January, 2004 and December, 2005 to calculate T.

Discussion

Seasonal Breeding in Lemurs

In this study, reproduction in *Eulemur rubriventer* indicated that they respond to exogenous cues, as predicted. They bred seasonally ($r=0.87$), though births were distributed less seasonally than that reported previously ($r=0.92$, Janson and Verdolin, 2005), with a unimodal birth peak. The mean birth date (d 284, October 11) was also similar to that in previous reports (d 282, October 9, Janson and Verdolin, 2005). Births peaked in late August–October, as reported previously for this species in this park (Durham, 2002). Each birth during the birth peak occurred within 1 wk of the other births. Breeding corresponded to short days and reproductive inactivity corresponded to long and decreasing days (lack of conceptions January–March, inferred from lack of births in May–July), as in other lemurids such as *Lemur catta* (van Horn, 1975). Captive studies have shown that in *Microcebus murinus* increasing day length stimulates reproduction (Petter-Rousseaux, 1980), whereas in *Lemur catta* decreasing day length stimulates reproduction, increasing day length inhibits cycles, and cycling resumes 105 d after the onset of day length reduction (van Horn, 1975, 1980). After the austral summer solstice, estimated latency to activation of cycling in wild *Eulemur rubriventer* similarly spanned 101 d, providing indirect evidence of some entrainment to reliable exogenous cues, and in this respect they fit the lemurid pattern of strict seasonal breeding.

As suggested broadly for lemurs, the presence of a birth season in *Eulemur rubriventer* may be an adaptation to avoid seasonal nutritional stress when the demands of food scarcity and reproduction converge. Though the eastern rain forests are less seasonal than those in the west, food is scarce for up to 5 or 6 mo and may necessitate careful timing of reproduction (Overdorff *et al.*, 1999; Wright, 1999; Wright *et al.*, 2005). However, with such irregularity in the timing of rainfall and

food availability, additional mechanisms such as energy storage also may be necessary for successful reproduction (Pereira *et al.*, 1999; Tecot, 2008).

Extended Breeding in *Eulemur rubriventer*

Though *Eulemur rubriventer* bred seasonally, the temporal breadth of the breeding season indicates that they responded to additional endogenous cues. Though some lemur species in captivity continue to have narrow birth seasons (income breeders), others tend to have wide birth seasons compared with their wild counterparts (relaxed income breeders), suggesting that they are responding to endogenous, as well as exogenous, cues (Brockman and van Schaik, 2005). For instance, Boskoff (1978) found that individual captive female *Eulemur fulvus* had the potential to cycle throughout much of the year (mean 8.5 cycles/female), and Stanger and colleagues (1995) found that births in captive *Mirza coquerelii* were distributed throughout 9 mo. Both studies noted a 2–3 mo period of anestrus either just preceding the period when all individuals regularly cycled (*Eulemur fulvus*), or during a potential period of lactation (*Mirza coquerelii*), indicating some level of seasonality. Wild *Eulemur rubriventer* in this study are distinct from the majority of wild lemurs to date in that they regularly breed in several months, and they more closely resemble captive lemur species that have been classified as relaxed income breeders (Brockman and van Schaik, 2005), showing a period of anestrus, a clear birth peak, and a broad birth season. Though feeding, phenological, and hormonal data indicate that females store energy prebreeding (Tecot, 2008), researchers have not directly measured seasonal weight change in wild reproductive females (N.B.: Though a 5% seasonal weight loss was reported in *Eulemur rubriventer* [Glander *et al.*, 1992], this female did not reproduce and died the following year; Overdorff, *unpub. data*). Such data would help determine the influence of body condition on reproduction. The reproductive schedules observed in wild *Eulemur rubriventer* can fit a simple lemur model incorporating photoperiod stimulation (austral summer solstice), followed by a latency period of reproductive inactivity (minimum 92 d) leading to cycling, and mating, the timing of which may be modified by fetal loss or social and ecological environments.

Though lemurs usually conceive during their first estrus, once per year (Brockman and Whitten, 1996; Curtis *et al.*, 2000; Foerg, 1982; Perry *et al.*, 1992; Richard, 1974; Shideler *et al.*, 1983), a second estrus may occur *ca.* 39 d after failed conception (Koyama *et al.*, 2001; Pereira, 1991). Within each species, individual females typically give birth during the same month, within a range of 1–3 mo across years (Pereira, 1991; Whitten and Brockman, 2001). In Ranomafana National Park, *Propithecus edwardsi* give birth in June, and occasionally May and July; only two births occurred as late as September over the course of 23 yr (Morelli *et al.*, 2009). But the temporal breadth of reproduction exhibited by *Eulemur rubriventer* (births in 8 different months) cannot be explained by fertilization following intraseason failed conception or fetal loss.

Social factors can impact reproductive timing (Whitten and Brockman, 2001). *Hapalemur* reproductive output and timing differed depending upon group composition, size, or fluidity (Grassi, 2001; Mutschler *et al.*, 2000), and captive male *Lemur catta* stimulated photoinhibited female cycling (van Horn, 1975, 1980).

However, group dynamics in these *Eulemur rubriventer*, including social behavior, hierarchy, and group composition, were markedly stable (Overdorff and Tecot, 2006; Tecot, 2008). No social instability or novelty occurred in groups breeding out of peak season, with the exception of the emigration of a young adult male that occurred after an infant's birth and before its death. Further, two newly formed pairs in this study successfully conceived in season, a few months after formation (Tecot *unpub. data*).

Food availability and quality also may modify strictly timed breeding (Brockman and van Schaik, 2005; Janson and Verdolin, 2005; Negus and Berger, 1972). Relaxed breeding seasonality can indicate a particularly resource-rich year (Brockman and van Schaik, 2005; Daan and Tinbergen, 1997). Exogenously cued breeders can breed without maintaining high energy balance, but in unusually productive years with abundant available energy, i.e., food, they might be more flexible in when they breed. Captive lemurs that do not experience food scarcity show seasonal birth peaks as they do in the wild, but several of these species—strict seasonal breeders in the wild—also have wider birth seasons under the captive feeding regimen, e.g., *Propithecus coquereli* and *Lemur catta* (Brockman and van Schaik, 2005). Wild *Hapalemur griseus* in Ranomafana National Park also have broader birth seasons when food is more abundant (Grassi, 2001). However, there was no indication of increased food availability in years when out-of-peak births occurred in *Eulemur rubriventer*. In fact, in 2004 all such births occurred in the more disturbed, less fruit-abundant, less predictable site (Tecot, 2008).

Durham (2002) suggested that breeding out of peak season might be a response to cyclone-induced reductions in fruit availability. She observed 100% intraseason births in 1999 (August 21–September 14) and 2001 (September 11–October 24), years in which cyclones did not impact Ranomafana National Park; but in 2000 she observed only 2 births after a cyclone, and neither occurred during the typical birth peak (November 20, December 3). Similarly, 2004 was a cyclone year, and several infants were born out of peak season (this study). However, some births preceded the cyclone and cannot easily be explained by this event. Moreover, other out-of-peak births documented in this study did not coincide with cyclones.

The environment may vary not only in terms of the amount and quality of food available, but also in when it is available, and thus the optimal time for reproduction may differ year to year. Variation in the timing of births across years may be explained by differences in the timing of food availability, as external and internal states interact to promote or inhibit breeding. However, differences in the timing of reproduction were not consistent among all individuals living in the same habitat at the same time, as would be expected if all out of peak births resulted from temporal shifts in food availability from year to year, though individual differences in territory quality and body condition cannot be ruled out. Longer-term and more detailed data on nutritional intake or nutritional status of mothers that breed in and out of season, coupled with precise dates of conception or birth, would more directly test for a link between food and the timing of breeding.

Intriguingly, all lemur species for which births have been reported >4 mo apart in the wild range in eastern Madagascar and adopt a cathemeral or nocturnal activity pattern (Table II). Butynski (1988) suggested that the distribution of rainfall vs. total rainfall impacts the breadth of the guenon birth season, where guenons living in areas with 2 rainy seasons have wider birth seasons. Climate has been dismissed as a

Table II Characteristics of temporally reproductively relaxed lemur species

Species	Habitat	Main component of diet	Activity	Social structure	Group size	Birth season (other months births observed)	No. of offspring per birth ^a	References
<i>Daubentonia madagascariensis</i>	Eastern rain forest, western deciduous forest, scrub, plantations, mangroves	Seeds, larvae, fruit	Nocturnal	Solitary+female-male and male-male associations (dispersed multimale)	1+	? [February, June/July, 1 August/September (East); April (West)] ^b	1	Mittermeier <i>et al.</i> , 2006; Peter, 1977; Petter and Peyrières, 1970; Sterling, 1993, 1994
<i>Eulemur coronatus</i>	Northern dry and moist forests	Fruit	Cathemeral	Multimale and female	5–6 up to 15	September–October (January, May)	1–2	Arbelot-Tracqui 1983, as cited in Sterling, 1994; Freed, 1996; Mittermeier <i>et al.</i> , 2006
<i>Eulemur rubriventer</i>	Eastern rain forest	Fruit	Cathemeral	Family groups (gregarious monogamous)	2–5	September–October (January, March, April, August, November, December)	1–2	Durham, 2003; Marenzeller, 1993; Overdorff, 1991; Tecot, 2008; Tecot and Overdorff, 2005
<i>Hapalemur daonensis</i>	Marsches in eastern rain forest	Reeds, grass	Cathemeral	Family groups+ multimale and female	2–9	September–February (May)	1–2	Mutschler, 1999; Mutschler <i>et al.</i> , 2000
<i>Hapalemur griseus</i>	Eastern rain forest	Bamboo, leaves, fruit	Cathemeral	Family groups+ multimale and female	3–11	November–February (April)	1	Grassi, 2001; Tan unpubl. data
<i>Microcebus murinus</i>	Northwestern and western dry deciduous and southeastern littoral rain forest	Insects, fruit, gums	Nocturnal	Solitary (dispersed, female sleeping associations)	1 up to 15 in sleeping hole	November/ December, January/February (April–May)	1–3	Eberle and Kappeler, 2004; Lahann <i>et al.</i> , 2006; Radetspiel, 2000; Schmelting <i>et al.</i> , 2000

Data for species in which births >4 mo apart have been reported in the wild

^aThe number 2 indicates regular twinning in the wild^bBased on captured infants' estimated growth from captive growth curves and average gestation length (Sterling, 1994)

single factor selecting for seasonal breeding in lemurs due to the combination of island-wide strict seasonality and variable climates. However, if some species are more flexible than others or predisposed to year-round breeding, this hypothesis might be better tested by comparing *Eulemur* or *Hapalemur* spp. living in seasonal dry forest with conspecifics in eastern rain forest, which, though a drier season is present, experience relatively evenly distributed rainfall (Martin, 1972). Interestingly, when temperature and rainfall are less closely tied to food availability, births in *Alouatta carya* become less seasonal (Kowalewski and Zunino, 2004). Clearly, more data on a variety of species are necessary to determine the extent of relaxed breeding seasonality and elucidate what might predispose certain lemur species to less restricted breeding.

Potential Causes of Infant Mortality

My results do not support the hypothesis that relaxed breeding seasonality is adaptive, potentially enabling *Eulemur rubriventer* to survive and reproduce in a stochastic environment (Durham, 2002). Instead, breeding outside peak season appears to be disadvantageous. Infant mortality was higher when births occurred outside the birth peak (ranging from 67% to 100%) than when births occurred inside the birth peak (ranging from 5% to 11%). Sources of out-of-peak season infant mortality remain unknown. No males or females immigrated into groups, and I did not observe infanticide, predation, and injurious falls. Infants born into poor ecological conditions may nurse longer and grow at lower rates (Borries *et al.*, 2001). Infants in this study that were born outside the August/September/October birth peak appeared very small in size (Overdorff *pers. obs.*; Tecot *pers. obs.*). The small sizes of *Eulemur rubriventer* and other lemur infants born out of peak season (*E. cinereiceps*, S. Martin, *pers. comm.*) or that died shortly after birth (*Propithecus edwardsi*, P. Wright, *pers. comm.*) might indicate under- or malnourishment, supporting the suggestion that out-of-season births in this study may result from suboptimal conditions, rather than increased food availability. Nonetheless, differences in infant mortality between infants born within and outside the birth peak are notable, and importantly indicate that such extended breeding is not adaptive.

The birth peak in *Eulemur rubriventer* corresponds with the most resource-poor period. Recent research of fecal cortisol level elevations—indicators of increased stress that may reflect increased energetic demand—in *Eulemur rubriventer* identifies parturition through mid-lactation as a highly energetically demanding period, wherein the most intense food scarcity period is met with reproductive demands (Tecot, 2008). Though reproductive demands may not be as great as those imposed later when infants are nursing at larger body sizes, the convergence of these demands has a profound impact on lemur physiology, with cortisol levels increasing almost 2-fold compared with elevated levels during late gestation (Tecot, 2008). When births occur outside the peak birth season, early to mid-lactation months are likely met with greater food abundance, yet these infants die. Thus, in this species, the successful birth and weaning of infants is likely dependent in part upon food availability before birth.

Analysis of the theoretical overlap indices (T) supports this. T indicated that reproduction of *Eulemur rubriventer* is timed such that overlap with fruit abundance

relative to the duration of each reproductive stage is maximized, as predicted. Specifically, 100% of prebreeding and infant independence stages and 0–50% of each of the other stages overlapped with fruit abundance. This may explain Overdorff's (1991) observation in which the timing of the mating season remained consistent in 1989 and 1990, despite differences in fruit availability during that reproductive stage (Overdorff, 1991); interannual variation in food availability before breeding, instead of during the mating season, may determine variation in the timing of births from year to year.

T indicates that the intersection of reproduction with fruit abundance is maximized for 3 mo, providing 3 mo in which this species can optimize reproduction. Three months is also the approximate duration of the birth peak, and while other foods may play a role in reproductive timing, e.g., flowers, (Pereira *et al.*, 1999), these results suggest that fruit availability may indeed exert strong selection on the timing of breeding. Breeding outside of this 3-mo window reduces T, and prebreeding and infant independence stages are met with little to no fruit. As noted previously, small body sizes of infants born outside of the birth peak indicate some disadvantage at birth, initiated before parturition. Since most infants born out of peak season died within the first 3 mo of life, the amount of energy available to mothers prebreeding, or to infants as they become more independent, may have been insufficient. If energy is stored before conception for use post-parturition, the pressure of insufficient resources may also act on the infant via low-quality milk (King *et al.*, 2005). Previous studies of infant mortality have found that a peak in lemur infant mortality occurs soon after birth, and also may be associated with small infant body sizes (Koyama *et al.*, 2001; Richard *et al.*, 2002); whether these results are related to prebreeding food availability is unknown. Lemurs may also reduce energetic maintenance needs during the late dry season (Pereira *et al.*, 1999), which coincides with gestation. If breeding occurs out of peak season and physiological adjustments do not coincide with gestation, energetic needs may be elevated, and prebreeding energy stores may be insufficient to support healthy offspring from conception through weaning. Thus, prebreeding and infant independence are critical stages during which maximizing energy intake is essential. Our understanding of how lemurs time reproduction in seasonal yet unpredictable environments would be greatly enhanced by additional analyses of phenological interannual variation, such as 1) whether some months are more predictable from year to year and 2) whether peaks and troughs merely shift slightly in time, e.g., within a 3-mo range, or are erratic. The applicability of T in an environment with high interannual variability can be tested using annual data on plant phenological patterns and births in several years.

Potential Ultimate Sources of Out-of-Season Breeding

Why does this pattern of reproduction occur? A seasonal strategy with some relaxation might be optimal if the environment is largely seasonal but the overall quality of the environment varies year to year, vs. random throughout each year, such that flexibility in which years animals reproduce maximizes fitness. On a smaller scale, reproduction outside of the peak season may be a by-product of such a strategy (entrainment to exogenous cues modified by internal condition), rather than

a strategy in itself. Lemur interbirth intervals are typically 1–2 yr (Overdorff *et al.*, 1999; Pochron *et al.*, 2004; Richard *et al.*, 2002), reaching up to 5 yr (Ratsimbazafy, 2003) in harsh environments. Brockman and van Schaik (2005) found that primate birth rates were higher in good vs. bad years, and that these differences were most pronounced in relaxed income breeders. The mechanism behind such bet-hedging (Stearns, 1976) is unknown, but may result from energetic condition or food availability. Future research on intra- and interannual maternal condition, infant survival, phenology, and climate would help test how reproductive strategies work on different timescales with different selective pressures.

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