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Authors: Frasier, Cynthia L., Rakotonirina, Jean-Norbert, Razanajatovo, Lamaherisolo Gervais, Nasolonjanahary, Theoluc Stanislas, Rasolonileniraka, , et al.

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Expanding Knowledge on Life History Traits and Infant Development in the Greater Bamboo Lemur (*Prolemur simus*): Contributions from Kianjavato, Madagascar

Cynthia L. Frasier[1], Jean-Norbert Rakotonirina[2], Lamaherisolo Gervais Razanajatovo[2],
Theoluc Stanislas Nasolonjanahary[2], Rasolonileniraka[2], Stephanson Bertin Mamiaritiana[2],
Jean Fulbert Ramarolahy[2] and Edward E. Louis Jr.[1,2]

[1]*Omaha's Henry Doorly Zoo and Aquarium, Department of Conservation Genetics, Omaha, NE, USA*
[2]*Madagascar Biodiversity Partnership, Manakambahiny, Antananarivo, Madagascar*

Abstract: Data are lacking on intraspecific variability in life history traits for the Critically Endangered greater bamboo lemur (*Prolemur simus*). Until now, detailed investigations on wild individuals had only been published for Ranomafana National Park, limiting the predictive power on the greater bamboo lemurs' possible responses to threats such as habitat loss and climate change. In this study, data were compiled on vital statistics and basic aspects of infant development for a 48-month period in Kianjavato, Madagascar. The area is mixed-use lowland forest with dense pockets of bamboo amid a disturbed landscape. Four core social groups, which would frequently coalesce into two larger groups, were monitored intensively. The birth pulse occurred in mid- to late September, nearly one month earlier than in Ranomafana National Park. Interbirth intervals and rates of attainment of infant developmental landmarks such as locomotor independence and weaning are discussed. Infant mortality averaged 47% with most deaths concentrated in December and January, while adult mortality was low with most deaths occurring during the dry season. Annual female adult mortality ranged from 0% to 22%. The mortality of adult males could not be assessed due to their dispersal.

Key Words: infant development, infant mortality, interbirth interval, life history, vital rates

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Introduction

Knowledge on basic life history traits is a stepping-stone to the effective conservation of endangered species as well as an exploration of evolutionary and ecological questions. For organisms with long generation times, developing a comprehensive understanding of their life history requires long-term commitment of resources and personnel. Studies can continue for decades, as in the monitoring efforts on ring-tailed lemurs (Jolly *et al.* 2002; Gould *et al.* 2003) or Verreaux's sifaka (Richard *et al.* 2002). In great apes, Gombe's chimpanzees have been tracked for more than 50 years (Pusey *et al.* 2007), and Rwanda's mountain gorillas (Stewart *et al.* 2005) and Borneo's orangutans (Galdikas 1988) have been studied for more than 40. The opportunity for research of this nature on Madagascar's greater bamboo lemur (*Prolemur simus*) was uncertain as there were no reported sightings of this species in the twentieth century until 1964 (Meier and Rumpler 1987). Pivotal field studies in the late 1970s and 1980s identified two populations of *P. simus* in southeastern Madagascar in Ranomafana and Kianjavato (Petter *et al.* 1977; Meier and Rumpler 1987; Wright *et al.* 1987), enabling future investigations on life history values that will contribute to the protection of greater bamboo lemurs in their native habitat.

The greater bamboo lemur is once widely distributed across vast areas of Madagascar and is the most abundant lemur in the subfossil record (Godfrey and Vuillaume-Randriamanantena 1986; Godfrey *et al.* 2004). The extensive historical range of *P. simus* suggests that it was well-adapted to this island nation's natural disturbance regime marked by cyclones, re-occurring droughts, and generally unpredictable precipitation patterns (Wright 1999; Dewar and Richard 2007). However, the recent decades of deforestation coupled with hunting are believed to be the leading causes of the greater bamboo lemurs' near disappearance, resulting in its classification as Critically Endangered (Mittermeier *et al.* 2010; Andriaholinirina *et al.* 2014). Recent surveys have located previously unknown populations, but this species is today restricted to pockets in the eastern humid forests (Andriaholinirina *et al.* 2003; Dolch *et al.* 2004, 2008; King and Chamberlan 2010; Rajaonson *et al.* 2010; Ravaloharimanitra *et al.* 2011; Rakotonirina *et al.* 2011, 2013; Olson *et al.* 2012; Randrianarimanana *et al.* 2014).

Prolemur simus is an elusive, group-living, cathemeral lemur (Santini-Palka 1994; Tan 1999, 2000). Evidence of its presence at sites is often limited to signs of their feeding and to interviews with local people (Dolch *et al.* 2004; Ravaloharimanitra *et al.* 2011) as they are rarely encountered during site surveys. More than 3,000 human hours were invested at Torotorofotsy in the northern part of the species' current range to locate the first documented individual at this site (Dolch *et al.* 2008). Not only is the greater bamboo lemur difficult to locate, habituation is a lengthy process taking up to four times longer than for other bamboo lemur species (Tan 1999). Due to these obstacles, there are few sites with habituated groups of *P. simus*, and most published vital statistics and behavioral data are from a social group in the Talatakely parcel of Ranomafana National Park (Tan 1999, 2000; Bergey and Patel 2008). Additional information recently became available on more northerly groups (Bonaventure *et al.* 2012; Lantovololona *et al.* 2012; Mihaminekena *et al.* 2012; Randrianarimanana *et al.* 2012; Andrianandrasana *et al.* 2013; Randriahaingo *et al.* 2014).

Studies on wild *P. simus* have shown shown that it is a seasonal breeder, with births mostly confined to October and November at Ranomafana (Tan 1999, 2000) and near the villages of Ranomainty and Sakalava more than 350 km north in the Ankeniheny-Zahamena Corridor (Randrianarimanana 2012). These locations are all in eastern humid rainforests and at similar elevations, ranging from 900 m to 1160 m (Tan 1999; Randrianarimanana *et al.* 2012). Recorded gestation lengths in captivity (150 ±3 days; Roullet 2012) and at Ranomafana (148−150 days; Tan 2000) are consistent, and so most conceptions would evidently occur in May or June in the wild. At Ranomafana, females give birth to a single infant annually, having their first infant in their third year (Tan 2000). In captivity, estrus can begin as early as 1.5 years old, with the youngest individual giving birth at two years (Roullet 2012). Females are philopatric and males disperse when they are approximately 3.5 years old (Tan 2000). In captivity, males are removed from their natal groups at maturity at 2.5 years old when tensions with their father become apparent (Roullet 2012).

Differences in age of maturation in captive versus wild populations are likely related to provisioning, which has been reported to accelerate development (Altmann *et al.* 1993; Borries *et al.* 2001; Altmann and Alberts 2005). In Beza Mahafaly, for example, ring-tailed lemurs (*Lemur catta*) reproduce at three years old, while in Berenty where there are introduced food resources and provisioning, they have been seen to give birth when only two years old (Gould *et al.* 2003). The effects of provisioning in *P. simus* may be reflected in the recommended captive weights for males ranging from 2.7−2.8 kg (Roullet 2012), while the average weight for both sexes in the wild is 2.4 to 2.6 kg (Tan 2000, 2007).

Differences in infant maturation have also been noted in captive versus wild populations. In Ranomafana, infants were weaned at 7.5 months old (Tan 2000) versus 8.5 to ten months in captivity (Roullet 2012). Accelerated infant maturation has been linked to nutritional stress at one end of the spectrum, but also to good ecological conditions on the other end of the spectrum (Lee 1996). It is likely that the prolonged period of lactation in captivity is also due to provisioning, especially as lactating females were possibly pregnant. Interbirth intervals are approximately one year in both the wild and captivity, and the total time of gestation plus nursing exceeds one year (Tan 2000; Roullet 2012).

Another aspect of infant development is the time of attainment of locomotor independence. Highly arboreal primate infants tend to have slower rates of physical development than more terrestrial species as arboreality has been implicated in promoting greater amounts of physical contact between primate infants and mothers (Chalmers 1972; Sussman 1977; Karssemeijer *et al.* 1990). Tan (2000) reported that *P. simus* in Ranomafana engage in many activities while on the ground and infants attain complete locomotor independence by 16 weeks of age. This would occur in February and March based on the birth pulse in October and November. Although not explicitly stated by Tan, locomotor independence coincides with a spike in terrestriality. *Prolemur simus* in Ranomafana spends up to 24% of its time on the ground in February (Tan 2000), and it is predicted that similar patterns of physical development will be seen in other populations of greater bamboo lemurs with infants becoming increasingly independent during periods of increased terrestriality. However, it is not expected that they will mature in this regard as quickly as the most terrestrial lemur species, *Lemur catta*, which spends up to 35% of its time on the ground. *Lemur catta* infants are skillful at leaping and playing by week eight, and increase locomotor independence during group travel by week ten (Gould 1990).

Although limited, the existing published baseline life history data on *P. simus* are extraordinarily valuable. Data on intraspecific plasticity of wild greater bamboo lemur populations are sparse, yet interpopulation variability has been identified as an important safeguard against extinction for mammal species (González-Suárez and Revilla 2013). The Ranomafana *P. simus* study population has declined since 2003 (Wright *et al.* 2008, 2012) to a current low of just two individuals in the park as reported in popular sources (Conway-Smith 2013; Douglas 2014) and reiterated at the *Prolemur simus* Working Group 2015 meeting. This draws attention to the pressing need of expanding knowledge on this species in its natural habitat and gathering data to facilitate exploration of local population declines (Cowlishaw *et al.* 2009).

This study's objective was to characterize basic life history patterns of a population of greater bamboo lemurs; monitoring wild, yet habituated, social groups living in a disturbed low-elevation evergreen humid forest in Kianjavato, Madagascar (McGuire *et al.* 2009). The submontane rainforests of Ranomafana are only 70 km west of Kianjavato, but the elevation drops as one descends from the eastern escarpment of the central plateau towards Kianjavato, and this change is accompanied by shifts in weather (Donque 1972) that may affect seasonality and thus the life history patterns of wildlife populations. Our multi-year data set will provide insight into variability from the population level down to the individual. When possible, these data are compared to those from Ranomafana to assess intraspecific variation in life history parameters between different forest types and disturbance regimes. The data from this study can direct attention to factors affecting population viability in a critically endangered species.

Methods

All research was authorized by Madagascar's Ministère de l'Environnement et des Forêts, and was documented in a series of permits issued over the duration of the work (066/10/MEF/SG/DGF/DCB.SAP/SLRSE, 100/11/MEF/SG/DGF/DCB.SAP/SCB, 078/12/MEF/SG/DGF/DCB.SAP/SCB, 039/13/MEF/SG/DGF/DCB.SAP/SCB). All interactions with the study subjects abided by Omaha's Henry Doorly Zoo and Aquarium's IACUC (97-001, 12-101).

Study site and subjects

The Kianjavato Commune in southeastern Madagascar is characterized by a patchwork of lowland evergreen humid forest and agricultural land. At least 12 social groups of greater bamboo lemurs have been identified across the commune (Petter *et al.* 1977; Meier and Rumpler 1987; Wright *et al.* 1987; McGuire *et al.* 2009; this study). These lemurs are spread over an 8-km distance. An additional, but lesser known group, was observed at Tsitola at Kianjavato's western boundary near the Antaretra Commune. Of these groups, four were part of a long-term monitoring program begun at the end of 2010.

The monitoring program was focused primarily on *P. simus* social groups at the FOFIFA Kianjavato Coffee Plantation (21°22'43.2"S, 47°52'2.9"E), which is located on the southern aspect of the Sangasanga Mountain in Kianjavato Village (Fig. 1; McGuire *et al.* 2009). The monitored groups were referred to as West 1, West 2, East 1, and East 2. West 1 and West 2 frequently coalesced into a larger group, and the same was true for East 1 and East 2. The FOFIFA station includes areas of active agriculture near the mountain's base, progressing through secondary forest to a more mature intact forest near the summit approximating the less disturbed

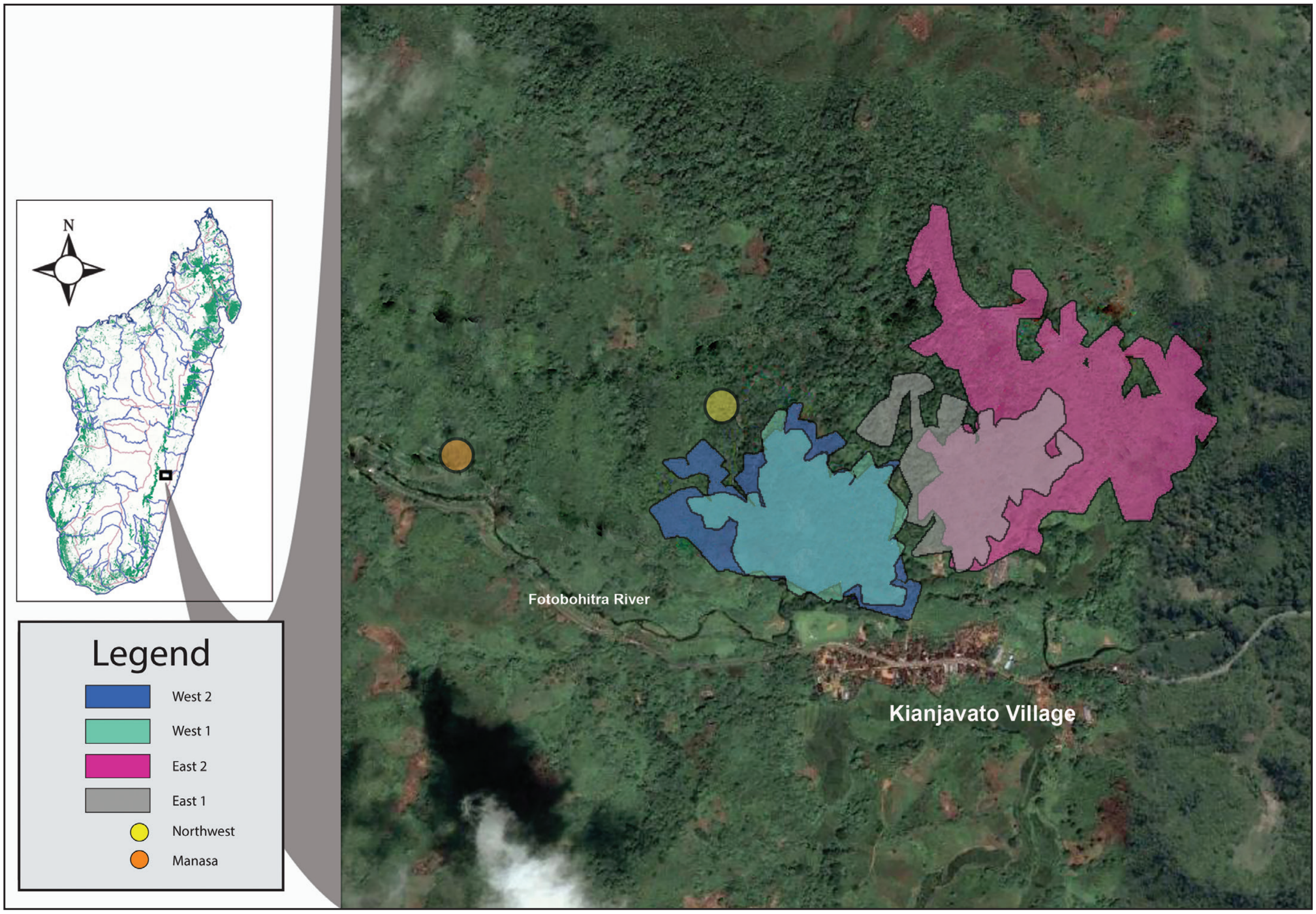

Figure 1. The study site was located on Sangasanga Mountain within the FOFIFA Kianjavato Coffee Plantation. The occurrence distributions of the four monitored *P. simus* groups are outlined, and the locations of two additional, nearby groups are indicated with circles. The northern side of Sangasanga Mountain was deforested.

vegetation found on the nearby mountain of Vatovavy. The forest at Sangasanga is used by residents of Kianjavato as a source of fuel wood, bamboo, and non-wood products.

Captures and measurements

Eighty-seven different immature and mature *P. simus* individuals were immobilized between 2000 and 2015 following methods described by Louis *et al.* (2006). Biomedical and morphometric data were recorded. Immature individuals less than three years old were identified based on size, weight, molar eruption and, when possible, known date of birth, and were excluded from calculations for average adult weight.

On first capture, microchips were placed subcutaneously into the interscapular space during the initial sedation to aid in the identification of each individual in ensuing recaptures. To facilitate monitoring, female greater bamboo lemurs in the behavioral groups were recognized by color combinations of nylon collars and aluminum pendants; male lemurs were outfitted with ATS radio collars (model M1545; Isanti, MN, USA).

Behavioral and census data

Behavioral data used in this study were collected by the authors from January 2011 through December 2014 from four habituated *P. simus* social groups. Censuses were recorded on behavioral groups a minimum of three to four times monthly during the behavioral monitoring program. Individuals received a score of zero if they were absent or one if they were present; presence of unknown individuals was always noted. These data were also used to calculate population growth rates (λ) as in Lawler (2011). Focal individuals were followed for two hours daily over three consecutive days every two weeks or monthly as the program expanded, such that data was distributed evenly for every individual throughout the monitoring duration. The hours of the follow per individual varied systematically to obtain behavioral data at different times during the diurnal portion of its activity cycle.

Data were recorded via instantaneous sampling at five-minute intervals (Altmann 1974), with rare behaviors recorded whenever they were seen (*ad libitum*). If an activity occurred on the ground during a scan, it was noted, and the percent of terrestrial observations per month was calculated. Activities recorded included resting, feeding (plant identification and part consumed), traveling, and social behaviors. Female-specific activities relating to interactions with infants were also recorded. The distance between mothers and infants was noted during the infant's first year of life, and three general categories were assessed: in physical contact, within one body length of mother, and greater than one body length away from mother but within visual and hearing distance. Occurrences of nursing or if the infant was mounted on the mother while she was moving were also recorded.

Life history data

Based on preliminary data from 2010, beginning the second week of September we checked *Prolemur simus* females in the four core social groups every day for the presence of newborn infants. The daily checks, including weekends, continued for five weeks or until an infant was observed. If an infant was born after mid-October its presence was recorded during subsequent censuses, but resulting in less precise birth date estimates. Birthing seasons were identified by the year that the season begins with the caveat that the interval could continue into the following year. The midpoints between the first and last dates of possible parturition were used to calculate the interbirth interval (IBI) in days, which were converted to months as in Fürtbauer *et al.* (2010).

Prolemur simus females were often absent from their groups prior to the birth of an infant. All downstream calculations were, therefore, based on the average birth date of an individual, which was the day that fell between the last time a mother was observed without an infant and the first day she was seen with an infant. The week of birth was estimated to be the week including the infant's average birthdate with week 1 starting on January 1 (Tecot 2010). The week of conception was estimated by counting back 149 days from the average birth date—the average length of gestation reported in the wild (Tan 2000) and within the documented range for captivity (Roullet 2012).

Infants were presumed dead if mothers were repeatedly seen without them before the infants attained an age of one year. At Sangasanga, the adult female membership of a social group was consistent with no known incidences of immigration during the study period. Therefore, if an adult female went missing from a group she was considered deceased, although females and their offspring in Ranomafana have been noted to migrate on rare occasions (Wright *et al.* 2012). The male membership was much more fluid, with males frequently moving between groups, especially the subordinate males. Missing males were not considered deceased unless their remains were found.

Data analysis

Circular statistics are recommended for cyclical data (Berens 2009) and were used to determine seasonality in births. This method allows one to take into account the proximity of December 31st to January 1st, which would otherwise be on opposite ends of a linear scale. For this analysis, births were grouped according to month making the circular axis one year composed of 12 equal parts each 30°. Although the data were grouped, a correction factor was not calculated as this is not problematic for most applications as long as groupings are less than 45° (Jammalamadaka and SenGupta 2001). The R-package CircStats (Agostinelli 2009) was used and the Rayleigh test was implemented to check for seasonality. Yearly data from 2011 to 2014 were analyzed separately and then combined.

Results

Captures and measurements

In Sangasanga Mountain in Kianjavato, greater bamboo lemurs were immobilized in every month of the year except March between 2000 and 2015 (Table 1, Fig. 2). The average weight of an adult female *P. simus* at Sangasanga was 2.61 kg (range 2.20–3.25 kg; 48 measurements representing 29 individuals), and the average weight of an adult male was 2.75 kg (range 2.15–3.55 kg; 76 measurements representing 32 individuals). The average weight of males was significantly higher than that of females (t = 2.6353, df = 122, p <0.05), but the size difference was not readily observed in the field.

Behavioral data

In total, there were six groups of *Prolemur simus* with abutting territories occupying Sangasanga. Four of these groups were habituated and had in total from 29 to 55 individuals in 46 ha in 2014 (Fig. 1). The number varied throughout the year due to births, deaths, and dispersals. Group composition is shown in Table 2. Overall, the population of the focal groups expanded 19.0% from 2011 to 2014. Lambda was 1.06 and 1.17 for 2012 and 2013, respectively, showing positive growth rates, but dropped to 0.99 in 2014 hovering near equilibrium. A combined total of 5788 hours of behavioral data were recorded.

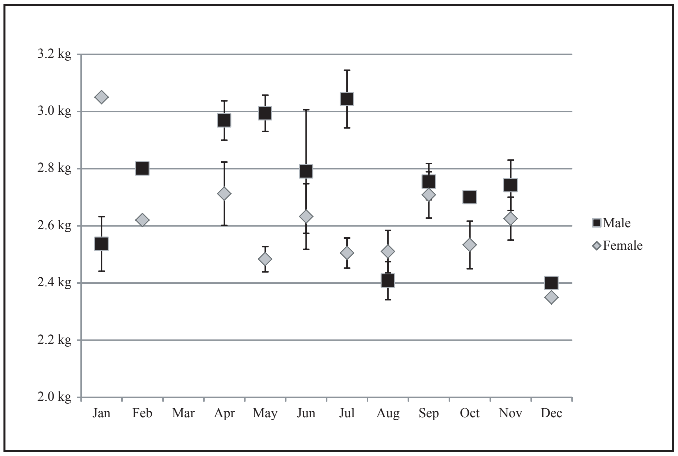

Figure 2. Averaged weights of captured male and female adult *P. simus* from the Kianjavato Commune by month from 2000 to 2015. See Table 1 for accompanying data.

Infants were in physical contact with their mothers for 100% of observations during the first two weeks of their life, declining to 83% on average by week five. Infants began spending more than 50% of their time out of physical contact with their mothers by week 12, typically occurring in mid- to late December (Fig. 3). Around this same time, infants were no longer dependent on their mothers to transport them, with the last observation of being mounted on their mothers during movement occurring on average at 11.8 weeks of age (n = 18, SD = 0.63); although simplistic, this was deemed to be the point of locomotor independence. Simultaneously, the percentages of observations occurring on the ground began to increase markedly in December, peaking in January with a high of 11.10% in 2013, and an overall average of 8.46% for this month. Average percent terrestriality decreased to less than 1% from June to September (Fig. 4).

Life history data

Females typically reproduced annually, giving birth to single infants. Two sets of twins were reported, however, in social groups outside of Sangasanga, but within the Kianjavato Commune. The average fecundity rate for the four social groups monitored from 2011 to 2014 was 94.0% ranging from 91.7% to 100.0%, and resulting in 45 births. These were minimum fecundity rates, as it was possible for an infant to be stillborn or to have died before its presence was noted. Two female greater bamboo lemur individuals became reproductively mature during this study and had their first infants during their third year, agreeing with previous reports (Tan

Table 1. Average weights of captured adult greater bamboo lemurs from Sangasanga, Kianjavato from 2000 to 2014.

Month	Female (kg)	Standard error	n	Male (kg)	Standard error	n
Jan	3.05	0.00	1	2.54	0.10	6
Feb	2.62	0.00	1	2.80	0.00	1
Mar						
Apr	2.71	0.11	4	2.97	0.07	12
May	2.48	0.04	3	2.99	0.06	7
Jun	2.63	0.11	8	2.79	0.22	5
Jul	2.51	0.05	6	3.04	0.10	12
Aug	2.51	0.07	7	2.41	0.07	6
Sep	2.71	0.08	12	2.75	0.06	13
Oct	2.53	0.08	3	2.70	0.00	2
Nov	2.63	0.08	2	2.74	0.09	11
Dec	2.35	0.00	1	2.40	0.00	1
Total			48			76

2000). Also in his third year, one male dispersed from his natal group into an adjacent group as seen at Ranomafana (Tan 2000). Two additional males moved between closely linked subgroups in their third year, for example from West 1 to West 2, and then emigrated from their overall social group in their fourth year. It was not possible to calculate adult mortality for male greater bamboo lemurs as their disappearance from a group could be attributed to either death or dispersal. No females died in 2011 and 2014. One female died in 2012 (9.0%) and the remains were recovered. Three females died in 2013 (22.0%), and the remains of two were found. The third was temporarily outfitted with a radio collar to assist with locating her during the birth season. The collar was cut and hidden in a small hole under a rock; she was considered a victim of poaching and her dependent infant was also lost.

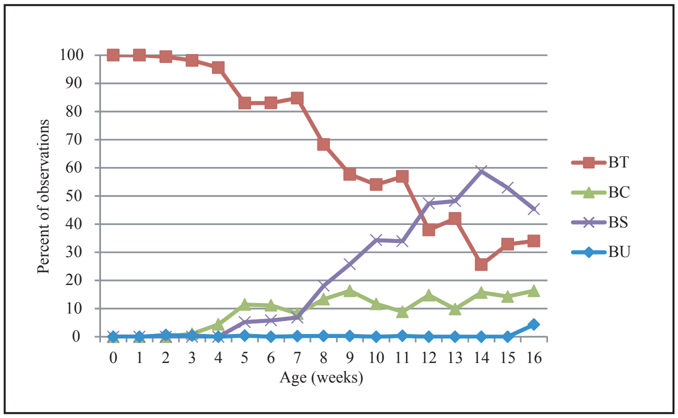

Figure 3. Proximity of an infant *P. simus* to its mother according to its age. BT – infant in physical contact with its mother; BC – infant within one body length of the mother; BS – infant greater than one body length from the mother but within sight or hearing distance; BU – infant's location is unknown.

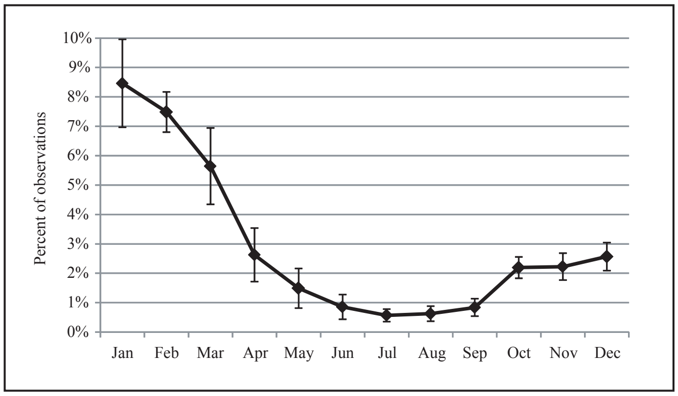

Figure 4. Percent of *P. simus* observations occurring on the ground by month with standard error of the mean.

Length of gestation, birth synchrony, and interbirth intervals

Birth dates were estimated, on average, to within a 7.8 day interval over four seasons and to within hours for exceptional cases. It was rare to have such narrow windows as *P. simus* females were often absent from their group for up to six days prior to returning with a new infant. The first of these exceptional cases was an infant born to a female 148 to 150 days after a witnessed copulation event. The narrowest birth window was 14 hours, 149 days after she mated with the dominant male of her group. This is in agreement with previously recorded gestation periods (Tan 2000; Roullet 2012).

Timing of births in Kianjavato showed significant seasonality (Rayleigh test: $Z = 35.96$, $p < 0.05$) with 20 of the 43 observed infants from 2011 to 2014 estimated to have been born in weeks 38 and 39, from mid- to late September (Fig. 5). Forty-five births were mentioned earlier in this text, but the birth dates of two infants could not be estimated due to a short disruption in the monitoring efforts due to unsafe field conditions. The average birthdate of infants to multiparous females was September 28 ($n = 41$, $SD = 22.0$) or 99 days after June 21st, which is the winter solstice in the southern hemisphere. The winter solstice was used as a reference point by Tan (2000), and so also used here to permit comparison. The average birth date occurs significantly earlier (two-sample t, $df = 48$, t-value $= 4.06$, $p = 0.0002$) in Kianjavato than in Ranomafana, where the average birthdate was 131 days after the winter solstice ($n = 9$, $SD = 18.2$; Tan 2000). Infants born to first-time mothers ($n = 2$) were not included in the calculation of average birthdates for Sangasanga as there is a general trend suggesting that estrus occurs later for *P. simus* primiparous females in comparison to multiparous females. For example, one female had her first infant in January, while another had her first infant near the end of November. By subtracting 149 days from the average birth date of infants born to multiparous females, most successful copulation events were found to occur during weeks 17 and 18, corresponding to the end of April and beginning of May (Fig. 5).

Table 2. Composition of *P. simus* study groups from 2011 through 2014. The number of animals in each age category was recorded monthly then averaged for each year.

	2011			2012			2013				2014			
	East	West 1	West 2	East	West 1	West 2	East 1	East 2	West 1	West 2	East 1	East 2	West 1	West 2
Adult males	6.3	3.0	2.0	5.9	2.3	2.0	3.5	3.3	2.8	2.0	4.3	2.5	2.0	2.3
Adult females	4.3	3.5	2.3	4.4	4.4	2.8	4.9	2.6	3.2	2.8	6.1	3.4	2.0	2.0
Juveniles & subadults	1.8	2.3	1.0	3.6	2.5	1.4	3.9	1.2	2.4	3.0	2.7	1.9	1.9	2.1
Infants	4.0	3.0	1.3	3.8	1.8	1.6	3.9	1.8	0.8	0.8	3.9	2.3	1.4	1.9
Total	16.3	11.8	6.5	17.7	11.0	7.8	16.3	8.9	9.1	8.6	16.9	10.1	7.3	8.3

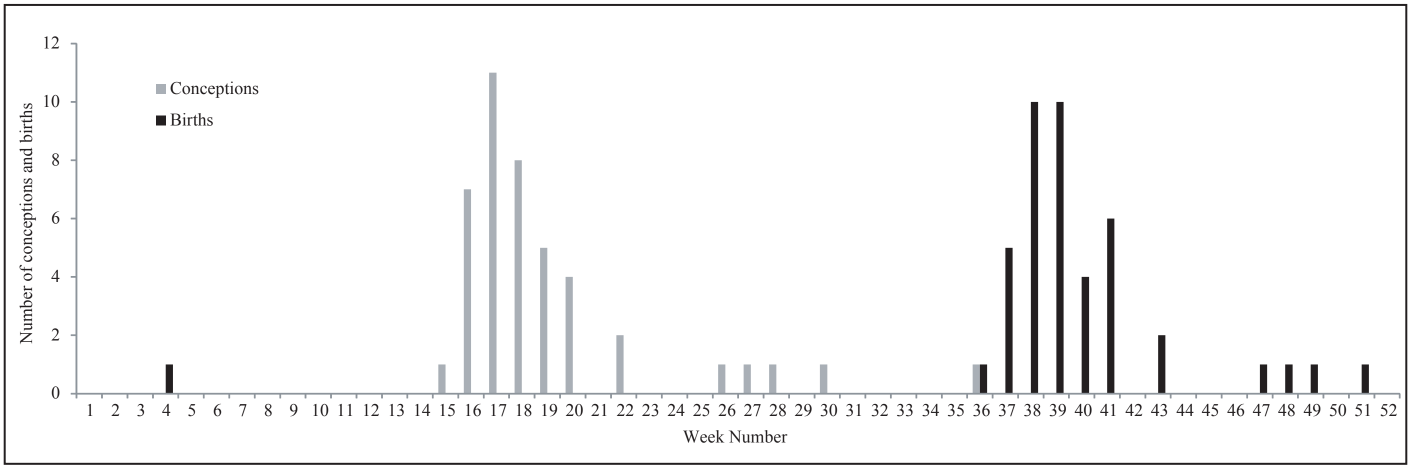

Figure 5. Distribution of conception and births for *P. simus* at Sangasanga, Kianjavato.

Average IBI of multiparous females from 2011 to 2014 was 363.7 days (n = 22, SD = 23.7). New mothers varied in the adjustment of their IBI to synchronize with the following year's birth pulse. One individual had a curtailed IBI of just 10.4 months between her first and second infant, while the IBI of another was reduced by a smaller increment to 11.0 months. The loss of an infant did not significantly influence the subsequent IBI (two-sample t, df = 20, t-value = 2.045, $p < 0.05$), although a difference was observed with an average duration of 12.1 months if an infant survived (n = 11) and 11.5 months if an infant died (n = 13).

The IBI is influenced by lactation (Thompson *et al.* 2012); thus, it is useful to note that the age of weaning was roughly estimated to be the date nursing was last observed and on average occurred 7.0 months after birth (n = 14, SD = 0.98). During most of this time, infants were consuming milk as well as provisioning for themselves. The last date of observed suckling is a simplistic view of the weaning process (Lee 1996); however, it is unlikely the infants derived much of their nutrition from their mothers beyond this point even with occasional bouts of nursing.

Minimum infant mortality rates

Infant mortality in Kianjavato increased from 45.5% for the 2011 birthing season to 54.5% for the 2012 season. The mortality rate for infants born in 2013 was 40.0%, for an overall average infant mortality rate of 46.7%. As of December 2014, four of 13 infants died. Half of all infant deaths occurred in December and January, with an average age at death of 3.2 months (n = 24, SD = 1.64). An additional five infants died in March and April, perhaps related to weaning. No infants died between May and July.

Discussion

Conception and birth

Comparisons of data between and within populations of greater bamboo lemurs demonstrated previously undocumented plasticity in this species' life history. With conception and birth as the starting point for comparison, we found that the timing of birth pulses varied between greater bamboo lemur populations at Ranomafana and at Sangasanga, but was consistent within locales. The later average date of conception and, hence, birth pulse in Ranomafana may reflect adaptations to the different environments at these mid- and low elevation forests, respectively. The coolest months at both sites are from June to August with temperatures at Ranomafana dipping down to 4–6°C (Tan 1999) while dropping to only 11°C in Kianjavato (data from the local weather station).

The basal metabolic rate (BMR) is the minimum energy cost of living (Frappell and Butler 2004) and as ambient temperatures decrease, this cost of living increases for endotherms that must maintain a specific body temperature (Frappell and Butler 2004; Naya *et al.* 2013). The BMR also increases during pregnancy, and more so during lactation (Frappell and Butler 2004; Speakman 2008).

Additionally, cooler temperatures affect the assemblage of plant communities and timing of phenophases, affecting the availability of certain food sources. For example, *Cathariostachys madagascariensis*, an endemic woody bamboo, is the staple of the *P. simus* diet at Ranomafana (Tan 1999). This bamboo is associated with lower montane forests where it grows in disturbed areas or gaps (Dransfield 1998; King *et al.* 2013; Olson *et al.* 2013). In Kianjavato, *Valiha diffusa* is the dominant woody bamboo and the staple food of *P. simus* at Sangasanga (Tan 2007). This species grows in low elevation areas, frequently in highly disturbed habitats (Dransfield 1998; King *et al.* 2013).

In Sangasanga, the first infants of the birth season were observed during the second week of September, while births in Ranomafana were well synchronized and occurred one month later during October and November (Tan 1999, 2000). The delayed conception at Ranomafana, and therefore the birth pulse, may result in the increased BMRs of mothers coinciding with increasing food supplies and the onset of warmer weather. Shifting the birth pulse may also ensure that infants have a sufficient food supply when nutritionally independent, as predicted with the classic reproductive strategy (Lewis and Kappeler 2005).

Infant developmental landmarks

The last observation of nursing in Sangasanga was recorded on average 7.0 months after birth, or 213 days, which is typically late April. In Ranomafana, infants were weaned at 7.5 months (Tan 2000), which should be around early June. A statistical comparison was not possible between these two sites due to limited information on the Ranomafana population. We do not predict, however, that these time frames were significantly different, as multiple infants at Sangasanga did nurse for a similar duration. In Sangasanga, weaning coincides with the consumption of the fruits of a native palm, *Dypsis* sp., as well as the fruits of the alien invasive herb *Clidemia hirta* (this study). Both of these food sources are accessible to infants, in contrast to woody bamboo culms or the large tips of new culms that require the strength of an adult to break. Although these fruits only constitute less than 10% of the adult diet from February to June (this study), they may be important for infant nutrition. More detailed observations on immature individuals would be necessary to address differences in diet between adults and infants as they develop.

The attainment of locomotor independence occurred over a protracted period in Sangasanga (n = 18) in comparison to Ranomafana (n = 9), which may, in part, be related to sample sizes (Fig. 6). On average, infants in Sangasanga traveled independently of their mothers (but with the group) at 2.8 months, or nearly 12 weeks of age, typically mid- to late December. At this time there is also a marked decrease in physical contact between infants and mothers. In Ranomafana, infants attained complete locomotor independence by four months, but as early as 13.5 weeks of age (estimated from a graphical representation; Tan 2000). As predicted, the attainment of this physical developmental landmark coincided with increasing terrestriality by adults, which peaks in January in Sangasanga (11.1%) and February in Ranomafana (24.1%; Tan 2000), and is likely related to the eruption of bamboo shoots from the ground. This period of increased terrestriality may play a valuable role in refining *P. simus* infant locomotor skills.

By creating a simple diagram of conception, birth, locomotor independence, and weaning using data from *P. simus* at Ranomafana and Sangasanga some intriguing patterns emerge (Fig. 6). It appears that it is possible for *P. simus* mothers to be nursing and pregnant concurrently. In Sangasanga, concurrent lactation and pregnancy has occurred with some individuals nursing an estimated 25 days into their subsequent pregnancy. This is also supported by average duration of reproductive phases in captivity (Roullet 2012).

Concurrent pregnancy and lactation has been observed in other social primates such as humans (Merchant *et al.* 1990), macaques (Tanaka *et al.* 1993), and marmosets (Saltzman and Abbott 2005). Although not explicitly stated, it may also occur in *Propithecus verreauxi verreauxi* (see Lewis and Kappeler 2005). It has been suggested that macaques wean their current infant once the developing fetus survives the greatest at-risk period for abortion, which is during the first month of pregnancy (Tanaka *et al.* 1993). This may also hold true for *P. simus*.

Mortality

Infant mortality rates at Sangasanga were higher than those reported from Ranomafana where mothers successfully reared all their infants during the study period (n = 9; Tan 2000). Over the duration of the study at Sangasanga infant mortality was nearly 50%, which was similar to mortality rates for ring-tailed lemurs and sifakas (Gould *et al.* 2003; Richard *et al.* 2002). There is no evidence of infanticide.

In Sangasanga, half of all infant deaths occurred in December and January. This may be related to increasing independence of infants from their mothers that leaves the infants more vulnerable to predation. Threats of predators and intragroup aggression have been proposed to be highly influential in the rate of infants attaining independence (Förster and Cords 2002), which may also explain the acquisition of locomotor independence at nearly the same time as a peak in infant mortality rates. Additionally, in late December and early January, researcher presence decreased due to the Christmas and New Year holidays, when field hours were reduced. It is possible that researchers acted as inadvertent sentinels driving away possible predators.

As noted by Lawler (2011) in an overview of demographic concepts, the population growth rate in the majority of primate species is mostly affected by adult survival, with populations being more resilient to losses of immature individuals. Mortality rates for greater bamboo lemur males could not be estimated due to their frequent movement between

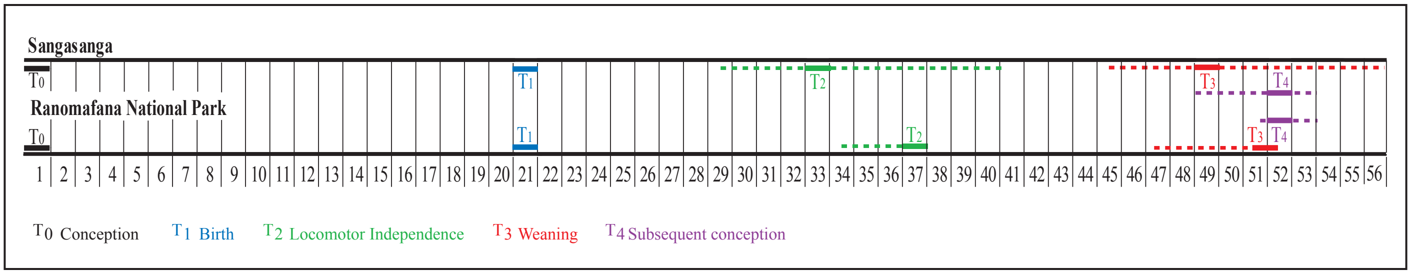

Figure 6. Scaled timeline of *P. simus* female reproductive cycle and infant developmental landmarks. Dotted lines cover the range of observed values from Sangasanga with solid bars over the average week. Dotted lines for Ranomafana reflect ranges noted in Figure 5.4 of Tan (2000) with bars over values reported in that text.

groups and possibly to groups outside the study area. Only males who died while wearing active radio collars within the study area were recovered. One such set of remains indicated predation by fossa (*Cryptoprocta ferox*). Predation of *P. simus* by raptors was reported in Ranomafana (Wright *et al.* 2012), and is suspected to occur at Sangasanga. At Sangasanga, the lemurs become highly agitated in the presence of these large birds, but an attack has never been witnessed.

It was possible to estimate female adult mortality, which was highest in group West 1 who lost half its breeding females (two of four) in 2013. The females were predated on during the same time period, in August, and both sets of remains were recovered, but the predator could not be identified due to the state of decomposition. All presumed natural deaths in the monitored groups occurred during the dry season, while the only known poaching event occurred at the beginning of the rainy season in West 2, and resulted in the loss of a breeding female and her infant. This incident coincided with the extraction of bamboo to make baskets to transport the litchi harvest to market, supporting the conclusion that most bushmeat collection in Madagascar is from opportunistic hunting while collecting non-meat forest products (Gardner and Davies 2013), but see Golden (2009).

Despite an infant mortality rate of nearly 50%, the population of *P. simus* in Sangasanga increased, with an overall growth rate of 19.0% from 2011 to 2014 in the focal groups. All groups monitored experienced growth in 2013, but with only East 1 and 2 continuing to expand through 2014. West 1 has not rebounded since the aforementioned precipitous decline in the number of its breeding females due to natural causes. West 2 also experienced faltering numbers due to the loss of one of its breeding females to a poacher. Since immigration of females into groups has not been observed in this study, it is predicted that these groups will not recover their numbers of breeding females until the two surviving infant females from 2013 reach sexual maturity. However, migration of females was seen for the first time after more than a decade of monitoring in Ranomafana, at a time when the population was plummeting (Wright *et al.* 2012).

These data shed light on intraspecific variation in greater bamboo lemurs at two sites with divergent disturbance regimes and ecological profiles. Flexibility in reproductive cycles as seen in the shift of the birth pulse as well as inter-individual variation in infant development may promote resilience in unpredictable environments. Infant mortality rates vary greatly between sites, but additional long-term information is needed as this can affect the ability of groups to rebound after a population decline. The identification of intraspecific differences highlighted here underscores the need for expanded long-term investigations at sites with differing selection pressures throughout the geographic range of greater bamboo lemurs. These data will be useful for population viability analyses, predicting resilience to hunting pressure and habitat loss, and for the development of conservation strategies.

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Authors' addresses:
Cynthia L. Frasier, Omaha's Henry Doorly Zoo and Aquarium, Department of Conservation Genetics, 3701 S. 10th Street, Omaha, NE 68107, USA, **Jean-Norbert Rakotonirina**, **Lamaherisolo Gervais Razanajatovo**, **Theoluc Stanislas Nasolonjanahary**, **Rasolonileninaka**, **Stephanson Bertin Mamiaritiana**, **Jean Philbert Ramarolahy**, Madagascar Biodiversity Partnership, Lot VO 12bis A, Manakambahiny, Antananarivo, Madagascar 102, and **Edward E. Louis Jr.**, Omaha's Henry Doorly Zoo and Aquarium, Department of Conservation Genetics, 3701 S. 10th Street, Omaha, NE 68107, USA, and Madagascar Biodiversity Partnership, Lot VO 12bis A, Manakambahiny, Antananarivo, Madagascar 102. E-mail: <mbp@madagascarpartnership.org>. *Corresponding author:* Cynthia L. Frasier, e-mail: <cynthiaf@omahazoo.com>.

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