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# Annual Variation in Ecology and Reproduction of Wild Simakobu (*Simias concolor*)

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**Abstract** Seasonal breeding in primates is related to the degree of environmental seasonality, particularly the availability and predictability of food. Southeast Asian species in general show moderate birth seasonality due to either low environmental seasonality or unpredictable fluctuations of mast-fruiting food resources. One Southeast Asian primate, the simakobu (*Simias concolor*), however, has been reported to be a strict seasonal breeder with births occurring in June and July only. It is unclear whether these observations are characteristic of the species or result from a sampling bias. To address this question, we documented the annual distribution of 11 births in eight groups of simakobu over two consecutive years at Pungut, an undisturbed site on Siberut Island, Indonesia. We assessed annual variation in ecology and reproduction via rainfall, temperature, food availability, feeding time, physical condition, conceptions, and births. Mean monthly temperature was nearly constant (26.3–27.1 °C), and monthly precipitation always high (219–432 mm). Although simakobu foods were abundant year-round, there were two fruit-feeding peaks in June and September. In contrast to previous reports, we documented births in 7 mo. Most births occurred in October (45 %), the wettest month of the year, and most conceptions in March and April, following a peak in unripe fruit availability. Although sample sizes are very small, females seemed to conceive when their physical condition was best, suggesting that simakobu time conceptions flexibly to the recovery of energy

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reserves. Across study sites, births occurred in 10 calendar months, indicating that simakobu reproduction is not strictly seasonal.

**Keywords** Birth distribution · Capital breeding · Conception · Food availability · Seasonal breeding · Southeast Asian colobines

## Introduction

The timing of reproduction is often related to the availability of foods, resulting in breeding seasons in populations in which plant productivity is seasonally restricted (Janson and Verdolin 2005). Breeding seasonality is typically indicated via measures of the evenness of the distribution of births across months. One quantitative measure that has often been used is the percentage of births observed during the 3-mo period with the most births, i.e., 3-mo birth peak, where 25 % indicates an even distribution, and 100 % indicates that births are restricted to ≤3 mo of the year (*cf.* van Noordwijk and van Schaik 2004). More recently, another measure, mean vector length ($r$), has been employed to indicate the degree of concentration of births in a circular distribution, where $r=0$ when births are evenly distributed across all intervals and $r=1$ when all births occur within the same interval (*cf.* Di Bitetti and Janson 2000; Janson and Verdolin 2005).

Among primates, most populations show at least some degree of seasonality in the timing of births (Janson and Verdolin 2005). Three general patterns in the annual distribution of births can be identified: 1) strict seasonality (*cf.* Lancaster and Lee 1965), in which births occur at around the same time every year and there are multiple consecutive months with no births, e.g., Hanuman langurs (*Semnopithecus entellus*: Koenig *et al*. 1997), Verreaux's sifakas (*Propithecus verreauxi*: Lewis and Kappeler 2005); 2) moderate seasonality, in which births occur in all or most months of the year, but with a clear peak that may or may not occur in the same months across years, e.g., long-tailed macaques (*Macaca fascicularis*: van Schaik and van Noordwijk 1985); and 3) no seasonality, in which births occur throughout the year with no peak in the distribution, e.g., mountain gorillas (*Gorilla beringei*: Watts 1998).

Birth seasonality in primates is related, in particular, to the length and predictability of the period of food abundance and is lowest for species that rely on nonseasonal resources and live in relatively aseasonal environments, such as those with folivorous diets living at low latitudes (Di Bitetti and Janson 2000; Lindburg 1987). Conversely, frugivores residing at high latitudes are among the most seasonal breeders (Di Bitetti and Janson 2000). Building on previous work (Drent and Daan 1980; Jönsson 1997; Stearns 1989), Brockman and van Schaik (2005) described two patterns of reproductive seasonality in primates in relation to environmental seasonality and predictability of seasonal food peaks: income and capital breeding (*cf.* Stearns 1992). Income breeders use current energy intake to offset the costs of reproduction, whereas capital breeders build up energy reserves before reproduction. Consequently, for income breeders, birth peaks coincide with or directly follow food peaks such that the most costly aspect of reproduction, i.e., early lactation (Lee *et al*. 1991) occurs when food is abundant, whereas for capital breeders, conception occurs when food is abundant, after females have built up their energy reserves, resulting in birth peaks and lactation occurring at less favorable times. Whereas the income breeding tactic is expected in habitats with predictable food peaks, the capital breeding tactic is expected when food peaks are unpredictable or when environmental seasonality is moderate or absent (van Schaik and van Noordwijk 1985). Thus, income breeders should respond to predictable environmental cues, e.g., photoperiod, to resume cycling, whereas capital breeders should respond to internal cues about their physical and energetic condition (Brockman and van Schaik 2005).

Most Southeast Asian primates have been characterized as capital breeders, often showing moderate birth seasonality (Brockman and van Schaik 2005). For example, long-tailed macaques in northern Sumatra gave birth year-round, with a peak between July and November, during or after the peak in fruit availability (van Noordwijk and van Schaik 1999). This pattern has been interpreted as being a consequence of highly unpredictable resources in habitats characterized by mast-fruiting events leading to reduced seasonality across years (Brockman and van Schaik 2005; Janson and Verdolin 2005). Although Brockman and van Schaik's (2005) capital breeding generalization was made about macaques and orangutans, it is likely that the pattern also holds for the less frugivorous Southeast Asian colobines, e.g., red-shanked doucs (*Pygathrix nemaeus*: Phiapalath *et al*. 2011).

In light of these observations it is surprising that one Southeast Asian colobine, the simakobu (*Simias concolor*) on Siberut Island, is reported to be a strict seasonal breeder with births occurring in just 2 mo of the year, June and July (Tilson 1977). This pattern suggests that lactation coincides with high food availability (as predicted for income breeders) because fruiting in the area was reported to peak in July (Whitten 1980). Although Tilson's study covered a 21-mo period, owing to very small group sizes, just five births were documented. A single birth occurred in one focal group, while the others were recorded during surveys throughout Siberut. An additional five births were reported by hunters, all during June and July. It is unclear, however, whether the surveys and hunts were distributed evenly across months, and if a potential bias in data collection could explain the reported bias in births. Two other studies suggested that simakobu births may be concentrated between November and February, following the wet season (Hadi *et al*. 2009; Watanabe 1981). As with the Tilson study, the data in these studies were limited to five or fewer infants and covered <2 yr each. Thus, it remains unclear whether and when a peak in births occurs for simakobu.

Here we present data on births recorded during systematic censuses of known wild simakobu groups over 25 consecutive months at an undisturbed site in northern Siberut, Indonesia. We aim to assess annual variation in simakobu ecology and reproduction by documenting year-round changes in rainfall, temperature, food availability, feeding time, physical condition, conceptions, and births in this population. Given the common Southeast Asian primate pattern, we do not expect to find strict birth seasonality. If, like other Southeast Asian primates, simakobu are capital breeders, we predict that conceptions occur during or immediately after food peaks when female physical condition is best. We further aim to compare the distribution of births in simakobu to those for other Southeast Asian colobines. Because simakobu reside at low latitudes, where periods of food abundance are generally longer and more predictable (Di Bitetti and Janson 2000), we predict their 3-mo birth peak to be lower than that of the other species.

## Methods

### Study Site and Species

We conducted research at the Siberut Conservation Programme’s Pungut study site in northern Siberut, Indonesia. The study area comprises 1100 ha of primary mixed evergreen rainforest (altitude: *ca*. 25–190 m), which lies within the 4500-ha area known as the Peleonan forest (0°56′–1°03′S, 98°48′–98°51′E). Although designated as production forest, it is currently protected from hunting and logging through agreements with the local community and Indonesian officials. Additional information about the study site is provided in Erb *et al*. (2012) and Waltert *et al*. (2008).

Simakobu are medium-sized Asian colobines (adult males, 7.7–8.9 kg; adult females, 5.2–7.1 kg: Hadi *et al*. 2009; Tenaza and Fuentes 1995). One-male–multifemale groups average 7.9 individuals, with a mean of three adult females, two juvenile females, and one or two infants. All-male groups average 4.5 individuals and comprise males of all noninfant age classes and occasionally juvenile females (Erb *et al*. 2012). Because to our knowledge the gestation length of simakobu has not yet been determined, we extrapolated a value of 201 d (6.6 mo) from the fitted function between body mass and gestation length in wild Asian colobines (Fig. 3 in Borries *et al*. 2011), assuming an average adult female body mass of 6.3–6.8 kg (Hadi *et al*. 2009; Smith and Jungers 1997; Tenaza and Fuentes 1995).

### Phenology and Climate

To describe annual patterns of food availability, we collected phenological data monthly for 13 mo (December 2007–December 2008) on 404 trees and lianas. The sample included up to 10 adult specimens of the most common species from nine botanical plots (0.9 ha total) established at the start of the study, plus feeding trees for species eaten by the monkeys but not present in the plots. For this study, we selected data from 152 tree and liana specimens representing the 21 top food species (accounting for 76 % of feeding time). We estimated each phytophase, e.g., leaf bud, flower, ripe fruit, on a 4-point scale (0 = nothing, 1 = items in 1/3 of the crown area, 2 = in 2/3 of the crown area, and 3 = crown area full). We calculated the availability of young leaves, leaf buds, flowers, and unripe and ripe fruits using an adaptation of Marsh’s index (Koenig *et al*. 1997; Marsh 1981), which weighs the mean phenological score of a given species by its importance percentage (includes density, area at breast height, and frequency; data collected from 15 botanical plots, which included the original nine plots plus six plots established later in the study, covering 1.5 ha representing *ca*. 25 % of the focal groups’ ranges). We did not consider mature leaves because they were always abundant.

Owing to equipment failure, weather data at the site were not available for the study period. We therefore obtained climate data from WorldClim (Hijmans *et al*. 2005). The WorldClim database compiles measurements recorded from weather stations between 1950 and 2000, which are interpolated for interlaying areas. We downloaded the following 30 arc-seconds data files: 1) Mean Temperature = average monthly mean temperature; 2) Precipitation = average monthly precipitation; 3) Altitude = elevation above sea level; and 4) Bioclim = annual mean temperature, mean diurnal temperature range, maximum temperature of warmest month, minimum temperature of coldest month, and annual precipitation. We extracted and averaged values from four point locations representing the boundaries of the Pungut study area from raster files using ESRI® ArcMap™ 9.3. Based on these data, we constructed a climate diagram following the procedures established by Walter (1994).

## Demography and Behavior

We contacted and made counts of eight wild one-male–multifemale simakobu groups on 373 group-census days from December 2006 through December 2008. Adult male membership in all groups remained stable over the study period. Two of these groups, H and S, were focal groups and were contacted during most months (H=25, S=20 mo) for an average of 5.2 d per group per month ($N$=262, range 0–21 d). A total of seven infants were born into these two groups during the study period. The remaining six groups were contacted at irregular intervals whenever the schedule, designed to collect data on the behavior of adult males, would allow ($N$=54 d, mean 0.74 contact days per group per month, range 0–8). Although infants were born into five of the six groups, the month of birth could be estimated only for four infants in three of these groups (J, P, and Z). Thus, the sample includes 11 births in five one-male groups.

Two of the 11 infants were found alone (alive, but later died) within the home range of one of the focal groups (S) in 2007. These infants had not been observed in the group beforehand and therefore the mothers were unknown. Based on known group ranging patterns (W. M. Erb, *unpubl. data*), these infants were assigned to group S. Both infants were estimated to be 2 wk of age when found.

Birth months were known for five infants, i.e., mother observed without infant on previous observation day in focal group. For the remaining six infants, we estimated their ages based on size, motor skills (begin moving away from mother at 6–7 wk: W. M. Erb, *unpubl. data*), and/or skin coloration (melanin appears on hands/feet at 6–7 wk, on faces at 2–3 mo: W. M. Erb, *unpubl. data*). Of these, we estimated three to be <1 mo old, and the other three to be <2 mo old. We did not estimate birth dates for infants >2 mo of age. We determined conception months by subtracting 201 d from the estimated date of birth for each infant.

To calculate monthly feeding time, we used focal animal data from December 2007 until November 2008 for six adult males from three one-male–multifemale groups and one all-male group. We recorded instantaneous data on feeding at 5-min intervals during all-day follows of the adult males. We recorded local names of food species and reported food item and age in broad categories, e.g., young leaves, ripe fruits, etc. We compiled a total of 1787 feeding points, averaging 149/mo (range 64–281), and could identify the food item in 94.4 % of the cases (range 81.8–98.4 %). From these values, we calculated the amount of time spent feeding on leaves, flowers, fruits, and other foods, e.g., fungus, insects, in each month as a percentage of the total feeding points. Although feeding data for reproductive females would have been a more direct measure in this context, our main study focused on adult males and consequently these data are of much better quality, i.e., cover a longer period, were collected using instantaneous vs. scan sampling, include more identified foods, and sample more individuals vs. those for females. In addition, adult males and females spent a similar amount of time feeding overall (Erb 2008). Further, instantaneous focal (male only) and group scan (all group members) data sets for monthly fruit feeding times yielded comparable results that did not differ significantly (Wilcoxon signed-ranks test: $T=32.00$, $P>0.10$, $N=12$ mo).

In addition to feeding data, we assessed the physical condition of adult and juvenile females once per month by visual inspection of the back and limbs (following Koenig *et al*. 1997) and recorded it on a 3-point scale (poor = lean, average = neither lean nor fat, good = fat). Female physical condition data were available for six females, five juveniles, and one adult, which we sampled in ≥6 of the 13 mo for which these data were collected. Although we also collected physical condition data for the other adult females in focal groups, we could not regularly assess these females and thus data were not continuous enough to document changes throughout the reproductive cycle. We included the data for juvenile females to document seasonal changes in physical condition unrelated to reproduction.

To describe the annual distribution of births, we calculated the average percentage of births during the three consecutive months with the most births as well as the circular statistic mean vector length ($r$). We tested the value of $r$ against a null hypothesis of no clustering via the Rayleigh test (Batschelet 1981) in CircStats 0.2-4 in R 2.12.0. We used Statistica 9.1 to conduct nonparametric analyses to test for the relationship between sampling effort and the number of births observed each month, and for that between latitude and 3-mo birth peaks among Southeast Asian colobine populations.

Research permits were issued by LIPI (Indonesian Institute of Sciences, permit no. 0604/SU/KS/2007) in accordance with the legal requirements of conducting research in Indonesia. All research methods were approved by Stony Brook University's Institutional Animal Care and Use Committee and complied with its regulations (no. 2006-2008-1451).

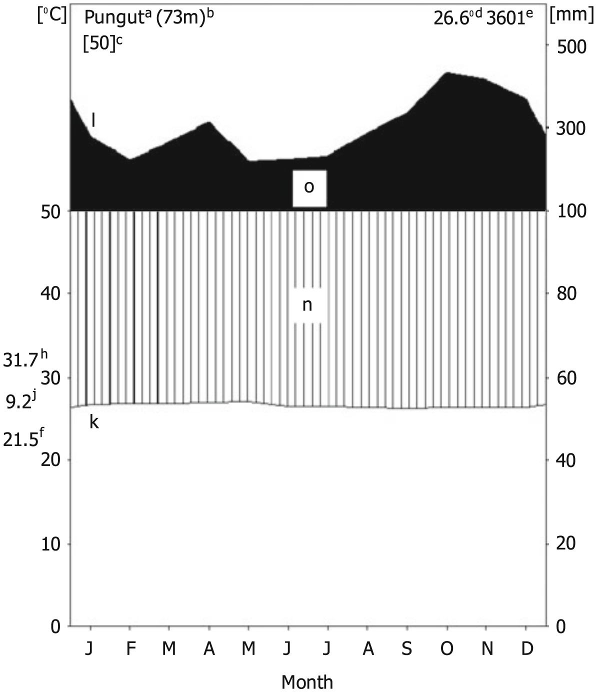
## Results

### Ecology

The climate at the Pungut study site was characterized by warm and wet conditions throughout the year (Fig. 1). Temperature showed almost no variation, with mean monthly temperatures varying between 26.3 and 27.1 °C. Rainfall, however, did vary throughout the year. The wettest period occurred between September and December with a peak in rainfall in October (432 mm). Even in the driest month, however, mean precipitation was >200 mm (219 mm in May) and the climate remained perhumid throughout the year.

Similarly, the phenology of simakobu food species lacked distinct annual variation (Fig. 2). Young leaves and leaf buds were abundant throughout the year (Fig. 2a). Flowers, although less abundant, were also available during most months of the year (Fig. 2b). They were least abundant in December 2008, but most abundant in December 2007, suggesting considerable interannual differences in phytophase availability. This high abundance of flowers was followed by a rise in the availability of unripe fruits 2 mo later, but this was not the largest fruit peak of the year (Fig. 2b). Either unripe or ripe fruits were available in most months, with the exception of May, June, and December 2008. Unripe fruits were most abundant between June and

**Fig. 1** Climate at Pungut between 1950 and 2000 (data obtained from WorldClim), plotted following Walter (1994): a = station; b = elevation above sea level; c = number of observation years; d = mean annual temperature; e = mean annual precipitation; f = mean daily minimum of the coldest month; h = mean daily maximum of the warmest month; j = mean daily temperature fluctuation; k = plot of mean monthly temperature; l = plot of mean monthly precipitation; n = humid period; o = perhumid period.



September, and were also elevated between February and March, while ripe fruits were most abundant in April, October, and November. Taken together, fruits were abundant during 9 mo of the year.

In spite of limited annual variation in food abundance, simakobu feeding time showed high variation across months (Fig. 3). Fruits accounted for an average of 17.1 ± SD 11.80 % (CV=68.9) of feeding time throughout the year, with monthly values ranging from 4.5 % to 42.2 %. Ripe fruits contributed to 25.4 % (range 0–66.7 %) and unripe fruits 70.5 % (range 11.1–100 %) of monthly fruit feeding time. Two distinct peaks of fruit feeding occurred in June (42.2 %) and September (39.5 %) at the start and end of the peak in unripe fruit availability. Flower feeding time was slightly less variable throughout the year (CV=58.5), with flowers accounting for 25.5 ± SD 14.9 % of the average monthly feeding time. Flower feeding peaked in August (59.7 %) and was lowest in June (0 %). Leaves contributed to 50.5 ± SD 12.0 % of average monthly feeding time (range 25.4–67.7 %; CV=23.7), with young leaves and leaf buds accounting for 79.0 % (range 62.2–97.9 %) and mature leaves 11.0 % (range 0–32.4 %) of monthly leaf feeding time. Leaves were the most commonly eaten foods throughout the year, except in January and August, when flowers contributed most to feeding time. Other foods, such as insects, fungus, and moss accounted for 1.1 ± SD 1.3 % (range 0–3.2 %; CV=124.7) of monthly feeding time, and were highest in February (3.1 %) and November–December (3.2 %).

## Reproduction

Births occurred in seven calendar months, with births in the two focal groups —for which data were collected most systematically— covering six of these months (Fig. 4).

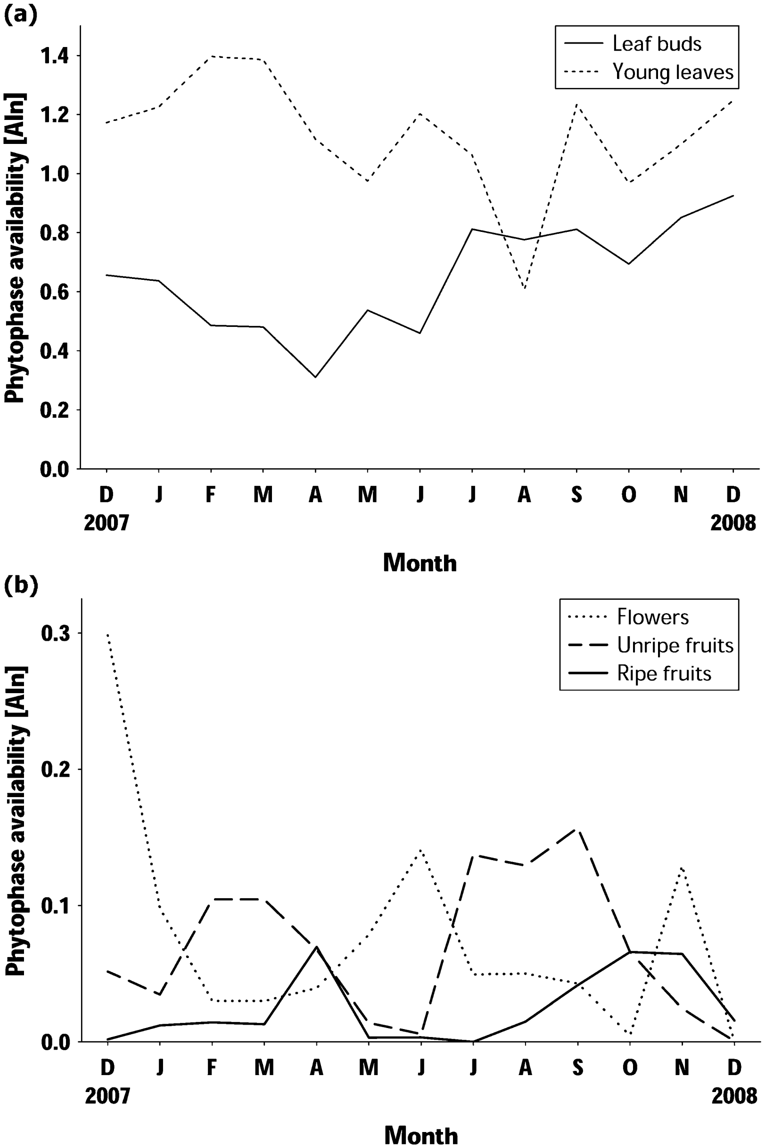
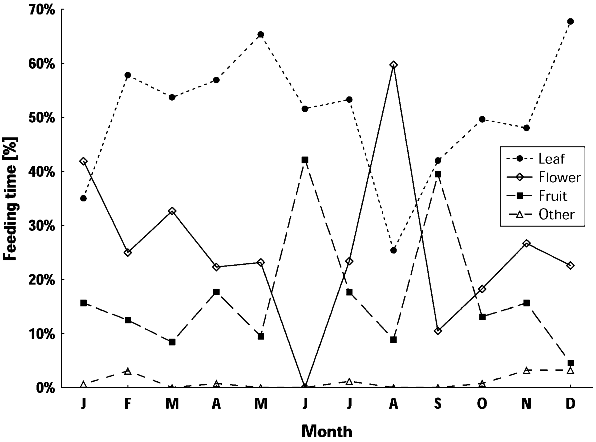


**Fig. 2** Phytophase availability (Marsh's index) for December 2007–December 2008 of the top 21 food species. (**a**) Young leaves and leaf buds. (**b**) Flowers, unripe fruits, and ripe fruits.

There was a peak of six births (55 %) during September and October, which represents the 3-mo birth peak, because there were no births in August or November. This result cannot be explained by a sampling bias, as these 2 mo accounted for 15 % of our observation days (where 16.7 % represents an even distribution) and there was no relationship between the number of days groups were censused and births observed each month (Fig. 4, Kendall's $\tau$=0.06, $P$=0.79, $N$=12). Five of these births (45 %) were in October alone, which is the wettest month of the year (Fig. 1). The circular statistics, however, indicate that the distribution of births did not deviate

**Fig. 3** Percent of feeding time devoted to leaves, flowers, fruits, and other items. Feeding data for December 2007–November 2008.

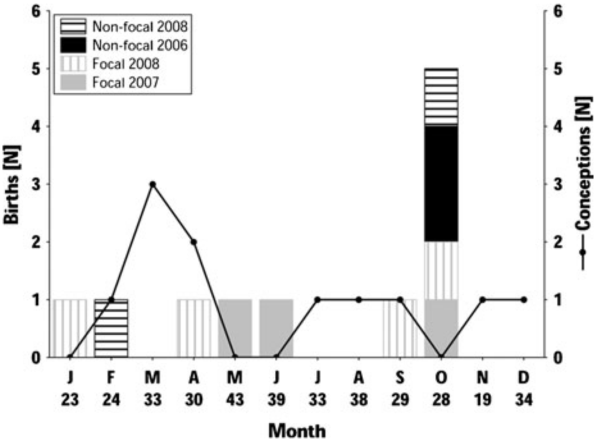


significantly from a uniform distribution (mean vector length $r=0.276$, Rayleigh test of uniformity: $P=0.44$).

Other Southeast Asian colobines for which data are available show similar 3-mo birth peaks, ranging from 33 % to 63 % of births, 45.5 % on average (silvered leaf monkeys, *Trachypithecus cristatus*=33 % [3°21′, $N=76$]: Wolf 1984; Thomas' langurs, *Presbytis thomasi*=38 % [3°30′, $N=13$]: Gurmaya 1986; Javan surili, *Presbytis comata*=50 % [7°11′, $N=12$]: Ruhiyat 1983; red-shanked doucs=63 % [17°15′, $N=19$]: Phiapalath *et al.* 2011). Even within this small data set, we found a positive correlation between latitude and the extent of the birth peak (Kendall's $\tau=1.00$, $P=0.04$, $N=4$), similar to that reported across Hanuman langur populations (Newton and Dunbar 1994). Although simakobu at Pungut reside at a lower latitude (1°3′S) than the other species, their 3-mo birth peak is of greater magnitude than all but the northernmost species (red-shanked doucs at 17°15′N), and when simakobu were added to the aforementioned data set, the correlation disappeared (Kendall's $\tau=0.40$, $P=0.33$, $N=5$).

The 3-mo period with the most conceptions was between February and April, when six (55 %) conceptions occurred (Fig. 4). An additional three (27 %) conceptions occurred between July and September. Both periods coincided with or immediately followed a peak in unripe fruit availability.

**Fig. 4** Annual distribution of births and conceptions in focal and nonfocal groups. Number of group census days indicated below each calendar month.



Juvenile female physical condition was good from April to June and in November 2008, following the two peaks in ripe fruit availability; and poor in March and July (Fig. 5). The adult female conceived after her physical condition had been good for ≥2 mo. It dropped to average for most of her gestation and declined further after parturition, when juvenile females reached their best physical condition of the year.

## Discussion

Siberut has been described as having four indistinct seasons: "two wet, one very wet, and one incredibly wet" (Whitten 1982a, p. 76). We confirmed this characterization by constructing a climate diagram for our study site, which showed consistently warm temperatures and abundant rainfall throughout the year. Most rain fell between September and December, but there was never a month averaging <200 mm of rain. Food was abundant throughout the year. Although there were periods when fruits were more abundant, these peaks were relatively shallow, and even when fruits were scarce, flowers and young leaves were available.

In light of this limited environmental variation, the variation in simakobu feeding behavior, particularly on fruits, is surprising. Although the monthly feeding time on fruits was low during most months (10–20 %), there were 2 mo when fruits accounted for >39 % of feeding time (June and September). The second of these peaks coincided with an increase in ripe fruits as well as the 3-mo birth peak. Although both fruit-feeding peaks coincided with the period of high fruit availability, it is unclear why fruit feeding was low in the 2 mo between peaks. Because one group fed heavily on a rare species of *Ficus* in June, this peak could be a sampling artifact, and the fruit-feeding peak in September might be a better representation of the population on the whole.

As expected, simakobu breeding was not strictly seasonal. Despite an early report that births were restricted to June and July (Tilson 1977: Table I), we documented just one of 11 births in these 2 mo. This difference can likely be attributed to the smaller sample size in the Tilson study, i.e., one birth in one focal group observed year-round.

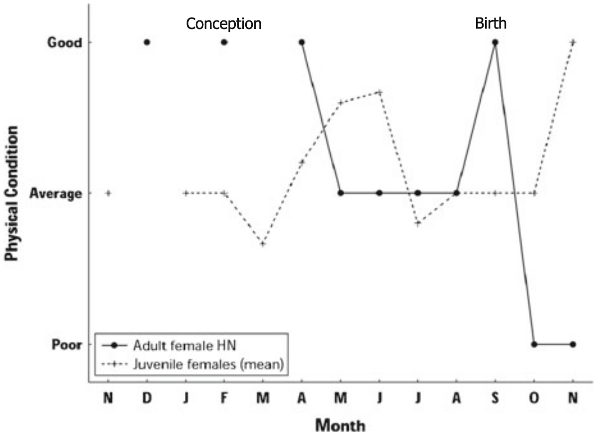


**Fig. 5** Monthly average physical condition for juvenile females vs. that of an adult reproductive female. Adult female's conception and birth months indicated.

**Table I** Known birth months for simakobu

| Month | Tilson 1977 | Watanabe 1981 | Hadi *et al.* 2009 | present study |
|---|---|---|---|---|
| January |  | x |  | x |
| February |  | x |  | x |
| March |  |  |  |  |
| April |  |  |  | x |
| May |  |  |  | x |
| June | x |  |  | x |
| July | x |  |  |  |
| August |  |  |  |  |
| September |  |  |  | x |
| October |  |  |  | x |
| November |  |  | x |  |
| December |  | x | x |  |

The remaining births were based on surveys throughout Siberut and on information from hunters, so there may have been a sampling bias.

It is also possible, however, that ecological differences exist between the study locations that could affect reproduction. For example, birth rates at Sirimuri in southern Siberut (Tilson 1977) were much lower than those at our site in northern Siberut (Erb *et al.* 2012). Though the two sites are only *ca.* 45 km apart, the compositions of the forests are different. Sirimuri is dominated by trees of the family Dipterocarpaceae (Whitten 1982b), which do not produce fleshy fruits and probably do not provide much energy for simakobu, but flowers may be an important fallback food during severe drought (Paciulli 2010). In contrast, Pungut lies within a mixed forest with a higher proportion of fruit trees, and presumably higher food availability (Whittaker 2005). Further, phenology may differ between sites. Data collected at a site *ca.* 6 km from Sirimuri showed patterns in young leaf production nearly identical to those in Pungut, but very different patterns in fruit production, with peaks occurring between April and July (Whitten 1980).

The possibility of intersite differences is further supported by the fact that two other studies in northern Siberut reported that births were concentrated between November and February (Hadi *et al.* 2009; Watanabe 1981; Table I). At Pungut, conversely, only two of 11 births occurred during these months, despite being situated only *ca.* 10 km from the other northern Siberut sites. Alternatively, the differences between studies could indicate differences on a temporal rather than spatial scale. Significant interannual variation, as occurs in habitats characterized by mast-fruiting, could further explain shifts in reproduction across years. We were unable to confirm the occurrence of mast-fruiting events in our study area, as we documented only a single year of phenology and masting cycles are irregular, occurring every 2–10 yr (Ashton *et al.* 1988). The fact that availability of flowers varied greatly between December 2007 and December 2008, however, suggests that there could be considerable variation across years.

Taken together, these studies suggest that simakobu are capable of giving birth in almost every month of the year (Table I). The variation across sites and over time, however, indicates that the timing of birth is most likely influenced by local fluctuations in food availability. Thus, although the population at Pungut and the species collectively lack distinct seasonality of reproduction, individual populations may still display moderate seasonality in the form of seasonal birth peaks whose timing is determined by factors operating at a local level that may vary from year to year.

In the current study, births occurred throughout the year, in most months and were not significantly clustered. However, our sample size was very small and as such this result should be viewed as preliminary. With a sample size of 11 births, an $r$ value >0.50 would have been needed to reach statistical significance. At the same time, the $r$ we observed (0.28) would require a sample size of $N\approx40$ for this result to have been significant. Nonetheless, there was a 3-mo birth peak during the wettest period of the year, when 55 % of births occurred. The fact that at least one birth occurred within October in each year of our study suggests that this may be an important time for reproduction. October was characterized by a decrease in the availability of fruits and an increase in leaves, and occurred *ca*. 6 mo after the first fruit peak of the year (Fig. 2). These observations suggest that simakobu may be capital breeders with conceptions flexibly timed to the recovery of energy reserves of individual females, an idea supported by the data on female physical condition. Although the adult female in this study was in good physical condition before and at conception, and average through most of gestation, she quickly declined to poor condition after birth, which indicates that she was not able to compensate for the increased energetic demands of lactation by increasing energy intake (income breeding). More data covering multiple years are required to confirm this hypothesis.

Although simakobu at Pungut reside at lower latitude than the other Asian colobine species we examined, their 3-mo birth peak was unexpectedly higher. Although this result is perhaps an artifact of small sample sizes, we cannot rule out the possibility that some ecological factors could be responsible for a more seasonal restriction of births in simakobu vs. most other Southeast Asian colobines. The Mentawai Islands differ from other parts of Southeast Asia in having very high rainfall and less fertile soils as well as fewer legumes (Whitten 1980). Thus, although the environment appears to exhibit little seasonality and relatively abundant food year-round, it is possible that low-quality food on Siberut constrains simakobu reproduction. This idea is supported by the observations that leaf quality decreases with increasing rainfall, and that primate population growth is more strongly limited by food quality during the lush season than by food quantity during the lean season (Ganzhorn *et al*. 2003). Future studies of the intra- and interannual patterns of both food quantity and quality are needed to address this hypothesis.

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