

Reproductive Parameters of Wild *Rhinopithecus bieti*

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Keywords

Yunnan snub-nosed monkey · Interbirth interval · Sex ratio · Infant mortality · Age at first parturition · Seasonal birth

Abstract

Animal life activities are rhythmic and affected by seasonal periodicity. Based on 9 years of observations, we estimated the reproductive parameters of a wild, but provisioned Yunnan snub-nosed monkey (*Rhinopithecus bieti*) group at Xiangguqing in Baimaxueshan National Nature Reserve, Yunnan Province, China. We observed 84 infants (43 males and 41 females) from 41 females between 2010 and 2018. We found the birth sex ratio was 1:1, the female age at first birth was 6.13 years and infant mortality was about 15.5%. Nine years of data showed that the maximum birth season lasted 126 days, and the average length per year was 98.57 ± 18.71 days. *R. bieti*, characterized by strictly seasonal reproduction, started giving birth on February 1, and this ended on June 7, with a peak reached from March 4 to March 11 (10th week). The mean birth date was March 20 (79.21 ± 29.54 days), and the median birth date was March 11 (71st day). The mean interbirth interval (IBI) was approximately 2 years, and the IBIs among females whose infants had survived for 1 year were found to be significantly longer than those found in females who lost their infant within 1 year. Comparing the reproduction parameters among Asian and African colobines, we concluded that Asian and African colo-

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bines tend to have an IBI of 2 years or more, females tend to give birth at the age of 5–6 years, *Rhinopithecus* species had a strict seasonal reproductive pattern concentrated in February to April. Seasonal changes in food resources and climatic factors may be the main reasons for the variation in reproductive parameters in intraspecific and interspecific comparisons of Asian and African colobines.

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Introduction

Understanding reproductive parameters is critical for evaluating the conservation status of primate populations [Dunbar, 1988]. For example, knowing reproductive parameters can allow scientists to evaluate population growth, analyze population dynamics, and predict future population trends; they are useful for in situ and ex situ management of wildlife populations [Zhang et al., 2015]. They are also necessary to examine metapopulation dynamics, such as determining the reproductive output of source populations and estimating the minimum viable population size [Smith and McDougal, 1991]. Age at first parturition, interbirth interval (IBI) and infant mortality are critical factors influencing the effectiveness of animal breeding [Fedigan and Griffin, 1996]. To obtain data on reproductive parameters, it is necessary to continuously record the reproductive histories of known individuals for several years, which is extremely difficult for wild primates [Jin et al., 2009]. Long-term reproductive data for colobine species are particularly scarce [Newton and Dunbar, 1994; Kirkpatrick, 2007]. Most Asian and African colobines are not strictly seasonal breeders, but rather have distinct birth peaks during the year, with IBIs of approximately 2 years (Table 1) [Jin et al., 2009]. In contrast, infant mortality and age at first parturition are variable among Asian and African colobines [Jin et al., 2009] (Table 1).

Bias in birth sex ratio has been a highly debated topic in mammalian research, especially in primates [Bercovitch, 2002]. Recent empirical and theoretical work has suggested that, under certain circumstances, females adjust the sex ratio of their progeny [Qi et al., 2008]. The sex allocation theory predicts that in some species, females in good condition (i.e., superior nutrition and health, and low stress) will tend to produce more sons than daughters [Fisher, 1930; Trivers and Willard, 1973]. Such female reproductive flexibility results in diverse sex-biased birth patterns that act to balance fitness benefits and maternal investment [Clutton-Brock et al., 1984; McFarland, 1987; Robinson, 1988; Di Bitetti and Janson, 2001].

Animals' daily activities are rhythmic and affected by seasonal periodicity. Environmental variables such as food supply and climatic factors (e.g., ambient temperature, precipitation and photoperiod, and variation in energy balance) are the ultimate causes of seasonal breeding in all mammals and the proximate cause in many [Herdon, 1983; Crockett and Rudran, 1987a, b; Bronson, 1989; Gevaerts, 1992; Brockman and van Schaik, 2005; Bronson, 2009; Xiang and Sayers, 2009; Tecot, 2010; Huang et al., 2012; Li et al., 2014a]. Relying on external cues such as photoperiod and internal cues such as food abundance, Brockman and van Schaik [2005] proposed two seasonal birth modes – income breeders (give birth before the food peak) and capital breeders (give birth at the end of the food peak). Seasonally breeding species usually inhabit higher latitudes, where food availability and abiotic factors vary as local environments change [Herdon, 1983]. Facing cyclical and hence predictable conditions,

Table 1. Reproduction parameters of African and Asian colobines

Species	Site	Birth season/ birth peak	Age at first parturition, years	IBI, months	Infant mortality	Birth sex ratio (F:M)	Reference
<i>Colobus guereza</i>	Kibale			25.2			Struhsaker and Leland, 1987
<i>Colobus polykomos</i>	Tiwai			24			Dasilva, 1989
<i>Procolobus badius</i>	Kibale	Apr to Jun and Nov (peak)		25.5			Struhsaker and Leland, 1987
<i>Procolobus verus</i>	Tiwai	Nov? to Feb? (peak)					Struhsaker and Leland, 1987
<i>Presbytis thomasi</i>	Ketambe		5.4	22		1:1	Wich et al., 2007
<i>Semnopithecus entellus</i>	Abu			25.4			Hrady, 1974, 1977
	Dharwar	Nov to May (peak)					Sugiyama, 1966, 1967
	Jodhpur	Mar (peak)	3.5	16.7			Sommer et al., 1992
	Kaukori	Apr to May					Dolhinow, 1972
	Kanha	Dec to May			40%		Newton, 1987
	Orcha	weak			24		Dolhinow, 1972
<i>Semnopithecus schistaceus</i>	Melemchi	Feb to Apr		20–24			Bishop, 1979
	Ramnagar	Jan to Jun	6.7	28.8			Borries et al., 1999, 2001
<i>Trachypithecus pileatus</i>	Arunachal Pradesh	Dec to Apr		23.3			Solanki et al., 2007
	Madhupur	Dec to Apr		24			Stanford, 1993
<i>Trachypithecus vetulus</i>	Polonnaruwa	May to Aug (peak)		23			Rudran, 1973
	Horton Plains	no		16.5			Rudran, 1973
<i>Trachypithecus johnii</i>	Nilgiri district	May to Jun		21			Poirier, 1970
<i>Trachypithecus phayrei</i>	Phu Khieo	Dec to Apr (peak)		21.3–24.5			Borries et al., 2008
<i>Trachypithecus leucocephalus</i>	Chongzuo	Nov to Mar (peak)	5–6	23.2	15.80%		Jin et al., 2009
<i>Pygathrix nemaeus</i>	Hin Namno	Jun to Sep					Phiapalath et al., 2011

Table 1 (continued)

Species	Site	Birth season/ birth peak	Age at first parturition, years	IBI, months	Infant mortality	Birth sex ratio (F:M)	Reference
<i>Rhinopithecus bieti</i>	Wuyapiya	Mar/Apr		36	55–60%		Kirkpatrick et al., 1998
	Captive	Dec to Jun	5	20.5	30%	1:4.4	Cui et al., 2006
	Xiaochangdu	Feb to Mar					Xiang and Sayers, 2009
	Mt Lasha	Feb to Apr		24			Huang et al., 2012; Li et al., 2014a
	Xiangguqing	Feb to Apr	5–6	24	15.50%	1:1	our research
<i>Rhinopithecus roxellana</i>	Qinling	Mar to May	5–6	21.9	22.40%	1:1.71	Qi et al., 2008
	Captive	Mar to Jun		18–20			Ren et al., 2003; Zhang et al., 2000
<i>Rhinopithecus brelichi</i>	Captive	Mar to Apr	8.6	38.2			Yang et al., 2009
<i>Simias concolor</i>	Pungut	Sep to Oct (peak)					Erb et al., 2012
<i>Nasalis larvatus</i>	Kinabatangan/ Sukai	weak					Boonratana, 1994

animals tend to align reproduction with periods of relatively abundant resources and suitable climate, improving offspring survival and reducing the risk of maternal death [Crockett and Rudran, 1987a; Goldizen et al., 1988; Di Bitetti et al., 2000; Schoech and Hahn, 2008]. This strategy can allow greater energy storage prior to gestation or minimize nutritional stress during lactation [Huang et al., 2012]. Since animals do not always have enough energy to maintain both reproductive capacity and their own metabolic needs, seasonal breeding maximizes individual fitness by synchronizing energetically demanding periods of the breeding cycle with the season of greatest food availability [Lancaster and Lee, 1965; Di Bitetti et al., 2000; Brockman and van Schaik, 2005; Tecot, 2010].

The endangered Yunnan snub-nosed monkey (*Rhinopithecus bieti*) lives in the eastern Himalayan highlands, bounded by the upper Yangtze River and Mekong Rivers [Long et al., 1994; Xiao et al., 2003; Li et al., 2010; Huang et al., 2012]. *R. bieti* is characterized by a multilevel society [Kirkpatrick et al., 1998; Kirkpatrick and Grueter, 2010; Ren et al., 2012], that is composed of 5–41 breeding units (one-male units, OMUs) and 1 or more all-male units (AMUs) [Grueter and Zinner, 2004; Ren et al., 2012; Grueter, 2013]. In *R. bieti*, females transfer between OMUs, and male offspring also emigrate from their natal unit before sexual maturity [Kirkpatrick, 2007]. More than two decades of studies on wild and captive groups have characterized the reproductive behavior of *R. bieti*. With regard to seasonal birth patterns in captive groups,

Ji et al. [1998] reported that *R. bieti* living at the Kunming Zoo gave birth from January to June. Subsequently, Cui et al. [2006] reported a birth period from December to June, with a birth peak observed from March to May, based on a 10-year study at the Kunming Institute of Zoology and the Kunming Zoo. In wild groups, however, Kirkpatrick et al. [1998] reported a birth season of March to April for *R. bieti* at Wuyapiya. Xiang and Sayers [2009] found tightly synchronized births in their study population as well, with newborns observed from February to March. Huang et al. [2012] and Li et al. [2014a] suggested that wild *R. bieti* typically give birth from February to April.

In this article, we present data on births recorded during systematic censuses of known wild *R. bieti* groups over 9 consecutive years at Xiangguqing, Baimaxueshan National Nature Reserve. We aimed to obtain accurate reproductive parameters of *R. bieti* in Xiangguqing, including (i) birth sex ratio and infant mortality, (ii) birth timing and length of the breeding season and (iii) the IBI of adult females. We also compare these reproductive parameters to those calculated for other Asian and African colobines, then describe the differences among colobines and discuss the proximate factors.

Materials and Methods

Study Areas and Species

Xiangguqing is located in the southernmost region of Baimaxueshan National Nature Reserve, Yunnan Province, China (99°22' E, 27°37' N). The site is approximately 10 km long and 9 km wide, about 90 km² in total area [Li et al., 2014a; Xia et al., 2016]. Xiangguqing contains multiple habitat types including mixed coniferous and deciduous broad-leaf forest, subalpine fir forest, montane sclerophyll oak forest, subtropical evergreen broad-leaf forest, and pine forest. The study group inhabits subtropical evergreen broad-leaf forest, mixed deciduous broad-leaf and conifer forest, and pine forest ranging from 2,600 to 3,200 m in altitude [Xia et al., 2016]. In 2008, staff at Baimaxueshan successfully split a small group of 95 individuals away from a larger wild group, forming a wild-living provisioned group at Xiangguqing [Ren et al., 2012], including 1 AMU with approximately 30 males and 8 OMUs [Li et al., 2013]. The staff fed a small amount of food to them to habituate the monkeys to the researchers. Reserve management has occasionally released individuals from this provisioned group into the wild [Zhu et al., 2016]. From 2010 to 2018, data on a total of 20 OMUs and 1 AMU were collected, from 45 to 93 individuals. Each year, the study group consisted of 5–10 OMUs and 1 AMU. The demographic data recorded each July are shown in Table 2.

Data Collection and Statistical Analyses

We recorded birth data in this group of *R. bieti* over a period of 9 years as part of long-term population monitoring efforts. Rangers provisioned the study group twice daily (around 9:00 and 17:00) in one of several 30 m by 30 m areas located in nearby forest patches where the group naturally ranges and feeds. The monkeys generally used the same provisioning site for 2–3 consecutive days, then moved to another part of their range [Zhu et al., 2016]. When feeding every day, we counted the number of individuals in each unit, identified them and recorded birth data. Birth data included the date of birth along with the sex of the newborn and the name of its mother. We monitored the infant's condition, and in the case of death, we recorded the date of death.

Circular statistics were used to test birth seasonality [Batschelet, 1981; Zar, 1999; Huang et al., 2012; Li et al., 2014b]. We transformed birth dates into the degrees of a circle (360° = 1 year), then calculated mean vector length r to determine whether the birth data were evenly distributed throughout the year. The length of r indicates how observations are spread across the annual cycle. When $r = 1$, all births occur on the same day of year, and when $r = 0$, the births are evenly

Table 2. The demographic data for July of each year in the one-male units (OMUs) and all-male unit (AMU) (2010–2018)

2010					2013					2016				
OMU	AM	AF	J	I	OMU	AM	AF	J	I	OMU	AM	AF	J	I
DGZ	1	2	3	2	DGZ	1	3	3	1	DGZ	1	2	2	1
YDH	1	4	2	3	HL	1	4	2		XS	1	4		1
DB	1	4	2	1	DB	1	5	1		HL	1	4	1	4
SB	1	2	3	1	LHG	1	2	1		DB	1	1	1	
HLG	1	4	3		HC	1		2		LHG	1	1	1	1
XW	1	4	4	3	PG	1	3	2		DS	1	1	1	1
HC	1	4	3	2	AMU	4		7		HD	1	6		3
GS	1		3							LB	1	1	3	1
AMU	7		12							AMU	1		4	
2011					2014					2017				
OMU	AM	AF	J	I	OMU	AM	AF	J	I	OMU	AM	AF	J	I
DGZ	1	4	3		DGZ	1	5	5		DGZ	1	2	3	1
YDH	1	4	5	1	HL	1	5		3	XS	1	4		3
BL	1	3	4		DB	1	3	1	2	HL	1	2	2	
SB	1	3	1		LHG	1	1	1	1	DB	1	1		1
LHG	1	4	3	2	DS	1	4		1	LHG	1	1	2	
XW	1	2	4		AMU	3		5		DS	1	1	2	
HC	1	4	5	2						HD	1	6	3	4
PG	1	2	3							LB	1	1	2	
HD	1	3	6							ML	1	1	2	
AMU	8		8							JG	1	1	2	
										AMU	2		4	
2012					2015					2018				
OMU	AM	AF	J	I	OMU	AM	AF	J	I	OMU	AM	AF	J	I
DGZ	1	6	2	2	DGZ	1	4	5	2	DGZ	1	2	3	1
YDH	1	4	4	2	HL	1	4	3		XS	1	5	3	2
BL	1	2	1	1	DB	1	2	1		HL	1	2	2	2
DZ	1	4	3		LHG	1	2	1		DB	1	1	1	
LHG	1	5	3	1	DS	1	1	1		LHG	1	1	1	1
XW	1	3	3		HD	1	7	1		HD	1	6	7	2
HC	1	7	4	2	LB	1	1	1		LB	1	2	1	1
PG	1	3	2		AMU	3		2		ML	1	3		1
AMU	4		6							CG	1	1	1	
										JG	1	2	1	1
										AMU	2		4	

AM, adult male; AF, adult female; J, juvenile; I, infant; other abbreviations are codes for resident males (i.e., for OMUs).

distributed across the 12 months [Batschelet, 1981]. We used the Kolmogorov-Smirnov test to compare the difference in IBI between females whose infants died before the age of 1 year and those whose infants survived for more than 1 year. All data are presented as means \pm SD. The binominal test was used to detect differences in birth sex ratio. As miscarriages are difficult to observe in the wild, only pregnancies leading to births, including stillbirths, were used for analysis [Qi et al., 2008]. All data were analyzed in SPSS 19.0. Statistical tests were two-tailed, with $p < 0.05$ taken as the threshold for significance:

$$r = \sqrt{\left(\frac{\sum_{i=1}^n f_i \cos a_i}{n}\right)^2 + \left(\frac{\sum_{i=1}^n f_i \sin a_i}{n}\right)^2},$$

where n is the mean of birth dates, and a_i is the angle conversion value of day i .

Results

Sex Ratio and Infant Mortality

During the study period, 41 *R. bieti* females gave birth to 84 infants (43 males and 41 females). The number of males and females born did not significantly differ, so we could not reject the null hypothesis that the birth sex ratio was 1:1 (51.19 vs. 48.81%, binomial test, $p = 0.913$). Among those 84 infants, 13 died in their first year (Fig. 1), a 15.5% mortality rate.

IBIs and Age at First Parturition

On the basis of 43 birth records from 27 continuously fertile mothers, the mean IBI of the monkeys was 719.7 ± 239.7 days (mean \pm SD, $n = 43$, range 293–1,502 days). These IBIs were divided into two categories. The IBI of females whose infants survived for at least 1 year (category A) was 760.5 ± 226.1 days (mean \pm SD, $n = 36$, range 399–1,502 days), whereas the IBI of females who lost their infants within the first year (category B) was 510.1 ± 206.6 days (mean \pm SD, $n = 7$, range 293–740 days). The IBI of category A was significantly longer than that of category B (Kolmogorov-Smirnov test: $Z = 1.381$, $p = 0.023$) (Fig. 1, 2).

Subadult females left their natal unit and began breeding behavior as early as 3–4 years of age, but they did not conceive until they were 5 years of age. The age at first parturition was known for 15 primiparous females, and the mean age was 6.13 years (range: 5–9 years). Of the 15 primiparous females, 4 females first gave birth at the age of 5, 8 females at 6, 1 female at 7, 1 female at 8, and 1 female at 9 (Fig. 1).

Seasonal Birth and Length of the Reproduction Period

Circular statistical tests of periodicity in birth showed that $r > 0.8$, and as births only occurred between February and June (Fig. 3), we conclude that reproduction in *R. bieti* is strictly seasonal. From 2010 to 2018, monkeys began giving birth on the 32nd day of the year (February 1) and finished on the 157th day (June 7), with a peak between March 4 and March 11 (the 10th week of the year). The mean birth date was March 20 (mean \pm SD, 79.21 ± 29.54 , $n = 84$), and the median birth date was March 11 (the 71th day). Out of 84 births for which the date of birth was confirmed, 73 births (86.9%) occurred from February to April. Detailed information for each year is shown in Figures 1 and 4 and Table 3.

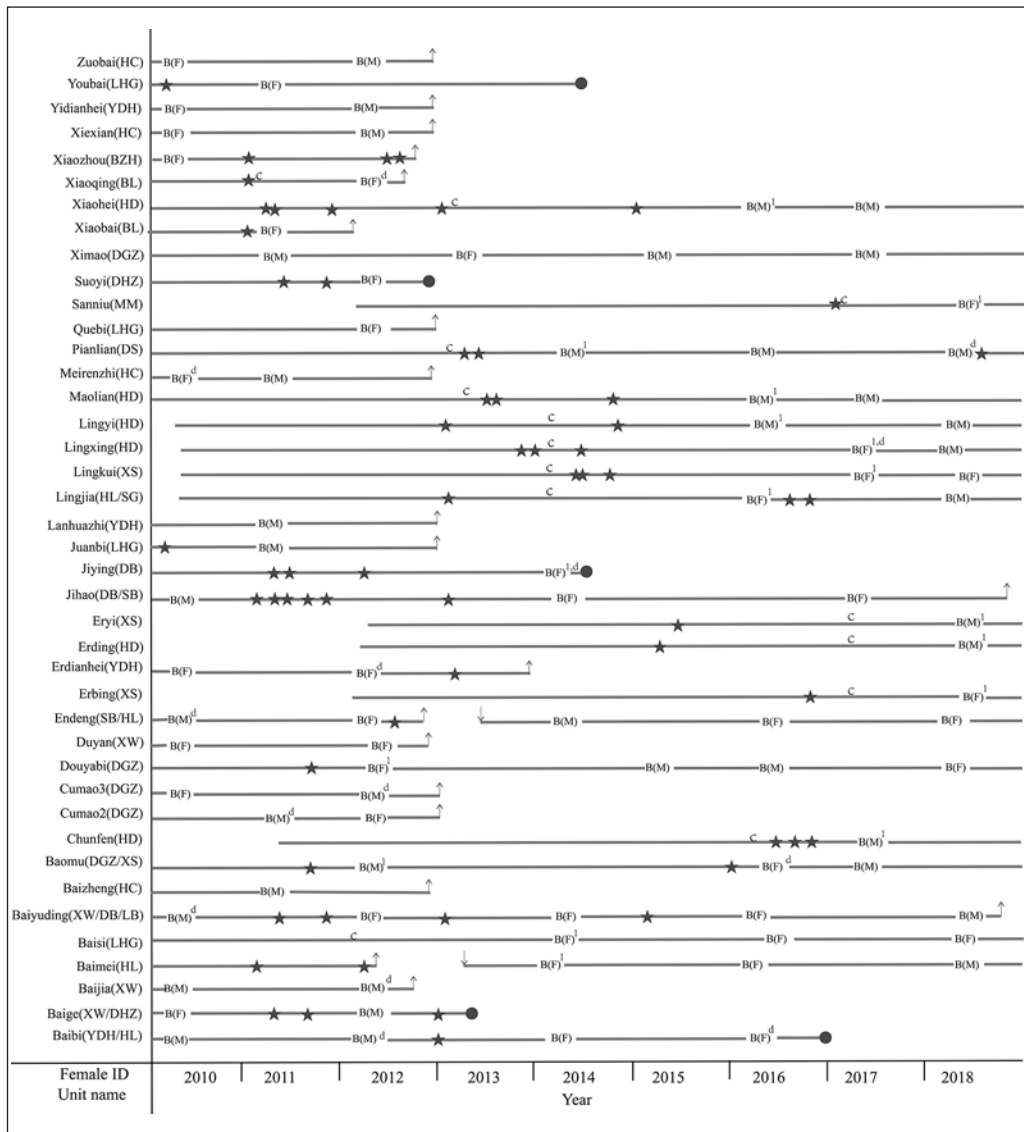
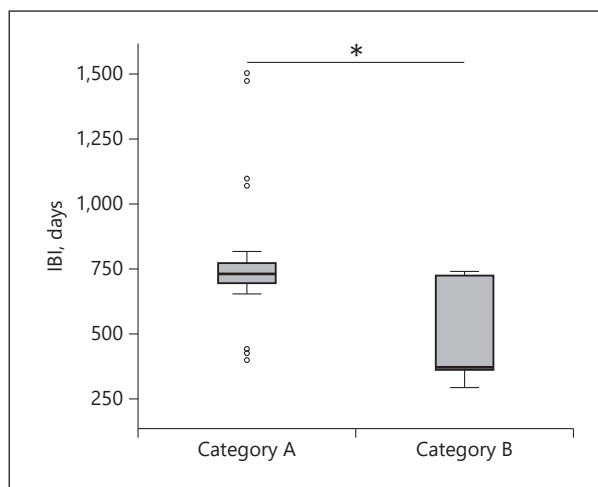


Fig. 1. The birth events during the 9 years from 2010 to 2018. Capital letters in parentheses are codes for the infants' fathers; a different code after a slash represents a replacement male which sired new infant(s). B: birth of infant, F and M in parentheses are sexes of the infants. C: The female reached maturity. ¹First birth; ★, replacement of the original resident male by a new male; ^dInfant died during first year; ●, adult female dead, ↑, emigrated from this troop; ↓, immigrated to this troop.

Fig. 2. Difference in interbirth interval (IBI) for females whose infants survived within the first year (category A) and IBI for females whose infants died within the first year (category B). * $p < 0.05$.



Seven years of observational data indicated a breeding season of 126 days, with mean length per year of 98.57 ± 18.71 days (mean \pm SD, $n = 7$; because only 1 infant was born in 2013 and just 2 were born in 2015, we excluded these years as outliers) (Table 3). Based on Brockman and van Schaik [2005], who proposed two seasonal birth modes, *R. bieti* belongs to the income breeders.

Comparing the Reproduction Parameters among Asian and African Colobines

Limited previously published data suggest that most Asian and African colobines are not strictly seasonal breeders. In contrast, members of the genus *Rhinopithecus* have a strictly seasonal reproduction pattern, mainly concentrated from February to April of each year (with some variation between populations and species: see Table 1). Age at first parturition is relatively uniform among the Asian and African colobines except for captive Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*: 8.6 years) and the gray langur (*Semnopithecus entellus*) in Jodhpur (3.5 years); all other species first give birth around the age of 5–6 years (Table 1). The mean IBI of Asian and African colobines taken together is approximately 2 years except for *R. bieti* at Wuyapiya and captive *R. brelichi* (Table 1).

Discussion and Conclusion

Even Birth Sex Ratio and Lower Infant Mortality in R. bieti

Females in good condition tend to produce more sons than daughters in polygynous species [Fisher, 1930; Trivers and Willard, 1973]. However, we found a newborn sex ratio close to 1:1 at Xiangguqing from 2010 to 2018, with no significant bias toward male infants, and the proportion of males in our study was smaller than that found in captive *R. bieti* [Cui et al., 2006] and wild *R. roxellana* [Qi et al., 2008]. Wild members of the genus *Macaca* seldom produce a biased sex ratio at birth, while macaques living in captivity often do [Zhao and Deng, 1988]. Unlike captive popula-

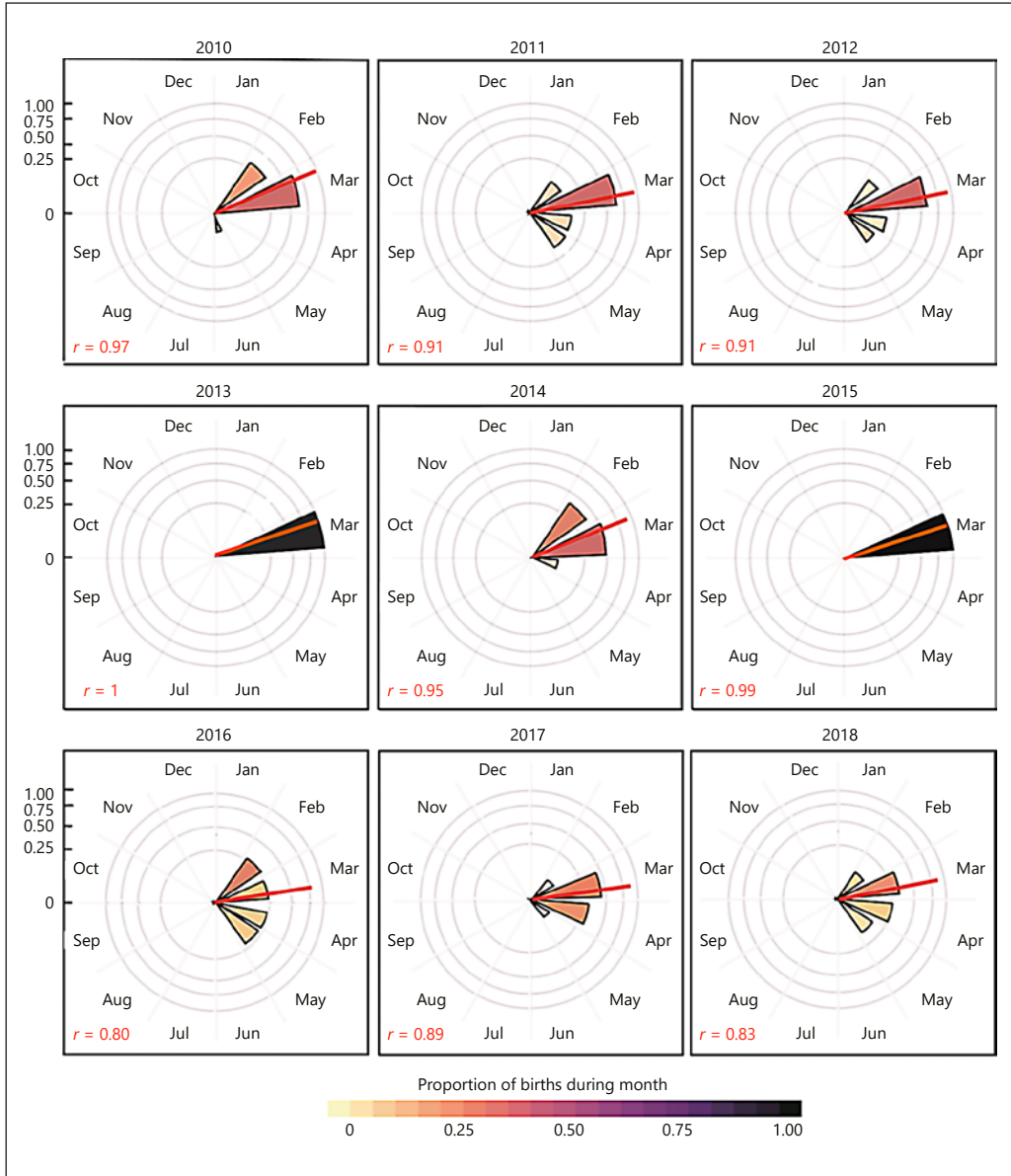


Fig. 3. Circular histograms showing the proportion of births in each month from 2010 to 2018. Note that the radial axis is the proportion of births during the month transformed to exaggerate differences in the lower end of the scale. The red lines show the mean vector (r).

Table 3. Reproductive parameters of *R. bieti* at four study areas

Site	LAL	AMSL, m	Year	Begin	End	Length, days	Mn	Md	Nnb	Nm	Nf	IM	IBI, days	BSR	Data algorithm	Reference
Xiaochangdu (wild)	29°15' N, 98°37' E	3,500–4,250	2005	Feb 4	Mar 14	38	58±6.5	54	37						I/F estimation	Xiang and Sayers, 2009
Xiangguling (provisioned)	27°38' N, 99°21' E	2,600–3,200	2010	Feb 10	Jun 3	114	67±27.19	63	14	5	9	15.5%	722.6±236.9	1:1	accurate data	our research
			2011	Feb 4	May 11	97	76±24.84	72	8	6	2					
			2012	Feb 19	May 30	102	83±25.66	76	17	8	9					
			2013	Mar 20		1	77	77	1	0	1					
			2014	Feb 2	Apr 4	62	61±19.79	62	8	2	6					
			2015	Mar 8	Mar 9	2	66±0.71	66	2	2	0					
			2016	Feb 4	May 27	114	82±37.95	72	13	7	6					
			2017	Feb 24	May 23	89	88±27.75	77	9	7	2					
			2018	Feb 16	Jun 7	112	90±36.25	85	12	6	6					
Mt. Lasha (wild)	26°20' N, 99°15' E	2,900–3,600	2009	Feb 21	Apr 3	42	84±11.58	79	11						I/F estimation	Huang et al., 2012; Li et al., 2014
			2010	Feb 15	Apr 4	49	81±19.48	89	16							
			2011	Feb 19	Apr 12	53	82±17.23	75	13							
			2012	Feb 17	Apr 6	50	86±17.27	86	15							
			2013	Feb 20	Apr 8	48	82±16.9	77	13							
Kunming Zoo (captive)	25°03' N, 102°42' E	1,891	1991–2003	Dec	Jun	~210	107±43		27	22	5	30%	624±150	1:4.4	accurate data	Cui et al., 2006

LAL, latitude and longitude; AMSL, above mean sea level; Begin, End, Length indicate dates of beginning and end of the birth season and its length, respectively; Mn, mean birth date (mean ± SD); Md, median birth date; Nnb, number of newborns; Nm, number of males; Nf, number of females; Im, infant mortality; IBI, interbirth interval; BSR, birth sex ratio (female:male); I/F, infant-to-female ratio.

tions, wild populations lack consistent access to high-quality food, shelter from extreme climates and protection from predators [Berman, 1988; Aureli et al., 1990; Koyama et al., 1992; Nevison et al., 1996]. Harsh conditions in the wild may eliminate the advantage of a male-biased sex ratio at birth.

Infant mortality of *R. bieti* was 15.5% in this study, lower than that observed in another wild population at Wuyapiya [55–60%, Kirkpatrick et al., 1998] and a captive population [30%, Cui et al., 2006]. It was also lower than that found in other colobine species, such as *Semnopithecus entellus* at Ramnagar [50%, Borries, 1997], Kanha [40%, Newton, 1987], *R. roxellana* [22.4%, Qi et al., 2007] and *Trachypithecus leuco-*

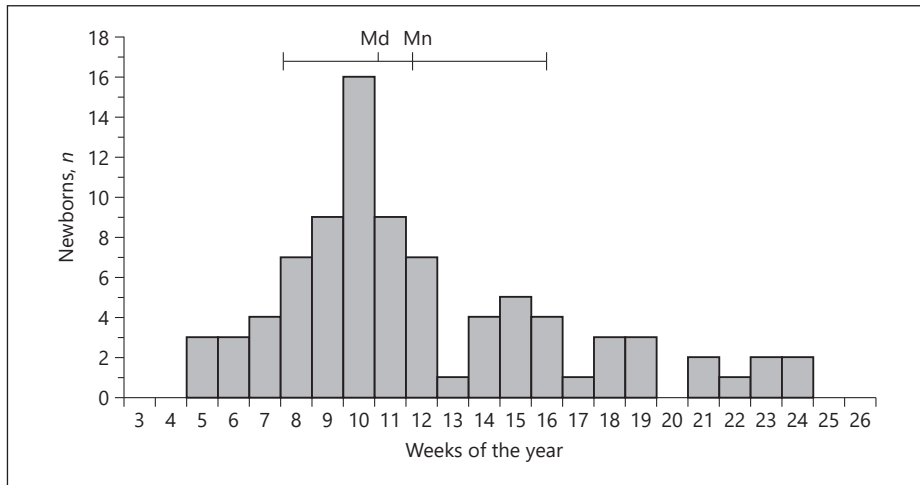


Fig. 4. Birth distribution from 2010 to 2018. Md, median; Mn, mean.

cephalus [15.8%, Jin et al., 2009]. The climate and available food during the birth peak (February to April) are not ideal for wild *R. bieti*, but many can find young leaves to eat during this period [Li et al., 2011]. Jin et al. [2009] speculate that low infant mortality may result from a prolonged lactation period. We hypothesize that infant mortality is a function of lactation period [Jin et al., 2009], infanticide [Ren et al., 2011] and the rate of inexperienced females giving birth, but this requires further testing. A low infant mortality can also be a consequence of the additional food available [Warren et al., 2011], and our result was consistent with the hypothesis that the infant mortality rate of the provisioned group is lower than that of the wild *R. bieti* group at Wuyapiya.

Consistent Mean IBIs in Asian and African Colobines and the Proximate Cause of IBI Length

Previously published data show that the mean IBI across all the Asian and African colobines is approximately 2 years. In primates, prolonged lactation inhibits ovulation and thus prevents pregnancy [Nadler et al., 1981; Frawley et al., 1983; Ziegler et al., 1990]. Maternal infertility during lactation and the mother's own nutritional status determine birth interval length [Clutton-Brock et al., 1984; McFarland, 1987; Robinson, 1988; Di Bitetti and Janson, 2001]. We found the mean IBI for *R. bieti* at Xiangguqing was approximately 2 years, similar to that found in other wild populations of this species [Xiang and Sayers, 2009; Huang et al., 2012; Li et al., 2014a, b], in *R. roxellana* [Qi et al., 2008] and in species such as *M. fuscata*, *M. mulatta* [Takahata et al., 1998] and *M. cyclopis* [Hsu et al., 2001].

In the wild, food is scarce, and infants are highly dependent on their mothers for nutrition in their first year of life [Li et al., 2005]. Wild colobines mainly feed on low-quality food, which barely meets the nutritional requirements of both a newborn and a female preparing for pregnancy. In these cases, the mother preferentially directs

energy towards the infant's growth until it is weaned. Only then will the female begin to build physiological reserves for her next pregnancy. This explains why the mean IBI of females who lose their infants within the first year of birth is significantly shorter than that of females whose infants survive. Similar results were reported for captive *R. bieti* in Kunming [Cui et al., 2006] and in *R. roxellana* [Qi et al., 2008].

Environmental Conditions and Seasonal Reproduction

Brockman and van Schaik [2005] characterize most southeast Asian primates as capital breeders showing moderate birth seasonality. According to this analysis (Table 1), members of the genus *Rhinopithecus* are strictly seasonal breeders, concentrating their births from February to May of each year. Seasonal breeding in primates is related to seasonal variations in climate and the availability of food [Brockman and van Schaik, 2005; Qi et al., 2008; Jin et al., 2009; Xiang and Sayers, 2009; Huang et al., 2012; Erb et al., 2012; Li et al., 2014a, b]. *Rhinopithecus* spp. live at higher altitudes and latitudes than most other colobines, where temporal patchiness in food availability and changes in climate are more pronounced over the course of a year [Newton and Dunbar, 1994; Li et al., 2000]. The pattern of seasonal reproduction for high-latitude species is more apparent than in low-latitude species [Di Bitetti and Janson, 2000], and this may be the proximate cause of seasonality in the births of snub-nosed monkeys as opposed to other colobines.

There are also different reproduction parameters in different geographic populations of the same species (as in *Rhinopithecus* and *Semnopithecus*; Table 1). In addition to the environmental factors mentioned above, other reasons for the differences in reproductive patterns between the populations of *R. bieti* include whether they are wild, provisioned or captive, and how these parameters are calculated. Acquisition and allocation of nutrients are considered the limiting factors controlling the timing of reproduction [Di Bitetti and Janson, 2000; Brockman and van Schaik, 2005; Bronson, 2009]. Synchronizing energy-demanding periods of the breeding cycle with the season having the greatest food availability or quality promotes offspring survival [Lancaster and Lee, 1965; Di Bitetti et al., 2000; Brockman and van Schaik, 2005; Tecot, 2010]. Therefore food supplementation, especially in periods of nutritional stress, will likely improve the body condition of *R. bieti*, thus affecting their reproduction. Our results show an actual breeding season longer than what would be estimated using the infant-to-female ratio (a method of inferring reproductive parameters by the change in the ratio of infants to females) in wild *R. bieti* [Xiang and Sayers, 2009; Huang et al., 2012; Li et al., 2014a, b]. Due to the limitations of field observations, including distance and poor weather conditions, the value of the infant-to-female ratio fluctuates greatly, sometimes yielding estimates that deviate substantially from observed birth patterns and underestimate the length of the birth season [Wang et al., 2012].

In conclusion, we present the first detailed analysis of the reproductive parameters of *R. bieti* in its natural habitat, demonstrating that *R. bieti* has strictly seasonal reproduction. Females typically gave birth for the first time at 6.13 years old, the birth sex ratio was 1:1, 15.5% of infants died within their first year, and IBIs were approximately 2 years. Comparing the reproduction parameters among Asian and African colobines, we concluded that the colobines generally have an IBI of 2 years or more, with females also giving birth for the first time at the age of 5–6 years. Compared with other colobines, snub-nosed monkeys' reproduction is more strictly seasonal, with

births concentrated between February and April. Seasonal changes in food resources and climatic factors most likely drive the variation in reproductive parameters throughout the Asian and African colobines.

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Statement of Ethics

The authors have no ethical conflicts to disclose.

Disclosure Statement

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Author Contributions

Wancai Xia and Dayong Li wrote the manuscript; Wancai Xia, Hong Zhou, Hao Feng and Xinming He collected field data; Xiaofeng Luan, Baoping Ren, Ali Krzton and Majda Aouititen revised the manuscript.

References

- Aureli F, Schino G, Cordischi C, Cozzolino R, Scucchi S, van Schaik CP (1990). Social factors affect secondary sex ratio in captive Japanese macaques. *Folia Primatologica* 55: 176–180.
- Batschelet E (1981). *Circular Statistics in Biology*. London, Academic Press.
- Bercovitch FB (2002). Sex-biased parental investment in primates. *International Journal of Primatology* 23: 905–921.
- Berman CM (1988). Maternal condition and offspring sex ratio in a group of free-ranging rhesus monkeys: an eleven-year study. *American Naturalist* 131: 307–328.
- Bishop NH (1979). Himalayan langurs: temperate colobines. *Journal of Human Evolution* 8: 251–281.
- Boonratana R (1994). *The Ecology and Behaviour of the Proboscis Monkey (Nasalis larvatus) in the Lower Kinabatangan, Sabah*. PhD dissertation, Mahidol University.
- Borries C (1997). Infanticide in seasonally breeding multimale groups of Hanuman langurs (*Presbytis entellus*) in Ramnagar (South Nepal). *Behavioral Ecology and Sociobiology* 41: 139–150.
- Borries C, Koenig A, Winkler P (2001). Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). *Behavioral Ecology and Sociobiology* 50: 391–402.

- Borries C, Larney E, Lu A, Ossi K, Koenig A (2008). Costs of group size: lower developmental and reproductive rates in larger groups of leaf monkeys. *Behavioral Ecology* 19: 1186–1191.
- Borries C, Launhardt K, Epplen C, Epplen JT, Winkler P (1999). Males as infant protectors in Hanuman langurs (*Presbytis entellus*) living in multimale groups – defense pattern, paternity and sexual behaviour. *Behavioral Ecology and Sociobiology* 46: 350–356.
- Brockman DK, van Schaik CP (2005). Seasonality and reproductive function. In *Seasonality in Primates: Studies of Living and Extinct Human and Non-human Primates* (Brockman DK, van Schaik CP, eds.), pp 269–306. Cambridge, Cambridge University Press.
- Bronson FH (1989). *Mammalian Reproductive Biology*. Chicago, University of Chicago Press.
- Bronson FH (2009). Climate change and seasonal reproduction in mammals. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 364: 3331–3340.
- Clutton-Brock TH, Albon SD, Guinness FE (1984). Maternal dominance, breeding success and birth sex ratios in red deer. *Nature* 308: 358–360.
- Crockett CM, Rudran R (1987a). Red howler monkey birth data. I. Seasonal variation. *American Journal of Primatology* 13: 347–368.
- Crockett CM, Rudran R (1987b). Red howler monkey birth data. II. Inter annual, habitat, and sex comparisons. *American Journal of Primatology* 13: 369–384.
- Cui LW, Sheng AH, He SC, Xiao W (2006). Birth seasonality and inter-birth interval of captive *Rhinopithecus bieti*. *American Journal of Primatology* 68: 457–463.
- Dasilva GL (1989). *The Ecology of the Western Black and White Colobus (Colobus polykomos Zimmerman 1780) on a Riverine Island in Southeastern Sierra Leone*. PhD thesis, University of Oxford.
- Di Bitetti MS, Janson CH (2000). When will the stork arrive? Patterns of birth seasonality in neotropical primates. *American Journal of Primatology* 50: 109–130.
- Di Bitetti MS, Janson CH (2001). Reproductive socioecology of tufted capuchins (*Cebus apella nigrinus*) in northeastern Argentina. *International Journal of Primatology* 22: 127–142.
- Di Bitetti MS, Vidal EML, Baldovino MC, Benesovsky V (2000). Sleeping site preference in tufted capuchin monkeys (*Cebus apella nigrinus*). *American Journal of Primatology* 50: 257–274.
- Dunbar RIM (1988). *Primate Social Systems*. London, Croom Helm.
- Dolhinow PJ (1972). The North Indian langur. In *Primate Patterns* (Dolhinow PJ, ed.), pp 181–238. New York: Holt, Rinehart & Winston.
- Erb WM, Borries C, Lestari NS, Hodges JK (2012). Annual variation in ecology and reproduction of wild simakobu (*Simias concolor*). *International Journal of Primatology* 33: 1406–1419.
- Fedigan LM, Griffin L (1996). Determinants of reproductive seasonality in the Arashiyama West Japanese macaques. In *Evolution and Ecology of Macaque Societies* (Fa JE, Lindburg DG, eds.), pp 369–388. Cambridge, Cambridge University Press.
- Fisher RA (1930). *The Genetical Theory of Natural Selection*. New York, Dover Publications.
- Frawley LS, Mulchahey JJ, Neill JD (1983). Nursing induces a biphasic release of prolactin in rhesus monkeys. *Endocrinology* 112: 558–561.
- Gevaerts H (1992). Birth seasons of *Cercopithecus*, *Cercocebus* and *Colobus* in Zaire. *Folia Primatologica* 59: 105–113.
- Goldizen AW, Terborgh J, Corejo F, Porras DT, Evans R (1988). Seasonal food shortage, weight loss, and the timing of births in saddleback tamarins (*Saguinus fuscicollis*). *Animal Ecology* 57: 893–901.
- Grueter CC (2013). *The Biology of Snub-Nosed Monkeys, Douc Langurs, Proboscis Monkeys, and Simakobu*. New York, Nova Biomedical.
- Grueter CC, Zinner D (2004). Nested societies, convergent adaptations of baboons and snub nosed monkeys. *Primate Report* 70:1–98.
- Herndon JG (1983). Seasonal breeding in rhesus monkeys: influence of the behavioral environment. *American Journal of Primatology* 5: 197–204.
- Hrdy SB (1974). Male-male competition and infanticide among the langurs (*Presbytis entellus*) of Abu, Rajasthan. *Folia Primatologica* 22: 19–58.
- Hrdy SB (1977). *The Langurs of Abu: Female and Male Strategies of Reproduction*. Cambridge, Harvard University Press.
- Hsu MJ, Agoramoorthy G, Lin JF (2001). Birth seasonality and interbirth intervals in free ranging Formosan macaques, *Macaca cyclopis*, at Mt. Longevity, Taiwan. *Primates* 42: 15–25.
- Huang ZP, Cui LW, Scott MB, Wang SJ, Xiao W (2012). Seasonality of reproduction of wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Mt. Lasha, Yunnan, China. *Primates* 53: 237–245.
- Ji WZ, Zou RJ, Shang EY, Zhou HW, Yang SC, Tian BP (1998). Maintenance and breeding of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in captivity. In *The Natural History of the Doucs and Snub-Nosed Monkeys* (Jablonski NG, ed.), pp 323–335. Singapore, World Scientific.
- Jin T, Wang DZ, Zhao Q, Yin LJ, Pan WS (2009). Reproductive parameters of wild *Trachypithecus leucocephalus*: seasonality, infant mortality and interbirth interval. *American Journal of Primatology* 71: 558–566.

- Kirkpatrick RC (2007). The Asian colobines: diversity among leaf-eating monkeys. In *Primates in Perspective* (Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK, eds.), pp 186–200. New York, Oxford University Press.
- Kirkpatrick RC, Grueter CC (2010). Snub-nosed monkeys: multilevel societies across varied environments. *Evolutionary Anthropology* 19: 98–113.
- Kirkpatrick RC, Long YC, Zhong T, Xiao L (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *International Journal of Primatology* 19: 13–51.
- Koyama N, Takahata Y, Huffman MA, Norikoshi K, Suzuki H (1992). Reproductive parameters of female Japanese macaques: thirty years data from the Arashiyama troops, Japan. *Primates* 33: 33–47.
- Lancaster JB, Lee RB (1965). The annual reproductive cycle in monkeys and apes. In *Primate Behavior* (Devore I, ed.), pp 486–513. New York, Holt, Rinehart & Winston.
- Li BG, Chen C, Ji WH, Ren BP (2000). Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatologica* 71: 375–386.
- Li DY, Ren BP, Li BG, Li M (2010). Range expansion as a response to increasing group size in the Yunnan snub-nosed monkey. *Folia Primatologica* 81: 315–329.
- Li DY, Ren BP, He XM, Hu G, Li BG, Li M (2011). Diet of *Rhinopithecus bieti* at Xiangguqing in Baimaxueshan National Nature Reserve (in Chinese). *Acta Theriologica Sinica* 31: 338–346.
- Li JF, He YC, Huang ZP, Wang SJ, Xiang ZF, Zhao JJ (2014a). Birth seasonality and pattern in black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Mt. Lasha, Yunnan. *Zoological Research* 35: 474–484.
- Li TF, Ren BP, Li DY, Zhu PF, Li M (2013). Mothering style and infant behavioral development in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in China. *International Journal of Primatology* 34: 681–695.
- Li YH, Li BG, Tan LC (2005). Behavioral development of individuals within one-year-old individuals of Sichuan snub-nosed monkeys *Rhinopithecus roxellana* in the Qinling Mountains. *Acta Zoologica Sinica* 51: 953–960.
- Li YH, Li DY, Ren BP, Hu J, Li BG, Krzton A, Li M (2014b). Differences in the activity budgets of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) by age-sex class at Xiangguqing in Baimaxueshan Nature Reserve, China. *Folia Primatologica* 85: 335–342.
- Long YC, Kirkpatrick RC, Zhong T, Xiao L (1994). Report on the distribution, population, and ecology of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*). *Primates* 35: 241–250.
- McFarland SM (1987). Sex ratio and maternal rank in wild spider monkeys: when daughters disperse. *Behavioral Ecology and Sociobiology* 20: 421–425.
- Nadler RD, Graham CE, Collins DC, Kling OR (1981). Postpartum amenorrhea and behavior of apes. In *Reproductive Biology of the Great Apes* (Graham CE, ed.), pp 69–81. London, Academic Press.
- Nevison CM, Rayment FDG, Simpson MJA (1996). Birth sex ratios and maternal social rank in a captive colony of rhesus monkeys (*Macaca mulatta*). *American Journal of Primatology* 39: 123–138.
- Newton PN (1987). The social organization of forest Hanuman langurs (*Presbytis entellus*). *International Journal of Primatology* 8: 199–232.
- Newton PN, Dunbar RIM (1994). Colobine monkey society. In *Colobine Monkeys: Their Ecology, Behaviour and Evolution* (Davies AG, Oates JF, eds.), pp 311–346. Cambridge, Cambridge University Press.
- Phiapalath P, Borries C, Suwanwaree P (2011). Seasonality of group size, feeding, and breeding in wild red-shanked douc langurs (Lao PDR). *American Journal of Primatology* 73: 1134–1144.
- Poirier FE (1970). The Nilgiri langur (*Presbytis johnii*) of South India. In *Primate Behavior: Developments in Field and Laboratory Research* (Rosenblum RA, ed.), pp 251–383. New York, Academic Press.
- Qi XG, Li BG, Ji WH (2008). Reproductive parameters of wild female *Rhinopithecus roxellana*. *American Journal of Primatology* 70: 311–319.
- Ren BP, Li DY, Garber PA, Li M (2012). Fission-fusion behavior in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) in Yunnan, China. *International Journal of Primatology* 33: 1096–1109.
- Ren BP, Li DY, He XM, Qiu J, Li M (2011). Female resistance to invading males increases infanticide in langurs. *PLoS One* 6: e18971.
- Ren BP, Zhang SY, Xia SZ, Li QF, Liang B, Lu MQ (2003). Annual reproductive behavior of *Rhinopithecus roxellana*. *International Journal of Primatology* 24: 575–589.
- Robinson JG (1988). Demography and group structure in wedge-capped capuchin monkeys, *Cebus olivaceus*. *Behaviour* 104: 202–232.
- Rudran R (1973). The reproductive cycles of two subspecies of purple-faced langurs (*Presbytis senex*) with relation to environmental factors. *Folia Primatologica* 19: 41–60.
- Schoech SJ, Hahn TP (2008). Retracted article: Latitude affects degree of advancement in laying by birds in response to food supplementation: a meta-analysis. *Oecologia* 157: 369–376.
- Smith JLD, McDougal C (1991). The contribution of variance in lifetime reproduction to effective population size in tigers. *Conservation Biology* 5: 484–490.

- Solanki GS, Kumar A, Sharma BK (2007). Reproductive strategies of *Trachypithecus pileatus* in Arunachal Pradesh, India. *International Journal of Primatology* 28: 1075–1083.
- Sommer V, Srivastava A, Borries C (1992). Cycles, sexuality, and conception in free-ranging langurs (*Presbytis entellus*). *American Journal of Primatology* 28: 1–27.
- Stanford CB (1993). The capped langur in Bangladesh: behavior ecology and reproductive tactics. *International Journal of Primatology* 14: 511–512.
- Struhsaker TT, Leland L (1987). Colobines: infanticide by adult males. In *Primate Societies* (Smuts B, Wrangham RW, Cheney DL, Struhsaker TT, Seyfarth RM, eds.), pp 83–97. Chicago, University of Chicago Press.
- Sugiyama Y (1966). An artificial social change in a hanuman langur troop (*Presbytis entellus*). *Primates* 7: 41–72.
- Sugiyama Y (1967). Social organization of hanuman langurs. In *Social Communication among Primates* (Altmann S, eds.), pp 221–236. Chicago, University of Chicago Press.
- Takahata Y, Suzuki S, Agetsuma N, Okayasu N, Sugiura H, Takahashi H, Yamagiwa J, Izawa K, Furuichi T, Hill DA, Maruhashi T, Saito C, Saito S, Sprague DS (1998). Reproduction of wild Japanese macaque females of Yakushima and Kinkazan Islands: a preliminary report. *Primates* 39: 339–349.
- Tecot SR (2010). It's all in the timing: birth seasonality and infant survival in *Eulemur rubriventer*. *International Journal of Primatology* 31: 715–735.
- Trivers R, Willard D (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science* 179: 90–92.
- Wang SJ, Huang ZP, He YC, He XD, Li DH, Sun J, Cui LW, Xiao W (2012). Mating behavior and birth seasonality of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Mt. Lasha (in Chinese). *Zoological Research* 33: 241–248.
- Warren Y, Higham JP, Maclarnon AM, Ross C (2011). Crop-raiding and commensalism in olive baboons: the costs and benefits of living with humans. In *Primates of Gashaka II* (Sommer V, Ross C, eds.), pp 359–384. New York, Springer.
- Wich SA, Steenbeek R, Sterck EHM, Korstjens AH, Willems EP, van Schaik CP (2007). Demography and life history of Thomas langurs (*Presbytis thomasi*). *American Journal of Primatology* 69: 641–651.
- Xia WC, Ren BP, Li YH, Hu J, He XM, Krzton A, Li M, Li DY (2016). Behavioural responses of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) to tourists in a provisioned monkey group in Baimaxueshan Nature Reserve. *Folia Primatologica* 87: 349–360.
- Xiang ZF, Sayers K (2009). Seasonality of mating and birth in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Xiaochangdu, Tibet. *Primates* 50: 50–55.
- Xiao W, Ding W, Cui LW, Zhou RL, Zhao QK (2003). Habitat degradation of *Rhinopithecus bieti* in Yunnan, China. *International Journal of Primatology* 24: 389–398.
- Yang MY, Sun DY, Zinner D, Roos C (2009). Reproductive parameters in Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*). *American Journal of Primatology* 71: 266–270.
- Zar JH (1999). *Biostatistical Analysis*, 4th ed. Upper Saddle River, Prentice Hall.
- Zhang FH, Wu SB, Yang L, Zhang L, Sun RY, Li SS (2015). Reproductive parameters of the Sunda pangolin, *Manis javanica*. *Folia Zoologica* 64: 129–135.
- Zhang SY, Liang B, Wang LX (2000). Seasonality of matings and births in captive Sichuan golden monkeys (*Rhinopithecus roxellana*). *American Journal of Primatology* 51: 265–269.
- Zhao QK, Deng ZY (1988). *Macaca thibetana* at Mt. Emei, China. II. Birth seasonality. *American Journal of Primatology* 16: 261–268.
- Zhu PF, Ren BP, Garber PA, Xia F, Grueter CC, Li M (2016). Aiming low: a resident male's rank predicts takeover success by challenging males in Yunnan snub-nosed monkeys. *American Journal of Primatology* 78: 974–982.
- Ziegler TE, Widowski TM, Larson ML, Snowdon CT (1990). Nursing does affect the duration of the postpartum to ovulation interval in cotton-top tamarins (*Saguinus oedipus*). *Journal of Reproduction and Fertility* 90: 563–570.