



# Mothering Style and Infant Behavioral Development in Yunnan Snub-Nosed Monkeys (*Rhinopithecus bieti*) in China

Tengfei Li · Baoping Ren · Dayong Li ·  
Pingfen Zhu · Ming Li

Received: 11 December 2012 / Accepted: 17 April 2013 / Published online: 16 June 2013  
© Springer Science+Business Media New York 2013

**Abstract** Considerable variation in mothering styles is found among primate species, which may be directly related to species-typical differences in social structure, dominance style, patterns of infant development, and rates of intragroup aggression. We predicted that, as egalitarian Asian colobines, mothers of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) would adopt a mothering style characterized by low restrictiveness and low rejection. We followed six mother–infant dyads in a provisioned group of *Rhinopithecus bieti* inhabiting the Baimaxueshan National Nature Reserve, Yunnan, China, and collected 717.2 h of observational data on maternal care and infant development. In the first month after birth, infants were completely dependent on their mothers for nutrition and movement. They began to locomote clumsily during their second month of life. Mothers restricted the movements of their infants only during their first 2 mo of life. Maternal rejection occurred infrequently and never exceeded a mean of two events per hour for a given infant over any 1-mo period. Most rejections were mild, and did not result in a cessation of nursing. Infants were not weaned when they were 12 mo old. Our study offers support for the contention that females of *Rhinopithecus bieti* adopt a relaxed mothering style in caring for offspring during their first year of life.

**Key words** Infant development · Maternal behavior · Mothering style · *Rhinopithecus bieti*

---

T. Li · B. Ren · D. Li · P. Zhu · M. Li (✉)

Key Laboratory of Animal Ecology and Conservation Biology, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China  
e-mail: lim@ioz.ac.cn

T. Li · P. Zhu

Graduate School of the University of Chinese Academy of Sciences, Beijing 100049, China

D. Li

College of Life Sciences, China West Normal University, Nanchong, Sichuan 637002, China

## Introduction

Mother–infant interactions are critical for offspring survival and female reproductive success (Hrdy 1999). Compared with other mammals of similar body size, primate infants are altricial for a prolonged period of time before they can survive independently (Kappeler *et al.* 2003; Ross 1998). The age when the infants are capable of independent foraging, locomotion, and social interaction with group members varies among primate species, and postnatal maternal care can last for 2 mo to several years, while weaning generally occurs when infants have reached about one-third of adult body mass (Kappeler *et al.* 2003).

Marked variation in mothering styles is found among primate species both in captivity and in the wild (Maestriperieri 1994b). Generally, mothering style is evaluated based on two main factors: protectiveness and rejection (Fairbanks and McGuire 1987; Simpson and Howe 1980; Tanaka 1989). Protectiveness is positively associated with maternal postnatal investment and the type of care and protection mothers provide their dependent offspring (Bardi *et al.* 2001). Rejection, in contrast, occurs as mothers begin to discourage ventral contact with their infants, refuse to provide milk, and reduce other forms of caregiving either temporarily or permanently (Su *et al.* 1992). The mother–infant conflict hypothesis suggests that maternal rejection ensues because of a trade-off that mothers experience between investing in current infants and future offspring (Lee 1996; Trivers 1974). The timing hypothesis (Altmann 1980; Dunbar and Dunbar 1988) posits that mother–infant conflict is more about the timing rather than the amount of investment in offspring, i.e., maternal rejection adjusts infant suckling time so that nursing behavior does not interfere with the mother's activity. Spatial (proximity to infant) and temporal (length of period of infant care) differences in the manner in which mothers interact with, protect, and reject their offspring, especially during weaning, are used to distinguish maternal style across primate species (Maestriperieri 1994b).

Previous studies of cercopithecines have shown that rhesus macaques (*Macaca mulatta*) adopt a controlling mothering style, in which mothers are both highly protective of their infants and actively reject them (Hinde and Simpson 1975). Maternal rejection in *Macaca mulatta* began as early as in the first month of infant life and peaked between 10 and 12 mo of age, which resulted in significantly reduced infant contact seeking behavior (Hinde and Spencer-Booth 1967). In contrast, stump-tail macaque mothers (*Macaca arctoides*) scored low on both protectiveness and rejection measures, so the mothering style was characterized as laissez-faire or relaxed (Altmann 1980; Maestriperieri 1994a). The differences in mothering styles between macaque species were related to differences in the species-typical social structure and dominance hierarchies (Maestriperieri 1994a). For example, conflicts in *Macaca mulatta* have been characterized as severely aggressive, with individuals displaying reduced social tolerance and less frequent affiliative interactions (despotic social style) compared with *M. arctoides*, which are described as expressing high rates of affiliative behaviors that reduce social tension (de Waal and Luttrell 1989; Thierry 1990). Under these conditions, mothers of *Macaca mulatta* are expected to be highly vigilant and protect their infants from intragroup aggression, but in addition encourage offspring independence by frequent rejection in order for them to achieve the ability to self-protect early (Maestriperieri 1993a,b). Given that the frequency and severity of aggression are significantly lower in egalitarian species such as *Macaca arctoides*,

mothers are expected to be more relaxed and permissive in allowing their offspring to be socially and temporally separated from them and in expanding the set of social partners their offspring interact with (Maestriperieri 1994a).

Female colobines are generally noted for their lower rates of intragroup aggression, less pronounced dominance hierarchies, and more egalitarian social relationships when compared with many species of cercopithecines (Newton and Dunbar 1994; Struhsaker and Leland 1987). The interactions among factors including phylogeny, feeding ecology, digestive strategies, opportunities for infanticide, and reproductive competition are expected to exert a strong influence on primate social structure and dominance style (Maestriperieri 1994b). Colobines heavily exploit foliage, but also turn to fruits and seeds whenever available (Kirkpatrick 2007). Leaves are often described as a relatively abundant and nonpatchily distributed resource that could blunt the food competition and reduce intragroup aggression in colobines (Sterck *et al.* 1997; Yeager and Kool 2000).

The most common form of social structure reported for Asian colobines is a one-male, multifemale group (OMU), with extragroup males forming all-male, nonreproductive units (AMU) (Yeager and Kool 2000). Because colobine females do not regularly engage in aggressive competition with females of their own group, it has been hypothesized that colobine mothering styles should be more permissive than that of cercopithecine females (Moore 1992). The ecological and behavioral differences between colobines and cercopithecines offer a framework for investigating mothering styles in primate species characterized by different types of social relationships (Maestriperieri 1994b). Mother–infant relationships and infant development have been described in several colobine species, such as Hanuman langurs (*Semnopithecus entellus*: Sugiyama 1965), Nilgiri langurs (*Trachypithecus johnii*: Poirier 1968), white-headed langurs (*Trachypithecus leucocephalus*: Zhao *et al.* 2008), and Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*: Li *et al.* 2005, 2011) (Table I).

**Table I** Major landmarks in infant behavioral development for *Rhinopithecus bieti*, *R. roxellana*, *Trachypithecus leucocephalus*, *Macaca mulatta*, and *Cercopithecus miti*

	Yunnan snub-nosed monkey ( <i>R. bieti</i> )	Sichuan snub-nosed monkey ( <i>R. roxellana</i> )	White-headed langur ( <i>T. leucocephalus</i> )	Rhesus monkey ( <i>M. mulatta</i> )	Blue monkey ( <i>Cercopithecus mitis</i> )
Exploring ventrum	2	2	14–35	3	3
Break contact with mothers	17	15	28–35	9	5
Move more than an arm’s reach from their mothers	39	37	56–63	13	9
Social play	81	92	63–70	21–28	—
Swallow solid food	98	99	21–42	21	44
Source	This study	Li <i>et al.</i> (2005)	Zhao <i>et al.</i> (2008)	Hinde <i>et al.</i> (1964)	Forster and Cords (2002)

Ages are in days

We present data on maternal behavior and infant development in Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), an endangered species of Asian colobine. These monkeys inhabit northwestern Yunnan and southeastern Tibet, China, where they live at the highest altitude of any nonhuman primate species (2650–4500 m a.s.l.) (Li *et al.* 2008; Long *et al.* 1994). *Rhinopithecus bieti* appears to be a highly seasonally breeder, with the birth season beginning in February and ending in April (Huang *et al.* 2012; Xiang and Sayers 2009). The mean interbirth interval is *ca.* 24 mo (Cui *et al.* 2006). *Rhinopithecus bieti* has a diet dominated by lichens, which are seasonally complemented with young leaves, fruits, and flowers (Grueter *et al.* 2009; Kirkpatrick *et al.* 2001). Lichens are abundant and nonpatchily distributed in the habitat of *Rhinopithecus bieti* (Kirkpatrick *et al.* 1998). The lichen-eating habit probably has profound influences on the social system of *Rhinopithecus bieti*, as it relaxes food competition and thus permits the formation of large groups (Kirkpatrick *et al.* 1998). Group size varies from 50 to 480 individuals (Li *et al.* 2010; Long *et al.* 1994), and groups comprise several distinct OMUs and AMUs (Kirkpatrick *et al.* 1998). This multi-level system is upheld via mutual tolerance among neighboring units, but aggression does occur when units approach each other too closely or a contestable resource is at stake (Grueter *et al.* 2013; Kirkpatrick 1996). Compared with many cercopithecines, *Rhinopithecus bieti* is a “tolerant” Asian colobine with low levels of aggression within family units, rare severe conflict, and high conciliatory tendency (Grueter 2004; Kirkpatrick *et al.* 1998). Aggression toward infants is rare, and infanticide does not appear to represent a common male or female reproductive strategy (Ren *et al.* 2011). Only two cases of infanticide have been reported in *Rhinopithecus bieti*, and one of these appears to have been accidental (Ren *et al.* 2011; Xiang and Grueter 2007). Given high levels of intragroup social tolerance, and the absence of adult male or female aggression directed at infants, we predicted that females of *Rhinopithecus bieti* adopt a relaxed mothering style characterized by low restrictiveness and low rejection compared with *Macaca mulatta*. If mothers rejected infants in favor of sexual behavior, then this would support the mother–infant conflict hypothesis. If mothers rejected infants when mothers were feeding, then this would provide some support for the timing hypothesis.

## Materials and Methods

### Study Site and Subjects

We conducted this study at Xiangguqing (99°20'E, 27°30'N) in Baimaxueshan National Nature Reserve, Yunnan Province, China from December 2009 to March 2011. The focal group of Yunnan snub-nosed monkey (*Rhinopithecus bieti*) has been provisioned two or three times per day since 2008, but the provisioning food accounts for only a small proportion of their diet. The monkeys are well habituated to observers and can be approached to within 5–30 m (Ren *et al.* 2011). The focal group consists of *ca.* 90 monkeys belonging to seven to nine OMUs and one AMU. We classified the individuals into six age/sex categories: adult males, adult females, subadult males, subadult females, juveniles, and infants (Kirkpatrick 1996; Li *et al.* 2010). Each individual can be recognized by its unique set of physical features, which include distinctive hair patterns, facial features, scars, and body size. During the 2010 birth season, we selected six mother–infant dyads as our focal subjects for which we knew the birth dates of the

infants and the mothers' parity and rank (Table II). Maternal rank was based on the feeding superiority and displacement behaviors in their OMU (Zhang 2012).

Data Collection and Analysis

Behavioral observations began at 08:00 and 09:30 h, and ended at 17:30–19:00 h when the monkeys returned to their nocturnal sleeping sites. We divided the day into three periods (morning feeding time: 08:00–11:00 h; resting time: 11:00–15:30 h; afternoon feeding time: 15:30–19:00 h) based on the routine diurnal activity pattern of this species. We attempted to obtain equal amounts of data on each of the different dyads across all three activity periods.

Using a focal sampling method (Altmann 1974), we began by selecting a mother–infant dyad that was nearby and recorded data continuously until they moved out of view. The mean length of a focal observation session was  $62.6 \pm SE 4.0$  min ( $N = 688$ ). Data collection included mother–infant interactions, the mother's activity, and infant's behavior (Table III). For behavioral states, we recorded the type of behavior and its duration in seconds, so the percentage of time spent performing it could be calculated. For behavioral events, we described the discrete incident, from which we determined the frequency of occurrence. We recorded aggression toward infants *ad libitum* (Martin and Bateson, 1993).

We followed each mother–infant dyad for 1 yr after the birth of the infant, yielding a total of 717.2 observation hours (mean =  $119.53 \pm SE 1.82$  h per dyad). We used the Kruskal–Wallis test to analyze differences in mother–infant behaviors between difference infant ages (SPSS 16.0). All tests were two-tailed and we set the level of significance at 0.05.

Our study complied with protocols approved by the State Forestry Administration of China and adhered to the legal requirements of China.

Results

Nipple Contact and Physical Contact with Mothers

During their first day of life, infants spent the majority of their daylight time (95.3%) in contact with their mother's nipple. Mothers sometimes held the newborn's head to facilitate nursing. There was a significant difference in the percentage of time infants

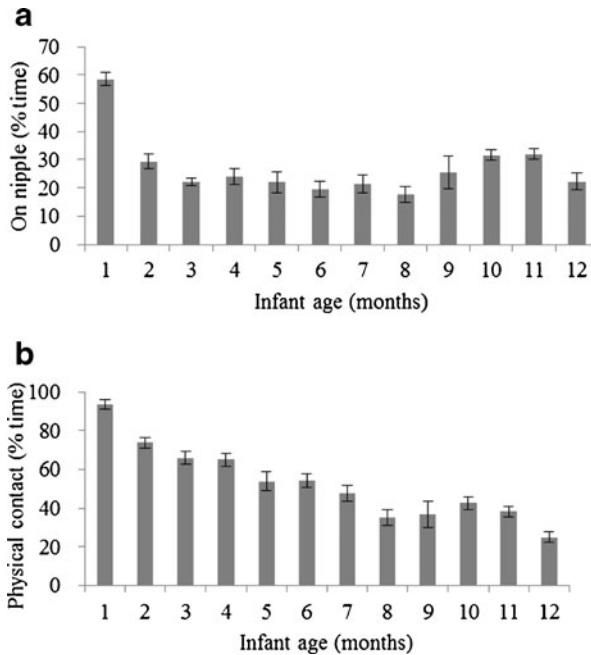
**Table II** Mother–infant dyads of *Rhinopithecus bieti* observed at Xiangguqing from February 2010 to March 2011

Infant's name	Jiu	Yao	Lan	Hong	Lv	Qiu
Sex	Female	Female	Male	Female	Female	Female
Birthdate (yy/mm/dd)	2010/2/9	2010/3/11	2010/3/11	2010/3/18	2010/3/10	2010/3/14
Mother's name	Jiumu	Yaomu	Lanmu	Hongmu	Lvmu	Qiumu
Mother's age	Old	Mid	Young	Mid	Young	Mid
Mother's parity	multiparous	Multiparous	Primiparous	multiparous	primiparous	multiparous
Mother's rank	High	Medium	Medium	Medium	Low	High
Unit	YDH	YDH	YDH	HC	HC	BL

**Table III** Ethogram of mother–infant behavior in *Rhinopithecus bieti*

Behavior	Definition	Category
On nipple	The infant has nipple in mouth.	Behavioral state
On ventrum	The infant on its mother's ventrum, without nipple in mouth.	Behavioral state
Exploring ventrum	The infant crawls on its mother's ventrum, without nipple-seeking movements.	Behavioral state
Body Contact	The infant is in contact with some portion of its mother's body, but not on her ventrum.	Behavioral state
Within an arm's length	The infant is within an arm's length from its mother but not in contact.	Behavioral state
Greater than an arm's length	The infant is within 1 m from its mother but more than an arm's length.	Behavioral state
Greater than 1 m	The infant is >1 m from its mother.	Behavioral state
Forage	The mother searches for or swallows food.	Behavioral state
Move	The mother travels >10 m and for >30 s.	Behavioral state
Rest	The mother sits on the ground or on a tree, not engages in foraging.	Behavioral state
Carry	The mother carries the infant when she is moving.	Behavioral state
Groom	The mother grooms the infant.	Behavioral state
Restrain	The mother prevents the infant from moving out of contact with her.	Behavioral event
Reject	The mother prevents the infant from establishing or continuing nipple contact or physical contact with her.	Behavioral event
Solicitation	The mother glances at a male and runs a short distance away, then prostrates herself on a branch or on the ground.	Behavioral event
Copulation	The mother is mounted by a male.	Behavioral event
Explorative feed	The infant handles and mouths food objects in a playful manner, without swallowing.	Behavioral state
Infant feed	The infant searches for, manipulates, and swallows food objects.	Behavioral state
Social play	The infant plays with peers.	Behavioral state
Allogroom	The infant grooms other individual.	Behavioral state
Threat	The infant threatens other individual by staring or exposing teeth.	Behavioral event
Submission	The infant crouches on the ground when it is threatened or attacked.	Behavioral event
Infant sexual behavior	The female infant glances at a male and runs a short distance away, then prostrates herself on a branch or on the ground. The female infant is mounted by a male. The male infant mounts a female.	Behavioral event

spent on nipple between different infant ages (Kruskal–Wallis test:  $\chi^2 = 33.437$ ,  $P < 0.001$ ,  $N = 12$  mo; Fig. 1a). The infants spent 58.5% of their time on the nipple during their first



**Fig. 1** Mean ( $\pm$  SE) percentage of time infant *Rhinopithecus bieti* spent **(a)** in nipple contact and **(b)** in physical contact with their mothers from February 2010 to March 2011 at Xiangguqing in Yunnan, China.

month of life, and the percentage decreased to 29.4% in the second month, then remained relatively constant ( $23.8 \pm 0.5\%$ ) for the next 10 mo. During their first year of life, the infants always returned to their mother’s ventrum when resting and usually kept a nipple in their mouth.

Infants remained on their mother’s ventrum and exhibited little movement during the first day after birth. Newborns began to explore their mother’s body on the second day while maintaining ventro-ventral contact. By d 3, infants became more active and attempted to crawl on their mothers when the mother was sitting. The infants first broke tight contact with their mothers at a mean age of  $17 \pm 2.1$  d (range 8–22 d,  $N = 6$ ). During this time, infants could climb or jump only very short distances, and were always within an arm’s reach of their mothers. The mean age at which infants started traveling more than an arm’s reach from their mother was  $39 \pm 3.7$  d (range 26–53 d,  $N = 6$ ). Infants began to walk clumsily during their second month of life. At  $41 \pm 3.0$  d infants were first observed to travel  $>1$  m from their mothers (range 35–55 d,  $N = 6$ ).

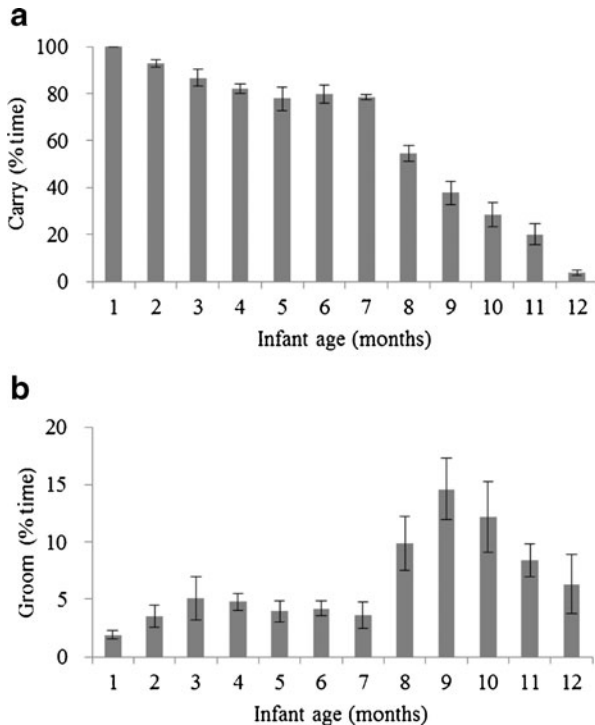
There was a significant difference in the percentage of time infants spent in contact with the mother between different ages ( $\chi^2 = 56.189, P < 0.001, N = 12$  mo, Fig. 1b). In mo 1, the infants spent 93.4% of their time in contact with their mother, and the percentage decreased to 24.9% in mo 12.

### Maternal Carrying and Grooming

Mothers carried their infants exclusively in a ventro-ventral position. Although the newborn infants could grasp the mother’s stomach hair with their hands and feet as soon as they were born, mothers always supported their infants with one hand while

climbing, running, or jumping during their first week of life. As the infants developed, the mother's support decreased and it ceased during the second month of life. During the first month of life, mothers retrieved their infants when they began to travel, but by mo 2 they started to leave the infants behind. From mo 8 onwards, infants began to follow the group regularly on their own when the group moved. The percentage of time an infant was carried by its mother when she moved showed significant differences between infant ages ( $\chi^2 = 64.216$ ,  $P < 0.001$ ,  $N = 12$  mo; Fig. 2a). By 12 mo of age, infants were carried only 3.6% of the time. Nevertheless, 1-yr-old infants were still dependent on their mother's carrying under conditions in which mothers traveled long distances, when infants needed assistance in climbing large trees, or the infants were attacked by group members.

Mothers began grooming their infants soon after birth. The relative amount of maternal grooming, i.e., grooming time per time spent in contact, showed significant differences between infant ages ( $\chi^2 = 36.781$ ,  $P < 0.001$ ,  $N = 12$  mo; Fig. 2b). Maternal grooming occurred infrequently in the first 7 mo; the percentage varied from 1.9% to 5.1% among these months. From mo 8 to mo 12, the infants received more grooming, and the percentage varied from 6.3% to 14.6%. Maternal grooming directed by mothers toward their infants occurred only during resting, particularly before the mothers fell asleep and after they woke up. Mothers groomed the infant's head, back and limbs when the infant had a nipple in its mouth, and mothers did not use grooming to prevent nursing.



**Fig. 2** Mean ( $\pm$  SE) percentage of time infant *Rhinopithecus bieti* were (a) carried by their mothers, calculated as carrying time per time mothers were moving, and (b) groomed by their mothers, expressed as a percentage of time spent in contact with the mother, from February 2010 to March 2011, Xiangguqing.



We first observed infants groom themselves at mo 6, and autogrooming bouts from mo 6 to mo 12 were very rare (only 11 cases) and of short duration (<30 s/event).

Maternal Restriction

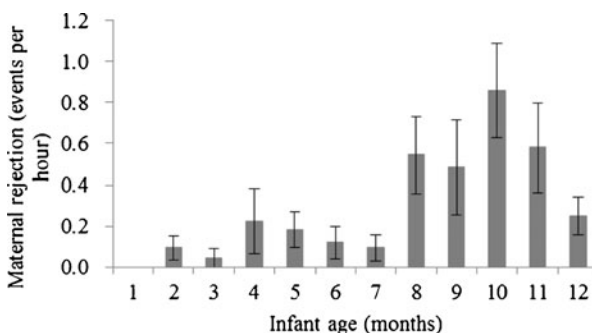
We observed maternal restriction in the first 2 mo of the infant’s life when an infant tried to break contact with its mother. All six infants experienced maternal restriction during their first month of life ( $0.38 \pm 0.12$  events/h). In the second month, three of the six infants were restricted by their mothers, and the frequency of maternal restriction declined to  $0.13 \pm 0.07$  events/h for these six infants. The mean age when the infants were last seen being restricted was  $28 \pm 4.2$  d (range 13–37 d,  $N = 6$ ). When infants were 3 mo old, the mothers allowed them to move away freely, but would still pick them up if other members alarm called or attacked the infants.

Maternal Rejection and Mother’s Reproductive Behaviors

We first observed maternal rejection when the infants were 2 mo old (Fig. 3). Rejection frequencies were very low from mo 2 to 7, which varied from 0.04 to 0.22 events/h. The infants received more rejection in the subsequent 5 mo, and the frequency varied from 0.25 to 0.86 events/h. Rejection peaked when the six infants were 10 mo old (mean = 0.86 events/h).

We recorded 272 cases of rejection. In 53% of cases, mothers turned around or left the infants, resulting in a loss of nipple contact or physical contact. In 41% of cases mothers pushed the infants away. Mothers gently hit or nibbled the infants on the head in only 6% of cases. Most rejection events occurred when the mothers were feeding or began to forage (62%), 27% occurred during resting, and 11% occurred when mothers were moving. We first observed “tantrum” behavior at the age of 5 mo. The infant screamed loudly while jumping and jerking its head suddenly. We observed 11 cases of such behavior, and in 6 cases, the mothers responded by allowing the infants to suckle.

Mothers started to solicit adult males and copulate when infants were 8 mo old. Eight of 15 sexual solicitations resulted in copulation. On one occasion a mother carried her infant when she copulated with the adult male in her OMU.



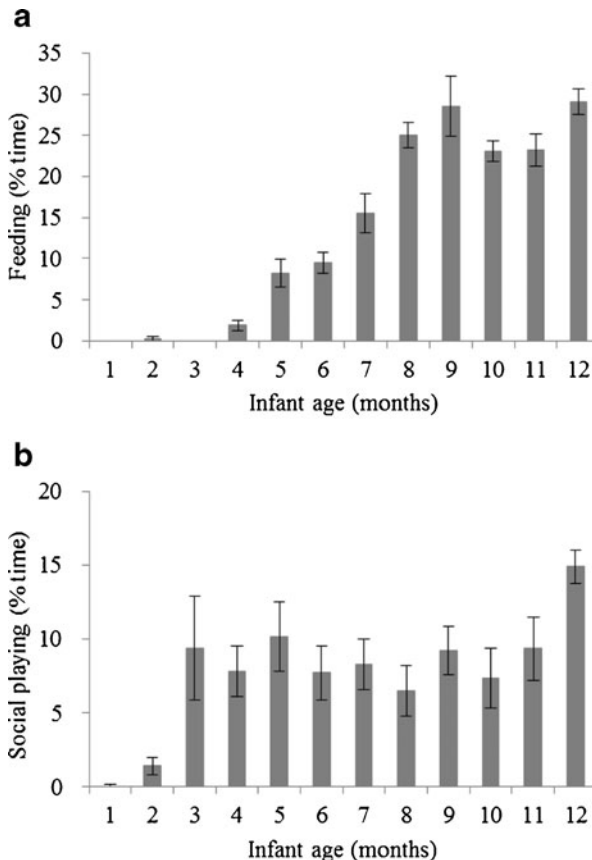
**Fig. 3** Mean ( $\pm$  SE) frequency of maternal rejection in *Rhinopithecus bieti* from February 2010 to March 2011, Xiangguqing.

## Mouthing and Feeding

In their first month after birth, infants handled and mouthed objects like leaves or twigs but did not eat them. The mean age when we first observed the infants swallowing solid food was at  $98 \pm 13.2$  d (range 60–143 d,  $N = 6$ ). Infants often tried to grab food from their mothers or other nearby conspecifics, with the exception of the dominant male in their OMU. The percentage of time infants spent feeding showed significant differences between infant ages ( $\chi^2 = 64.010$ ,  $P < 0.001$ ,  $N = 6$ ; Fig. 4a), reaching 25.0% in mo 8, and peaked in mo 12, when the infants spent 29% of their time feeding.

## Social Behavior

We first observed social playing when infants were aged  $81 \pm 13.9$  d (range 29–118 d,  $N = 6$ ) (Fig. 4b). Infants sought other infants and juveniles as playmates, but never played with adults. Social play included wrestling, mock-biting, and chasing. The percentage of time infants spent in playing showed significant differences between



**Fig. 4** Mean ( $\pm$  SE) percentage of time infants of *Rhinopithecus bieti* spent (a) feeding and (b) social playing from February 2010 to March 2011, Xiangguqing.

infant ages ( $\chi^2 = 33.236$ ,  $P < 0.001$ ,  $N = 12$  mo). Time spent in social play increased over time, from a low of <1% in mo 1 to a maximum of 15% in mo 12.

We first observed allogrooming by infants when infants were 5 mo old. Grooming by infants was rare and hasty (<1 min/event). We did not observe threat, submission, or sexual behavior in infants.

We observed no direct threats or attacks on infants before the age of 8 mo. From mo 8 to mo 12, we recorded three threats and eight cases of infant aggression from other OMU members. On six occasions an infant was gently hit or bitten when it tried to grab food from subadult females or non-mother adult females. Only the male infant was attacked by the adult male from its OMU. The infant approached the male closely while the male was foraging. The male grasped the infant's head and the infant screamed loudly. The mother retrieved the infant immediately. Other females in the OMU gathered round and screamed at the adult male. We also noted three cases of infants being threatened by non-OMU members, once by a subadult male from the AMU, while the other two cases involved adult males from other OMUs. None of the six infants were injured during these aggressions.

## Discussion

Newborn *Rhinopithecus bieti* were dependent on their mothers for nutrition, travel, hygiene, and safety. We compared the infant behavioral development of *Rhinopithecus bieti* with several representative species of Asian colobines and cercopithecines for which the relevant data were available and comparable (Table I) and found the infant behavior patterns in the first 12 mo after birth of *Rhinopithecus bieti* were similar to those of *R. roxellana*. Unlike infant *Macaca mulatta*, neither *Rhinopithecus bieti* nor *R. roxellana* (Li *et al.* 2005) show mounting, presenting, threatening, and submission during their first year of life (Hinde and Spencer-Booth 1967). This suggests that social behaviors develop more quickly in *Macaca mulatta* than in *Rhinopithecus*. However, as infant sex influences maternal behavior and infant behavioral development in other primate species (Bercovitch 2002; Mithcell 1979), and our data set included only one male infant of *Rhinopithecus bieti*, future studies should include more male infant subjects. Further, the provisioning food of our focal group might have potential influences on infant development, so investigation of a wild troop of *Rhinopithecus bieti* on this subject is still needed.

Drawing on studies of maternal styles in cercopithecines, we predicted that the egalitarianism with low risk of intragroup aggression in *Rhinopithecus bieti* would predispose mothers to low levels of protectiveness to their infants compared with *Macaca mulatta*. Maternal restriction of *Macaca mulatta* peaked at the end of the first month (5 events/h) (Berman 1980) and could last for >10 mo (Hinde and Spencer-Booth 1967). In our study, mothers of *Rhinopithecus bieti* showed restrictive behavior to their infant only in the first 2 mo after birth, and the frequency was much lower than in *Macaca mulatta*, consistent with our hypothesis. Maternal restriction in the first 2 mo might serve to ensure infant's safety, when the risk of injury and accident is high. Newborn *Rhinopithecus bieti* are extremely vulnerable, as exemplified by a case in 2010 when a newborn infant died after accidentally falling off a tree (*personal observation*). We observed no severe attacks on infants during the study period and mothers were

more permissive after the infants were 3 mo old. However, the mothers protected their infants immediately whenever danger occurred in the first year after birth.

Protective behaviors (nipple contact, physical contact, and carrying) declined with infant age except for maternal grooming. Because most maternal grooming occurred during resting and it was not used to reject suckling attempts, we suggest that the increased maternal grooming frequency from mo 8 to mo 12 is for hygiene reasons. The infants were feeding and playing but their autogrooming skills were not yet fully developed. Maternal grooming could ensure good hygiene of the infants and prevent parasitic infection (Dunbar 1991). Allogrooming also leads to higher levels of  $\beta$ -endorphins in the brain, which could give the infants a sense of comfort and well-being (Keverne *et al.* 1989), so it is also possible that maternal grooming has some psychological function during infant development.

Mothers of *Rhinopithecus bieti* were more permissive than mothers of *Macaca mulatta*, in which maternal rejection began as early as wk 1 and increased during the infant's first year of life (1–3 events/h) (Berman 1980; Hinde and Spencer-Booth 1967). Maternal rejections are thought to facilitate infant independence (Nicolson 1987), so that the infant would not obstruct the mother's future reproduction (Trivers 1974). We observed sexual behavior in mothers of *Rhinopithecus bieti* when the infants were 8 mo old, and mothers also rejected infant proximity more than in the first 7 mo, which seems to be consistent with the mother–infant conflict hypothesis. However, because the interbirth interval (IBI) of female *Rhinopithecus bieti* is *ca.* 2 yr (Cui *et al.* 2006), and none of these six mothers conceived in 2011, we doubt whether the mothers rejected their infants in this period in an attempt to save energy for future reproduction. Most maternal rejections occurred when the mothers were feeding, the activity most likely to be disrupted by the presence of an infant, which partly supports the timing hypothesis. In addition, neither nipple time nor physical contact declined rapidly when maternal rejection increased at mo 8, suggesting that nipple and physical contact was not the source of the mother–infant conflict. Owing to limited visibility, we could not distinguish between sucking the nipple and just holding it, so time on nipple contact does not represent the amount of milk transfer (Cameron 1998; Cameron *et al.* 1999). However, based on the IBI of *Rhinopithecus bieti*, we can infer that maternal investment remains elevated despite the mother's resumed copulation in mo 8, and maternal rejection increased from mo 8 to mo 12. The infants were not weaned by the end of their first year, and juveniles at the age of 3 still hold their mother's nipple occasionally (*unpubl. obs.*). Mothers of *Rhinopithecus bieti* appeared to tolerate nursing if it did not hinder their activities. A similar behavior pattern was also found in *Trachypithecus johnii* (Poirier 1968), in which mild maternal rejection initially increased rather than decreased dependent behavior in infants, and although most infants were weaned at around 12 mo, juveniles >1 yr old often retained strong ties with their mothers and had a nipple in their mouth while resting and sleeping. We conclude that maternal rejection plays only a marginal role in infant independence during the first year in *Rhinopithecus bieti*.

Our data suggest the mothering style of *Rhinopithecus bieti* can be characterized as relaxed. Maternal protectiveness was not high and maternal restriction was limited. Infant *Rhinopithecus bieti* were still dependent on their mothers at the end of the first year of life, and maternal rejection did not play a major role in promoting infant independence during this period. Future studies should include additional subjects, particularly male infants.

**Acknowledgments** This study was supported by Project of Public Benefit (201104073), the Natural Science Foundation of China (No. 30970442), and the State Forestry Administration of China. We thank the Baimaxueshan National Nature Reserve for work permits. Special thanks are due to Prof. Paul Garber (University of Illinois), Dr. Cyril Grueter (University of Western Australia), and two anonymous reviewers for their valuable comments and English revision for the manuscript. We are very grateful to our field assistants for data collection.

## References

- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *69*, 227–267.
- Altmann, J. (1980). *Baboon mothers and infants*. Cambridge, MA: Harvard University Press.
- Bardi, M., Shimizu, K., Fujita, S., Borgognini-Tarli, S., & Huffman, M. A. (2001). Hormonal correlates of maternal style in captive macaques (*Macaca fuscata* and *M. mulatta*). *International Journal of Primatology*, *22*, 647–662.
- Bercovitch, F. B. (2002). Sex-biased parental investment in primates. *International Journal of Primatology*, *23*, 905–921.
- Berman, C. M. (1980). Mother-infant relationships among free-ranging rhesus monkeys on Cayo Santiago: a comparison with captive pairs. *Animal Behaviour*, *28*, 860–873.
- Cameron, E. Z. (1998). Is suckling behaviour a useful predictor of milk intake? A review. *Animal Behaviour*, *56*, 521–532.
- Cameron, E. Z., Stafford, K. J., Linklater, W. L., & Veltman, C. J. (1999). Suckling behaviour does not measure milk intake in horses, *Equus caballus*. *Animal Behaviour*, *57*, 673–678.
- Cui, L., Sheng, A., He, S., & Xiao, W. (2006). Birth seasonality and interbirth interval of captive *Rhinopithecus bieti*. *American Journal of Primatology*, *68*, 457–463.
- de Waal, F. B. M., & Luttrell, L. M. (1989). Toward a comparative socioecology of the genus *Macaca*: different dominance styles in rhesus and stump-tail macaques. *American Journal of Primatology*, *19*, 83–109.
- Dunbar, R. I. M. (1991). Functional significance of social grooming in primates. *Folia Primatology*, *57*, 121–131.
- Dunbar, R. I. M., & Dunbar, P. (1988). Maternal time budgets of gelada baboons. *Animal Behaviour*, *36*, 970–980.
- Fairbanks, L. A., & McGuire, M. T. (1987). Mother-infant relationships in vervet monkeys: response to new adult males. *International Journal of Primatology*, *8*, 351–366.
- Forster, S., & Cords, M. (2002). Development of mother-infant relationships and infant behavior in wild blue monkeys (*Cercopithecus mitis stuhlmanni*). In M. E. Glenn & M. Cords (Eds.), *The guenons: Diversity and adaptation in African monkeys* (pp. 245–272). New York: Kluwer Academic.
- Grueter, C. C. (2004). Conflict and postconflict behaviour in captive black-and-white snub-nosed monkeys (*Rhinopithecus bieti*). *Primates*, *45*, 197–200.
- Grueter, C. C., Li, D., Ren, B., Wei, F., Xiang, Z., & van Schaik, C. P. (2009). Fallback foods of temperate-living primates: a case study on snub-nosed monkeys. *American Journal of Physical Anthropology*, *140*, 700–715.
- Grueter, C. C., Li, D., & Ren, B. (2013). Insights into the social system of Yunnan snub-nosed monkeys. In C. L. Tan, C. C. Grueter, & B. W. Wright (Eds.), *Odd-nosed monkeys: Recent advances in the study of the forgotten colobines*. New York: Springer.
- Hinde, R. A., and Simpson, M. J. A. (1975). Qualities of mother-infant relationships in monkeys. In (CIBA Symposium 33) "Parent-Infant Interaction" pp. 39–67. Elsevier, Amsterdam.
- Hinde, R. A., & Spencer-Booth, Y. (1967). The behaviour of socially living rhesus monkeys in their first two and a half years. *Animal Behaviour*, *15*, 169–196.
- Hinde, R. A., Rowell, T. E., & Spencer-Booth, Y. (1964). Behaviour of socially living rhesus monkeys in their first six months. *Proceedings of the Zoological Society of London*, *143*, 609–649.
- Hrdy, S. B. (1999). *Mother nature: A history of mothers infants, and natural selection*. New York: Pantheon Books.
- Huang, Z., Cui, L., Scott, M. B., Wang, S., & 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.
- Kappeler, P. M., Pereira, M. E., & van Schaik, C. P. (2003). Primate life histories and socioecology. In P. M. Kappeler & M. E. Pereira (Eds.), *Primate life histories and socioecology* (pp. 1–20). Chicago: University of Chicago Press.

- Keverne, E. B., Martensz, N. D., & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology*, *14*, 155–161.
- Kirkpatrick, R. C. (1996). Ecology and behavior of the Yunnan snub-nosed langur (*Rhinopithecus bieti*, Colobinae). Ph.D. dissertation, University of California, Davis.
- Kirkpatrick, R. C. (2007). The Asian colobines: Diversity among leaf-eating monkeys. In C. J. Campbell, A. Fuentes, C. K. MacKinnon, M. Panger, & S. K. Bearder (Eds.), *Primates in perspective* (pp. 186–200). Oxford: Oxford University Press.
- Kirkpatrick, R. C., Long, Y., 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.
- Kirkpatrick, R. C., Zou, R., Dierenfeld, E. S., & Zhou, H. (2001). Digestion of selected foods by Yunnan snub-nosed monkey *Rhinopithecus bieti* (Colobinae). *American Journal of Physical Anthropology*, *114*, 156–162.
- Lee, P. C. (1996). The meaning of weaning: Growth, lactation, and life history. *Evolutionary Anthropology*, *5*, 87–96.
- Li, Y., Li, B., & Tan, C. L. (2005). Behavioral development within one-year-old individuals of Sichuan snub-nosed monkeys *Rhinopithecus roxellana* in the Qinling Mountains. *Acta Zoologica Sinica*, *51*, 953–960.
- Li, D., Grueter, C. C., Ren, B., Long, Y., Li, M., Peng, Z., & Wei, F. (2008). Ranging of *Rhinopithecus bieti* in the Samage Forest, China. II. Use of land cover types and altitudes. *International Journal of Primatology*, *29*, 1147–1173.
- Li, D., Ren, B., Grueter, C. C., Li, B., & Li, M. (2010). Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. *American Journal of Primatology*, *72*, 1092–1099.
- Li, Y., Guo, S., Ji, W., He, G., Wang, X., & Li, B. (2011). Social play behavior in infant Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in Qinling Mountains, China. *American Journal of Primatology*, *73*, 845–851.
- Long, Y., Kirkpatrick, R. C., Zhong, T., & Xiao, L. (1994). Report on the distribution, population, and ecology of the Yunnan snub-nosed monkeys (*Rhinopithecus bieti*). *Primates*, *35*, 241–250.
- Maestripieri, D. (1993a). Maternal anxiety in rhesus macaques (*Macaca mulatta*). I. Measurement of anxiety and identification of anxiety-eliciting situations. *Ethology*, *95*, 19–31.
- Maestripieri, D. (1993b). Maternal anxiety in rhesus macaques (*Macaca mulatta*). II. Emotional bases of individual differences in mothering style. *Ethology*, *95*, 32–42.
- Maestripieri, D. (1994a). Mother-infant relationships in three species of macaques (*Macaca mulatta*, *M. nemestrina*, *M. arctoides*). I. Development of the mother-infant relationship in the first three months. *Behaviour*, *131*, 75–96.
- Maestripieri, D. (1994b). Social structure, infant handling, and mothering styles in group-living old world monkeys. *International Journal of Primatology*, *15*, 531–553.
- Martin, P., & Bateson, P. (1993). *Measuring behaviour: An introductory guide*. Cambridge, U.K.: Cambridge University Press.
- Mithcell, G. (1979). *Behavioral sex differences in nonhuman primates*. New York: Van Nostrand Reinhold.
- Moore, J. (1992). Dispersal, nepotism, and primate social behavior. *International Journal of Primatology*, *13*, 361–378.
- Newton, P. N., & Dunbar, R. I. M. (1994). Colobine monkey society. In G. Davies & J. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour, and evolution* (pp. 311–346). Cambridge, U.K.: Cambridge University Press.
- Nicolson, N. A. (1987). Infants, mothers, and other females. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 330–342). Chicago: University of Chicago Press.
- Poirier, E. E. (1968). The Nilgiri langur (*Presbytis johnii*) mother-infant dyad. *Primates*, *9*, 45–68.
- Ren, B., Li, D., He, X., Qiu, J., & Li, M. (2011). Female resistance to invading males increases infanticide in langurs. *PLoS One*, *6*, 1–4.
- Ross, C. (1998). Primate life histories. *Evolutionary Anthropology*, *6*, 54–63.
- Simpson, M. J. A., & Howe, S. (1980). The interpretation of individual differences in rhesus monkey infants. *Behaviour*, *72*, 127–155.
- Sterck, E. H. M., Watts, D. P., & van Schaik, C. P. (1997). The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, *41*, 291–309.
- Struhsaker, T. T., & Leland, L. (1987). Colobines: infanticide by adult males. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 83–97). Chicago: University of Chicago Press.
- Su, Y., Ren, R., Qi, H., Liang, B., & Bao, W. (1992). Development of social relationship of infant golden monkeys in breeding group: a case study. *Acta Psychologica Sinica*, *24*, 66–72.

- Sugiyama, Y. (1965). Behavioral development and social structure in two troops of Hanuman langurs (*Presbytis entellus*). *Primates*, 6, 213–247.
- Tanaka, I. (1989). Variability in the development of mother-infant relationships among free ranging Japanese macaques. *Primates*, 30, 477–491.
- Thierry, B. (1990). Feedback loop between kinship and dominance: the macaque model. *Journal of Theoretical Biology*, 145, 511–521.
- Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, 14, 249–264.
- Xiang, Z., & Grueter, C. C. (2007). First direct evidence of infanticide and cannibalism in wild snub-nosed monkeys (*Rhinopithecus bieti*). *American Journal of Primatology*, 69, 249–254.
- Xiang, Z., & Sayers, K. (2009). Reports on seasonality of mating and birth events in wild black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Xiaochangdu, Tibet. *Primates*, 50, 50–55.
- Yeager, C. P., & Kool, K. (2000). The behavioral ecology of Asian colobines. In P. F. Whitehead & C. J. Jolly (Eds.), *Old world monkeys* (pp. 496–521). Cambridge, U.K.: Cambridge University Press.
- Zhang, Y. (2012). Female-female relationships of Yunnan snub-nosed monkeys (*Rhinopithecus bieti*) within one-male units. Master's thesis. Beijing: University of Chinese Academy of Sciences.
- Zhao, Q., Tan, C. L., & Pan, W. (2008). Weaning age, infant care, and behavioral development in *Trachypithecus leucocephalus*. *International Journal of Primatology*, 29, 583–591.