

Chapter 2

Social and Life History Strategies of Tibetan Macaques at Mt. Huangshan



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2.1 Introduction

Among the more than 25 species of *Macaca*, the Tibetan macaque (*Macaca thibetana*) is relatively late to be known in primatology. There are several reasons for this. First, it had been considered as a subspecies of *Macaca speciosa* until Fooden (1983), based on his re-examination of the form and size of the glans penis and baculum and the structure of the female reproductive tract, elevated it to species status. Second, Tibetan macaques are endemic to east central China, where most of them inhabit high mountains with dense forests and cliff ledges, making field studies very challenging. Third, as argued above (Sun et al. 2019), there were few Chinese researchers interested in studying primates until the 1980s. As a result, the population status, life history, and social organization of *M. thibetana* have remained relatively poorly known.

Existing information, though still limited, indicates that the Tibetan macaque may be special in many ways. Morphologically, it resembles the stump-tailed macaque, *M. arctoides* (Delson 1980). Phylogenetically, it is close to the Assamese macaque, *M. assamensis*, as indicated by both morphological (Delson 1980) and genetic

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analyses (Hoelzer et al. 1992). Ecologically and behaviorally, it is more similar to the Barbary macaque, *M. sylvanus*, because both live in montane habitats near the subtropical/temperate boundary, have a similar diet, and share intensive infant care with “bridging behavior,” which involves two adults simultaneously lifting up an infant (Ogawa 2019). Yet, the four abovementioned species have been placed into different species groups within the genus *Macaca* by Fooden (1980) and Delson (1980), leading Wada et al. (1987) to suggest that the Tibetan macaque is a key species for understanding the evolution of Asian *Macaca*. These are the main reasons why *M. thibetana* has attracted much interest among primatologists lately.

Tibetan macaques have been listed as a Class II protected species in China since 1988, and they were classified as “Near Threatened” by the IUCN Red List of Threatened Species in 2017. Four subspecies of Tibetan macaque (*M. t. thibetana*, *M. t. guizhonensis*, *M. t. huangshanensis*, and *M. t. pullus*) have been identified based on morphological comparisons (Jiang et al. 1996) and mtDNA analyses (Sun et al. 2010). These subspecies represent distinct conservation units (Liu et al. 2006). Since *M. t. huangshanensis* is the most genetically distinctive and geographically isolated taxon (Sun et al. 2010), it deserves particular attention (Li et al. 2008) (Fig. 2.1).

2.2 Long-term Study of Tibetan Macaques at Mt. Huangshan

The Mt. Huangshan study site is located in southern Anhui province in East China (118.3E, 30.2 N, elevation 1841 m), about 1000 km south of Beijing. It covers an area of 154 km² with a south-north dimension of 40 km and an east-west extension of 30 km. This region is primarily made up of granite with many separate, sharp peaks and cliffs, which prevent people from gaining access to most parts. The weather in the mountain changes with altitude, from subtropical near the bottom, to temperate on the slopes, and to cold at the peak. Correspondingly, the vegetation changes from evergreen broad-leaved forest near the base, to deciduous and evergreen broad-leaved mixed forest on the slopes, and to montane grassland at the top. Mean temperature is 7.8 °C with the highest mean temperature in August (25.6 °C) and the lowest in January (−19.8 °C) (Li 1999). Mt. Huangshan is a well-known scenic spot and a popular tourist destination in China and is listed as a World Cultural and Natural Heritage Site, a World Geological Park, and is in the Man and the Biosphere Programme (MAB) (Fig. 2.2).

Two primate species inhabit these mountains: the Tibetan macaque and the rhesus macaque (*M. mulatta*). Tibetan macaques inhabit higher altitudes above 600 m asl with rocky cliffs, whereas the rhesus macaques live in lower areas with a relatively continuous distribution (Wada et al. 1987). Both have been strictly protected from hunting and trapping since the 1940s and have no known large predators.

Nine social groups of Tibetan macaques are currently living in Mt. Huangshan, where they maintain apparently nonoverlapping home ranges (Wada et al. 1987).

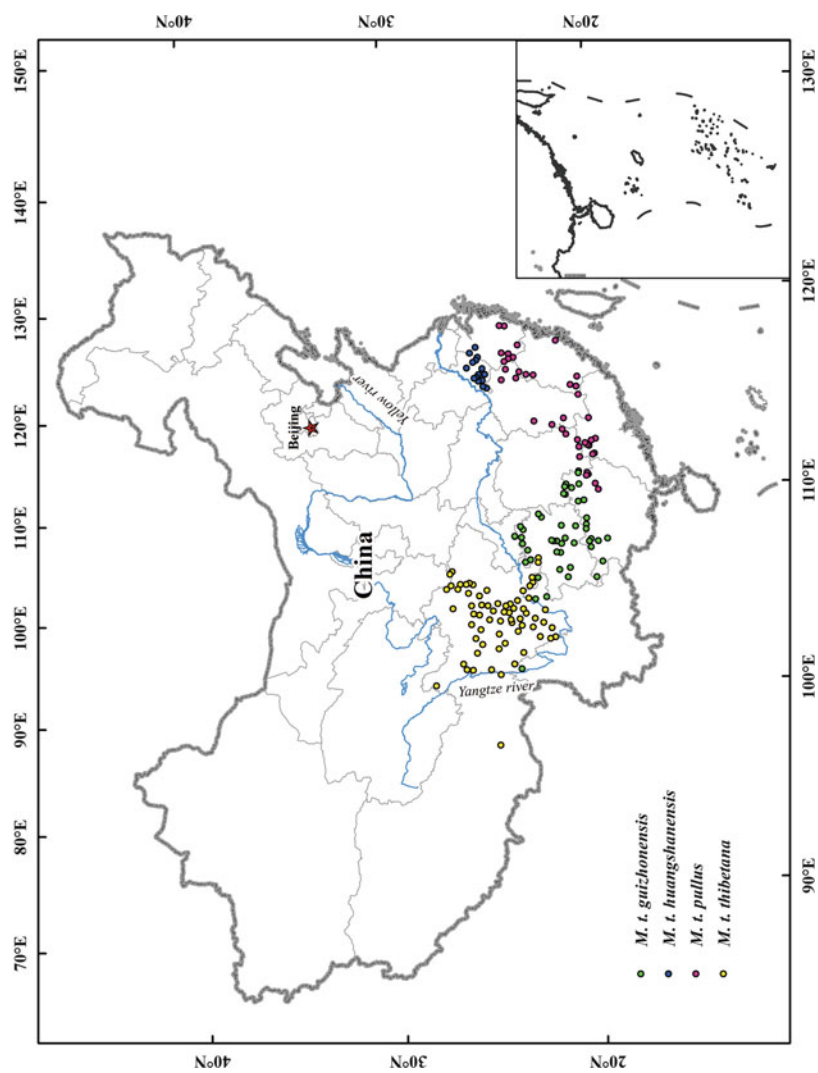


Fig. 2.1 Geographical distribution of the four subspecies of *Macaca thibetana* in China. The species sporadically inhabits in the mid-east region of China, along the Yangtze River



Fig. 2.2 Tibetan macaques inhabit high mountains with evergreen broad-leaved forest (left) and rocky cliffs (right)

They occur in two types of forest and mixed forest: the evergreen broad-forest between 500 and 1000 m asl and deciduous and evergreen mixed broad-forest between 800 and 1200 m asl. They are heavily reliant on structural plant parts for food with marked seasonality: bamboo and grass shoots in spring; fruits, nuts, acorns, and tubers in fall; and bark and mature leaves in winter, supplemented with invertebrates year-round (Xiong and Wang 1988). Geophagy has been observed in terms of ingesting yellow clay from well-established spots and licking rocks that are in contact with soil (Wang et al. 2007). In winter, Tibetan macaques huddle together and sleep on the terraces of rocky cliffs (Xiong 1984), but in summer, they spend the night in trees, which are cool and are safe from venomous snakes (Li and Wang 1994).

Our long-term study group is named Yulingken group (lately Yulingken A or YA1 following a recent group fission) at the village of Fuxi in the southern part of the mountain. The group has been monitored continuously since 1986. To facilitate observation, we have provisioned the group with dried maize to attract them to an open area by a stream. An amount of 5–6 kg of maize per day, which is about 1/3 of the daily food intake of the group, has been given by local wardens 3–4 times a day on a set schedule. When not being fed, the macaques spend most of their time in the forest near the provisioning area. Provisioning has made it possible for us to study the group in a steep terrain and has prolonged our observational time, though it may inevitably affect their natural activities to some extent (Matheson et al. 2006).

We set up a standard study protocol for long-term collection of consistent data within and among researchers at the beginning of the study in 1986. Since then, we have recognized individuals from birth on (natal individuals) or first discovery (immigrated individuals) and given them Chinese names. We have identified each group member based on individually specific physical characteristics such as body size, fur color, facial features, and body scars and taken pictures for confirmation and comparison over time. Furthermore, since Tibetan macaques have broad faces and long fur, both of which change with age, we can fairly reliably sort them into age-sex groups: infant (< 1 year), juvenile (1–3 years), adolescent (♂3–7 years, ♀3–5 years),

young adult (♂7–10 years, ♀5–10 years), middle-aged adult (10–15 years), and old adult (>15 years). Our records show that a male can live up to 28 years (Gaoshan) and a female up to 33 years old (Hua). They both died of old age. Because all females in the group have been identified after their births, we have been able to trace matrilineal relationships among all group members since 1983. Recently, we used microsatellite DNA markers to determine paternity for most group members (Appendix I). For behavioral data collection, we have followed Altmann's methods (Altmann 1974) and recognized and defined 33 distinct social behaviors (Li 1999, see Appendix II). In order to conduct genetic, physiological, and microbiological analyses, we have developed noninvasive techniques to collect cell or hormone samples from the feces and saliva of living monkeys (Zhao et al. 2005; Simons et al. 2012).

The long-term study of Tibetan macaques at Mt. Huangshan has been ongoing for over 30 years. It is the longest research project for wild primates in China. More than 150 researchers and students from the United States, Japan, Australia, England, and Germany as well as China have visited or conducted research at our field site, and 50 theses and 12 dissertations have been completed. This project is now recognized among the eight sites in the world for the long-term study of free-living monkeys (Kappeler and Watts 2012). Recently, as an integral part of the International Research Center for Huangshan Biodiversity and Tibetan Macaque Behavioral Ecology, the project has been approved by the Anhui provincial government.

2.3 Social Life History Strategies

2.3.1 *The Largest Macaca*

It is difficult to study Tibetan macaques in the wild because of their elusiveness and aggression, so catching and weighing them is nearly impossible. An unexpected opportunity to obtain morphometric data presented itself in July 1988, however, when 17 individuals of our study group died within 10 days for a reason that is still unknown. We obtained morphometric data from 14 of the 17 corpses. The average weight for adult males, adult females, and neonates are 16.4 ($n = 4$), 11.0 ($n = 3$), and 0.60 kg ($n = 2$), respectively. They were all heavier than members of the same age-sex classes in other *Macaca* species (Table 2.1). Apparently, the Tibetan macaque is the heaviest species in the genus *Macaca*. This may be the reason why local people call them “bear monkeys.” This result has been verified by morphometric analysis of 72 linear dental and cranial variables of 11 macaque species, showing that the two stump-tailed species (*M. thibetana* and *M. arctoides*) are the largest of the macaques (Pan et al. 1998).

Table 2.1 Body weights (kg) of some *Macaca* species

Species	Adult male	Adult female	Neonate
<i>M. thibetana</i>	16.4	11.0	0.60
<i>M. fuscata</i>	11.7	9.1	0.50
<i>M. sylvanus</i>	11.2	10.0	–
<i>M. nemestrina</i>	10.4	7.8	0.47
<i>M. nigra</i>	10.4	6.6	0.49
<i>M. maura</i>	9.5	5.1	–
<i>M. arctoides</i>	9.2	8.0	0.49
<i>M. silenus</i>	6.8	5.0	–
<i>M. radiata</i>	6.6	3.7	0.40
<i>M. sinica</i>	6.5	3.4	–
<i>M. mulatta</i>	6.2	3.0	0.48
<i>M. fascicularis</i>	5.9	4.1	0.35

Note: the data for species other than *M. thibetana* are from Smuts et al. (1987)

2.3.2 Medium-Sized Group with Even Adult Sex Ratios

We monitored the size and composition of Yulingken group annually and found a fluctuation of 21–51 individuals with an average of 35.3 individuals ($SE = 1.6$) over the 30 years from 1987 to 2017. Whenever group size reached about 50 individuals, it fissioned into two subgroups and the smaller one of the two subgroups left the study area. During this period, we recorded four fission events happening in 1993, 1996, 2001, and 2003, respectively (Li et al. 1996; Li 1999; Berman and Li 2002), and noticed that males and females who were relatives tended to separate on these occasions (Li et al. 1996). Thus, Tibetan macaques at Mt. Huangshan appear to live in medium-sized groups, in comparison with the 70–80 and sometimes more than 100 individuals found in groups of other macaque species (Macintosh et al. 2012; Waters et al. 2015). Group size is an important component of social organization that determines how many individuals a group member can potentially interact with, which in turn contributes to social complexity (Kappeler and Watts 2012).

Like other species of *Macaca*, Tibetan macaques are organized into multi-male, multi-female groups with female philopatry and male dispersal (Li et al. 1996; Li and Wang 1996). However, male Tibetan macaques do not leave their natal groups until adulthood, later than most *Macaca* in which male transfers typically occur at puberty (Zhao 1993; Li et al. 1996). Thus, Tibetan macaque groups tend to include large proportions of natal adult males and relatively even sex ratios (0.91 ± 0.05), with an average of 8.52 ($SE = 0.67$) adult males to 9.35 ($SE = 0.51$) adult females (Fig. 2.3).

2.3.3 A Rich Repertoire of Affiliative and Ritualized Behaviors

An important feature of Tibetan macaques is their rich repertoire of affiliative and ritualized behaviors. Of the 33 social behaviors we have identified, at least

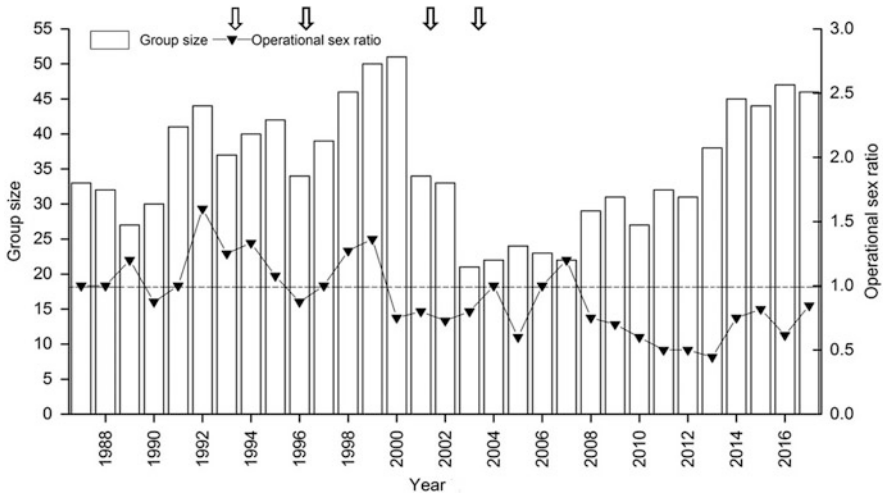


Fig. 2.3 Dynamic of group size and operational sex ratio of male to female in Yulingken A1 group during 1986 and 2017. Down arrow refers group fission events

17 (> 50%) include affiliation (Li 1999). Like other macaques, *allogrooming* (social grooming) is widespread among all group members and takes up about 20% of daily time expenditure (Wang et al. 2007). Females and juveniles are more active groomers than males in peaceful situations. Grooming is more frequent between sexual partners than between other male–female pairs. Specifically, higher-ranking males, including alpha males, groom females for a short time after copulation or during consortship. Grooming between adult males is also frequent (Xia et al. 2013). When two individuals meet, the lower-ranking individual usually *presents* to the high-ranking individual. If the two individuals are both males, they may *embrace* each other, sometimes with their hands stretching out to grasp the genitals of their partners. Additionally, the lower-ranking individual may approach a higher-ranking one, *showing its penis* to be sucked by the partner, or the higher-ranking individual *touches* a part of the body (head, back, or shoulder) of the lower-ranking individual or *mounds* the lower-ranking individual with *teeth chattering*. If the two individuals are of the opposite sex, the male may *grimace* at the female, and the female approaches the male for *genital inspection*, before copulation ensues. Also, during conflicts between two females, a third, higher-ranking female may often *approach* and *hold the bottom* of the attacking female to stop further aggression.

Tibetan macaques show an intense interest in infants. Group members, regardless of sex or age, often *hold infants*. Sometimes, an individual picks up an infant and carries it to another individual to perform the ritualized behavior of *bridging*. This behavior can occur between males, between females, and between a male and a female (Ogawa 1995a; Li 1999). The infants used in bridging are predominantly younger than 6 months, but occasionally 2–3-year-old juveniles may also be used



Fig. 2.4 Infant-holding behavior in Tibetan macaques is common. Left: three infants are attracted to two adult males, apparently waiting to be held or used in bridging. Right: a male Tibetan macaque living alone in Kowloon in Hong Kong holds an infant long-tailed macaque

(Zhang et al. 2018). Infants appear to be willing for bridging and mothers appear to be tolerant of infant handling by all group members (Fig. 2.4).

2.3.4 *Despotic Dominance Style*

The dominance style concept has proven useful for understanding covariation patterns in relationship qualities, particularly among macaques (Berman et al. 2004). As a member of the *sinica* lineage, Tibetan macaques are predicted to have a relaxed dominance style (Matsumura 1999; Thierry 2000). Previous studies did indicate relaxed dominance in this species. For example, males frequently engage in ritualized greetings in which they groom, mount, embrace, or touch each other's genitalia (Li 1999). In addition, both sexes engage in frequent bridging, and infants' mothers appear to be tolerant of infant handling by a wide range of group members (Ogawa 1995a).

However, a detailed study indicated that Tibetan macaques are more despotic than previously suspected. Bidirectional aggression, including counter-aggression (1.9%) and conciliatory tendency (6.4%), was consistently low in frequency across partner combinations, seasons, and locations (Berman et al. 2006). Females consistently displayed high levels of kin bias in affiliation and tolerance. Compared to other macaque species with better known dominance styles, data from Tibetan macaques generally fall within the range characteristic of despotic species and outside the range of relaxed species (Berman et al. 2004).

Despotic dominance of Tibetan macaques is consistent with our field observations. First, mating of low-ranking males was inhibited by high-ranking males. If a low-ranking male surreptitiously mated with a female in the forest but happened to be seen by a high-ranking male, the high-ranking male would immediately rush to punish him by scratching and biting. Second, when a series of conflicts happened,

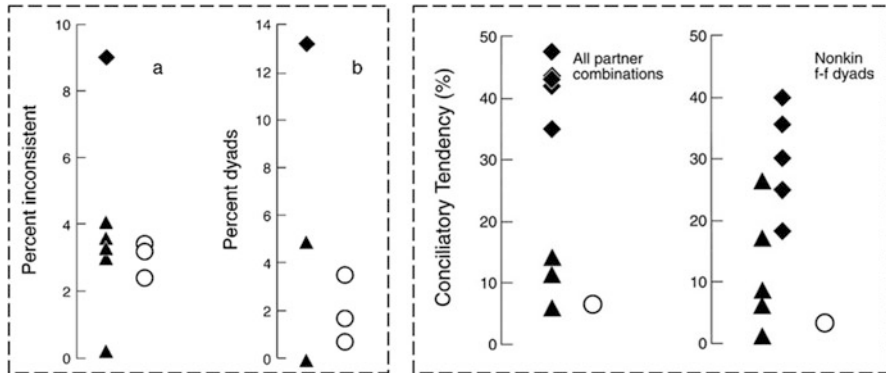


Fig. 2.5 Bidirectionality of aggression (left) and conciliatory tendencies of Tibetan macaques (right). Both a directional inconsistency index (a) and dyads-up index (percentage of dyads in which the primary direction of aggression is up the hierarchy of three data points representing three study periods for Tibetan macaques (circles)) fall within the range of despotic macaques (rhesus, long-tailed and Japanese macaques) (triangles) and are considerably lower than the one relatively relaxed species (stump-tailed macaques) (diamonds). Conciliatory tendencies of Tibetan macaque in (1) all partner combinations and degrees of relatedness combined, and (2) unrelated female–female partners (circles) are relatively low, even compared to values for despotic macaques (triangles). Data from Berman et al. (2004)

male Tibetan macaques often formed a “power coalition,” in which several high-ranking males support one another to defeat low-ranking ones (Li 1999). Third, serious fresh wounds on Tibetan macaques were frequently seen immediately after intense aggressive interactions (Fig. 2.5).

2.3.5 *Reproductive Pattern with Year-Round Mating but Seasonal Births*

It took a long time for us to understand the reproductive pattern of Tibetan macaques. At first, based on intermittent field observations, they were thought to be nonseasonal breeders (Wada and Xiong 1996). After intensive year-round observations, we found that, although mating indeed takes place throughout the year, mating with high frequency and with ejaculation occurs only between July and December, with subsequent births mostly occurring between January and April (Li 1999; Li et al. 2005). Thus, Tibetan macaques are seasonal breeders (Fig. 2.6).

In order to explain this unusual reproductive pattern of Tibetan macaques, we investigated changes in the female sexual skin and nonreproductive matings in more detail. We found that adult females had a slight but detectable sexual skin in the perineal region, but the sexual skin lacked the regular changes characteristic of the physiological cycle of a female or the reproductive season. Females also had no typical behaviors to show their sexual motivation during estrus. This led to the

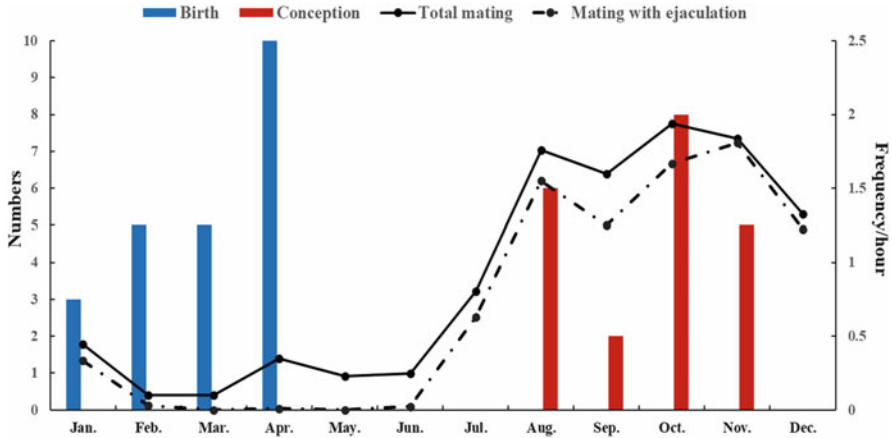


Fig. 2.6 Annual reproductive cycle of Tibetan macaques. Though Tibetan macaques mate year-round (solid line), mating with ejaculation (dotted line) is confined to a period from July to December. Therefore, the mating season is from July to December, and the birth season is from January to April

conclusion that Tibetan macaques have concealed ovulation (Li et al. 2005). Further study revealed that males could discriminate between potentially receptive females, but that they could not recognize the reproductive status of a given female (Li 1999; Zhang et al. 2010). Concealed ovulation may result in a higher mating frequency during a female's receptive period.

Compared with sexual behavior in the mating season, nonreproductive matings occurred at a lower frequency, with less frequent ejaculation, less harassment, shorter mount duration, and an absence of pauses with vocalization. It often took place in a situation in which non-lactating females were involved in social conflict or approached males for mating. Neither pregnant nor lactating females were observed to mate in the birth seasons. Copulation during the birth season did not affect a sexually receptive female's delivery the next year, nor was it associated with increased proximity, grooming, or agonistic aid within the mating pair. However, mating pairs spent more time co-feeding, presumably reflecting increased male tolerance (Li et al. 2007). Adolescent males, who rarely copulated in the mating season, engaged in mating activities during birth seasons as well. Therefore, even though birth season copulations have no reproductive function, they might fulfill social functions for females, such as post-aggression appeasement by males or improving access to resources. They may also offer good opportunities for adolescent males and females to develop their sexual skills (Li et al. 2007) (Fig. 2.7).

It is worth noting that an important aspect of the mating pattern of Tibetan macaques at Mt. Huangshan is a single mount ejaculation (SME), with average duration and thrust numbers of 23.2 s and 20 times, respectively (Xiong and Wang 1991). High-ranking males copulate more often with more females than do low-ranking males, and alpha males monopolize over 2/3 of all matings (Xiong



Fig. 2.7 Inconspicuous sexual skin in adult females (left) and large testes in adult males (right) in Tibetan macaque

and Wang 1991; Li et al. 2005). However, it has been reported that Tibetan macaques at Mt. Emei exhibit serial or multiple mount ejaculation with a mean duration and thrust number of mounts with 30.3 s and 43.3 times (MME), respectively (Zhao 1993). Since no data on the number of mounts in a MME have been provided, we do not know whether the difference is due to a difference in populations per se or observation methods.

Finally, females at the age of 7–12 years have the highest birth rate. Not only are birth rates of high-ranking females higher, but those of high-ranking females are also earlier than those of low-ranking ones in the birth season (Li et al. 1994).

2.4 Potential Contributions to Understanding Behavioral Mechanisms in Primate Societies

2.4.1 *Bridge and Bond Role of Infant*

Tibetan macaques exhibit some interesting and unique behavior patterns. Bridging behavior is one of them. Bridging involves two individuals and an infant and is a triadic interaction. Bridging behavior is common in Tibetan macaque society, and it can be performed between males, between females, between a male and a female, and even between an adult and a juvenile. Infants of both sexes are involved in the “bridge.” Despite this variation in bridging partners, bridging lasts only a few seconds. Once bridging has ended, the two bridging individuals often groom each other or sit together, ignoring the infant. Obviously, the “bridge” between monkeys is not for infant care, but for social contact or communication. In other words, infants are a “social tool” used to facilitate older group members’ associations and interactions (Ogawa 1995b). Zhao (1996) even compared infants in bridging behavior to a cigarette-like social facilitator in human social interactions.

Primatologists have always paid particular attention to the role of infants in nonhuman primate societies. However, most studies have focused on infant care or handling (Ogawa 1995a). For example, in capped langurs, *Presbytis pileata*, newborn infants of less than one month old spend nearly the same amount of time with alloparental females as with their own mothers (Stanford 1992). Likewise, young, female vervet monkeys, *Chlorocebus aethiops sabaesus*, without infants hold or carry newborn infants, which has been explained as alloparental investment (Fairbanks 1990). Bridging behavior has also been observed in *M. sylvanus* (Deag and Crook 1971). Clearly, infants in Tibetan and Barbary macaques play an active part in enhancing social relationships among group members. This is a relatively new and important research direction that is worthy of further exploration.

2.4.2 Male-Female Friendships in a Promiscuous Mating System

During the mating season from July to December, high-ranking Tibetan macaque males often follow sexually receptive females (usually those without unweaned infants). They move, feed, and rest together, often accompanied by mating; that is, they form a temporary consortship. The duration of such a consortship varies from a few days up to over 2 weeks (Li 1999). During a consortship, the male always keeps close with the female, and the male's activities are restricted by the female's movements. Sometimes, when a consorting male realizes that his female has disappeared, he shows signs of anxiety and searches for the female everywhere.

The role of consortship is unclear at present. On the one hand, the duration of consortship in Tibetan macaque is rather long, lasting as much as 18 continuous days (Li 1999). This does not only exceed the time needed to impregnate a female, but is also longer than the duration in other *Macaca* species (Li 1999). On the other hand, although a male follows one female at a time, usually he cannot monopolize all of her matings even though he is the alpha male. So why do high-ranking males use consortship as a mating tactic?

We already mentioned that female Tibetan macaques tend to conceal their ovulation by neither showing cyclical fluctuation of sexual skin nor estrus-related behaviors (Li et al. 2005). Although high-ranking males form consortship with females, they are able to opportunistically mate with other sexually receptive females, too. Thus, the co-occurrence of consort behavior and opportunistic mating may indicate a male mating tactic that is effective when mating is promiscuous and males cannot accurately detect ovulation in females from morphological and behavioral signs. That is, consortship may be a tactic related to the assurance of paternity. From an evolutionary perspective, consortship in Tibetan macaques appears to be a special type of sexual relationship, which has also been reported for some baboons, where they have been labeled as "friendships" (Smuts 1985).

2.4.3 *Competitive and Cooperative Relationships Among Males*

Male Tibetan macaques exhibit stable, linear dominance hierarchies typical of despotic species. On the one hand, aggression is frequent and can be accompanied by serious wounds in all sex/age classes (Berman et al. 2004; Li 1999). Additionally, the large body, large testes, and short tenures of alpha males (on average about 10 months) indicate intense competition among males (Li and Wang 1996). On the other hand, Tibetan macaque males frequently engage in friendly behaviors, such as grooming and sitting together, and engage in ritualized greetings involving mounting, embracing, and sucking penis. Many of these behaviors are rarely seen in other *Macaca* males. Tibetan macaque males also quickly reconcile after aggression. The conciliatory tendency is 19.7% in male–male dyads, compared to 4.2% in female–female dyads, and most male–male reconciliations occur within 1 min after aggression (Berman et al. 2004). It is evident that male Tibetan macaques show both competitive and cooperative relationships. This appears to agree with observations taken from other primate societies with relatively male-biased adult sex ratios.

2.4.4 *Behavioral Mechanism Promoting Genetic Diversity in a Small Group*

Like most nonhuman primates in China, Tibetan macaques live in small, isolated populations. Theoretically, a small population or group may suffer the detrimental effects of inbreeding and the loss of genetic diversity (Spielman et al. 2004). Our study group is a medium-sized one with 20–50 individuals and that ranges in a small habitat (Li et al. 1996). However, we have not found conspicuous changes in behavior during the 30-year period, except the sudden death of 17 individuals in the spring of 1988. Although we have noticed a decline in the frequency of affiliative interactions among group members and an increase in infant mortality in recent years, these appear to be a side effect of provisioning, which increases the rate of aggression among group members (Berman and Li 2002).

Additionally, we found that our study group has a relatively high haplotype diversity ($H_d = 0.341$) when compared to other subspecies (*M. t. pullus*, $H_d = 0.222$; *M. t. guizhouensis*, $H_d = 0.478$) (Sun et al. 2010). As such, loss of genetic diversity may not be a major concern in our study group at present. It is likely that some behavioral mechanisms in this group may play an important role in preventing or slowing down the loss of genetic diversity that is often observed in small groups. For instance, we found that the transfer of males into and out of the group occurs annually (Li et al. 1996). Also, kin recognition may prevent mating between matrilineal relatives. In fact, one of our studies demonstrates that no copulation involved mother-son dyads, and only 2.1% (7/329) of copulations were

between maternal siblings. Females may be more averse to copulating with relatives than are males (Zhu et al. 2008).

2.5 Conclusions

Long-term studies of primate populations are essential for documenting important events or phases of individual life histories that are critical for our understanding of subtle and complex relationships of group members that determine the nature and dynamic of social organization and, as a result, variation in individual reproductive success. The medium-sized group of Tibetan macaques we study facilitates censuses and unambiguous identification of all group members in the field. As the largest macaque species with a relatively male-biased adult sex ratio and year-round mating but seasonal birth, this species offers a large spectrum of sociodemographic conditions conducive for testing hypotheses related to dominance style and group fission. Furthermore, a rich repertoire of affiliative and ritualized behaviors and a complex interplay of competitive and cooperative relationships, especially among males, can provide primatologists with a wealth of opportunities to pursue additional behavioral, ecological, and evolutionary research projects focused on Tibetan macaques.

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Appendix II

Ethogram of social behaviors in Tibetan macaque

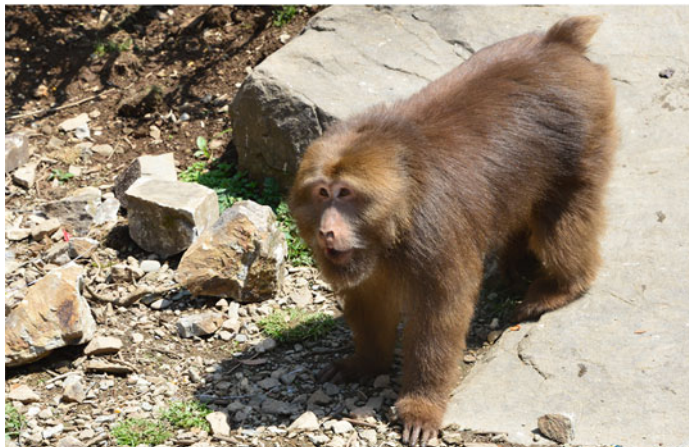
No.	Repertoire	Definition	Picture
1	Stare	An individual looks directly at another individual with its eyes wide open and with its shoulders raised for about 3–5 s. The staring individual appears as if it is preparing to lunge or chase the recipient of the stare.	Picture 1
2	Ground slap	An individual places one hand on the ground and slaps the ground, a rock, or some grassy vegetation with the other while staring at the recipient. The ground slap may be repeated several times.	Picture 2
3	Chase	An individual stares at the recipient and rushes at him/her at great speed. The recipient typically flees.	
4	Seize	The performer grabs the body, face, neck, or ear of the recipient with one hand, shakes it, and then releases it. Sometimes the performer also comes very close (face to face) and stares at the recipient.	Picture 3
5	Bite	The performer grabs the receiver tightly, preventing him/her from fleeing, and bites the recipient vigorously.	Picture 4
6	Avoid	The performer turns its body away from the attacker as if preparing to flee while displaying a “horrified” facial expression toward the attacker.	Picture 5
7	Flee	The target of an attack will run in the opposite direction from the attacker.	
8	Scream	A vocal reaction to an attacker. The scream is high pitched and of long duration. This may be accompanied by fleeing.	Picture 6
9	Redirection	When A is attacked by B, A responds immediately by attacking C. C is an individual that is nearby and lower-ranking than both A and B. In some cases, B will join the attack against C.	Picture 7
10	Solicit support	When an individual is attacked by another individual, it intermittently scans the attacker and a higher-ranking individual nearby with screams. The higher-ranking bystander may respond by interrupting the attack on the scanner.	Picture 8
11	Hold bottom	The performer (usually the alpha female) approaches one of two other females that are engaged in a fight. She approaches from behind and holds the bottom of the female. Both females typically teeth-chatter to one another. This tends to interrupt the fight.	Picture 9
12	Approach	An individual moves directly toward another individual, coming within 1 m.	
13	Leave	An individual moves from within 1 m to more than 1 m of another individual.	Picture 10
14	Proximity	Two or more individuals are sitting or lying within 1 m or between 1 and 5 m (depending on studies).	Picture 11

(continued)

No.	Repertoire	Definition	Picture
15	Following	When one individual begins to travel from one location to another, another individual nearby immediately goes in the same direction.	Picture 12
16	Teeth chatter	The performer opens his/her mouth, places the tongue close to the teeth, and moves his/her jaw rapidly, thereby making clicking noises with his/her teeth. The eyelids are lowered, the chin is raised, and the tongue is moved rapidly back and forth across the teeth. This behavior accompanies same-sex mounting, embracing, and infant carrying. It appears to function as a friendly invitation to interact.	Picture 13
17	Play	Brief sequence of rapid, repetitive, and exaggerated movements, without clear objectives. Interacting play movements involving two or more individuals include chase, mock fight, and combinations of previous behavior.	Picture 14
18	Social grooming/ allogrooming	One individual uses his/her fingers and palms to groom the fur of another individual. The groomer may pick out small objects from the recipients fur and eat them.	Picture 15
19	Embrace	Two individuals, usually adult males, hold each other while face to face. Each partner will reach with one hand and attempt to touch the genitals of the other. Both partners typically teeth-chatter and vocalize excitedly.	Picture 16
20	Touch	A ritualistic behavior between males in which the lower-ranking individual approaches the higher-ranking individual in front. The higher-ranking male touches some part of the body of the lower-ranking individual (head, back, shoulder). Then the lower-ranking individual leaves. This may be used in a tense situation and appears to be a means by which the lower-ranking individual obtains "permission" to proceed on its pathway or with its apparent goal.	
21	Present	One individual approaches the front of the other and shows his bottom to the other. Usually the presenter is the lower-ranking of the two partners. Females also present to males.	Picture 17
22	Mount	One male (usually the lower-ranking) grabs the back hair of another male and mounts from behind, using the full ankle clasp posture. Both males teeth-chatter and scream excitedly. Then the mounter dismounts. The duration of the mount is about 3–5 s. This may be a simple friendly gesture or a post-conflict behavior.	Picture 18
23	Show penis	This is a ritualized behavior shown by juvenile males toward adult males. Usually, the lower-ranking male approaches the higher-ranking male, raises one leg, and displays his penis. The higher-ranking male puts his head on the belly of the lower-ranking male and licks or touches the penis with his hand. The juvenile may show his penis from a reclining position.	Picture 19
24	Suck penis	A young male approaches an adult male and jumps on his head. The adult male holds the younger male by the waist in such a way that his mouth can reach the young male's penis. The adult sucks the young male's penis and then the younger male leaves.	Picture 20

(continued)

No.	Repertoire	Definition	Picture
25	Hold infant	An adult male holds an infant and may carry it ventrally. Usually the infant is male. This apparently serves to invite other adult males to engage in social interaction with the adult male.	Picture 21
26	Bridge	Bridging involves three individuals, an infant or young juvenile and (a) two adult males, (b) one adult male and one subadult male, or (c) two adult females. The two older individuals hold the infant on its back, lower their heads, and lick the belly and/or genitals of the infant. They will often teeth-chatter and vocalize excitedly. The infant is usually male and his penis becomes erect immediately. Other infants, particularly females, will approach a bridging triad with excitement as if they wish to participate.	Picture 22
27	Genital inspection	One individual will touch the genitals—the vagina of a female or the anus of a male—and sniff it or lick it directly. When a male inspects a female in estrus, it is called a sexual inspection.	Picture 23
28	Sexual inspection	A genital inspection by an adult male of an estrus female.	Picture 24
29	Sexual chase	An adult male chases a female and attempts to mate with her. The sexual chase differs from the aggressive chase in that it is slower and is interrupted by pauses. In addition, although the female attempts to avoid the male, she is less likely to scream.	Picture 25
30	Sexual grimace	An individual directs a grimace toward an adult of the opposite sex that may be either nearby or far away. The male sways his body in a manner that makes him more noticeable to the female. The grimace differs from a fear grimace in that the corners of the mouth are not drawn back as far. This is a sexual solicitation.	Picture 26
31	Mating	Three types of mating are described: (1) intromission and thrusting only; (2) intromission, thrusting, and pausing; and (3) intromission, thrusting, pausing, and calling.	Picture 27
32	Harassment	Individuals approach a mating pair excitedly, touch the heads, lick, or stick their faces in the faces of the mating partners. They may also grimace or scream. This does not generally interrupt the copulation of the mating partners.	Picture 28
33	Consortship	An adult male and female form a temporary close affiliative and sexual relationship during the mating season. They will move, feed, mate, and groom together, but do not necessarily mate exclusively with one another. Their frequencies of following one another are much higher than during non-mating periods.	Picture 29



Picture 1 An individual stares another animal



Picture 2 The right adult male slaps toward his front individual



Picture 3 An adult male (middle) seizes another adult male (right)



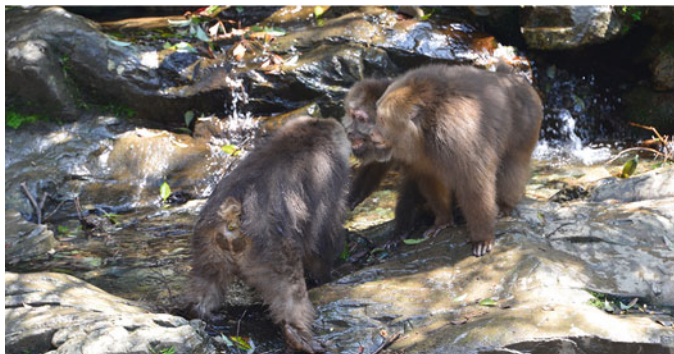
Picture 4 An adult male bites another adult male (two monkeys in right)



Picture 5 An adult male (right) avoids adult male's (middle) aggression



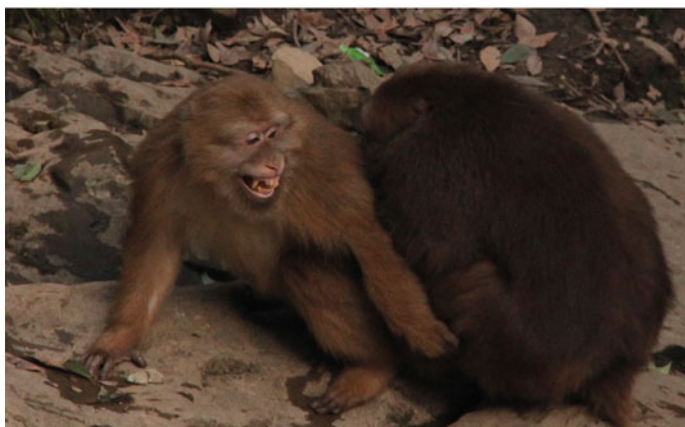
Picture 6 An adult female (right) screams when she is attacked by adult male (left)



Picture 7 The middle adult male redirects aggression from right adult male to the left adult male



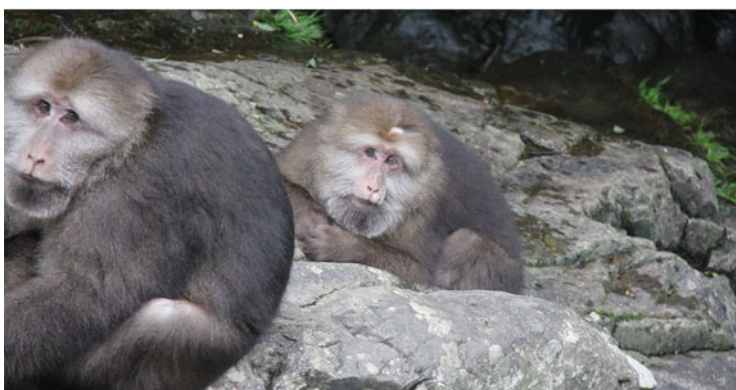
Picture 8 The middle adult male is getting the left male's support when he is in conflict with the right adult male



Picture 9 An adult male holds the button of a juvenile male (left)



Picture 10 The right adult male is leaving left adult male



Picture 11 An adult male (left) is in proximity with an adult female within 1 m



Picture 12 An adult female (left) is following an adult male



Picture 13 Teeth chatting



Picture 14 Three juveniles play together



Picture 15 Social grooming between two females



Picture 16 Embrace



Picture 17 An adult male presents to another male



Picture 18 Male–male mount



Picture 19 Show the penis



Picture 20 A juvenile (left) is sucking an infant's penis



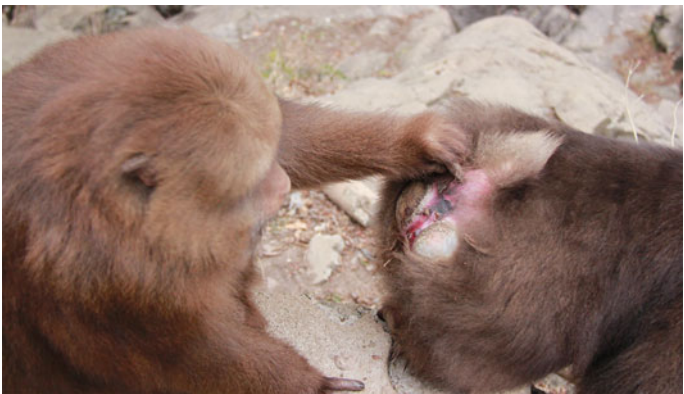
Picture 21 An adult male holds an infant



Picture 22 Male–male bridging



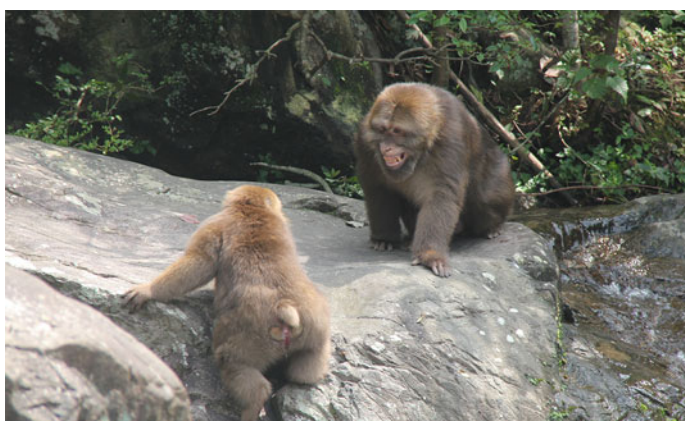
Picture 23 Genital inspection



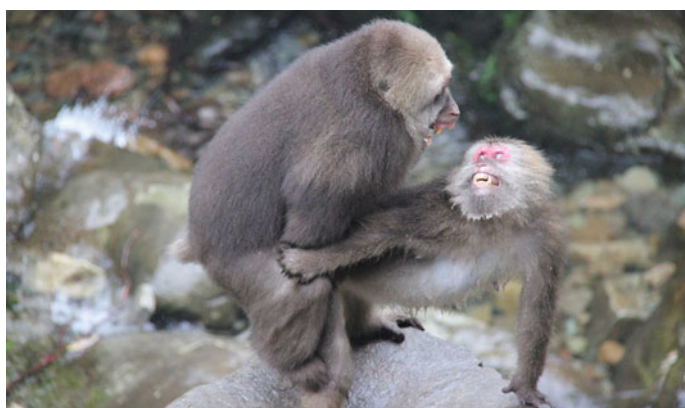
Picture 24 Sexual inspection



Picture 25 An adult male (left) chases an adult female (right) for mating



Picture 26 An adult male (right) grimace to an adult female (left)



Picture 27 An adult male (left) is mating with an adult female (right)



Picture 28 An adult male (left) is harassing a mating pair



Picture 29 An adult male (right) forms consortship with an adult female (left)

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