Comparison of genital contact behaviors among *Macaca assamensis pelops* in Nepal, *M. a. assamensis* in Thailand, and *M. thibetana* in China

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Abstract

We studied the social behaviors of western Assamese macaques (*Macaca assamensis pelops*) at Shivapuri Nagarjun National Park, Nepal from 2014 to 2017 and of eastern Assamese macaques (*M. a. assamensis*) at Wat Tham Pla, Thailand from 2008 to 2012. The behaviors of both subspecies of *M. assamensis* were compared to those of Tibetan macaques (*M. thibetana*) at Huangshan, China from 1989 to 1993. The study groups were free-ranging, provisioned daily, and habituated to observers. We observed adult males and adult females for 10 h each during both the birth and mating seasons using focal-animal sampling as well as all-occurrence-behavior sampling. All three species of macaque formed multi-male multi-female social groups with female philopatry, male dispersal, and a linear dominance hierarchy among adult females. Additionally, although they did not make genital–genital or oral–oral contact, all three species performed various affiliative behaviors with genital touching and genital showing during not only the mating season but also the birth season. However, we found more differences in the repertoire of social behaviors between western and eastern Assamese macaques than between eastern Assamese and Tibetan macaques. Bridging behavior, in which two adults simultaneously lift up an infant, was recorded in Tibetan and eastern Assamese macaques. Males of these two macaques sucked the infant's genitalia during bridging behavior and dyadic male–infant interactions, whereas this behavior was not observed in western Assamese macaques. In addition, only male Tibetan macaques directly sucked the penis of another male, although males of all three macaque species inspected female genitalia and the genital inspection was occasionally accompanied by oral–genital contact. These results indicate that bridging behavior and the sucking of an infant's genitalia by adult males evolved in a *sinica* species-group of the genus *Macaca*, particularly in the clade of Tibetan and eastern Assamese macaques, and that penis sucking between adult males occurred last in Tibetan macaques. Digital video images related to this article are available at <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma09a>, <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt06a>, <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt01a>, <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma01a>, <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma10a>, <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma04a>, and <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma07a>.

Keywords Genital contact · *Macaca assamensis* · *M. thibetana* · Affiliative behavior · Bridging behavior · Inter-species difference · *sinica* species-group

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Introduction

The genetic and morphological traits of focal species provide important evidence for understanding the evolutionary processes in and the phylogenetic relationships of primates and other animals. Additionally, information regarding inter-species differences in social behaviors, patterns of social interactions, and social relationships is also crucial, as social relationships in non-human primates are strongly affected by both ecological and phylogenetic factors (Balasubramaniam et al. 2018). Based on the behavioral repertoires of each species, we may be able to reconstruct the social relationships and social structure of the common ancestor (Mori 1983).

Studies of various species in the genus *Macaca*, Cercopithecidae, Primates, have revealed that all macaques share the common features of forming a multi-male multi-female social group with female philopatry, male dispersal, and a linear dominance hierarchy (Thierry et al. 2004). However, variations exist in their “dominance style” and the degree of kin-biased social relationships between females (Berman and Thierry 2010; de Waal and Luttrell 1989). Recent studies have systematically examined the variations in social relationships between females (Balasubramaniam et al. 2012). In addition to differences in social relationships between females, many inter-species differences occur in the social relationships between males and also between males and females. Compared to females, however, fewer comparative studies have examined the social interactions between males and between males and females. For example, genital touching and oral–genital contact have been reported in Tibetan (*Macaca thibetana*) (Ogawa 1995, 2006) and stump-tail macaques (*M. arctoides*) (Estrada and Sandoval 1977), but these behaviors have not been reported for most other macaque species. Similarly, frequent triadic male–infant interactions have been reported only in Barbary (*M. sylvanus*) (Deag and Crook 1971), Tibetan (Ogawa 1995, 2006), and Assamese (Kalbitz et al. 2017) macaques.

Macaques are divided into several species-groups, one of which is a *sinica* species-group composed of Toque macaques (*M. sinica*) in Sri Lanka, Bonnet macaques (*M. radiata*) in India, Assamese macaques in India eastward to Southeast Asia, and Tibetan macaques in China (Fooden 1982). Delson (1980) also included stumptail macaques, which are distributed in India eastward to Southeast Asia, in the *sinica* species-group. Additionally, Arunachal macaques (*M. munzala*) in the Arunachal area of India and white-cheek macaques (*M. leucogenys*) in Tibet were recently listed as new species in the *sinica* species-group (Li et al. 2015; Sinha et al. 2005).

Assamese macaques have been traditionally divided into two subspecies based on their morphological traits

(Fooden 1982). Eastern Assamese macaques (*M. assamensis assamensis*), which inhabit areas east of the Brahmaputra River, have shorter tails than western Assamese macaques (*M. a. pelops*), which inhabit areas west of the Brahmaputra River (Fooden 1982). Although Assamese macaques are widely distributed in Asia, direct observations of wild Assamese macaques are difficult, because they are patchily distributed in mountainous areas (Chalise et al. 2013; Wada 2005). However, some Assamese macaques are provisioned and habituated to humans at several locations, such as Shivapuri Nagarjun National Park in Nepal (Koirala et al. 2017), Wat Tham Pla in Thailand (Kaewpanus et al. 2015), and Tukreshwari (Tukeswari) Temple in India (Cooper and Bernstein 2000). Provisioned Tibetan macaques have also been observed at Huangshan in China (Ogawa 1995, 2006; Wada et al. 1987).

The present study focuses on comparative observations of the social behaviors of western and eastern Assamese macaques and Tibetan macaques. Similarities and inter-species/subspecies differences among these three macaques are compared, and the potential evolutionary processes involved in the observed social behaviors are discussed.

Materials and methods

Study sites and study subjects

We studied the social behaviors of western and eastern Assamese macaques and Tibetan macaques as described below.

Western Assamese macaques (*Macaca assamensis pelops*) in Nepal

Nagarjun (27°44'N, 85°17'E, 1350–2093 m above sea level), one of two areas in the Shivapuri Nagarjun National Park, Kathmandu District, Nepal, was selected for this study (Fig. 1, Table 1). The study site is 16 km² and is covered by mixed broadleaved forests, pine forests, and dry oak forests. Air temperatures ranged from 3.9 to 29.6 °C (Koirala et al. 2017). In addition to several social groups of western Assamese macaques, other mammals, such as rhesus macaques (*M. mulatta*) and common leopards (*Panthera pardus*), also inhabit Nagarjun (Chalise et al. 2013; Koirala et al. 2017; Wada 2005).

Eastern Assamese macaques (*M. a. assamensis*) in Thailand

The study site, Wat Tham Pla (Tham Pla Temple) (20°19'N, 99°51'E, 843 m), is located in Pong Ngam Subdistrict, Mae Sai District, Chiang Rai Province, Thailand (Fig. 1, Table 1). Wat Tham Pla is oriented in front of a steep cliff and a broadleaved forest and is surrounded by a village and

Fig. 1 Maps of the study sites. **a** The Nagarjun area of Shivapuri Nagarjun National Park in Nepal. **b** Wat Tham Pla (Tham Pla Temple) in Thailand. **c** The valley of monkeys at Huangshan (Mt. Huang) in China

Table 1 Study subjects, sites, and study periods

Species	<i>Macaca assamensis</i>		<i>Macaca assamensis assamensis</i>		<i>Macaca thibetana</i>	
Subspecies	<i>Macaca assamensis pelops</i>		<i>Macaca assamensis assamensis</i>		Huangshan in China	
Study site	Nagarjun in Nepal		Wat Tham Pla in Thailand		Yulingkeng	
Location	27°44'N, 85°17'E		20°19'N, 99°51'E		30°29'N, 118°11'E	
Study group	AA		A, B, C, D		Birth	
Study season	Birth	Mating	Birth	Mating	Birth	Mating
Study period	30th July–11th September 2014	13th November 2014–15th January 2015	25th July–7th September 2009	23rd December 2010–8th January 2011 31st December 2011–13th January 2012	16th February–26th April 1992	16th September–4th November 1992
Observer	HO	HO and SK	HO	HO	HO	HO
Number of focal animals	7 Males	7 Males	10 Males (5 in A, 2 in C, 3 in D groups)	10 Males (4 in A, 2 in C, 4 in D groups)	5 Males	6 Males
	7 Females	7 Females	5 Females (2 in A, 1 in C, 2 in D groups)	5 Females (3 in A, 1 in C, 1 in D groups)	9 Females	9 Females
Observation time (hours)	362.1	353.7	324.3	212.8	574.8	435.7

cultivated fields. Temperatures at the study site ranged from 23.0 to 33.9 °C during the study periods. The macaques at Wat Tham Pla were originally wild but have been provisioned and habituated to tourists and local people for more than 20 years (Kaewpanus et al. 2015). During the study periods, the macaques slept on steep hills behind the temple at night, and they often stayed in the temple area in the daytime, because they were given food, such as bananas and peanuts, every day. The macaques have no wild predators, but domestic dogs live in the village near the study area.

Females gave birth from April to July and conceived from October to February at Phu Khieo Wildlife Sanctuary, Thailand (Fürtbauer et al. 2010).

Tibetan macaques (*M. thibetana*) in China

The study site, called “the valley of monkeys” (30°29'N, 118°11'E, 700–800 m), is located at Huangshan (Mt. Huang) in Anhui Province, China (Fig. 1, Table 1). The 154-km² Huangshan area is registered as a UNESCO World Heritage Site. The study site is covered by deciduous and evergreen broadleaved forests. Temperatures at the study site ranged from −2.0 to 23.0 °C between February and April 1992 and from 4.0 to 27.0 °C between September and November in 1992. Wild Tibetan macaques inhabit this area in several social groups, as do wild rhesus macaques (Wada 2005). No predators of macaques were recorded during the study periods.

Study periods and sampling methods

We directly observed the macaques, using all-occurrence-behavior sampling (Martin and Bateson 1986) throughout the study periods at all three study sites. We recorded all social behaviors involving physical contact, genital showing, and genital inspection between adults within the visual field of the observer(s). We recorded supplanting behavior at the provisioning sites. When Monkey A approached Monkey B, if B immediately withdrew and A took the exact place of B, A was regarded as dominant to B and B was regarded as subordinate to A. We also recorded aggressive (biting, grabbing, hitting, chasing, lunging, open-mouth threat, etc.) and submissive (escaping, grimacing, fearful screaming, etc.) behaviors. We made a winner–loser matrix based on dyadic supplanting and aggressive–submissive interactions, and confirmed the dominance–subordinate relationships between adults.

Additionally, we used focal-animal sampling (Martin and Bateson 1986) of adult males and adult females for 10 h each during both the mating season and the birth season, as macaques are seasonal breeders (Fürtbauer et al. 2010; Li et al. 2005; Xia et al. 2010). During focal-animal sampling, we continuously recorded all social interactions that

involved the focal-animal. The study periods during which we conducted focal-animal sampling and the numbers of focal-animals are summarized in Table 1.

In addition to these study periods, (1) Hideshi Ogawa (HO) resided at Nagarjun for a total of 113 days between 2011 and 2017, (2) at Wat Tham Pla for a total of 110 days between 2008 and 2012, and (3) at Huangshan for a total of 382 days between 1989 and 1993. Kazuo Wada resided at Huangshan for a total of 312 days between 1985 and 1988.

Data analyses

We calculated the rate of each social behavior (number of behaviors of each focal-animal/hour) based on focal-animal sampling. We used a Kruskal–Wallis test to examine significant differences in the rate of each behavior among the three macaque species. We used a sign test to examine significant differences between dominant and subordinate individuals. We used a χ^2 test to examine significant differences between the observed and expected numbers of behaviors. For statistical tests, we considered p values < 0.05 to indicate statistical significance. When we used multiple tests to examine differences in each behavior in three sex combinations (male–male, male–female, and female–female) during two seasons, we used p values < 0.05/6 = 0.008, because we used a Bonferroni correction.

Study groups

Western Assamese macaques of the AA group in Nepal

Shivapuri Nagarjun National Park harbors a provisioned group of western Assamese macaques, named the “AA group” in the Nagarjun area. The AA group resides in an area near an army camp within the national park. When soldiers at this camp finish breakfast and dinner, they usually dispose of their leftovers at a dumping site in the camp. Macaques in the AA group consume the garbage and have become habituated to humans (Koirala et al. 2017). HO and Sabina Koirala (SK) identified all adult males and females in the AA group based on their physical characteristics. In January 2015, the group was composed of 56 monkeys, with 7 adult males and 13 adult females (Table 2).

Between 2014 and 2017, one adult male immigrated into the AA group, whereas no females immigrated into the AA group. When monkeys disappeared from the AA group, however, we were not sure whether they had died or emigrated from the group. Neither solitary males nor all-male groups have been found in this area (Ogawa et al. 2019). Females give birth from March to July (Ogawa unpublished data). Among adult females in the AA group, the improved Landau's index (h') of linearity in a dominance hierarchy (Appleby 1983; de Vries 1995) was 0.98, and hierarchical

Table 2 Age and sex composition of the study groups

Study subject		<i>Macaca assamensis pelops</i>										<i>Macaca assamensis assamensis</i>										<i>Macaca thibetana</i>					
Study site		Nagarjun in Nepal 7th Jan. 2015										Wat Tham Pla in Thailand 13th Jan. 2012										Huangshan in China 4th Nov. 1992					
Study group		AA group			A group			B group			C group			D group			Total of A–D groups						Yulingkeng group				
Age class	Estimated age of year	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total	Male	Female	Total		
Adult	≥5 (female), ≥7 (male)	7	13	20	8	18	26	4	14	18	3	9	12	6	16	22	26	54	80	10	9	19					
Subadult ^a	5–6 (male)	4	–	4	5	–	5	2	–	2	3	–	3	2	–	2	26	–	26	3	–	3					
Juvenile	3–4	3	2	5	7	7	14	4	3	7	5	3	8	5	5	10	16	17	33	4	3	7					
Infant	1–2	12	3	15	8	6	14	5	8	13	6	4	10	6	5	11	30	17	47	1	7	8					
Baby	<1 year	4	1	5	7	3	10	5	1	6	4	2	6	2	3	5	15	18	33	4	1	5					
Total		30	19	49	35	34	69	20	26	46	21	18	39	21	29	50	113	106	219	22	20	42					

^aMales aged 5–6 years old were regarded as subadults, whereas no subadult class was distinguished in females

^bOne adult female was *Macaca arctoides* who was a pet released to the B group when she was an infant

steepness based on the proportions of wins (P_{ij}) using normalized David's scores (de Vries et al. 2006) was 0.82 based on 302 supplanting and aggressive–submissive interactions in 2014–2015.

Eastern Assamese macaques of the A, B, C, D groups in Thailand

In Wat Tham Pla, there were 219 monkeys with 26 adult males and 54 adult females in four social groups (A, B, C, and D groups) in January 2012 (Table 2). These macaques formed stable multi-male multi-female groups, although the C group was temporarily a one-male group in 2009. HO identified all adult males and females in these social groups based on their physical characteristics. With the exception of mother–infant relationships, matrilineal kin relations remain unknown. HO did not observe solitary males or all-male groups during the study periods, although several peripheral males sometimes foraged apart from their social group. When monkeys disappeared from the study groups, we were not sure whether they had died or emigrated from the group. When we found a new adult male in the study groups, we were not sure whether he had immigrated into the group or whether a natal juvenile male of the group had become an adult, because HO did not completely identify all immatures. However, at least one adult male transferred from the A group to the D group, and another adult male transferred from the C group to the A group between 2009 and 2012, whereas no females transferred between the study groups. Among adult females in the A group, in which HO observed all adult females for 4 h each in 2009 by focal-animal sampling (Martin and Bateson 1986), the improved Landau's index (h') of linearity in a dominance hierarchy (Appleby 1983; de Vries 1995) was 0.83, and hierarchical steepness based on the proportions of wins (P_{ij}) using normalized David's scores (de Vries et al. 2006) was 0.75 based on 314 supplanting and aggressive–submissive interactions in 2009.

Tibetan macaques of the Yulingkeng group in China

Since 1986, one social group, the Yulingkeng group, has been provisioned for observations at Huangshan. The Yulingkeng group had 42 monkeys with 10 adult males and 9 adult females in November 1992 (Table 2). HO identified all monkeys based on their physical characteristics (Ogawa 2006). The macaques received corn 4 times a day at a feeding station. Matrilineal kinship and population changes in the study group caused by birth, death, and male transfer have been recorded since 1985. Several males immigrated into and disappeared from the Yulingkeng group, whereas females did not immigrate into the group (Ogawa 2006). The mating season occurred from July to December, and the non-mating season lasted from February to June (Li et al. 2005;

Xia et al. 2010). Among adult females in the Yulingkeng group, the improved Landau's index (h') of linearity in a dominance hierarchy (Appleby 1983; de Vries 1995) was 0.93, and the score of hierarchical steepness based on the proportions of wins (P_{ij}) using normalized David's scores (de Vries et al. 2006) was 0.66 based on 533 supplanting and aggressive–submissive interactions in 1992. The score of hierarchical steepness was 0.87 based on the proportions of wins (P_{ij}) and 0.96 based on the dyadic dominance index (D_{ij}), and the percentage of counter aggression was 0.76 among adult females in the same group in 1991 (Ogawa 1995; Balasubramaniam et al. 2012).

Results

During focal-animal sampling and all-occurrence-behavior sampling, we recorded a total of 9843 behavioral events involving physical contact between adults: 1984 events for western Assamese macaques, 3577 for eastern Assamese macaques, and 4282 for Tibetan macaques. Macaques performed hugging, genital touching, genital sucking, bridging, mounting, copulation, and social grooming, as well as aggressive behaviors with physical contact. Macaques also performed genital showing and genital inspection.

Affiliative and reproductive behavior between adults

We compared the presence/absence of each behavior using the all-occurrence-behavior sampling, whereas the rate of each behavior was analyzed using focal-animal sampling (Table 3). Figures 2, 3, 4, 5, 6, 7, and 8 show affiliated and sexual behaviors of Assamese and Tibetan macaques, although some of the individuals in the video images are not adults.

Hugging

Hugging is defined as using hands to hold the body of another individual and making physical contact with the individual.

Between adult males Males in all three macaque species hugged facing each other. Male Tibetan macaques usually shook their bodies when they were hugging, whereas the two subspecies of male Assamese macaques did not. Male Assamese macaques sometimes clung to another male's back and shoulder with their hands, whereas male Tibetan macaques rarely did so but usually hugged facing each other.

Between adult females Females of all three macaque species hugged another female. Female eastern Assamese macaques sometimes hugged each other while face to face. Female Tibetan macaques frequently hugged another female, but only when their dominance relationships were unstable (Ogawa 2006).

Between adult males and adult females Males and females in all three macaque species used their hands to hug each other.

Genital touching

Genital touching is generally defined as touching the penis and testes of another male with the fingers (penis touching), or touching the genitalia of another female with the fingers. However, when monkeys touched the genitalia of another individual during hugging, mounting, or genital inspection, this was not classified as genital touching.

Between adult males Males in all three macaque species touched the penis and testes of another male with their fingers. Male Tibetan macaques sometimes touched the penis and testes of another male when they were hugging each other. By contrast, male Assamese macaques frequently extended their arm and touched the penis and testes of another male (Fig. 2; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma09a>). Males of all three macaque species frequently touched the penis and testes of another male when they mounted another male or were mounted by another male (see below).

Between adult females None of the females in any of the three macaque species touched the genitalia of another female, although females did inspect the genitalia of another female (see below).

Between adult males and adult females None of the males in any of the three macaque species touched a female's genitalia, except for genital inspection. No females in any of the three macaque species touched a male's penis.

Genital sucking

Genital sucking is defined as sucking the penis and testes of a male (penis sucking), or sucking the genitalia of a female.

Between adult males Only male Tibetan macaques sucked the penis of another adult male. When one of the males lay down on his back and the other male put his head between the legs of the former male, the latter male moved his lips and sucked the tip of the penis of the former male. Male

Table 3 Rate of social behaviors between adults of *Macaca assamensis* and *M. thibetana*

Behavior	Subject	<i>Macaca assamensis pelops</i>			<i>Macaca assamensis assamensis</i>			<i>Macaca thibetana</i>			Kruskal–Wallis test		
		Combina- tion	Direction	Birth season	Mating season	Birth season	Mating season	Birth season	Mating season	Birth season	Mating season	<i>H</i>	<i>p</i>
(1) Hug- ging	Hugging each other	M&M		0.03±0.05	+	+	0.10±0.17	0.02±0.04	0.02±0.04	0.22	0.897	1.82	0.403
	Cling to another	M&M		0.01±0.04	0.03±0.05	0.03±0.05	0.02±0.04	+	+				
	Hugging each other	F&F		+	0.01±0.04	0.02±0.04	0.06±0.12	+	0.02±0.04	7.24	0.027	0.76	0.684
	Cling to another	F&F		+	0.03±0.08	0.03±0.05	0.02±0.04	+	+				
	Hugging each other	M&F		–	+	0.01±0.02	+	0.02±0.04	(+)	3.28	0.192	4.44	0.108
(2) Genital touching ^a	Cling to another	M&F	M to F	–	0.02±0.05	0.02±0.05	0.03±0.05	–	–				
		M&F	F to M	–	0.02±0.06	+	–	–	–				
	(Penis touch- ing)	M&M		+	+	0.01±0.03	0.10±0.07	+	+	1.20	0.549	3.84	0.147
		F&F		–	–	–	–	–	–				
(3) Genital sucking ^b		M&F	M to F	–	–	–	–	–	–				
	(Penis touch- ing)	M&F	F to M	–	–	+	–	–	–				
		M&M		–	–	–	–	+	+				
		F&F		–	–	–	–	–	–				
(4) Bridg- ing		M&F	M to F	–	–	–	–	–	–				
	(Penis sucking)	M&F	F to M	–	–	–	–	(+)	–				
		M&M		–	–	0.67±0.47	0.36±0.06	1.52±1.19	0.083±0.13	12.96	0.002**	13.11	0.001**
		F&F		–	–	0.41±0.41	0.34±0.25	1.47±1.46	0.24±0.25	12.34	0.002**	10.19	0.006*
		M&F		–	–	0.09±0.16	0.04±0.10	0.98±1.10	0.01±0.04	12.74	0.002**	2.79	0.248

Table 3 (continued)

Main-category	Sub-category	Subject	<i>Macaca assamensis pelops</i>		<i>Macaca assamensis assamensis</i>		<i>Macaca thibetana</i>		Kruskal–Wallis test	
			Birth season	Mating season	Birth season	Mating season	Birth season	Mating season	<i>H</i>	<i>p</i>
(5) Genital showing	Penis showing	M&M	+	–	0.01 ± 0.03	+	+	+	0.52	0.772
	Presenting	M&M	0.04 ± 0.11	0.07 ± 0.08	0.06 ± 0.11	0.06 ± 0.09	0.04 ± 0.15	0.07 ± 0.05		
	Presenting	F&F	+	0.03 ± 0.05	0.12 ± 0.09	0.02 ± 0.05	0.06 ± 0.07	0.03 ± 0.07	9.88	0.008**
	Penis showing	M&F	–	–	–	–	–	–	4.39	0.116
	Presenting	M&F	–	0.02 ± 0.08	+	–	–	–		
(6) Genital inspection	Presenting	M&F	–	0.39 ± 0.21	0.29 ± 0.25	0.24 ± 0.22	0.14 ± 0.18	0.10 ± 0.11		
	Presenting	M&F	–	–	–	–	–	–		
	F&F	F&F	+	+	+	0.04 ± 0.05	0.01 ± 0.03	0.06 ± 0.07	1.89	0.389
	M&F	M to F	0.06 ± 0.14	0.52 ± 0.37	0.14 ± 0.17	0.40 ± 0.37	0.11 ± 0.18	0.17 ± 0.17	2.72	0.257
	M&F	F to M	–	–	–	–	–	–		
(7) Mounting	M&M	M&M	0.14 ± 0.06	0.07 ± 0.08	0.10 ± 0.11	0.34 ± 0.29	0.06 ± 0.09	0.05 ± 0.08	0.90	0.637
	F&F ^c	F&F ^c	–	+	0.01 ± 0.03	+	(+)	(+)	1.60	0.449
	M&F	M to F ^d	+	0.05 ± 0.09	0.03 ± 0.07	0.02 ± 0.04	+	+	7.63	0.022*
	M&F	F to M	–	–	0.01 ± 0.02	0.02 ± 0.06	–	–		
	M&F	M to F	0.06 ± 0.12	0.26 ± 0.19	0.11 ± 0.20	0.46 ± 0.50	0.04 ± 0.09	0.47 ± 0.50	2.96	0.228
(8) Copulation									1.19	0.553

Behaviors between adults are shown

Figure: Mean ± SD. Mean = average number of occurrences of the behavior for each focal animal/hour, *M* male, *F* female, + no record of focal animal, but recorded by all-occurrence-behavior sampling, (+) no record during the study periods, but recorded during other study periods. – no record** $p < 0.008$, * $p < 0.05$ ^aMacaques touched the genitalia of another individual during hugging, mounting, or genital inspection; however these genital touching occurrences are not included here^bGenital inspection was occasionally accompanied by oral-genital contact; however this oral-genital contact is not included here^cHold-bottom behavior is included^dBoth social mounts and sexual mounts are included here, as the observers were unable to distinguish between them

Fig. 2 Genital touching of *Macaca assamensis assamensis*. An adult male touched the penis of a juvenile male (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma09a>)

Fig. 5 Bridging behavior of *Macaca assamensis assamensis*. Two adult males simultaneously lifted a male infant between them and touched and sucked the infant's penis (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma01ba>)

Fig. 3 Genital sucking of *Macaca thibetana*. Two juvenile males hugged each other and mutually sucked the penis of the other male (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt06a>)

Fig. 6 Presenting behavior of *Macaca assamensis assamensis*. An approaching female turned her buttocks to another female (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma10a>)

Fig. 4 Bridging behavior of *Macaca thibetana*. Two adult males simultaneously lifted a male infant between them, turned the infant face up, and touched and sucked the infant's penis (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt01ba>)

Fig. 7 Genital inspection of *Macaca assamensis assamensis*. An adult male inspected a female's genitalia (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma04a>)

Fig. 8 Mounting behavior of *Macaca assamensis assamensis*. An adult male mounted another adult male and the mounting male touched the penis and testes of the other male (<http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma07a>)

Tibetan macaques occasionally hugged each other and mutually sucked the penis of the other male (Fig. 3; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt06a>). Neither western nor eastern Assamese male macaques sucked the penis of another adult male, although males of eastern Assamese macaques sucked the genitalia of male and female infants (see below).

Between adult females None of females in any of the three macaque species sucked the genitalia of another female, although they occasionally licked a secretion on the genitalia of another female during genital inspection (see below).

Between adult males and adult females None of the males in any of the three macaque species sucked a female's genitalia, except for genital inspection. Neither western nor eastern Assamese female macaques sucked a male's penis, and we recorded only one event in which a female Tibetan macaque sucked a male's penis.

Bridging

Bridging is defined as two individuals simultaneously lifting an infant.

Between adult males Bridging behavior was recorded in males of both Tibetan macaques (Fig. 4; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430mt01a>) and eastern Assamese macaques (Fig. 5; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma01a>). That is, two males of these macaque species simultaneously lifted an infant between them when the male who was holding the infant approached another male or was approached by another male. One or both of the males frequently touched and/or sucked the genitalia of the infant dur-

ing bridging. Both macaques used a male infant in bridging more frequently than expected considering the number of male and female infants in the study group (chi-square test, $df=1$, $\chi^2=19.5$, $p<0.05$ for eastern Assamese macaques; $df=1$, $\chi^2=70.2$, $p<0.05$ for Tibetan macaques). Male Tibetan macaques usually turned the infant face up, whereas male eastern Assamese macaques did not necessarily do so. In contrast to Tibetan and eastern Assamese macaques, male western Assamese macaques never performed bridging behavior. The rate of bridging behavior between adult males was significantly higher in Tibetan and eastern Assamese macaques than in western Assamese macaques, who did not perform bridging behavior (Kruskal–Wallis test, $n_1=7$, $n_2=10$, $n_3=5$, $H=12.964$, $p<0.008$ during the birth season; $n_1=7$, $n_2=5$, $n_3=6$, $H=13.112$, $p<0.008$ during the mating season, Table 3).

Between adult females Female Tibetan and eastern Assamese macaques performed bridging behavior with females. When a mother was holding her infant offspring, another female approached the mother, clasped the infant's leg, and lifted the infant with the mother. One or both of the females touched and/or sucked the genitalia of the infant. Female Tibetan macaques used a male infant more frequently than expected (chi-square test, $df=1$, $\chi^2=53.8$, $p<0.05$), but no significant sex difference was found in eastern Assamese macaques (chi-square test, $df=1$, $\chi^2=1.1$, n.s.). Female western Assamese macaques did not perform bridging behavior. The rate of bridging behavior between females was significantly higher in Tibetan and eastern Assamese macaques than in western Assamese macaques, who did not perform bridging behavior (Kruskal–Wallis test, $n_1=7$, $n_2=10$, $n_3=9$, $H=12.341$, $p<0.008$ during the birth season; $n_1=7$, $n_2=5$, $n_3=9$, $H=10.189$, $p<0.05$ during the mating season, Table 3).

Between adult males and adult females Bridging behavior was recorded between males and females in Tibetan and eastern Assamese macaques. When a mother was holding her offspring infant, a male approached the mother, clasped the infant's leg, and simultaneously lifted the infant with the mother. Males sometimes carried an infant to its mother and lifted it with the mother. One or both of the individuals touched and/or sucked the genitalia of the infant. Male and female Tibetan macaques used a male infant more frequently than expected (chi-square test, $df=1$, $\chi^2=232.7$, $p<0.05$), but the difference could not be tested in eastern Assamese macaques due to a small sample size. Western Assamese macaques did not perform bridging behavior between males and females. The rate of bridging behavior between males and females was significantly higher in Tibetan and eastern Assamese macaques than in western Assamese macaques during the birth season, although the rate did not signifi-

cantly differ during the mating season (Kruskal–Wallis test, $n_1 = 14$, $n_2 = 20$, $n_3 = 14$, $H = 12.741$, $p < 0.008$ during the birth season; $n_1 = 14$, $n_2 = 10$, $n_3 = 15$, $H = 2.785$, n.s. during the mating season, Table 3).

Genital showing (penis showing and presenting)

Penis showing is defined as the behavior in which males in a quadrupedal posture raise one of their legs and show their penis to another individual. Presenting is defined as the behavior in which males or females in a quadrupedal posture turn their buttocks to another individual and take the same posture as female monkeys do for copulation.

Between adult males Males of all three macaque species performed penis showing behavior to another male. Males of all three macaque species also performed presenting behavior. In addition to subordinate males, dominant males performed presenting behavior to their subordinate male to solicit mounting.

Between adult females Females in all three macaque species performed presenting behavior in which they turned their buttocks to another female (Fig. 6; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma10a>). Females in eastern Assamese macaques performed presenting behavior to another female more frequently than other macaque species in the birth season, although the rate did not significantly differ during the mating season (Kruskal–Wallis test, $n_1 = 7$, $n_2 = 10$, $n_3 = 9$, $H = 9.876$, $p < 0.008$ during the birth season; $n_1 = 14$, $n_2 = 10$, $n_3 = 15$, $H = 0.101$, n.s. during the mating season, Table 3).

Between adult males and adult females None of the males in any of the three macaque species raised his leg and showed his penis to a female. None of the males in any of the macaque species turned his buttocks toward a female. Females in all three macaque species turned their buttocks toward males.

Genital inspection

Genital inspection is defined as the behavior in which males or females bring their face close to the genitalia of another individual and carefully look at the genitalia, sometimes while smelling, touching the genitalia with their fingers, licking a secretion on their fingers, and occasionally making physical contact between their mouth and the female genitalia to directly lick a secretion on the genitalia. However, oral–genital contact during genital inspection was not classified as genital sucking.

Between adult males Although males and females both inspected female genitalia, no males of the three macaque species inspected the penis of another male. When males touched the penis of another male (penis touching behavior), they did not carefully look at or smell it.

Between adult females Females in all three macaque species stared at, smelled, and/or touched the genitalia of another female, and occasionally licked a secretion on the genitalia of another female. Dominant females inspected her subordinate female's genitalia, whereas subordinate females did not inspect her dominant female's genitalia (sign test, $n_1 = 4$, $n_2 = 0$, n.s. for western Assamese macaques; $n_1 = 13$, $n_2 = 0$, $p < 0.05$ for eastern Assamese macaques; $n_1 = 29$, $n_2 = 0$, $p < 0.05$ for Tibetan macaques). Females inspected the genitalia of another female during both the birth and mating seasons. The significance of the difference between the two seasons could not be examined, due to the small sample size.

Between adult males and adult females Males in all three macaque species inspected a female's genitalia (Fig. 7; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma04a>). That is, males carefully looked at, smelled, touched with their fingers, licked a secretion on their fingers, and/or licked a secretion on female genitalia. They performed this behavior more frequently during the mating season than during the birth season, although the difference was not significant for Tibetan macaques (chi-square test, $df = 1$, $\chi^2 = 50.5$, $p < 0.05$ for western Assamese macaques; $\chi^2 = 19.9$, $p < 0.05$ for eastern Assamese macaques; $\chi^2 = 0.03$, n.s. for Tibetan macaques). No females in any of the three macaque species inspected a male's penis.

Mounting

Mounting is defined as the behavior in which males or females mount another individual, by clasping the feet of the recipient with their toes, and taking the same posture as copulation without inserting the penis into the female's vagina even if the mounter is a male.

Between adult males Males of all three macaque species mounted another male. During mounting, one male used his toes to grasp the other male's legs and mounted the back of the other male, which is a posture similar to that of copulation (Fig. 8; <http://www.momo-p.com/showdetail-e.php%3fmovieid%3dmomo090430ma07a>). Both the mounting and mounted males frequently touched the penis and testes of the other male, but did not touch their own penis or testes during mounting. They did not perform pelvic thrust and did not ejaculate during mounting. Anal penetration was never recorded. Not only did a dominant

male mount his subordinate male but a subordinate male would also mount his dominant male. A dominant male did not mount his subordinate male more frequently than vice versa (sign test, $n1 = 22$, $n2 = 34$, n.s. for western Assamese macaques; $n1 = 55$, $n2 = 49$, n.s. for eastern Assamese macaques; $n1 = 43$, $n2 = 50$, n.s. for Tibetan macaques).

Between adult females Female western and eastern Assamese macaques occasionally mounted another female. Only dominant females mounted subordinate females in eastern Assamese macaques (sign test, $n1 = 12$, $n2 = 0$, $p < 0.05$). We recorded one event in which a dominant female western Assamese macaque mounted her subordinate female, but we did not record a subordinate female mounting a dominant female. Female Tibetan macaques did not mount another female, with the exception of one female that frequently mounted another female between December 1990 and April 1991 (Ogawa 2006). When the dominance relationships were unstable in December 1990, instead of mounting, female Tibetan macaques performed hold-bottom behavior in which a female macaque did not mount but scratched another female's buttocks with her toes while clinging to the back of the other female with her hands from a sitting position behind the other female (Ogawa 2006). We did not record hold-bottom behavior in western or eastern Assamese macaques. None of the females in any of the three macaque species rubbed their genitals on the body of another female or showed signs of orgasm during the mounting and hold-bottom behavior.

Between adult males and adult females Males in all three macaque species occasionally mounted a female macaque. Because observers were unable to distinguish between social and sexual mounts, both are counted as mounting in Table 3. Female eastern Assamese macaques occasionally mounted a male macaque. However, neither western Assamese nor Tibetan macaque females mounted a male macaque.

Copulation

Copulation was defined as a male macaque mounting a female macaque and inserting his penis into the female's vagina.

Between adult males and adult females Males in all three macaque species copulated with females and ejaculated in a single mount. After the male finished thrusting his penis, he sometimes did not (or could not) immediately pull his penis out of the vagina and remained in that posture for a while (Li et al. 2005), like stump-tail macaques (Brereton 1994).

Social grooming between adults

Figure 9 presents the rate of social grooming between males, between females, and between males and females during each season. Grooming bouts were more frequently recorded between females than between males (chi-square test, $df = 1$, $\chi^2 = 170.2$, $p < 0.05$ for western Assamese macaques; $\chi^2 = 123.8$, $p < 0.05$ for eastern Assamese macaques; $\chi^2 = 69.7$, $p < 0.05$ for Tibetan macaques). Females groomed males more frequently than vice versa during the birth season (chi-square test, $df = 1$, $\chi^2 = 8.3$, $p < 0.05$ for western Assamese macaques; $\chi^2 = 33.3$, $p < 0.05$ for eastern Assamese macaques; $\chi^2 = 29.8$ for Tibetan macaques), but the difference was not significant during the mating season for western and eastern Assamese macaques (chi-square test, $df = 1$, $\chi^2 = 1.4$, n.s. for western Assamese macaques; $\chi^2 = 0.0$, n.s. for eastern Assamese macaques; $\chi^2 = 5.9$, $p < 0.05$ for Tibetan macaques). The lack of a difference during the mating season is due, in part, to the fact that males groomed females during the mating season more frequently than they did during the birth season (chi-square test, $df = 1$, $\chi^2 = 50.9$, $p < 0.05$ for western Assamese macaques; $\chi^2 = 27.7$, $p < 0.05$ for eastern Assamese macaques; $\chi^2 = 12.0$ for Tibetan macaques), whereas females did not necessarily groom males more frequently during the mating season than they did during the birth season (chi-square test, $df = 1$, $\chi^2 = 33.3$, $p < 0.05$ for western Assamese macaques; $\chi^2 = 0.0$, n.s. for eastern Assamese macaques; $\chi^2 = 2.7$, n.s. in Tibetan macaques).

Dyadic infant handling by adult males

Table 4 presents the rate of social behaviors by adult males toward infants based on focal-animal sampling.

Genital touching

Males in all three macaque species touched the genitalia of an infant during dyadic interactions. Male eastern Assamese and Tibetan macaques did so during bridging behavior as well (see above).

Genital sucking

Male Tibetan and eastern Assamese macaques sucked the genitalia of an infant during dyadic interactions as well as during bridging behavior (see above). They sometimes turned the infant upside down. The infant sometimes jumped onto an adult male's face to have his penis sucked. Male western Assamese macaques did not suck the genitalia of infants.

Fig. 9 Rate of grooming between adults of *Macaca assamensis pelops*, *M. a. assamensis*, and *M. thibetana*. **a** Social grooming between males. **b** Social grooming between females. **c** Social groom-

ing from male to female. **d** Social grooming from female to male. Rate of behavior = number of grooming bouts/hour. One bout is a contentious grooming without a > 10-s pause

Holding

Males in all three macaque species held an infant.

Social grooming

Males in all three macaque species groomed an infant.

Discussion

The age and sex compositions of the study groups show that western Assamese macaques in Nepal, eastern Assamese macaques in Thailand, and Tibetan macaques in China all form multi-male multi-female social groups. The records of transfer between social groups indicate that all macaque species form groups with female philopatry and

Table 4 Rate of social behaviors by adult males to infants of *Macaca assamensis* and *M. thibetana*

Study subject behavior	<i>Macaca assamensis pelops</i>		<i>Macaca assamensis assamensis</i>		<i>Macaca thibetana</i>		Kruskal–Wallis test			
	Birth season	Mating season	Birth season	Mating season	Birth season	Mating season	Birth season		Mating season	
							<i>H</i>	<i>p</i>	<i>H</i>	<i>p</i>
Genital touching	+	+	0.04 ± 0.07	0.01 ± 0.04	+	+	3.96	0.138	1.57	0.456
Genital sucking	–	–	0.08 ± 0.10	0.08 ± 0.11	0.28 ± 0.34	+	5.85	0.054	5.53	0.063
Holding	0.04 ± 0.19	0.01 ± 0.04	0.07 ± 0.16	0.12 ± 0.22	0.26 ± 0.43	0.02 ± 0.04	0.90	0.636	1.50	0.471
Grooming	0.13 ± 0.18	0.14 ± 0.16	0.11 ± 0.25	0.26 ± 0.32	0.24 ± 0.39	0.07 ± 0.10	0.86	0.650	1.38	0.502

Figure: mean ± SD. Mean = average number of occurrences of the behavior for each focal animal/hour

+ no record of focal animal, but recorded by all-occurrence-behavior sampling, – no record

male dispersal (Ogawa 2006). The social relationships within these groups were also similar to one another: each had a linear dominance hierarchy among adult females and kin-biased relationships among females (Balasubramaniam et al. 2012, 2018). The relative frequencies of social grooming between males, between females, and between males and females were similar in the three species. Cooper and Bernstein (2000) reported that adult male Assamese macaques at the Tukeswari (Tukreshwari) Temple in the West Bengal state in India groomed adult females more frequently than the reverse. In the present study, however, neither western nor eastern male Assamese macaques groomed females more frequently than vice versa, which is common among macaque species.

One of the conspicuous features of the social behavior of these macaque species is that they performed various affiliative behaviors with physical contact between adult males, between adult females, and between adult males and adult females. Additionally, they touched the genitalia of another individual during the interactions. A variety of genital contact behaviors have been reported in other primates (Dixon 1998; Vasey 1995). For example, pygmy chimpanzees (*Pan paniscus*) perform gg (genito–genital) rubbing behavior between females and rump–rump contact between males (Kano 1980; Kuroda 1980). However, none of the three macaque species made genital–genital contact. Unlike kissing in humans (*Homo sapiens*), none of the three macaque species made oral–oral contact, although western and eastern Assamese macaques sometimes put their lips on or very close to the body of another individual (Ogawa unpublished data). Instead, when they showed affiliative behaviors such as hugging and mounting, they frequently touched the genitalia of the other individual. In addition, eastern Assamese and Tibetan macaques sucked the genitalia of infants, and male Tibetan macaques sucked the penises of other adult males.

In addition to copulation, some of the male–female interactions involving genital contact could be regarded as reproductive efforts. During some interactions involving a male macaque mounting a female, the male did not actually insert his penis into the female's vagina, primarily because the female rejected copulation. Males inspected a female's genitalia more frequently during the mating season than during the birth season, whereas females did not inspect a male's penis. These findings indicate that males may try to monitor the timing of ovulation in the female sexual cycle.

On the other hand, other behaviors that involved genital contact, such as penis sucking, penis touching, hugging, and mounting, did not appear to be reproductive efforts but rather ritualized affiliative behaviors (Ogawa 1995, 2006). During genital contact, males did not engage in pelvic thrusts or ejaculation, and females did not rub their genitals or show signs of orgasm. Unlike the mounting between

female Japanese macaques (Vasey 2006), the genital contact behaviors of the three macaque species in the present study may serve social functions in that they may regulate social relationships with another individual. Only dominant females inspected the genitalia of another female. Females might assert their dominance rank via genital inspection rather than by monitoring the sexual cycles of another female. In contrast to female genital inspection, the mounting rate of the dominant male onto the subordinate male did not differ from the reverse interaction, indicating that these males were not asserting their dominance rank by mounting.

We also observed several differences in genital contact behaviors among the three macaque species. Bridging behavior was recorded between males, between females and between males and females in Tibetan macaques (this study; Ogawa 1995, 2006) and in eastern Assamese macaques in Thailand (this study; Kalbitz et al. 2017). Males in these macaque species also sucked the genitalia of an infant during bridging behavior and during dyadic interactions with an infant. The nature of bridging did differ somewhat between eastern Assamese macaques and Tibetan macaques. Although males do not necessarily have to turn the infant face up in order to suck the genitalia of the infant, male Tibetan macaques usually turned the infant face up, whereas male eastern Assamese macaques did not necessarily do so. Bridging appeared to be more ritualized in Tibetan macaques than in eastern Assamese macaques. Additionally, only male Tibetan macaques directly sucked the penis of another adult male.

In contrast to eastern Assamese and Tibetan macaques, western Assamese macaques in Nepal did not perform either bridging or genital sucking. The absence of a certain behavior cannot be logically demonstrated. At the very least, however, western Assamese macaques performed these behaviors significantly less frequently compared to Tibetan and eastern Assamese macaques. Additionally, field observations at Ramdi Village (27°54'N, 83°38'E), Pyuthan District, Nepal and at Wat Tham Pha Tha Pol (16°31'N, 100°40'E), Phitsanulok Province, Thailand, supported our observations that eastern Assamese macaques engage in bridging behavior, whereas western Assamese macaques do not (Ogawa et al. 2019). The occurrence of bridging and genital sucking behaviors in Tibetan and eastern Assamese macaques is generally consistent with genetic and morphological evidence that Tibetan and eastern Assamese macaques share a close phylogenetic relationship (Biswas et al. 2011; Sukmak et al. 2014). Assuming that Tibetan macaques split from eastern Assamese macaques, bridging and genital sucking behaviors may have evolved in the clade containing Tibetan and eastern Assamese macaques in the *sinica* species-group, although it is also possible that western Assamese macaques lost the bridging behavior. On the other hand, the fact that only western Assamese macaques in Nepal did not exhibit

bridging behavior is consistent with a genetic study demonstrating that the Nepal population of Assamese macaques was unique in its genetic diversity compared to other populations (Khanal et al. 2018).

Similar to Tibetan and eastern Assamese macaques, stump-tail and Barbary macaques also exhibit a behavior similar to bridging. Two female stump-tail macaques handle a newborn baby together (Estrada and Sandoval 1977; Chokechaipaisarn et al. 2016). Male Barbary macaques handle an infant together, which is referred to as “triadic male–infant interaction” and “agonistic buffering” (Deag and Crook 1971; Paul 1999; Taub 1980). Such interactions have rarely been reported in other species-groups of macaques. These findings suggest that the origin of these behaviors may have occurred in the common ancestral species of the *sinica* species-group (possibly including the clade containing stump-tail and Barbary macaques) and that some species lost the behavior while others evolved a more ritualized version of the behavior. To determine whether these behaviors are homologous or analogous, further studies are needed in other populations of Assamese macaques and other macaques of the *sinica* species-group.

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