

RESEARCH ARTICLE

Variation in Body Mass and Morphological Characters in *Macaca mulatta brevicaudus* From Hainan, China

PENG ZHANG^{1,2,3*}, MU-YANG LYU², CHENG-FENG WU¹, YUAN-MENG-RAN CHU², NING HAN⁴, DANHE YANG¹, AND KAIJIN HU¹

¹School of Sociology and Anthropology, Sun Yat-sen University, GuangZhou, China

²School of Life Sciences, Sun Yat-sen University, GuangZhou, China

³Key Lab of Human Evolution and Archaeometry in Guangdong Province, Sun Yat-sen University, GuangZhou, China

⁴Faculty of Foreign Languages and Culture, Kunming University of Science and Technology, Kunming, China

The rhesus macaque (*Macaca mulatta*) is the most widely distributed nonhuman primate species in the world, with six subspecies distributed through China. From 2012 to 2014, we conducted studies on the body mass and morphological variation of the southernmost subspecies *M. m. brevicaudus* in Nanwan Nature Reserve for Rhesus Macaque, Hainan, China. We compared measurements with other populations of this species. We also investigated the inter-group body mass variation from seven provisioned free-ranging groups in our study site. Our results show that *M. m. brevicaudus* has the smallest body size, the smallest body mass, and the shortest tail among rhesus macaque subspecies. Its sexual dimorphism score is also among the lowest, which is similar to other southern distributed subspecies in China, but smaller than northern distributed subspecies. We found that the average body mass of female macaques is not correlated with their dominance ranks. There are significant differences in body mass among the seven adjacent study groups at the same site, suggesting the existence of inter-group competition. Average body mass of a group is better described by a quadratic function of group size than a linear one as predicted by the socio-ecological model. *Am. J. Primatol.* 78:679–698, 2016. © 2016 Wiley Periodicals, Inc.

Key words: primates; rhesus macaque; Hainan subspecies; body size; sexual dimorphism

INTRODUCTION

Body mass and morphological traits provide the most extensive materials for comparative studies in primates [Feeroz et al., 2010; King et al., 2011; Leigh, 1994; Smith & Jungers, 1997; Soligo, 2006; Vančata et al., 2000]. There are numerous studies on the morphology and body mass of primate species. These include Orangutans (*Pongo pygmaeus*) [Fooden & Izor, 1983], Bonobos (*Pan paniscus*) [Leigh & Shea, 1995], Chimpanzees (*P. troglodytes*) [Pusey et al., 2005], Gorillas (*Gorilla gorilla*) [Zihlman & McFarland, 2000], Olive baboons (*Papio anubis*) [Dunbar, 1990; Strum, 1991], Yellow baboons (*P. cynocephalus*) [Altmann & Alberts, 1987; Altmann et al., 1993], Chacma baboons (*P. ursinus*) [Barrett & Henzi, 1997], Mandrills (*Mandrillus sphinx*) [Setchell et al., 2001], Rhesus macaques (*Macaca mulatta*) [Vančata et al., 2000], Japanese macaques (*M. fuscata*) [Jaman & Huffman, 2011; Kurita et al., 2002; Mori, 1979], Bonnet macaques (*M. radiata*) [Cooper et al., 2004], Pig-tailed macaques (*M. nemestrina*) [Tokuda & Jensen, 1969], Grey mouse lemurs (*Microcebus murinus*) [Lahann et al., 2006], Sichuan snub-nosed

monkeys (*Rhinopithecus roxellana*) [Peng et al., 1988], and Tibetan macaques (*M. thibetana*) [Zhao, 1994].

Patterns of large-scale variation in primate body mass and other morphological traits are summarized

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*Correspondence to: Peng Zhang, Martin Hall, Department of Anthropology, Sun Yat-sen University, GuangZhou 510275, China. E-mail: zhangp99@mail.sysu.edu.cn

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in biogeographical rules such as Bergmann's rule (increase of body size with increasing latitudes, [Bergmann, 1847; Fernandez-Duque, 2011; Villano et al., 2009]), Allen's rule (decrease of relative appendage length with increasing latitudes [Allen, 1907; Clarke & O'Neil, 1999; Fooden & Albrecht, 1999]), and the island rule (large species get smaller and small species get larger after colonizing an island [Bromham & Cardillo, 2007; Welch, 2009]). Both Bergmann's rule and Allen's rule are statements related to thermoregulation. Because lower surface to volume ratio and relatively shorter appendages contribute to better heat retention for larger size animals in a cold climate, the body size should increase with increasing latitude, and relative appendage length should increase with decreasing latitude. Some have also suggested alternative mechanisms such as primary productivity and environmental predictability to explain latitudinal size patterns [Meiri, 2011]. The island rule mainly results from an increased level of intra-specific competition among larger-sized animals and avoidance of predation by smaller size animals combined with their specific resource requirements [Bromham & Cardillo, 2007; Van Valen, 1973]. Therefore much of this large-scale variation could be explained by environmental factors such as precipitation [Gordon et al., 2013], annual temperature [Soligo, 2006], seasonality [Gordon et al., 2013], and habitat types [Olupot, 2000]. On the other hand, small-scale body mass variation is subject to influences of socio-ecological factors such as group size and social dominance rank. The socio-ecological model predicts that animals respond to increased intensity of competition by increasing foraging efforts in order to maintain constant net food intake; as groups become larger, the compensatory response becomes insufficient and net food intake starts to decline [Sterck et al., 1997; van Noordwijk & van Schaik, 1999]. Group size was found to be positively correlated with inter-group competitiveness in several studies (*S. entellus* [Koenig, 2000], *M. fuscata* [Sugiura et al., 2000], and *M. radiata* [Cooper et al., 2004]), indicating that larger groups often have greater access to food resources and greater net food intake. They also often have greater mean body mass when group sizes are not so large as to affect food availability. The degree of impact of social dominance on body mass varies in different primate species and between sexes: a positive correlation of body mass and social status had been observed in captive populations, but less so in wild populations (*M. sinica* [Dittus, 1998]; *M. fascicularis* [Morgan et al., 2000]; *M. radiata* [Cooper et al., 2004]; *P. troglodytes* [Pusey et al., 2005]).

Sexual dimorphism has been one of the most focused phenomena in evolutionary biology [Clutton-Brock et al., 1977; Plavcan & van Schaik 1997]. Body mass dimorphism (BMD) is closely related to

ontogeny, sexual selection, and habitat type [Kamilar & Cooper, 2013; Smith & Cheverud, 2002]. Rensch's rule states that the degree of sexual dimorphism increases with body size [Rensch, 1950]. Such a scaling relationship is expected if the level of sexual selection increases with increasing body size or natural selection is stronger against male as size increases [Clutton-Brock et al., 1977; Gordon, 2006; Smith & Cheverud, 2002]. Because of strong phylogenetic signals in BMD, it is often characterized as a biologically meaningful subspecific trait in some macaque species, such as *Macaca nigra*, *M. fascicularis*, *M. nemestrina*, *M. mulatta* and *M. arctoides* [Plavcan & van Schaik, 1997; Plavcan, 2001; Smith & Jungers, 1997; Turner et al., 1997].

Rhesus macaque (*Macaca mulatta*) provides a good primate species for examining biogeographical rules and socio-ecological models regarding body mass and morphological traits, because it is the most widely distributed non-human primate species in the world. Its natural range extends from East to South Asia, with substantial variation of both body mass and morphological traits among populations in different geographical locations [Fooden, 1982]. Rhesus macaques currently inhabiting China most likely dispersed from northern Asian populations during the Pleistocene, which distinguish themselves with shorter tails than other populations in South Asia [Fooden & Albrecht, 1999]. Among the six subspecies distributed in China (*M. m. mulatta*, *M. m. breviceaudus*, *M. m. lasiotis*, *M. m. littoralis*, *M. m. vestita* and *M. m. tcheliensis*), *M. m. breviceaudus* is the southernmost distributed subspecies [Fooden, 1982; Jiang et al., 1991]. While previous studies about *M. m. breviceaudus* have provided qualitative descriptions of their morphological traits based on several museum specimens [Jiang et al., 1991], a full account of variation on both body mass and morphological traits in wild populations of *M. m. breviceaudus* is still lacking.

In this study, we measured body mass and morphological characteristics of *M. m. breviceaudus* from seven adjacent, free-ranging groups living in Nanwan Nature Reserve for Rhesus Macaque in Hainan, China. Our first main objective was to present basic body mass and morphological data for *M. m. breviceaudus*. We hypothesized that as the southernmost distributed subspecies in China, *M. m. breviceaudus* should have the smallest body size and lowest body mass among Chinese rhesus populations (Hypothesis I). We reviewed sexual dimorphism of body mass in the genus *Macaca* and tested whether it is a sub-specific trait in *M. mulatta*. Our second main objective was to examine inter-group variation in body mass among adjacent groups. The mean group size of wild populations in *M. m. breviceaudus* was 38 ± 6 [Jiang et al., 1989]. We hypothesized that body mass may vary more among groups associated with

strong inter-group competition, and that mean body mass will decline as group size becomes too large (Hypothesis II). We also examined the correlation between body mass and dominance rank. In addition, we attempted to develop an efficient procedure and method for measuring body mass in free-ranging primates.

METHODS

Animal Ethics Statement

The research protocol was reviewed and approved by the institutional animal care and use committee and animal ethical and welfare committee of Sun Yat-sen University, met the legal requirements of 'Law of the People's Republic of China on the Protection of Wildlife,' and adhered to the American Society of Primatologists Principles for the Ethical Treatment of Non-Human Primates.

Study Site and Subjects

We carried out the study at Nanwan Nature Reserve for Rhesus Macaque, which is located in Nanwan peninsula with an area of about 10km² in southeastern Hainan Island, China (109°59'E, 18°24'N) (Fig. 1). The climate is characterized by alternating dry and rainy seasons. The coldest month is January, and the hottest month is July. The monthly mean temperatures in January and July were 22.2°C and 28.1°C respectively. The landscape is mainly made up of coastal mesas and hills with the

highest altitude of 255m in the Reserve (see more details in [Jiang et al., 1989; 1994; 1998]).

Since the founding of the Nature Reserve in 1964, there has been a great improvement in the living conditions of macaques [Jiang et al., 1994]. About 19 groups live in the Reserve and the total population had reached approximately 1,900 in 1998 [Jiang et al., 1998]. Some groups have been habituated and provisioned since the 1980's. Seven monkey groups (named as SJB, AC, JZ, HZ, GS, XBL and HL groups, respectively) visited the Monkey Park daily and spent hours around the park during our study periods. Since they were provisioned and habituated to humans, they were not strictly "wild" populations. These seven groups are referred to as provisioned, free-ranging groups throughout this article. Although aggressive inter-group encounters occurred sometimes, these groups were often tolerant of one another from distances of 10–300 m, and their home ranges appeared largely overlapped (Peng Zhang, unpublished data). The park staff feed the monkeys with sweet potatoes, wheat grains, and vegetables three times per day, at 0800, 1200, and 1730 hr, respectively. They distribute food to two regular provisional sites according to the number of visiting monkeys and no preference is given to any particular group. The amount of provisioned food is 80g per individual per day. Tourists are not allowed to feed monkeys. Monkeys also continue to consume natural foods in the forest and bushes around the park. At night, they leave and rest in the mountains outside the park. There were 10 individuals in the captive group (2 adult females, 6 adult males, 2 juveniles), all

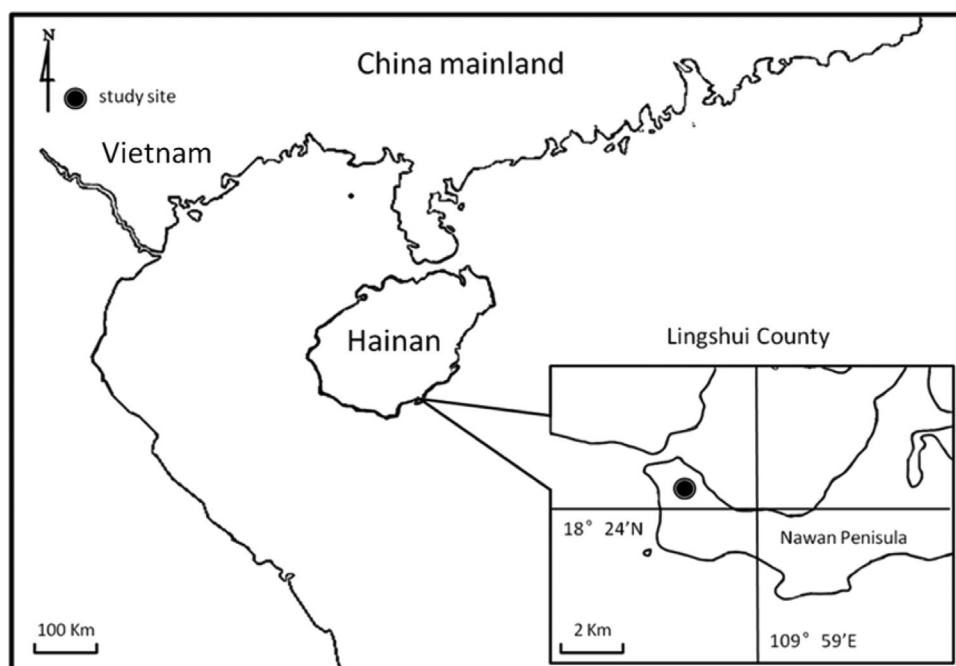


Fig. 1. The study site.

of which were captured from nearby wild populations. They were leashed by ropes and fed by staff in the Monkey Park. These captive individuals had little chance to consume foods in natural habitats.

We classified the monkeys into five age-sex groups: adult males (estimated to be more than 4 years old), adult females (estimated to be more than 4 years old with fertility experience), juveniles (estimated at 1–4 years), infants (estimated at 0.5–1 years with frequent breastfeeding), and neonates (estimated at under 0.5 years and often move around with their mothers). All individuals of the other study groups were individually identified by their physical traits. Only limited numbers of individuals in the rest subject groups were identified.

Data Collection

We conducted our study from July 2 to July 31 in 2012, from July 9 to August 6 in 2013, and from July 9 to August 5 in 2014, for a total of three months. We used a photogrammetric method modified from Mori [1979] to obtain morphometric data (Fig. 2). An anatomical landmark was placed horizontally on the digital scale, and photos were taken when the camera axes and subject were oriented vertically. Trunk length (linear distance between sternal notch and the

superior margin of the pubic symphysis), tail length (length from tip of the tail to junction of the base of the tail), forearm length (length of the segment between elbow and wrist joints), and leg length (length of the segment between knee and ankle joints) were then measured from the photos (units: cm). This method has the advantage of reducing the risk of injury, death and stress for animals compared with invasive methods such as anesthesia and capture [Kurita et al., 2012], and is more preferable in large scope investigations in wild populations.

We measured body mass with a Zhongqingda ACS type electronic scale (units: kg, accuracy: 0.005 kg). We placed small amounts of peanuts and rice on top of the scale to entice the monkeys. The bait was no longer needed after monkeys were habituated to the electronic scale. The digital display was recorded while the monkey was standing or sitting on the scale for more than 3 sec (Fig. 2). Body mass of neonates was calculated by subtracting the body mass of the mother from the total body mass of a mother carrying a baby. We estimated the female body mass by subtracting the mean body mass of neonates from total body mass when the mother's body mass was not available. Since not all individuals were identified during our study period, we carefully avoided measuring the same individual



Fig. 2. Measuring a macaque's body mass. The digital display was recorded while the monkey was standing or sitting on the scale for more than 3 sec (units: kg).

repeatedly by using techniques such as non-toxic hair dye spray on the back fur of measured individuals. The hair dye lasts for more than one month. We removed dubious data points in further analysis. Each member of JZ group was identified and named by their physical characteristics. The dominance rank of adult females in JZ group was determined by submissive behavior during dyadic, unidirectional interactions (Chengfeng Wu, unpublished data). We identified all females of HL groups and randomly measured 12 females, and grouped them into high-ranking (4 individuals), middle-ranking (4 individuals) and low-ranking females (4 individuals). We documented the inter-group encounters from April 2 to April 30, 2014. Dominance rank of each group was determined by unidirectional interactions such as avoidance and aggression. We obtained dominance rank of the seven groups from 71 unidirectional aggressive interactions among them, and found that their dominance ranks and group size were highly correlated ($\rho = 0.96$, $P < 0.05$). We summarized body mass data of other species in genus *Macaca* from the literature (Appendices I and II).

Data Analysis

We examined the differences between adult males and adult females using a two-sample t-test. We examined variation in inter-annual and inter-group body mass using a Kruskal-Wallis test when data were not normally distributed. In order to control the type I error of doing multiple simultaneous inferences, Pairwise t-tests with Holm correction were conducted when comparing body mass of specific groups [Wright, 1992]. We compared sexual dimorphism between *M. m. brevicaudus* and the mean sexual dimorphism of other species in genus *Macaca* using a one-sample t-test. We also examined the sexual dimorphism difference between *M. m. brevicaudus* and other subspecies of *M. mulatta* in China using a Wilcoxon test. If an individual was measured more than once, the

individual's mean body mass was used in calculating the population mean body mass. We calculated dimorphism scores by dividing mean numerical values of male by mean numerical values of female. We took the arithmetic mean of body mass dimorphism scores from 2012 to 2014 as the final value of BMD of *M. m. brevicaudus*. We used a Spearman rank test to examine correlation between dominance rank and body mass in JZ group, as well as correlation between group dominance rank and group size. We also performed a Kruskal-Wallis test to examine whether body mass is correlated to dominance rank in HL group. We used linear regression to analyze the relationship between group size and the mean body mass of a group. The degree of freedom used in this regression analysis was reduced correspondingly to account for the potential data dependency caused by repeated measurements of an identical group. We performed a *t*-test to show the difference between captive and provisioned free-ranging individuals. All analyses were performed in R. *P* values were based on two-tailed tests when not particularly indicated. The significance level was set to 0.05 throughout this study.

RESULTS

Body Mass and Morphological Traits of *M. m. brevicaudus*

More than 100 individuals from seven free-ranging groups were measured each year in 2012, 2013 and 2014. The ratio of measured individuals to total individuals in each group ranged from 20% to 70% (Table I). There was no significant inter-annual body mass difference in any age-sex group (adult males, $H = 3.62$, $df = 2$, $P = 0.16$; adult females, $H = 2.46$, $df = 2$, $P = 0.29$; juveniles, $H = 3.22$, $df = 2$, $P = 0.20$; infants, $H = 4.30$, $df = 2$, $P = 0.12$; neonates, $H = 0.42$, $df = 2$, $P = 0.81$) from 2012 to 2014. The average body mass of the study population was 6.33 kg for males, 5.24 kg for females, 2.90 kg for

TABLE I. Group Size and Proportion of Measured Individuals

	SJB	AC	JZ	XBL	HL	GS	HZ
2012							
n	90 ± 9	38 ± 3	22 ± 2	20 ± 2	112 ± 7	—	—
Percentage	21.1	36.9	45.5	50.0	30.4		
2013							
n	65 ± 4	49 ± 1	25 ± 0	—	130 ± 10	25 ± 5	38 ± 1
Percentage	44.6	32.7	48.0		24.6	48.0	71.1
2014							
n	74 ± 5	47 ± 6	22 ± 0	—	115 ± 8	25 ± 1	29 ± 0
Percentage	62.2	46.8	45.5		44.4	56.0	51.7

Note. The group size is n. Percentage (unit: %) shows the proportion of measured individuals to the entire group. SJB, AC, JZ, XBL, HL, GS, and HZ are the names of studied groups.

juveniles, 1.62 kg for infants, and 0.58 kg for neonates (Table II).

Table III summarizes adult body mass and morphological variables of rhesus macaques in China and India, and shows that *M. m. brevicaudus* was significantly different from most mainland populations in many aspects and is characterized by smaller body size, smaller body mass, shorter tail and shorter limbs than mainland populations.

The Spearman rank test showed that there was no significant correlation between adult female body mass and dominance rank in JZ group ($\rho = -0.11$, $P = 0.59$). The Kruskal-Wallis test also showed that there was no significant difference among high-ranking, middle-ranking, and low-ranking females in HL group ($H = 5.16$, $df = 2$, $P = 0.07$).

Inter-group Variation in Body Mass

Figure 3 shows that there was a significant difference in body mass of adult females among the seven study groups ($H = 29.12$, $df = 6$, $P < 0.05$). For instance, the mean female body mass in XBL group was 4.37 kg, which was significantly smaller than 5.97 kg in AC group (Pairwise t -tests, $t = 4.34$, $P < 0.05$) and 5.76 kg in SJB group (Pairwise t -tests, $t = 4.31$, $P < 0.05$), respectively. Nevertheless, there was no significant linear correlation between group size and mean adult female body mass. The relationship between body mass and group size is shown in Figure 4. When regression analyses were performed, we found that a quadratic equation described the trend much better than a linear equation (regression with first order terms: $R^2 = 0.015$, $P = 0.64$, $AIC = 34.34$; regression with second order terms: $R^2 = 0.42$, $P < 0.05$, $AIC = 27.04$).

Figure 5 shows the variation in body mass between the free-ranging groups and a captive group. Due to the small sample of captive females, only data from adult males were used in this comparison. The mean body mass of captive adult males was 7.76 kg ($n = 6$) and the mean body mass of provisioned free-ranging adult males was 6.33 kg ($n = 15$). Captive

macaques were 22.59% heavier than free-ranging macaques on average, and this difference is significant ($t = 2.45$, $P < 0.05$).

Sexual Dimorphism

Adult body mass dimorphism was 1.208 in the study population (average score for three years). Dimorphism scores for trunk length, tail length, forearm length, and leg length in the study population were 1.151, 1.038, 1.043, and 1.203, respectively (Males, $n = 7$; Females, $n = 24$). There were significant differences in body mass, trunk length, and leg length between adult males and adult females (Body mass: $t = -5.34$, $df = 51.41$, $P < 0.05$; Trunk length: $t = 3.72$, $df = 13.13$, $P < 0.05$; Leg length: $t = 2.81$, $df = 8.84$, $P < 0.05$), but not in tail length or forearm length (Tail length: $t = 0.61$, $df = 13.55$, $P = 0.55$; Forearm length: $t = 0.50$, $df = 7.56$, $P = 0.63$).

Comparisons With Other Subspecies of Rhesus Macaque

Body mass of adult male *M. m. brevicaudus* is significantly less than that of the subspecies *M. m. lasiotis* (7.99 ± 1.13 kg, $n = 37$ [Zhao et al., 2012]; Pairwise t -tests, $t = -6.10$, $P < 0.05$) at Ninglang County, Yunnan Province, than that of subspecies *M. m. littoralis* (8.79 ± 1.03 kg, $n = 20$ [Xu, 2013]; Pairwise t -tests, $t = -5.96$, $P < 0.05$) in Anhui Province, as well as that of subspecies *M. m. tcheliensis* in Taihang Mountains, Henan Province (8.8 ± 3.0 kg, $n = 14$ [Zhao and Zhang, 1989]; Pairwise t -tests, $t = -5.44$, $P < 0.05$). The same trend was found in female *M. m. brevicaudus*, when compared with the values of female *M. m. lasiotis* (6.27 ± 0.98 kg, $n = 68$ [Zhao et al., 2012]; Pairwise t -tests, $t = -6.00$, $P < 0.05$), *M. m. tcheliensis* (6.50 ± 1.0 kg, $n = 20$ [Zhao and Zhang, 1989]; Pairwise t -tests, $t = -3.38$, $P < 0.05$) and *M. m. littoralis* (7.36 ± 1.24 kg, $n = 20$ [Xu, 2013]; Pairwise t -tests, $t = -6.29$, $P < 0.05$), respectively.

TABLE II. Body Mass and Age-Sex Distribution of Three Years

	AM	AF	J	I	N
2012					
Mean (SD)	6.91 (1.13)	5.07 (0.88)	2.75 (0.72)	1.60 (0.28)	0.53 (0.20)
n	8	43	34	12	3
2013					
Mean (SD)	6.34 (1.26)	5.46 (1.12)	2.99 (0.68)	1.48 (0.10)	0.57 (0.10)
n	15	54	38	13	8
2014					
Mean (SD)	5.98 (0.96)	5.18 (1.03)	2.94 (0.64)	1.68 (0.35)	0.59 (0.15)
n	14	70	41	36	11

Note. AM means adult male, AF means adult female, J means Juvenile, I means Infant and N means neonate. The sample size is n. Body mass shown in units of kg.

TABLE III. Comparison of Morphological Variables Among Populations of *Macaca mulatta*

	Body mass (kg)			Trunk length (cm)			Tail length (cm)			Forearm length (cm)			Leg length (cm)		
	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD
Hainan															
Male	15	6.3	1.3	7	33.6	2.5	7	15.2	2	7	12.2	2.5	7	14	2
Female	54	5.5	1.1	24	29.2	3.4	24	14.7	2.7	24	11.7	1.6	24	11.7	1.8
Jingdong/Zhenyuan															
Male	67	6.7	1												
Female	103	5.3	0.7												
Ninglang															
Male	37	8.0*	1.1												
Female	68	6.3*	1												
Taihangshan															
Male	14	8.8*	3	14	40.4*	1.4	14	16.0	1.8	14	16.7*	2	14	17.3*	2.2
Female	20	6.5*	1	20	36.6*	0.7	20	14.1	1.6	20	15.1*	1.5	20	16.4*	1.4
Anhui															
Male	20	8.8*	1	20	39.5*	2	20	19.8*	1.5						
Female	20	7.4*	1.2	20	37.1*	1.5	20	17.8*	1.5						
Nepal															
Male	9	9.8*	1.5	8	40.1*	1.8	8	26.3*	2						
Female	5	6.9*	1.3	8	36.1*	2.4	8	22.0*	2.2						
India															
Male	6	9.8*	2.5	6	37.3*	3.8	6	25.0*	1	5	16.2*	2.3	5	16.7	2
Female	17	7.9*	1.9	16	34.2*	2.8	16	22.1*	1.8	13	14.5*	1.1	13	15.2*	1.3
Bangladesh															
Male	7	8.7*	2.7	7	37.1*	2.5	7	25.7*	4.2						
Female	10	7.7*	1.4	10	35.6*	2.2	10	23.1*	2.4						

Note. N represents the sample size. SD represents the standard deviation. Comparisons were made using a t-test based on published estimates of means and standard deviations. * Significant difference from those of Hainan populations. Hainan populations belong to subspecies *M. m. brevicaudus*, Taihangshan populations belong to *M. m. tcheliensis*, Anhui populations belong to *M. m. littoralis*, Ninglang populations belong to *M. m. lasiotis*, Jingdong and Zhenyuan populations belong to *M. m. mulatta*. Trunk length is the linear distance between the sternal notch and the superior margin of the pubic symphysis. Tail length is the length from the tip of the tail to the junction of the base of the tail. Forearm length is the length of the segment between elbow and wrist joints. Leg length is the length of the segment between the knee and ankle joints. Data for Nepal, India and Bangladesh populations were obtained from Feeroz et al. [2010]

We further review the distribution of BMD scores in genus *Macaca* in Figure 6. The BMD score of *M. m. brevicaudus* is 1.208, which is significantly lower than the mean dimorphism score in genus *Macaca* ($t = 9.85$, $df = 46$, $P < 0.05$; Appendix I), and also lower than the mean dimorphism score of *Macaca mulatta* (Wilcoxon Test: $V = 65$, $P < 0.05$). The score of *M. m. brevicaudus* is close to subspecies distributed in southern China such as *M. m. littoralis* in Anhui and *M. m. mulatta* in Yunnan, but different from populations in higher latitudes such as *M. m. tcheliensis* in Henan and *M. m. lasiotis* in northern Yunnan [Xu, 2013; Zhao & Zhang, 1989; Zhao et al., 2012]. It is also close to the score of the macaque population in Cayo Santiago, which has an obviously larger body mass than that of the study population (11.00 kg for adult males, $n = 59$ and 8.80 kg for adult females, $n = 28$ [Smith & Jungers, 1997]).

The correlation between sexual dimorphism and latitude was not significant (Pearson's correlation test: $r = 0.59$, $P = 0.16$), nor was the correlation between sexual dimorphism and mean body mass significant (Pearson's correlation test: $r = 0.28$, $P = 0.55$).

DISCUSSION

Hypothesis I states that, as the southernmost distributed subspecies in China, *M. m. brevicaudus* should have the smallest body size and lowest body mass among Chinese rhesus populations. Our results support this hypothesis. Body mass of *M. m. brevicaudus* is smaller than subspecies *M. m. lasiotis*, *M. m. littoralis* and *M. m. tcheliensis* in the Chinese mainland. This is consistent with Bergmann's rule. Table III and IV show that the variation of relative tail length is generally consistent with the prediction of Allen's rule. However, the populations in India, Bangladesh and Nepal have longer tails than populations in China (Table III). The ratios of their tail lengths to trunk lengths are also higher than those of populations in China (Table IV). The deviation of relative tail length variation from Allen's rule in *Macaca mulatta* has been noticed before, and was ascribed to different origins of current populations as a result of a major glacial advance [Fooden & Albrecht, 1999]. The *Macaca mulatta* populations now occupying the southern region (latitude: 15° to 20°) are referred to as "anomalously short tail populations" by Fooden

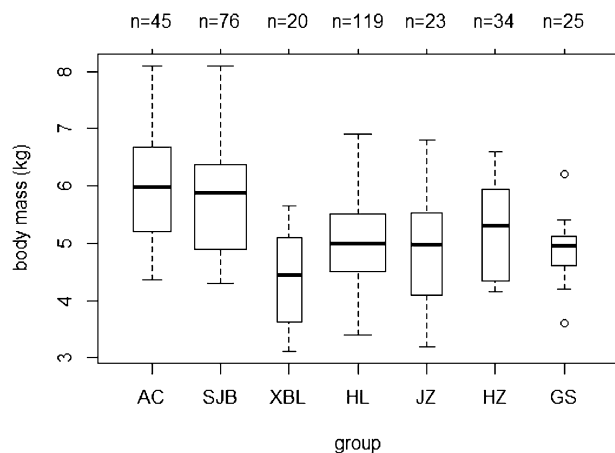


Fig. 3. Inter-group body mass difference of adult females of *Macaca mulatta brevicaudus*. n: average group size of three years. AC, SJB, XBL, HL, GS, JZ, and HZ refer to the names of the studied groups.

and Albrecht, and it is proposed that northern populations dispersed to this region after the original long tail populations went extinct [Fooden & Albrecht, 1999].

Some studies have suggested that morphological traits of primates follow the island rule [Bromham & Cardillo, 2007; Welch, 2009], while others argued the opposite [Meiri et al., 2008]. Schillaci et al. [2009] have shown that at least for one species in genus *Macaca*, the long-tailed macaque (*M. fascicularis*), the island rule does not apply. *M. m. brevicaudus* in Hainan Island provides a good opportunity to examine the effect of the island rule in rhesus macaques. The significantly smaller body mass and body size of *M. m. brevicaudus* as compared to other subspecies have tempted us to conclude that it is another example of dwarfism resulting from natural selection of island habitats. However, we cannot be

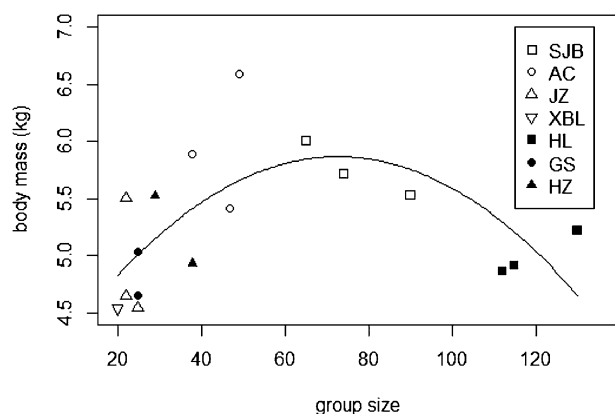


Fig. 4. Relationship between body mass of adult females and group size. Mean body mass and mean group size values plotted on the graph. Different symbols represent data points contributed by different groups. The smooth line shows the result of regression with second order terms. AC, SJB, XBL, HL, GS, JZ, and HZ refer to the names of the studied groups.

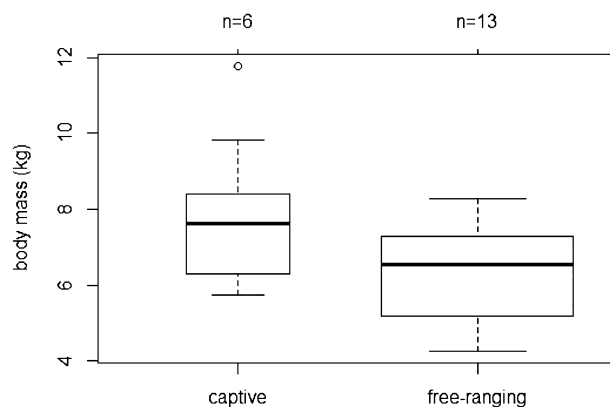


Fig. 5. Body mass difference between captive individuals and free-ranging individuals. n: average group size in three years.

sure whether adaptations to habitats of lower latitude alone contribute to its small size, or if the island effect also plays a role. Since populations in India, Bangladesh and those in inland China originated from different parts of South Asia [Fooden & Albrecht, 1999], the comparison between populations in India, Bangladesh and those in Hainan makes less sense than comparison between populations in Hainan and those on the Chinese mainland. It is also notable that the body mass of populations from Jingdong and Zhenyuan in Yunnan Province does not differ significantly from those in Hainan (Table III). Since we do not have more morphologic data of populations in lower latitudes on the Chinese mainland, further studies are still required to examine the effect of the island rule in *Macaca mulatta*. Data for populations in Guangxi, Yunnan, and other habitats of the Chinese mainland would also be helpful to investigate the island rule. However, we do not have the data for trunk length and tail length of populations in Yunnan Province to support this claim.

Some researchers have pointed out that BMD could be regarded as a species-level trait as well as a

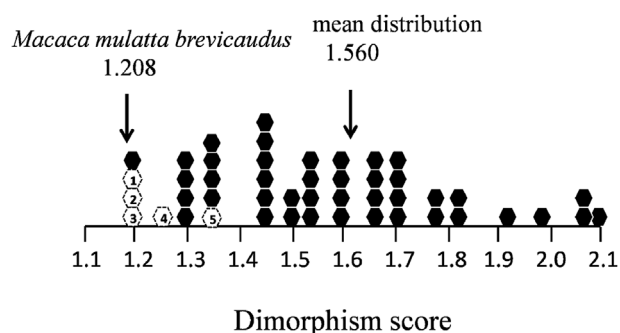


Fig. 6. Dot density plot describing body mass dimorphism scores of genus *Macaca*. 1 and 4 respectively for *M. m. mulatta* and *M. m. lasiotis* in Yunnan, 2 for *M. m. brevicaudus* in Hainan, 3 for *M. m. littoralis* in Anhui, and 5 for *M. m. tcheliensis* in Taihangshan Henan. This plot was adapted from Schillaci et al. [2007].

TABLE IV. Relative length of appendage to trunk of *Macaca mulatta*

	Tail length	Forearm length	Leg length
Hainan			
Male	0.454	0.364	0.418
Female	0.503	0.402	0.400
Taihang			
Male	0.396	0.413	0.429
Female	0.386	0.412	0.447
Anhui			
Male	0.500		
Female	0.481		
India			
Male	0.670	0.435	0.449
Female	0.645	0.422	0.443
Nepal			
Male	0.656		
Female	0.609		
Bangladesh			
Male	0.693		
Female	0.649		

Note. Mean relative lengths were the ratios of mean value of measured segments to mean value of trunk lengths (proportional fraction). Trunk length is the linear distance between sternal notch and the superior margin of the pubic symphysis. Tail length is the length from tip of the tail to junction of the base of the tail. Forearm length is the length of segment between elbow and wrist joints. Leg length is the length of segment between knee and ankle joints. Data for Nepal, India and Bangladesh populations were obtained from Feeroz et al. [2010].

biologically meaningful subspecific trait in some primate species [Plavcan, 2001] that has proven to be strongly correlated with phylogenetic signals [Cheverud et al., 1985; Kamilar & Cooper, 2013]. Our study lends support to this claim: southern and northern populations of macaques in China that dispersed from different parts of Asia during the Pleistocene have different levels of BMD. However, BMD alone does not suffice to distinguish *M. m. brevicaudus* from other southern-distributed subspecies. Correlations between latitude and sexual dimorphism were noticed in some previous studies [Albrecht, 1980; Schillaci, 2010]. In our study, this correlation is not significant (Pearson's correlation test: $r = 0.59$, $P = 0.16$). This could be the result of small sample size ($n = 7$). If such an association between latitude and sexual dimorphism does exist in *Macaca mulatta*, it seems that it has less to do with the body size gradient (Pearson's correlation test between body mass and sexual dimorphism: $r = 0.28$, $P = 0.55$) than with latitude itself. Thus Rensch's rule is less likely to hold in *Macaca mulatta*, which is consistent with the conclusions of previous studies on intra-specific level dimorphism variation in this species [Blanckenhorn et al., 2006; Fernandez-Duque, 2011; Schillaci, 2010]. Schillaci et al. [2007] concluded that the intra-specific dimorphism variation of *M. fascicularis* in Singapore and Thailand was mainly due to the resource availability at different sites rather than differentiation in male

size selection, because the feeding ecologies of their studying populations were very different. Resource availability might be the primary factor driving the latitudinal dimorphism gradient on an intra-specific level if such a gradient is detectable in *Macaca mulatta* populations.

Furthermore, our results show some inconsistency with previous experiences from captive populations in laboratories and medical centers, such as the relationship between body mass and dominance rank. Previous studies on captive groups of macaques showed that a higher body mass generally means a higher social status [Tokuda & Jensen, 1969; Morgan et al., 2000], which is not easily observed in populations living in their natural habitats [Morgan et al., 2000]. Our results on adult females show no significant correlation between body mass and dominance rank, as in the case of *Macaca radiata* [Cooper et al., 2004]. Altmann and Alberts's study on baboons came to a similar conclusion [Altmann & Alberts, 1987]. In most cases reproductive state and health condition play far more important roles in determining the dominance rank in adult female primates [Dittus, 1998; Tokuda & Jensen, 1969]. Sometimes the variation of body mass as a better indicator of health condition exhibits more correlation with dominance rank [Pusey et al., 2005]. Sexual selection usually has a larger impact on males than females [Gaulin & Sailer, 1984; Plavcan & van Schaik, 1997], which makes it more likely for body mass to indicate the social status of males. In our study, such influence is hard to detect in adult males due to fewer male members as well as the lack of stable social hierarchy in males among our study subjects. A longer-term surveillance on body mass in a larger scope still needs to be done to test this hypothesis.

Provisioning is likely to increase body mass relative to non-provisioned groups. It was one of our major concerns before conducting the study. We were not sure how much heavier the provisioned free-ranging groups were than the wild groups, as there were no data from wild populations of this sub-species. There were 10 individuals in the captive group, which were leashed by ropes and fed by staff in the Monkey Park. We obtained data for both provisioned free-ranging individuals and captive individuals for comparison. Free-ranging individuals weigh 22.59% less than captive individuals at the study site. This is consistent with the result of Leigh's analysis on 53 primate species [Leigh, 1994]. Works on *M. fuscata* and *M. radiata* showed a similar pattern [Cooper et al., 2004; Hazama, 1964]. Stable access to food resources and lack of exercise in captive individuals could lead to a higher body mass and sometimes even obesity [Altmann et al., 1993]. The acceleration of growth rates is often accompanied by earlier sexual maturity in captive population, which is likely to exaggerate the degree of body mass sexual dimorphism [Altmann & Alberts, 1987; Strum, 1991]. Though such a trend

cannot be statistically analyzed in our study due to the small sample of captive individuals, it is supported by the data collected by Rehg and Leigh [1999]. The highest body mass dimorphism score (sexual dimorphism: 1.691) with a statistically meaningful large sample size (AM/AF = 52/58) in Appendix I came from a captive population measured by Leigh [Rehg & Leigh, 1999]. Provisioned/captive populations of macaques have been studied for more than half a century, and previous studies have provided valuable morphological data on macaques for comparative analysis. Our results suggest that the average body mass of our study subjects is less affected by provisioning and is more reliable for making inter-group comparisons, thus bringing more confidence to our analyses.

We found obvious inter-group variation in female body mass among the seven adjacent groups at the same study site. A quadratic equation describes the relationship between group size and body mass better than a linear equation, which is predicted by the primate socio-ecological model [Sterck et al., 1997]. This result supports Hypothesis II, which states that body mass varies more among groups associated with strong inter-group competitions, and that mean body mass will decline as group size becomes too large. The primate socio-ecological model predicts that clumped resources will lead to inter-group competitions. The larger the group size is, the more likely it is for a group to outcompete their rivals [Sugiura et al., 2000]. Though a larger group would usually lead to a higher mean body mass value, an oversized group is more likely to intensify the level of intra-group competitions and thus reduce the mean body mass of the group members [Koenig, 2000; van Noordwijk & van Schaik, 1999]. In the case of our study, food is clumped in the two provisioning sites and leads to strong inter-group competitions among the seven groups. The smaller group was more likely to retreat when two groups encountered each other at our study site. The group with the largest mean body mass (AC group, $n = 45 \pm 6$) happened to have an intermediate group size, while both the largest group (HL group, $n = 119 \pm 10$) and the smallest group (XBL group, $n = 20 \pm 2$) had a lower mean body mass. This suggests that individuals in the intermediate-size group might have better food intake on average than those in either the oversized or small-sized groups. Our study suggests that there seems to be an optimal group size in *M. m. brevicaudus*, which is consistent with the prediction of ecological model [Terborgh & Janson, 1986; Wrangham, 1980].

In conclusion, this study explores an efficient procedure for measuring wild primate body mass and provides 3-years of data for more than 100 individuals from seven different provisioned, free-ranging groups of *M. m. brevicaudus*. We found: (1) Body mass and body size of *M. m. brevicaudus* is

significantly smaller than that of *M. m. tcheliensis*, *M. m. lasiotis*, and *M. m. littoralis*, but it is similar to that of subspecies *M. m. mulatta* on the Chinese mainland. It also has the shortest tail compared to other subspecies. There is no significant correlation between dominance rank and body mass in adult females; (2) the body mass sexual dimorphism of *M. m. brevicaudus* is similar to other southern-distributed subspecies but smaller than the northern-distributed subspecies *M. m. tcheliensis*; and (3) there is obvious inter-group variation in body mass among groups distributed in the same study site. The relationship between body mass and group size is better described by a quadratic equation than a linear equation, which could be shaped by inter-group competitions and the limits of net food intake posed by increased intra-group competitions of a given group size. It is noteworthy that a lack of seasonal investigation still puts limits on our study, as seasonality could impose a strong impact on body mass sexual dimorphism [Cooper et al., 2004; Dietz et al., 1994; Kurita et al., 2002; Zhao, 1994]. Body mass and morphological traits are fundamental data in studies on ontogeny, health condition, phylogeny, ecology, behavior, and conservation biology, and are worth further investigation among and within species measurement and comparative study.

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APPENDIX I. Body Mass Sexual Dimorphism Scores Reported in Literature for Genus *Macaca*

Species	n (M/F)	Body mass (M/F,unit:kg)	Body mass dimorphism (BMD)
<i>Macaca maurus</i> ^a	17/4	—	1.521
<i>Macaca tonkeana</i> ^a	5/2	—	1.711
<i>Macaca ochreata</i> ^b	9/10	10.14/6.34	1.587
<i>Macaca hecki</i> ^c	11/10	—	1.647
<i>Macaca nigra</i> ^d	3/3	7.99/4.69	1.700
<i>Macaca nigra</i> ^d	—	10.40/6.60	1.580
<i>Macaca nigra</i> ^c	11/21	—	1.808
<i>Macaca fascicularis</i> ^d	—	5.80/4.10	1.439
<i>Macaca fascicularis</i> ^d	5/1	5.32/3.90	1.364
<i>Macaca fascicularis</i> ^d	8/15	4.54/3.12	1.455
<i>Macaca fascicularis</i> ^d	3/3	6.20/4.54	1.366
<i>Macaca fascicularis</i> ^d	3/6	4.16/3.18	1.308
<i>Macaca fascicularis</i> ^d	6/6	4.93/3.13	1.575
<i>Macaca fascicularis</i> ^e	13/13	—	1.593
<i>Macaca nemestrina</i> ^d	—	10.40/7.80	1.333
<i>Macaca nemestrina</i> ^d	6/6	10.21/6.35	1.608
<i>Macaca nemestrina</i> ^d	1/3	9.99/5.98	1.671
<i>Macaca nemestrina</i> ^d	1/3	9.99/5.83	1.714
<i>Macaca nemestrina</i> ^d	—	13.00/7.00	1.857
<i>Macaca nemestrina</i> ^e	39/64	—	2.053
<i>Macaca nemestrina</i> ^d	2/1	9.75/4.65	2.096
<i>Macaca nemestrina</i> ^c	28/18	—	1.723
<i>Macacamulatta</i> [*]	8/43	6.33/5.24	1.208
	15/54		
	14/70		
<i>Macaca mulatta</i> ^f	67/103	6.69/5.26	1.230
<i>Macaca mulatta</i> ^f	37/68	7.99/6.27	1.274
<i>Macaca mulatta</i> ^g	20/20	8.8/7.4	1.189
<i>Macaca mulatta</i> ^c	24/45	—	1.313
<i>Macaca mulatta</i> ^h	59/28	11.90/9.60	1.250
<i>Macaca mulatta</i> ^d	4/6	6.80/5.18	1.313
<i>Macaca mulatta</i> ⁱ	14/20	8.8/6.5	1.354
<i>Macaca mulatta</i> ^d	8/9	7.71/5.37	1.436
<i>Macaca mulatta</i> ^d	7/10	8.72/5.86	1.488
<i>Macaca mulatta</i> ^e	52/58	—	1.691
<i>Macaca mulatta</i> ^d	3/3	10.91/5.49	1.987
<i>Macaca mulatta</i> ^d	—	6.20/3.00	2.066
<i>Macaca arctoides</i> ^d	6/3	12.20/8.40	1.452
<i>Macaca arctoides</i> ^e	52/58	—	1.530
<i>Macaca fuscata</i> ^d	—	11.00/9.20	1.196
<i>Macaca fuscata</i> ^d	—	11.70/9.10	1.285
<i>Macaca fuscata</i> ^e	64/71	—	1.443
<i>Macaca silenus</i> ^d	—	6.80/5.00	1.360
<i>Macaca silenus</i> ^a	39/41	—	1.686
<i>Macaca sinica</i> ^d	—	5.70/3.60	1.583
<i>Macaca sinica</i> ^c	—	—	1.774
<i>Macaca sinica</i> ^d	—	6.50/3.40	1.912
<i>Macaca radiata</i> ^e	28/26	—	1.822
<i>Macaca cyclopis</i> ^e	—	—	1.358
Mean			1.554

Note. The sample size is n, M is for male, F is for female. Body mass dimorphism is calculated by dividing male mean value by female mean value.

*Data from this study. “—” is used when data were not reported in the original literature.

^aData from M. A. Schillaci, J. W. Froehlich, and J. Supriatna [2007].

^bData from Schillaci and Stallmann [2005].

^cData from Plavcan [2002].

^dData from Plavcan and van Schaik [1997].

^eData from Rehg and Leigh [1999].

^fData calculated from Zhao and Wang [2012].

^gData calculated from Xu YR [2013].

^hData from J. Smith & William Jungers [1997].

ⁱData from Zhao and Zhang [1989].

APPENDIX II. Individual Data Points of Measured Body Mass of *Macaca mulatta brevicaudus* From 2012 to 2014

Date	Group	Age class	Sex	Body mass
2012.7		J	F	3.13
2012.7		I	M	2.8
2012.7		A	F	4.43
2012.7		N	F	0.51
2012.7	HL	A	F	4.35(C)
2012.7	HL	J	M	4.91
2012.7	HL	I	F	2.02
2012.7	HL	J	F	3.75
2012.7	HL	A	M	6.78
2012.7	HL	A	F	5.29(C)
2012.7	HL	J	M	3.06
2012.7	HL	I	M	1.98
2012.7	HL	J	F	3.07
2012.7	HL	J	F	2.85
2012.7	HL	I	M	2.33
2012.7	HL	A	F	5.4(C)
2012.7	HL	A	F	3.92(C)
2012.7	HL	A	M	6.62
2012.7	HL	A	F	5.74(C)
2012.7	HL	A	F	6.06(C)
2012.7	HL	I		1.45
2012.7	HL	I		1.92
2012.7	HL	A	F	5.53
2012.7	HL	I	F	1.53
2012.7	HL	I		1.44
2012.7	HL	A	F	4.68(C)
2012.7	HL	I	F	1.98
2012.7	HL	J		3.84
2012.7	HL	A	F	5.03
2012.7	HL	A	M	7.56
2012.7	HL	I	F	3.09
2012.7	HL	J	F	3.46
2012.7	HL	N		0.74
2012.7	HL	J	F	2.72
2012.7	HL	A	F	5.4
2012.7	HL	A	F	5.94(C)
2012.7	HL	A	F	5.23(P)
2012.7	HL	J	F	3.19
2012.7	JZ	A	F	5.49(C)
2012.7	JZ	A	F	5.43/5.54/5.63
2012.7	JZ	I	M	1.98
2012.7	JZ	J	F	2.75
2012.7	JZ	I	F	2.88
2012.7	JZ	I	F	2.75
2012.7	JZ	I	F	2.28
2012.7	JZ	A	F	5.55(C)
2012.7	JZ	A	M	7.13
2012.7	JZ	A	F	3.71(C)
2012.7	JZ	A	M	7.64
2012.7	SJB	J	F	3.47
2012.7		A	F	3.98
2012.7	XBL	J	F	3.38
2012.7	XBL	A	F	5.66
2012.7	XBL	J	M	3.7
2012.7	CAPTIVE	A	M	11.78
2012.7	XBL	I	F	0.98
2012.7	XBL	I	F	2.07
2012.7	XBL	A	F	5.52(C)
2012.7	XBL	I	F	2.21
2012.7	XBL	A	F	4.41(C)

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2012.7	XBL	I	M	1.85
2012.7	XBL	I	F	1.79
2012.7	XBL	A	F	3.63
2012.7	CAPTIVE	A	M	5.75
2012.7	CAPTIVE	A	M	6.33
2012.7	CAPTIVE	A	M	7.92
2012.7	CAPTIVE	A	M	7.21
2012.7	CAPTIVE	J	M	3.45
2012.7	AC	A	F	6.98(C)
2012.7	AC	A	F	6.08
2012.7	AC	I	M	1.7
2012.7	AC	I	M	2.38
2012.7	AC	I	F	2.04
2012.7	AC	A	F	5.49
2012.7	AC	I	F	1.92
2012.7	AC	I	F	1.64
2012.7	AC	J	F	3.07
2012.7	AC	A	M	8.21
2012.7	AC	A	F	6.81(C)
2012.7	AC	I	F	1.86
2012.7	AC	A	F	5.42
2012.7	SJB	A	F	5.28
2012.7	SJB	A	M	6.86
2012.7	SJB	A	F	7.02(C)
2012.7	SJB	A	F	4.46
2012.7	SJB	A	F	5.98
2012.7	SJB	N	M	0.35
2012.7	SJB	A	F	5.98
2012.7	SJB	I		2.25
2012.7	SJB	A	F	4.83(C)
2012.7	SJB	I	F	2.36
2012.7	SJB	A	F	6.38
2012.7	SJB	J	F	3.32
2012.7	SJB	A	F	6.5(C)
2012.7	SJB	A	F	5.87(P)
2012.7	SJB	A	F	5.92(C)
2012.7	SJB	I		2.06
2012.7	SJB	I	M	1.8
2012.7	SJB	A	F	4.79
2012.7		A	F	6.00(C)
2012.7	AC	A	F	5.63
2012.7		A	F	5
2012.7		I		1.37
2012.7		A	F	4.56(P)
2012.7		A	M	4.44
2012.7	SJB	I	F	1.51
2013.7	JZ	A	M	5.98/6.25/6.41/6.5/6.29
2013.7	JZ	A	M	6.80
2013.7	JZ	A	F	3.17
2013.7	JZ	A	F	3.58
2013.7	JZ	A	F	5.63
2013.7	JZ	A	F	4.05(C)
2013.7	JZ	A	F	5.17(C)
2013.7	JZ	A	F	5.71(C)
2013.7	JZ	A	F	6.79(C)
2013.7	JZ	I		1.55
2013.7	JZ	I		1.51
2013.7	JZ	N		0.71/0.67
2013.7	HL	A	M	7.77/7.81/7.80
2013.7	HL	A	M	6.95/6.79/6.88/7.01
2013.7	HL	A	M	5.89

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2013.7	HL	A	M	4.26
2013.7	HL	A	F	5.28
2013.7	HL	A	F	5.49
2013.7	HL	A	F	5.52(C)
2013.7	HL	A	F	6.32(C)
2013.7	HL	A	F	5.08(C)
2013.7	HL	A	F	6.40(C)
2013.7	HL	A	F	5.19(C)
2013.7	HL	A	F	6.25(C)
2013.7	HL	A	F	5.63
2013.7	HL	A	F	5.17
2013.7	HL	A	F	4.89
2013.7	HL	A	F	5.44
2013.7	HL	A	F	4.61
2013.7	HL	J		4.02
2013.7	HL	J		2.29
2013.7	HL	J		2.04
2013.7	HL	J		3.18
2013.7	HL	J		3.62
2013.7	HL	J		3.08
2013.7	HL	J		3.27
2013.7	HL	J		2.86
2013.7	HL	J		3.49
2013.7	HL	J		2.19
2013.7	HL	J		2.13
2013.7	HL	J		2.40
2013.7	HL	I		1.32
2013.7	HL	N		0.48
2013.7	HL	N		0.52
2013.7	CAPTIVE	A	M	7.64
2013.7	CAPTIVE	A	M	9.83
2013.7	CAPTIVE	A	M	8.59
2013.7	CAPTIVE	A	M	8.23
2013.7	CAPTIVE	A	M	5.80
2013.7	CAPTIVE	A	M	6.28
2013.7	CAPTIVE	A	F	4.28
2013.7	CAPTIVE	A	F	5.13
2013.7	CAPTIVE	J		4.04
2013.7	CAPTIVE	J		3.28
2013.7	SJB	A	M	6.89
2013.7	SJB	A	M	7.90
2013.7	SJB	A	M	5.26
2013.7	SJB	A	F	6.65
2013.7	SJB	A	F	6.50
2013.7	SJB	A	F	7.28
2013.7	SJB	A	F	7.29
2013.7	SJB	A	F	5.49
2013.7	SJB	A	F	7.70
2013.7	SJB	A	F	4.75
2013.7	SJB	A	F	6.16
2013.7	SJB	A	F	5.72
2013.7	SJB	A	F	5.14(C)
2013.7	SJB	A	F	5.61(C)
2013.7	SJB	A	F	6.85(C)
2013.7	SJB	A	F	5.17(C)
2013.7	SJB	J	F	2.93
2013.7	SJB	J	M	4.41
2013.7	SJB	J	F	3.75
2013.7	SJB	J		2.15
2013.7	SJB	J		2.68
2013.7	SJB	J		3.10

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2013.7	SJB	J		2.80
2013.7	SJB	J		3.23
2013.7	SJB	I		1.54
2013.7	SJB	N		0.67
2013.7	SJB	N		0.68
2013.7	SJB	N		0.50
2013.7	SJB	N		0.51
2013.7	HZ	A	M	7.11/7.57/7.46
2013.7	HZ	A	M	4.16
2013.7	HZ	A	F	6.05
2013.7	HZ	A	F	5.97
2013.7	HZ	A	F	4.37
2013.7	HZ	A	F	4.34
2013.7	HZ	A	F	4.16
2013.7	HZ	A	F	5.85(C)
2013.7	HZ	A	F	4.92(C)
2013.7	HZ	J		2.34
2013.7	HZ	J		2.65
2013.7	HZ	J		2.22
2013.7	HZ	J		2.06
2013.7	HZ	J		2.88
2013.7	HZ	J	M	4.06
2013.7	HZ	J		2.73
2013.7	HZ	J		3.89
2013.7	HZ	J		3.80
2013.7	HZ	J		2.01
2013.7	HZ	J		3.35
2013.7	HZ	I		1.44
2013.7	HZ	I		1.48
2013.7	HZ	I		1.34
2013.7	HZ	I		1.43
2013.7	HZ	I		1.58
2013.7	HZ	I		1.50
2013.7	HZ	I		1.48
2013.7	AC	A	M	8.34/8.22
2013.7	AC	A	M	5.15
2013.7	AC	A	F	5.97(C)
2013.7	AC	A	F	7.28/7.24(C)
2013.7	AC	A	F	8.16(C)
2013.7	AC	A	F	4.92(C)
2013.7	AC	A	F	4.47
2013.7	AC	A	F	6.56
2013.7	AC	A	F	6.04
2013.7	AC	A	F	7.95(P)
2013.7	AC	A	F	8.09(P)
2013.7	AC	J		3.91
2013.7	AC	J		2.75
2013.7	AC	J		2.75
2013.7	AC	J		2.80
2013.7	AC	J		2.44
2013.7	AC	J		4.27
2013.7	GS	A	M	7.23/7.46
2013.7	GS	A	F	6.20
2013.7	GS	A	F	4.92
2013.7	GS	A	F	4.20
2013.7	GS	A	F	5.68(C)
2013.7	GS	A	F	5.3(C)
2013.7	GS	A	F	5.59(C)
2013.7	GS	J		2.96
2013.7	GS	I		1.35
2013.7	GS	I		1.67

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2013.7	GS	N		0.48
2013.7	GS	A	M	5.18
2013.7		A	M	5.59
2014.7	AC	I		1.4
2014.7	AC	J		2.2
2014.7	AC	J		3.1
2014.7	AC	A	F	4.8
2014.7	AC	A	F	6.8
2014.7	AC	A	M	4.9
2014.7	AC	A	M	7.6
2014.7	AC	N		0.46
2014.7	AC	I		1.6
2014.7	AC	J		3.4
2014.7	AC	I		1.2
2014.7	AC	A	M	6.1
2014.7	AC	A	F	4.7
2014.7	AC	A	F	7.2
2014.7	AC	J		2.5
2014.7	AC	A	F	5.2
2014.7	AC	A	F	4.6
2014.7	AC	J		3.9
2014.7	AC	J		2.5
2014.7	AC	A	F	4.4
2014.7	AC	A	F	7.1
2014.7	AC	N		0.76
2014.7	AC	A	F	6
2014.7	GS	J		2.3
2014.7	GS	A	M	3.6
2014.7	GS	J		3
2014.7	GS	I		1.4
2014.7	GS	A	M	4.9
2014.7	GS	J		4.4
2014.7	GS	A	F	5.4
2014.7	GS	N		0.612
2014.7	GS	A	F	5.1
2014.7	GS	J		2.5
2014.7	GS	A	F	4.7
2014.7	GS	A	F	3.6
2014.7	GS	I		1.6
2014.7	GS	A	M	5.9
2014.7	GS	J		2.7
2014.7	HL	I		1.3
2014.7	HL	A	F	3.6
2014.7	HL	A	F	5
2014.7	HL	A	F	5.1
2014.7	HL	I		2
2014.7	HL	I		1.7
2014.7	HL	A	F	5.8
2014.7	HL	J		2.3
2014.7	HL	J		3
2014.7	HL	A	F	5.7
2014.7	HL	A	F	6.7
2014.7	HL	A	F	4.6
2014.7	HL	I		1.4
2014.7	HL	A	F	4.1
2014.7	HL	A	M	7.3
2014.7	HL	A	F	4.9
2014.7	HL	A	F	5.7
2014.7	HL	A	F	5.2
2014.7	HL	A	F	5.5
2014.7	HL	I		1.6

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2014.7	HL	A	F	3.4
2014.7	HL	N		0.41
2014.7	HL	J		2.3
2014.7	HL	A	F	4.8
2014.7	HL	A	F	6.4
2014.7	HL	A	F	3.7
2014.7	HL	N		0.89
2014.7	HL	I		1.5
2014.7	HL	J		2.1
2014.7	HL	I		1.4
2014.7	HL	A	M	6.2
2014.7	HL	J		2.4
2014.7	HL	N		0.58
2014.7	HL	A	F	4.8
2014.7	HL	J		3.4
2014.7	HL	I		2.2
2014.7	HL	A	M	4.9
2014.7	HL	I		1.6
2014.7	HL	A	F	4.4
2014.7	HL	A	F	4
2014.7	HL	I		2.3
2014.7	HL	I		1.7
2014.7	HL	J		2.2
2014.7	HL	A	F	6.9
2014.7	HL	N		0.61
2014.7	HL	I		2
2014.7	HL	A	F	4.4
2014.7	HL	J		2.2
2014.7	HL	J		3
2014.7	HL	A	F	4.2
2014.7	HL	A	F	4.5
2014.7	HZ	J		2.4
2014.7	HZ	A	M	6.7
2014.7	HZ	N		0.52
2014.7	HZ	A	F	5.4
2014.7	HZ	A	F	6.6
2014.7	HZ	A	F	4.2
2014.7	HZ	I		1.6
2014.7	HZ	J		3.1
2014.7	HZ	I		2.2
2014.7	HZ	A	F	5.9
2014.7	HZ	N		0.41
2014.7	HZ	I		2.1
2014.7	HZ	A	F	5.7
2014.7	HZ	I		1.4
2014.7	HZ	J		2.9
2014.7	JZ	A	F	5
2014.7	JZ	A	F	4.6
2014.7	JZ	A	F	5.7
2014.7	JZ	J		2.9
2014.7	JZ	J		2.3
2014.7	JZ	I		1.3
2014.7	JZ	J		3.4
2014.7	JZ	I		1.4
2014.7	JZ	A	F	6.8
2014.7	JZ	I		1.8
2014.7	JZ	A	M	6.1
2014.7	JZ	A	F	5.6
2014.7	JZ	N		1.1
2014.7	JZ	A	F	4.7
2014.7	JZ	A	F	5.2

APPENDIX II. Continued

Date	Group	Age class	Sex	Body mass
2014.7	SJB	J		3.1
2014.7	SJB	A	F	6.4
2014.7	SJB	J		2.4
2014.7	SJB	A	M	6.5
2014.7	SJB	J		3.4
2014.7	SJB	J		3
2014.7	SJB	I		2.3
2014.7	SJB	A	F	5.6
2014.7	SJB	J		4.8
2014.7	SJB	A	F	4.9
2014.7	SJB	I		2
2014.7	SJB	A	M	5
2014.7	SJB	J		3.5
2014.7	SJB	A	F	6.2
2014.7	SJB	A	F	4.4
2014.7	SJB	A	F	8.1
2014.7	SJB	A	F	4.6
2014.7	SJB	A	F	6.2
2014.7	SJB	I		1.6
2014.7	SJB	J		2.3
2014.7	SJB	A	F	6.9
2014.7	SJB	J		3.4
2014.7	SJB	A	F	5.4
2014.7	SJB	J		3.3
2014.7	SJB	J		3.5
2014.7	SJB	I		1.4
2014.7	SJB	J		2.4
2014.7	SJB	A	F	4.4
2014.7	SJB	J		3.7
2014.7	SJB	I		2.5
2014.7	SJB	I		1.7
2014.7	SJB	A	F	5.3
2014.7	SJB	A	F	6.1
2014.7	SJB	A	M	7.1
2014.7	SJB	I		1.6
2014.7	SJB	A	F	7.5
2014.7	SJB	J		2.3
2014.7	SJB	I		1.4
2014.7	SJB	N		0.71
2014.7	SJB	A	F	6.3
2014.7	SJB	N		0.58
2014.7	SJB	I		2.2
2014.7	SJB	A	F	5.3
2014.7	SJB	A	F	4.3
2014.7	XBL	A	F	4.2
2014.7	XBL	A	F	3.2
2014.7	XBL	A	M	5.4
2014.7	XBL	A	F	4.7
2014.7	XBL	A	F	5.3
2014.7	XBL	I		1.6
2014.7	XBL	A	M	5.1
2014.7	XBL	A	F	5.1

Note. The unit of body mass is kg. (w) means body mass measured together with baby. (p) means pregnant individual. A for adult, J for juvenile, I for infant, N for neonate, F for female and M for male. Since individuals were not identified in most cases, there could be a large proportion of overlap among different years. SJB, AC, JZ, XBL, HL, GS and HZ are the names of studied free-ranging groups. CAPTIVE refers to the captive group.