Int J Primatol (2008) 29:1271–1294
DOI 10.1007/s10764-008-9289-y

Morphological and Body Color Variation in Thai *Macaca fascicularis fascicularis* North and South of the Isthmus of Kra

Yuzuru Hamada · Bambang Suryobroto · Shunji Goto · Suchinda Malaivijitnond

Received: 20 September 2007 / Accepted: 4 April 2008 /
Published online: 3 September 2008

Abstract Long-tailed macaques (*Macaca fascicularis fascicularis*) are widely distributed in Southeast Asia and are morphologically and genetically (Tosi *et al.* in International Journal of Primatology 23:161–178, 2002) distinguishable on either side of the Isthmus of Kra (*ca.* 10.5°N). We compared the somatometry and body color of 15 local populations of long-tailed macaques in Thailand distributed over areas from 6.5°N to 16.3°N and also a Thai rhesus macaque population at 17.2°N. Limb proportions and body color variation follow the geographical trend. However, contrary to a previous report, body size does not decrease with latitude in the northern group and also in the southern (southerly distributed) rhesus macaque. Relative tail length (RTL) and color contrast in yellow between the back and thigh are the sole traits that distinctively separate the 2 groups: the southern group has a long relative tail length (RTL >125%) and small color contrast, whereas the northern group has a short RTL (<120%) and large color contrast. The southern rhesus macaques appear to have somatometric and body color traits that follow the geographical trend in long-tailed macaques, though they maintain their distinctive species-specific traits of shorter RTL (*ca.* 55%), shorter relative facial length, and a bipartite body color pattern. Researchers assume that the northern group of long-tailed macaques and the southern rhesus macaques had undergone partial introgression with each other. Montane refugia present during the glacial period are localities in which introgression occurred in long-tailed macaques.

Y. Hamada (✉)
Morphology Section, Primate Research Institute, Kyoto University, Inuyama, Japan
e-mail: hamada@pri.kyoto-u.ac.jp

B. Suryobroto
Faculty of Mathematics and Natural Sciences, Bogor Agricultural University, Bogor, Indonesia

S. Goto
Amami Wild Animal Research Center, Inc., Amami, Japan

S. Malaivijitnond
Primate Research Unit, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok, Thailand

Keywords geographical variation · hybridization · Isthmus of Kra · long-tailed Macaque · *Macaca fascicularis fascicularis*

Introduction

Macaca fascicularis have a wide geographical range both in peninsular and insular Southeast Asia (Fooden 1995). Researchers have classified the species into as many as 50 subspecies and even into several different species (Fooden 1995). However, Fooden (1995) classified them into 10 subspecies within *Macaca fascicularis* (Groves 2001), 3 of which range widely within the core area of the specific range. One of the 3, the nominotypical subspecies, *Macaca fascicularis fascicularis*, is distributed among the major islands of Indonesia and Malaysia, the southern part of the Philippines, the Malay Peninsula, the Isthmus of Kra area (*ca.* 10°N), and the Indochina Peninsula. The subspecies exhibits wide variation in morphology and body color (Fooden 1995, 1997; Fooden and Albrecht 1999). It is separated into northern and southern groups by the Isthmus of Kra based on morphological differences and susceptibility to malarial infection (Fooden 1995), and also on the pattern of female sexual skin swelling (Malaivijitnond *et al.* 2007a).

Fooden (1995) suggested that morphologically, intergradation occurred in *Macaca fascicularis fascicularis*, including intersubspecific intergradation with *M. f. aurea* in the west and south (*ca*. 11–13°N) and interspecific intergradation with rhesus macaques (*Macaca mulatta*) in the north (15–20°N). The latter may be one of the reasons for the characteristics of the northern group of long-tailed macaques and those of the southern rhesus macaques (Fooden 1964, 1995, 2000; Hamada *et al*. 2006). Genetic studies (Hayasaka *et al*. 1996; Tosi *et al*. 2000, 2002, 2003) and the morphological similarity, e.g., penile morphology, suggest phylogenetic closeness of the 2 species. Thus, the 2 species are members of the *fascicularis* species group in *Macaca*, which also includes Taiwanese (*M. cyclopis*) and Japanese macaques (*M. fuscata*; Fooden 1976, 1980).

Hybridization between long-tailed and rhesus macaques appears to be restricted to the area close to the boundary zone in the Indochina Peninsula, at *ca.* 15–20°N, and the spectrum of intermediate individuals does not occur in Laos (Duckworth *et al.* 1999). However, Tosi *et al.* (2002) claimed that all long-tailed macaque populations in the Indochina Peninsula (northern group) have experienced introgression from rhesus macaques, such that their Y-chromosomal genetic haplotype has been completely replaced by that of rhesus macaques. Thus, there is a need to examine the variations in both the long-tailed and rhesus macaques in the Indochina Peninsula, particularly the areas close to the boundary zone.

The Isthmus of Kra certainly played an important role in the evolution of *Macaca fascicularis fascicularis*; researchers have assumed it to be a barrier to gene flow between the northern and southern groups. Pleistocene climate changes also greatly influenced *Macaca fascicularis fascicularis*. In the Indochina Peninsula, it forced the macaques to retreat into refugia, e.g., the Dawna Range in Thailand (including the Huai Kha Khaeng Wild Life Sanctuary, 15°N, 99°E; Eudey 1980; Jablonski 1993; Koenig *et al*. 2004). However, researchers have not thoroughly examined the influence of climate and environmental change on long-tailed macaques.

We surveyed morphological variations in *Macaca fascicularis fascicularis* over a range that encompasses the Isthmus of Kra. We also compared the morphology of long-tailed macaques with that of rhesus macaques inhabiting northeastern Thailand (Hamada *et al*. 2006). We discuss the geographical pattern of variation in morphology and body color, and the implications for the evolutionary history of the long-tailed macaques distributed over the Indochina and Malay Peninsulas and the southern rhesus macaques.

Materials and Methods

Subjects

We conducted field surveys on *Macaca fascicularis fascicularis* at 15 localities in Thailand (Table I) between 6.5° and 16.5°N (Fig. 1; Malaivijitnond *et al*. 2005). The local populations represent the variation of long-tailed macaques between the Indochina and Sunda regions in peninsular Thailand. The southern sample, distributed south of the Isthmus of Kra (*ca.* 10.5°N), comprises 5 populations: Yala, Songkhla, Phang-nga, Surat Thani, and Chumphon. The northern sample, between 10.5° and 16.5°N, comprise 10 populations: Prachuab, Hua Hin, Petchaburi, Ratchaburi, Nakhonpathom, Saiyok, Petchabun, Nakhonsawan, Kosumphi, and Pichit.

In Thailand, there are 3 subspecies of *Macaca fascicularis*: *M. f. fascicularis*, *M. f. aurea*, and *M. f. atriceps* (Fooden 1995). *Macaca fascicularis fascicularis* and *M. f. aurea* have different hair patterns on the cheeks: a transzygomatic crest pattern in *M. f. fascicularis* and an infrazygomatic pattern in *M. f. aurea* (Fooden 1995). Because *Macaca fascicularis aurea* occurs in only 3 locations in Thailand (Malaivijitnond *et al*. 2005; *unpub. data*), we selected *M. f. fascicularis* for our study. *Macaca fascicularis aurea* may have influenced some of them. We also compared southern rhesus macaques in the Loei troop (Hamada *et al*. 2006; 17.2°N) with long-tailed macaques. The focal populations inhabit Buddhist temples or recreational parks, and they are habituated and provisioned to different degrees. We temporarily caught a total of 811 macaques for the collection of data and samples via nets and box traps; however, we used data from 778 postinfant subjects (403 males and 375 females).

We anesthetized the macaques via intramuscular injection with 10 mg/kg body mass of ketamine hydrochloride (Ketalar; Sankyo). After we inspected them and confirmed their full awakening, we released them back to their habitats. We followed the guidelines of Chulalongkorn University, Thailand, for handling research subjects and the chief monks and the local government permitted our surveys.

Dimensions Measured and Indices

We measured 20 somatometric dimensions (Hamada 1982, Iwamoto 1972), including skinfold thickness at 3 sites: belly, back (subscapular), and waist (suprailiac: Table 2). We used an anthropometer, spreading calipers, sliding calipers, a tape measure, skinfold calipers, and a balance for measurements. We estimated the age of the subjects via standard dental eruption tables (Smith *et al*. 2007). In addition

Table I Locality of macaque troops and number of individuals inspected

Locality No	Locality	Province	Population code	Date	GPS		Infant		Juvenile		Subadult and adult		Total		
					Latitude (N)	Longitude (E)	F	M	F	M	F	M	F	M	Total
Long-tailed macaques (*Macaca fascicularis fascicularis*)															
1	Wat Kuhaphimuk	Yala	Yala	2003 May	6.51	101.35	0	0	8	9	2	1	10	10	20
2	Khao Noi & Khao Tang Kuan	Songkhla	Songkhla	2003 May	7.21	100.60	1	0	12	10	12	3	25	13	38
3	Wat Suwan Khuha	Phang-nga	Phang-nga	2003 May	8.43	98.47	1	4	11	19	12	3	24	26	50
4	Ban Pak Nam	Surat Thani	Surat Thani	2006 April	9.10	99.23	0	0	1	4	6	6	7	10	17
5	Suan Somdet Prasrinakharin Chumphon	Chumphon	Chumphon	2006 May	9.95	99.04	0	0	6	6	6	0	12	6	18
6	Wat Khao Chong Krachok	Prachuab Khirikhan	Prachuab	2003 April	11.81	99.80	0	0	1	16	8	7	9	23	32
7	Wat Khao Takieb	Prachuab Khirikhan	Hua Hin	2006 April	12.51	99.99	0	1	7	26	7	34	14	61	75
8	Wat Khao Thamon	Petchaburi	Petchaburi	2004 Feb.	13.04	99.96	11	3	44	50	30	9	85	62	147
9	Kao Ngu Rock Garden	Ratchaburi	Ratchaburi	2002 Sept.	13.57	99.77	0	2	21	32	6	2	27	36	63
10	Wat Thammasala	Nakhonpathom	Nakhonpathom	2004 Feb.	13.81	100.12	0	0	6	15	5	2	11	17	28
11	Saiyok	Kanchanaburi	Saiyok	2005 Sept.	14.12	99.16	0	0	2	5	7	0	9	5	14
12	Wat Tamtepbandaan	Petchabun	Petchabun	2004 Mar.	15.75	101.04	0	0	41	18	13	4	54	22	76
13	Wat Kao Nor	Nakhonsawan	Nakhonsawan	2002 Sept.	15.95	99.88	2	3	4	19	13	4	19	26	45
14	Kosumphi Forest Park	Mahasarakham	Kosumphi	2003 Mar.	16.25	103.07	0	2	25	50	15	10	40	62	102
15	Wat Haad Moon	Pichit	Pichit	2007 April	16.51	100.28	2	1	3	12	19	17	24	30	54
Rhesus macaques (*Macaca mulatta*)															
16	Wat Tham Pa Mak Ho	Loei	Loei	2003 Mar.	17.23	101.78	0	0	14	9	8	1	22	10	32
					Long-tailed macaque total		17	16	192	291	161	102	368	409	779
						Total	17	16	206	300	169	103	392	419	811

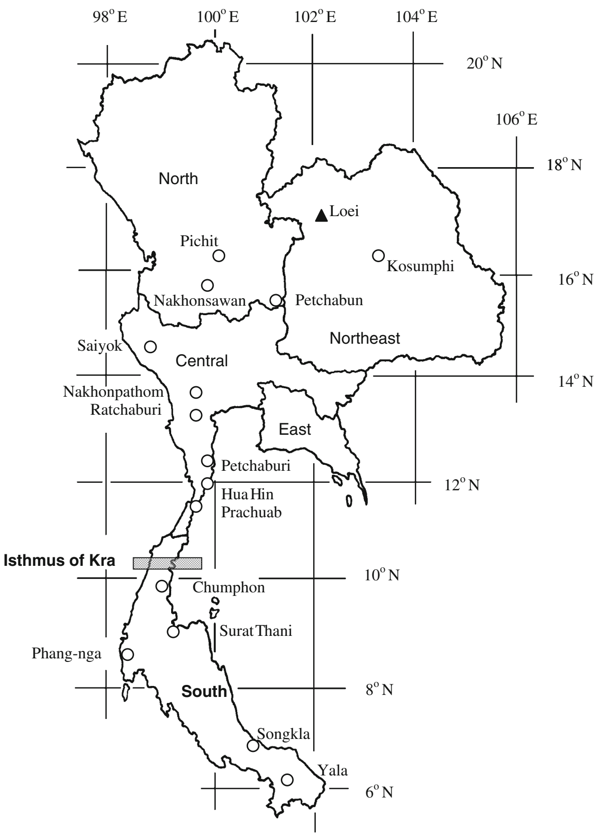


Fig. 1 Locations of sampled troops of long-tailed (circles) and rhesus (solid triangle) macaques in Thailand. The populations are indicated by the codes in Table 1.

to body mass, we used crown-rump length (CRL) to compare body size in linear dimensions, instead of the head and body length (HBL). We calculated relative sizes and indices and used them to compare body proportions. We obtained relative tail length (RTL in %) by dividing tail length by CRL, and multiplying by 100. We obtained intermembral index (%), which reflects the locomotor behaviors and substrates —arboreality or terrestriality (Fleagle 1999)— from [(arm length + forearm length)/(thigh length + leg length)] × 100. We obtained relative facial length (%) from [(upper facial height)/(head length)] × 100. Upper facial height is the distance between the foremost point on the maxilla (midsagittal point between the gingival central incisor contact points, a proxy for prosthion and a point at the nasal root (the midsagittal deepest point between the medial canthi; a proxy for nasion).

Body Color

We measured body color via a reflectometer (Color Analyzer^{TR} CR-200) at 11 sites: crown (vertex of the head), back (interscapular), arm, forearm, hand, waist (suprailiac part of trunk), thigh, leg, foot, posterior thigh (posterior aspect of the proximal one-third of the thigh), and face (side of nose; Hamada *et al.* 2005a, b,

Table II Somatometric sizes of Thai long-tailed and a rhesus macaques; mean (standard deviation)

Locality no.	Troop	*n*	Body mass (kg)	Total skinfold[a]	Crown-rump L[b]	Anterior trunk L	Tail L	Biacromial W	Bi-iliac W	Bitrochanteric W	Bimamalial W
Female											
1	Yala	2	3.68 (0.46)	7.10 (0.99)	420.00 (8.49)	284.00 (4.24)	541.00 (9.90)	94.00 (0.00)	70.00 (2.83)	91.50 (0.71)	42.00 (0.00)
2	Songkhla	12	5.58 (0.98)	18.22 (4.95)	436.17 (21.68)	291.67 (16.59)	559.00 (26.68)	102.58 (8.96)	84.42 (6.13)	104.67 (5.99)	51.67 (7.85)
3	Pang-nga	12	4.29 (0.89)	12.92 (4.15)	406.75 (19.19)	268.00 (20.58)	540.55 (28.26)	98.83 (5.61)	78.00 (7.08)	95.58 (6.01)	44.75 (6.51)
4	Surat Thani	6	4.33 (0.72)	16.55 (9.46)	406.67 (12.26)	270.50 (8.41)	520.33 (39.15)	94.00 (5.18)	77.50 (3.27)	93.17 (6.43)	42.17 (2.40)
5	Chumphon	6	4.71 (1.09)	14.33 (5.72)	430.67 (26.52)	279.50 (19.45)	565.83 (40.76)	109.00 (9.32)	84.83 (9.06)	98.50 (7.34)	45.67 (11.38)
6	Prachuab	8	6.18 (1.15)	16.34 (4.35)	455.63 (12.63)	300.75 (12.27)	498.50 (28.88)	107.75 (12.23)	89.50 (7.95)	106.88 (5.38)	50.00 (7.05)
7	Hua Hin	7	7.63 (1.25)	31.63 (9.19)	451.43 (17.57)	295.00 (16.15)	523.14 (28.39)	111.14 (7.01)	99.14 (6.44)	116.86 (7.22)	51.86 (6.44)
8	Petchaburi	31	4.94 (0.80)	10.80 (3.67)	441.65 (18.32)	293.21 (15.07)	518.67 (35.01)	96.20 (5.70)	82.76 (4.95)	104.32 (5.51)	42.88 (6.95)
9	Ratchaburi	6	4.53 (0.83)		426.50 (17.74)	277.67 (8.36)	465.33 (25.10)	116.33 (10.35)	81.50 (6.57)	103.00 (12.49)	
10	Nakhonpathom	5	6.91 (1.23)	29.92 (13.31)	444.20 (14.82)	290.80 (11.48)	525.50 (27.44)	110.80 (8.58)	94.80 (8.76)	108.60 (5.90)	59.60 (12.18)
11	Saiyok	7	4.16 (0.65)	9.17 (2.03)	423.71 (16.60)	273.57 (20.60)	499.71 (20.76)	99.29 (7.13)	78.29 (5.44)	94.86 (5.40)	43.71 (8.20)
12	Petchabun	13	4.58 (0.82)	13.79 (2.67)	417.92 (15.36)	281.00 (11.42)	470.15 (27.98)	90.83 (6.42)	72.50 (4.36)	100.00 (8.15)	49.00 (4.57)
13	Nakhonsawan	13	5.21 (0.94)		420.62 (14.45)	279.08 (11.69)	482.38 (30.80)	107.62 (7.09)	83.15 (4.65)	108.69 (9.40)	
14	Khosumphi	15	6.77 (1.27)	16.57 (7.16)	461.86 (20.71)	310.80 (13.85)	500.79 (33.12)	108.31 (7.54)	93.92 (6.87)	116.77 (9.43)	49.23 (6.98)
15	Pichit	14	5.22 (0.98)	16.71 (5.34)	448.50 (11.49)	299.21 (10.56)	486.93 (32.90)	100.43 (5.52)	84.36 (7.28)	103.43 (8.05)	50.50 (8.56)
16	Loei rhesus macaque	12	6.40 (1.16)	21.19 (6.29)	456.50 (22.06)	305.67 (18.24)	247.92 (18.73)	105.17 (8.64)	83.58 (6.04)	107.75 (6.55)	48.50 (5.47)
Male											
1	Yala	1	5.32	9.9	450	290	631	117	78	99	48
2	Songkhla	3	7.73 (0.87)	11.33 (1.50)	492.67 (8.08)	326.67 (5.51)	636.33 (8.39)	126.00 (5.20)	89.67 (5.13)	114.33 (2.52)	51.33 (10.41)
3	Pang-nga	3	7.57 (1.96)	18.47 (15.40)	482.00 (30.61)	325.00 (22.65)	636.67 (69.74)	118.00 (6.00)	89.33 (8.39)	111.67 (7.64)	52.67 (6.03)
4	Surat Thani[c]	3	4.75 (0.56)	7.33 (7.16)	430.33 (9.50)	275.00 (6.24)	578.00 (35.17)	106.67 (1.53)	79.67 (2.89)	98.33 (5.13)	46.67 (2.52)
5	Chumphon	0									
6	Prachuab	7	10.57 (2.26)	28.41 (14.15)	508.71 (28.20)	332.71 (24.84)	587.29 (35.25)	134.86 (8.88)	106.57 (10.69)	127.14 (7.13)	64.29 (10.16)
7	Hua Hin	35	10.93 (3.01)	35.71 (13.25)	508.20 (28.69)	330.40 (20.30)	556.66 (105.65)	128.04 (12.45)	107.85 (11.85)	132.19 (12.80)	55.07 (8.26)
8	Petchaburi	9	8.59 (0.84)	11.82 (0.96)	504.44 (10.48)	325.78 (13.01)	599.22 (34.46)	125.67 (6.71)	96.89 (5.58)	122.44 (6.29)	50.00 (5.48)
9	Ratchaburi	2	10.20 (0.99)		478.00 (7.07)	304.50 (6.36)	566.00 (15.56)	125.00 (2.83)	105.50 (14.85)	142.00 (14.14)	–
10	Nakhonpathom	2	9.03 (2.86)	19.65 (14.92)	507.50 (17.68)	323.50 (9.19)	608.00 (22.63)	127.50 (4.95)	95.50 (2.12)	122.00 (5.66)	62.50 (6.36)
11	Saiyok	0									
12	Petchabun	4	6.55 (0.60)	11.48 (3.01)	481.00 (22.20)	308.25 (10.18)	533.67 (33.31)	121.75 (5.38)	87.50 (3.87)	117.75 (6.40)	50.75 (5.06)
13	Nakhonsawan	4	8.90 (2.65)		480.25 (23.47)	307.00 (16.45)	495.00 (53.08)	131.75 (3.77)	97.25 (8.26)	125.75 (2.22)	–
14	Khosumphi	10	8.98 (1.18)	16.42 (4.89)	505.20 (31.24)	339.00 (24.00)	555.43 (24.28)	128.00 (5.66)	96.00 (7.21)	122.60 (8.04)	49.70 (5.21)
15	Pichit	13	7.62 (1.60)	16.17 (5.74)	498.08 (16.29)	325.46 (14.88)	566.54 (29.98)	121.77 (6.72)	92.23 (5.43)	120.92 (6.91)	53.23 (6.34)
16	Loei rhesus macaque	1	6.45	6.9	509	341	280	143	84	114	50

[a]Summed skinfold thickness at belly, back (subscapular), and supraiiac.

[b]L=length; W=width; G=girth.

[c]We measured only subadults.

Thoracic W	Thoracic depth	Thoracic G	Arm L	Forearm L	Thigh L	Leg L	Ulnar hand L	Radial hand L	Hand W
66.00 (2.83)	96.50 (3.54)	306.50 (6.36)	123.00 (1.41)	119.50 (0.71)	131.50 (4.95)	117.00 (1.41)	81.00 (1.41)	72.00 (1.41)	25.50 (0.71)
84.08 (6.16)	101.25 (10.15)	365.08 (31.90)	126.25 (4.09)	127.67 (5.50)	142.42 (7.45)	129.17 (6.39)	86.92 (1.83)	79.25 (2.18)	27.33 (1.50)
77.92 (5.30)	99.83 (7.70)	331.42 (32.41)	120.50 (4.34)	123.25 (4.63)	132.92 (6.26)	122.00 (4.63)	79.25 (3.05)	70.92 (3.32)	26.58 (1.98)
78.33 (3.98)	91.33 (5.50)	321.33 (31.85)	123.33 (1.63)	124.83 (2.99)	136.67 (4.41)	122.33 (6.09)	81.67 (3.56)	73.67 (2.58)	27.50 (1.38)
88.50 (11.00)	107.00 (12.47)	359.00 (47.94)	131.33 (7.09)	131.83 (4.26)	142.33 (7.89)	128.00 (5.33)	88.67 (3.27)	78.83 (2.93)	28.00 (1.90)
86.00 (12.93)	105.00 (12.36)	370.88 (37.75)	136.38 (5.95)	144.38 (4.10)	156.50 (8.57)	139.50 (4.24)	88.50 (3.82)	80.13 (3.18)	27.75 (1.83)
94.29 (11.28)	121.43 (12.09)	426.86 (29.13)	135.71 (5.19)	137.29 (5.22)	152.14 (5.11)	137.71 (3.77)	88.57 (2.64)	79.57 (3.82)	30.29 (1.70)
80.56 (6.71)	97.56 (6.90)	342.56 (23.07)	128.50 (4.59)	134.96 (5.80)	146.90 (5.68)	132.38 (5.00)	86.46 (3.67)	76.93 (2.93)	28.86 (1.18)
79.50 (7.89)	83.00 (5.97)		119.17 (6.62)	131.83 (3.60)	137.50 (10.01)	131.00 (7.35)			
94.00 (10.75)	103.40 (11.59)	400.00 (27.60)	130.60 (3.78)	132.20 (3.27)	145.40 (11.76)	128.20 (4.15)	85.40 (2.88)	76.40 (3.21)	29.20 (1.10)
78.71 (6.73)	96.57 (8.83)	327.57 (29.85)	125.14 (5.37)	129.43 (6.19)	139.29 (8.14)	126.43 (4.83)	79.43 (3.31)	70.86 (2.54)	27.29 (1.25)
78.42 (4.76)	95.17 (8.68)	336.69 (14.38)	126.23 (5.45)	129.08 (5.09)	144.54 (7.98)	127.92 (6.18)	82.85 (3.08)	75.31 (3.09)	26.85 (1.72)
82.00 (11.20)	87.15 (11.30)		118.54 (7.74)	127.54 (8.32)	140.15 (9.71)	136.69 (7.11)			
92.85 (8.32)	115.69 (10.03)	394.67 (31.91)	134.67 (5.18)	136.87 (3.40)	156.87 (7.57)	137.60 (5.03)	89.00 (4.37)	79.43 (3.92)	28.54 (1.51)
81.71 (9.01)	102.14 (8.46)	352.00 (31.59)	121.50 (8.60)	124.14 (5.30)	139.57 (6.99)	125.29 (6.32)	84.00 (3.46)	75.43 (3.11)	32.07 (15.89)
95.75 (11.57)	109.83 (10.50)	380.42 (30.24)	135.00 (6.69)	138.92 (6.65)	160.75 (6.76)	141.50 (5.65)	96.42 (3.06)	86.58 (2.71)	30.50 (1.73)
72	98	345	137	138	148	140	93	80	29
93.00 (5.57)	121.00 (6.08)	403.33 (30.02)	144.00 (3.61)	147.00 (8.72)	162.00 (5.00)	143.33 (1.53)	97.67 (2.52)	89.67 (1.53)	32.33 (1.15)
98.67 (5.51)	112.00 (9.64)	411.00 (66.57)	137.00 (4.36)	142.33 (4.04)	153.00 (12.17)	138.33 (5.86)	91.67 (6.03)	82.33 (6.11)	30.33 (4.16)
81.00 (4.36)	93.33 (10.12)	332.00 (18.73)	134.00 (3.00)	135.33 (5.13)	152.67 (7.57)	135.33 (2.31)	93.00 (1.00)	84.00 (1.00)	30.33 (0.58)
101.00 (8.74)	126.86 (9.96)	457.29 (33.22)	157.86 (11.52)	168.14 (11.80)	179.43 (13.83)	160.71 (7.04)	105.57 (2.76)	96.57 (2.30)	34.57 (1.51)
104.52 (11.86)	132.00 (16.30)	471.32 (58.99)	151.91 (9.43)	157.00 (8.79)	176.38 (8.79)	154.47 (7.86)	102.83 (5.40)	91.97 (4.70)	34.90 (2.37)
97.89 (6.27)	124.22 (5.83)	417.11 (18.40)	151.44 (7.72)	156.22 (8.01)	172.00 (4.09)	154.56 (4.33)	100.11 (4.59)	89.11 (4.11)	34.67 (2.92)
101.00 (2.83)	118.50 (9.19)		147.00 (14.14)	151.00 (2.83)	170.50 (6.36)	152.50 (2.12)			
102.00 (1.41)	121.00 (11.31)	444.00 (72.12)	165.00 (12.73)	156.50 (3.54)	176.00 (8.49)	154.50 (0.71)	96.50 (4.95)	87.50 (4.95)	33.50 (3.54)
84.25 (9.36)	112.00 (9.42)	384.50 (25.59)	154.00 (4.97)	155.25 (6.65)	172.75 (7.68)	151.25 (6.13)	100.25 (6.95)	89.50 (5.97)	31.00 (1.41)
97.75 (10.63)	103.50 (13.99)		137.25 (11.27)	146.25 (5.97)	166.75 (6.75)	156.25 (6.50)			
95.40 (5.93)	116.70 (7.51)	434.00 (20.74)	148.50 (4.65)	154.70 (6.68)	175.80 (9.04)	151.00 (5.42)	99.10 (4.86)	89.20 (3.94)	32.40 (1.26)
89.46 (9.47)	119.08 (8.22)	407.31 (39.06)	143.54 (5.78)	148.00 (5.35)	168.15 (7.12)	149.00 (5.46)	99.77 (4.57)	89.46 (4.18)	33.38 (1.89)
68	105	368	143	156	168	152	108	96	35

Table II (continued)

Locality no.	First fnger L	Third finger L	Foot L	Foot W	First toe L	Third toe L	Arm G	Thigh G	Max leg G	Min leg G	Head L
Female											
1	17.50 (0.71)	41.00 (2.83)	115.00 (1.41)	27.00 (1.41)	24.50 (2.12)	44.50 (0.71)	118.00 (5.66)	194.00 (5.66)	115.00 (1.41)	63.00 (0.00)	81.50 (3.54)
2	18.50 (1.17)	44.92 (1.93)	124.00 (3.19)	28.08 (1.83)	24.67 (1.72)	47.75 (2.49)	137.42 (13.20)	221.83 (15.65)	128.08 (10.13)	75.42 (7.49)	83.58 (2.23)
3	17.83 (1.60)	42.00 (2.90)	117.67 (4.70)	27.42 (2.07)	21.83 (1.17)	43.83 (2.14)	122.83 (18.58)	185.58 (17.66)	120.00 (12.74)	73.17 (8.08)	82.67 (3.47)
4	17.33 (1.03)	42.00 (1.67)	117.50 (3.51)	28.00 (1.26)	22.83 (1.47)	44.67 (2.07)	121.17 (14.33)	199.33 (17.73)	125.00 (10.70)	73.83 (8.13)	77.83 (1.17)
5	18.83 (0.98)	45.33 (1.21)	128.17 (4.67)	29.50 (2.07)	24.33 (1.37)	49.33 (3.20)	131.67 (16.68)	203.50 (17.35)	123.17 (10.11)	70.33 (7.20)	82.50 (4.55)
6	18.50 (2.00)	45.13 (2.64)	133.88 (3.60)	28.00 (1.93)	25.75 (2.12)	49.13 (2.30)	138.00 (12.54)	213.50 (18.56)	131.38 (6.23)	77.00 (1.77)	85.00 (3.12)
7	18.43 (1.72)	45.14 (1.07)	130.00 (3.11)	31.86 (1.57)	24.57 (2.44)	47.14 (1.77)	167.71 (19.30)	240.43 (19.92)	155.57 (14.71)	94.86 (11.77)	90.43 (2.88)
8	17.21 (1.52)	42.57 (2.06)	129.43 (4.41)	29.68 (1.39)	23.36 (1.97)	46.68 (2.13)	133.12 (11.24)	206.23 (15.54)	123.23 (8.64)	72.85 (5.54)	82.41 (4.16)
9											81.00 (3.41)
10	18.40 (1.14)	43.00 (2.45)	126.40 (4.67)	28.80 (1.48)	22.80 (0.84)	46.00 (2.55)	153.40 (12.07)	233.40 (28.90)	140.60 (17.04)	86.80 (4.97)	87.40 (2.07)
11	16.71 (1.38)	38.57 (0.98)	120.57 (2.76)	27.86 (0.90)	20.71 (1.80)	42.43 (2.44)	126.71 (7.99)	195.43 (12.46)	118.00 (7.48)	64.86 (3.34)	80.14 (3.18)
12	15.46 (1.56)	43.15 (2.41)	122.69 (4.21)	27.15 (1.77)	21.77 (2.55)	45.77 (1.96)	126.31 (7.67)	204.85 (15.16)	121.77 (6.22)	68.54 (4.24)	81.85 (3.48)
13											84.23 (2.80)
14	18.54 (1.90)	45.31 (2.93)	132.13 (5.10)	28.33 (2.06)	25.53 (2.03)	49.13 (3.00)	155.64 (17.56)	224.67 (18.67)	138.93 (12.23)	77.57 (6.43)	86.08 (3.75)
15	19.21 (9.03)	41.86 (3.16)	122.14 (4.69)	28.71 (1.49)	22.50 (2.28)	47.50 (2.59)	138.00 (15.11)	219.29 (18.52)	122.50 (9.12)	74.00 (6.48)	81.71 (3.05)
16	19.08 (1.98)	48.75 (2.49)	138.00 (3.54)	30.42 (1.31)	25.33 (1.37)	48.58 (7.65)	151.75 (13.39)	227.42 (29.79)	142.08 (14.49)	82.92 (11.11)	85.00 (3.30)
Male											
1	19	48	138	29	24	54	153	212	133	73	89
2	20.67 (2.08)	49.67 (1.15)	140.33 (3.79)	32.67 (1.53)	29.33 (2.08)	52.67 (1.53)	177.33 (13.32)	253.67 (8.62)	150.67 (6.66)	82.33 (4.62)	93.00 (6.56)
3	19.33 (1.53)	46.00 (3.46)	135.67 (7.51)	33.00 (3.00)	25.00 (2.00)	50.33 (3.79)	169.00 (13.11)	236.33 (5.77)	149.00 (12.53)	79.00 (8.72)	93.33 (5.69)
4	20.33 (4.04)	48.00 (1.00)	135.33 (5.51)	30.67 (0.58)	25.67 (0.58)	52.00 (2.00)	140.00 (15.13)	197.00 (30.81)	128.00 (10.15)	74.33 (4.04)	83.67 (6.03)
5											
6	21.71 (1.38)	51.00 (4.43)	154.86 (7.24)	35.00 (0.58)	31.57 (3.91)	56.57 (2.70)	187.00 (12.27)	275.86 (18.92)	164.29 (10.87)	95.14 (9.41)	97.00 (4.90)
7	21.70 (1.68)	51.56 (3.51)	150.94 (6.74)	35.85 (2.18)	29.64 (1.95)	55.14 (2.86)	202.41 (21.65)	285.24 (25.52)	177.63 (20.37)	103.52 (12.93)	97.82 (5.86)
8	20.67 (1.41)	50.11 (1.90)	147.89 (6.51)	34.44 (1.42)	26.67 (1.66)	54.78 (2.49)	180.89 (8.99)	249.56 (16.85)	153.56 (8.82)	90.89 (5.04)	95.11 (6.57)
9							–	–	–	–	95.00 (4.24)
10	21.50 (2.12)	46.00 (2.83)	149.00 (4.24)	34.00 (1.41)	26.00 (1.41)	53.50 (3.54)	181.00 (39.60)	263.50 (55.86)	156.00 (31.11)	93.00 (9.90)	96.00 (2.83)
11											
12	19.25 (0.96)	51.25 (2.22)	149.25 (6.55)	32.75 (0.96)	25.75 (2.22)	56.00 (2.58)	159.75 (13.62)	228.50 (14.66)	143.75 (3.77)	80.25 (8.77)	91.50 (3.11)
13							–	–	–	–	92.75 (4.03)
14	21.00 (1.05)	50.20 (3.29)	149.80 (6.61)	32.20 (1.40)	28.10 (2.23)	53.80 (2.86)	191.50 (9.83)	266.00 (22.73)	162.00 (10.78)	89.70 (3.89)	94.80 (3.29)
15	20.00 (2.27)	50.38 (2.84)	144.77 (6.97)	34.08 (2.29)	27.30 (2.29)	56.92 (3.73)	175.77 (15.87)	258.46 (23.69)	148.77 (11.86)	89.23 (6.78)	91.08 (3.62)
16	22	57	158	35	32	58	167	260	153	86	90

Head W	Bizygomatic W	Bigonial W	Upper facial height	Facial height	Nasal height	External canthic W	Interna; canthic W	Nasal W	Total head height	Head height	Ear L	Ear W
63.50 (0.71)	68.50 (0.71)	39.50 (6.36)	42.50 (3.54)	55.50 (0.71)	32.50 (3.54)	38.50 (0.71)	7.50 (0.71)	12.00 (0.00)	76.00 (1.41)	35.50 (2.12)	34.00 (1.41)	25.50 (0.71)
69.17 (2.29)	75.00 (2.34)	33.67 (2.39)	42.75 (3.25)	58.00 (2.66)	32.25 (2.09)	42.08 (1.24)	9.75 (1.22)	13.67 (1.07)	87.58 (4.93)	40.42 (4.32)	36.17 (2.25)	27.50 (1.68)
68.42 (2.11)	71.92 (3.00)	33.50 (4.19)	39.67 (3.96)	54.25 (3.22)	32.33 (3.58)	41.42 (2.61)	9.42 (1.00)	13.42 (1.00)	83.00 (3.52)	42.67 (3.14)	37.17 (2.52)	27.42 (2.15)
66.33 (2.07)	69.67 (2.42)	33.00 (2.83)	42.83 (4.17)	55.50 (2.88)	34.00 (4.00)	38.33 (2.25)	9.50 (0.84)	11.83 (1.17)	84.83 (4.45)	38.67 (5.75)	34.00 (1.79)	25.17 (1.17)
66.83 (2.23)	73.83 (1.17)	37.83 (2.56)	43.67 (3.33)	59.17 (3.13)	34.33 (1.63)	40.33 (1.03)	10.50 (1.05)	13.00 (1.41)	83.00 (6.03)	38.83 (1.83)	43.00 (5.18)	29.33 (1.75)
72.38 (2.56)	77.88 (2.75)	40.00 (2.73)	46.88 (5.17)	62.13 (4.82)	36.38 (3.89)	43.38 (3.34)	10.88 (2.10)	12.75 (0.89)	88.75 (3.62)	41.75 (3.01)	42.63 (2.33)	28.88 (1.25)
71.43 (3.99)	79.14 (2.79)	37.00 (3.37)	45.29 (3.64)	62.57 (2.51)	37.00 (3.92)	42.71 (2.50)	11.00 (1.91)	12.43 (1.40)	92.00 (3.74)	39.86 (5.67)	43.57 (2.23)	31.43 (2.99)
67.67 (2.65)	75.07 (3.10)	38.81 (3.86)	44.00 (3.82)	61.16 (3.29)	37.19 (3.07)	42.08 (2.58)	11.12 (1.58)	13.27 (1.28)	88.60 (4.09)	42.56 (3.40)	40.00 (2.93)	28.69 (2.15)
65.67 (1.51)	68.67 (2.07)	39.67 (5.47)	38.17 (3.37)	58.17 (4.17)	32.17 (3.06)	42.33 (1.75)	11.00 (1.26)	11.67 (0.52)	83.17 (6.21)	43.17 (6.62)		
70.60 (1.82)	75.20 (3.83)	37.20 (1.48)	42.80 (5.12)	60.80 (4.76)	33.80 (3.27)	45.40 (1.67)	11.00 (0.71)	13.20 (0.84)	91.80 (3.90)	44.40 (2.30)	41.80 (3.03)	30.00 (3.00)
65.43 (2.57)	71.14 (3.76)	35.00 (2.83)	45.71 (2.63)	57.71 (2.43)	34.14 (2.73)	42.57 (3.15)	10.29 (0.49)	13.57 (1.27)	83.86 (4.22)	38.57 (4.61)	37.86 (1.95)	28.57 (1.27)
65.85 (2.30)	72.15 (3.69)	34.77 (3.00)	41.46 (2.93)	57.08 (3.43)	35.62 (2.63)	42.00 (2.00)	11.85 (1.91)	13.50 (1.09)	85.08 (3.68)	39.85 (1.95)	38.69 (2.56)	30.54 (2.50)
63.31 (3.95)	70.69 (4.11)	38.23 (4.87)	39.38 (4.31)	60.23 (3.37)	35.08 (4.03)	43.62 (2.33)	11.31 (1.18)	12.69 (1.49)	83.23 (4.38)	35.15 (6.27)		
72.31 (2.63)	79.38 (2.57)	36.00 (4.88)	52.21 (4.58)	67.07 (4.84)	38.38 (3.45)	43.92 (2.87)	10.38 (1.19)	13.46 (1.76)	97.07 (5.28)	42.93 (2.23)	41.23 (3.52)	29.85 (1.99)
66.50 (3.16)	73.36 (3.00)	32.00 (2.86)	42.79 (3.60)	58.57 (4.03)	37.64 (2.95)	44.14 (1.29)	12.57 (0.94)	15.79 (1.19)	88.29 (4.08)	41.43 (2.53)	41.14 (3.13)	31.07 (2.56)
72.08 (2.71)	74.67 (3.31)	40.08 (7.12)	41.42 (4.19)	55.75 (3.02)	31.25 (4.41)	43.67 (2.02)	12.42 (1.78)	14.08 (1.31)	90.42 (3.75)	43.75 (2.80)	39.67 (3.63)	29.92 (2.43)
77	79	39	52	64	42	41	11	15	86	39	39	30
80.67 (6.11)	92.67 (4.04)	38.33 (1.15)	55.00 (4.58)	72.00 (3.61)	40.67 (2.31)	47.00 (3.61)	11.67 (0.58)	18.00 (0.00)	101.00 (6.24)	40.67 (3.06)	42.67 (4.62)	29.67 (3.06)
83.00 (4.58)	88.00 (1.00)	38.00 (1.00)	48.33 (5.03)	67.67 (6.11)	41.67 (4.16)	46.33 (1.15)	12.67 (2.08)	16.33 (1.53)	97.67 (4.16)	43.67 (4.04)	43.67 (0.58)	31.00 (1.00)
74.67 (2.52)	76.33 (2.08)	32.00 (4.36)	50.33 (0.58)	65.33 (1.53)	40.67 (0.58)	40.00 (2.00)	11.33 (0.58)	12.67 (0.58)	91.33 (2.52)	40.33 (0.58)	36.67 (2.52)	26.00 (1.73)
86.43 (2.07)	97.43 (3.36)	51.71 (4.23)	57.00 (2.83)	77.14 (3.63)	46.86 (2.61)	49.71 (1.60)	14.00 (1.73)	15.57 (0.79)	103.43 (4.43)	42.29 (3.64)	50.86 (3.02)	33.14 (3.13)
81.65 (5.43)	89.94 (7.59)	41.81 (4.97)	55.81 (6.34)	73.96 (5.68)	46.04 (3.93)	46.74 (3.08)	13.56 (2.21)	15.78 (1.63)	102.85 (6.70)	42.15 (3.35)	48.48 (4.64)	33.93 (2.70)
78.67 (3.16)	94.33 (4.53)	47.00 (5.59)	59.22 (5.19)	79.89 (4.83)	49.22 (4.27)	47.56 (2.74)	13.44 (1.51)	17.11 (1.69)	107.44 (7.80)	44.22 (2.54)	46.56 (4.67)	33.89 (2.09)
81.00 (4.24)	85.00 (2.83)	43.50 (4.95)	46.50 (0.71)	73.50 (0.71)	40.00 (1.41)	13.00 (0.00)	51.00 (2.83)	16.00 (2.83)	101.50 (9.19)	37.00 (2.83)		
83.00 (5.66)	94.00 (0.00)	48.00 (1.41)	54.50 (4.95)	76.00 (7.07)	46.50 (3.54)	49.50 (0.71)	15.00 (0.00)	17.50 (0.71)	105.50 (12.02)	43.50 (0.71)	45.50 (2.12)	29.50 (0.71)
75.00 (2.94)	87.00 (5.48)	45.00 (3.46)	53.50 (2.89)	72.25 (2.75)	45.75 (2.22)	47.00 (3.74)	14.25 (2.22)	17.25 (1.71)	96.25 (2.63)	39.00 (3.37)	46.25 (1.26)	35.75 (2.63)
78.00 (3.27)	84.50 (1.29)	43.50 (6.56)	48.00 (2.58)	73.00 (3.37)	43.50 (1.00)	14.50 (2.89)	47.25 (2.50)	15.25 (1.71)	93.50 (3.11)	38.75 (9.18)		
84.00 (3.33)	93.50 (3.06)	43.00 (4.24)	58.80 (3.97)	74.60 (4.33)	45.30 (3.43)	47.30 (1.64)	13.00 (1.63)	15.10 (1.37)	106.50 (4.74)	42.60 (3.31)	44.20 (3.94)	32.30 (2.00)
76.38 (3.07)	87.31 (3.07)	39.54 (3.23)	53.15 (3.29)	70.77 (4.46)	46.31 (3.28)	48.69 (2.56)	15.69 (1.49)	21.23 (9.88)	98.92 (5.35)	40.15 (6.00)	46.62 (2.79)	32.92 (1.89)
76	84	63	52	69	43	48	14	18	103	47	41	32

2006). In the limb segments, excluding the posterior thigh, we measured the color in the middle of each at the lateral or dorsal aspects. For feet and hands, we measured the color at the center of the third metatarsal and third metacarpal, respectively. The reflectometer illuminates a circular area 8 mm in diameter with a standardized flashing light (D65) and measures the reflected light. We used the $L^*a^*b^*$ color system (Hamada *et al*. 1988), wherein L^* represents lightness (0–100, blackish to whitish), a^* represents the hue of green (–60) to red (60), and b^* represents the hue of blue (–60) to yellow (60). We excluded data on 15 yellow monkeys in the Kosumphi population (Hamada *et al*. 2005a, b) from the quantitative comparison.

Statistical Analyses

We calculated fundamental statistics, means and standard deviations, and examined the significance of the differences in means via a *t*-test. We examined geographical clines using correlation and regression analyses, and applied principal component analysis and factor analysis to the somatometry and body color data, respectively, via S-Plus 4.0 (MathSoft).

Results

Body Size and Proportions

Body mass We used data from macaques ≥7 yr to compare body sizes between populations (Table II). Yala (6.5°N) long-tailed macaques are the lightest: females, 3.68 kg and males, 5.32 kg. Hua Hin (12.5°N) long-tailed macaques are the heaviest: females, 7.63 kg and males, 10.93 kg. The body masses of Loei (17.2°N) rhesus macaques are intermediate in the range of Thai long-tailed macaques: females, 6.40 kg and a male, 6.45 kg.

Body mass is greatly influenced by nutritional condition, as reflected by skinfold (SF). The average total skinfold thickness (sum of SFs of 3 body sites) ranges from 7.1 mm in Yala females and 8.1 mm in Surat Thani (9.1°N) males to 31.6 mm and 35.7 mm in Hua Hin females and males, respectively. The linear dimension of the body. e.g., CRL, also influences body mass. Via generalized linear model analysis, we described the relationship of the body mass (BM [kg]) of Thai long-tailed macaques with CRL (mm) and SF (mm) as follows: BM=0.028 CRL + 0.10 SF – 8.53 (R^2=0.69) for females, and BM=0.034 CRL + 0.12 SF – 10.53 (R^2=0.72) for males. Thus, the skinfold (subcutaneous fat) considerably influences body mass in long-tailed macaques.

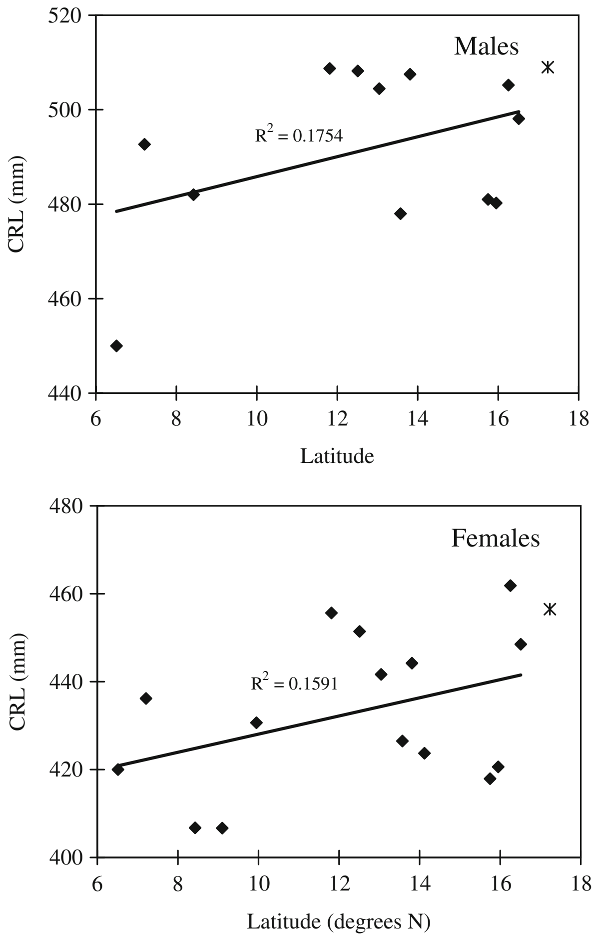
Crown-rump length (CRL) The Surat Thani (9.1°N) and Phang-nga (8.4°N) female populations had the shortest CRL, 406.7 mm and 406.8 mm, respectively, and the Kosumphi (16.3°N) and Prachuab (11.8°N) populations had the longest CRL, 461.9 mm and 455.6 mm, respectively (Table II). Yala (6.5°N) male long-tailed macaques were the shortest, 450.0 mm, and Nakhonpathom (13.8°N), Prachuab, and Hua Hin (11.8°N) male macaques were the longest, *ca.* 508 mm.

The CRL variation in Thai long-tailed macaques does not exhibit a simple, clear geographical cline (a relationship with latitude; R^2=0.18 and 0.16 in males and females, respectively; Fig. 2). The southern sample, comprising 5 populations south of the Isthmus of Kra (*ca*. 10.5°N), exhibits no geographical pattern with respect to CRL, with females ranging from 406.7 mm in Surat Thani (9.1°N) to 436.2 mm in Songkhla (7.2°N), and males ranging from 450.0 mm in Yala (6.5°N) to 492.7 mm in Songkhla. In the northern sample, with the exception of the Pichit and Kosumphi populations, CRL exhibits a significant negative correlation with latitude (R^2=0.788) in females. However, CRL in males of the northern sample exhibits no geographical trend (R^2=0.192; Fig. 2).

Loei rhesus macaques have CRL, 456.5 mm and 509 mm in females and males, respectively, comparable to those of the largest long-tailed macaques: 455.6 mm in Prachuab females and 508.7 mm in Hua Hin males, respectively.

Tail length (TL) and relative tail length (RTL) We compared tail lengths (TLs) via the data of subadult and adult subjects (≥6 yr) and relative tail lengths (RTLs) via the

Fig. 2 Geographical variation of the crown-rump length in long-tailed macaques (solid diamonds) with a population of rhesus macaques (*: Loei, Thailand).



data of all postinfant subjects (≥1 yr) because the growth change in RTL is insignificant after infancy. The northern populations tend to have shorter tails than those of the southern populations. Female long-tailed macaque TL is shortest in Ratchaburi (470.2 mm) and longest in Chumphon (565.8 mm, Table II). Male long-tailed macaque TL varies widely from the shortest in Nakhonsawan (495.0 mm) to the longest in Phang-nga and Songkhla (*ca.* 635.0 mm).

A comparison of RTL (Fig. 3) clearly reveals that there are 2 groups, northern and southern, of Thai long-tailed macaque populations. The 5 southern populations between 6.5°and 9.9°N have tails longer than 125% of the CRL (ranges: 129.2–140.2% in males and 128.2–132.5% in females). The 10 populations between 11.8° and 16.5°N have tails shorter than 120% of the RTL (ranges: 109.3–119.5% in females and 103.3–118.7% in males). Though the coefficient of correlation (R^2) calculated from all 15 populations is as high as 0.78, the variation within each of the southern and northern samples does not correlate significantly with the latitude because R^2 is <0.05 in each of them (Fig. 3). Therefore, the high correlation in Thai long-tailed macaques as a whole reflects the gap between the 2 samples. Loei rhesus macaques have RTLs (54.3% in females and 55.0% in males) only half those of the northern populations of Thai long-tailed macaques.

Limb proportion Long-tailed macaques exhibit no significant geographical cline in the intermembral index, with R^2=0.17 in males and 0.37 in females (p > 0.05, Fig. 4). However, there is a negative trend with latitude in females, and when we exclude the Songkhla data, which are outliers, the correlation is significant (R^2= 0.58). The maximum indices are 97.7% in Nakhonpathom males and 97.6% in Yala females, whereas the minimum indices are 92.3% and 91.9% in Kosumphi males and females, respectively.

The indices of Loei rhesus macaques (93.4% in males and 90.7% in females) are close to the minima of Thai long-tailed macaques, particularly to those of Kosumphi macaques.

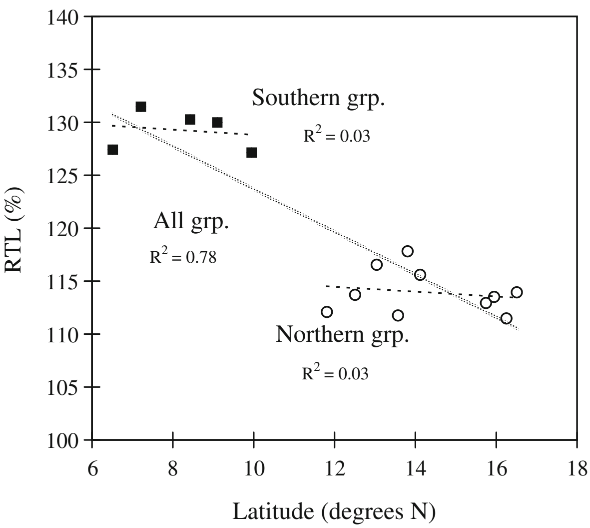


Fig. 3 Geographical variation of the tail length relative to crown-rump length in Thai long-tailed macaques. Regression lines are superimposed for all Thai long-tailed macaques and for the southern (solid squares) and northern (circles) samples.

Relative facial length Relative facial length exhibits no significant geographical cline: R^2=0.01 in females and R^2 < 0.01 in males. However, there are considerable differences between populations. Female Kosumphi macaques have the longest faces (60.5%), and Nakhonsawan (48.0%) and Phang-nga (49.0%) female macaques have the shortest faces. Male Chumphon (64.9%) and Petchaburi (62.4%) individuals have the longest faces, and Ratchaburi (49.0%) and Nakhonsawan (51.8%) macaques have the shortest faces.

Loei rhesus macaques have short faces (48.7% in females and 57.8% in males), comparable to the shortest-faced Thai long-tailed macaques.

Principal component analysis We applied principal component analysis to the somatometric data of 13 populations of female long-tailed macaques and a population of Loei rhesus macaques. We excluded the Ratchaburi and Nakhonsawan populations from the calculation because some somatometric data are missing. The 14 somatometric dimensions are crown-rump length, biacromial width, bi-iliac width, arm length, forearm length, thigh length, leg length, foot length, foot width, head length, head width, bizygomatic width, bigonial width, and upper facial height. The results for the males are similar to those for the females.

The first component accounts for 71.3% of all variance, and exhibits component loadings of large magnitude in almost all traits, e.g., 0.97 in crown-rump length. However, the magnitude for upper facial height (0.41) is rather small. Thus, the first component represents a size factor in general, excluding facial length. The second component, accounting for 9.71% of all variance, expresses limb segment lengths as shown by their positive loadings, e.g., arm length (0.51), forearm length (0.51), thigh length (0.42), and leg length (0.48). The third component, accounting for 6.30% of all variance, expresses biacromial width (–0.64) and bi-iliac width (–0.53).

Figure 5 is a scatterplot of the first and second component scores (population averages). A conspicuous deviant is the Pichit population, which has a much smaller second component score, indicating shorter limbs relative to other body dimensions; when we removed the score, the remaining populations exhibited a major trend

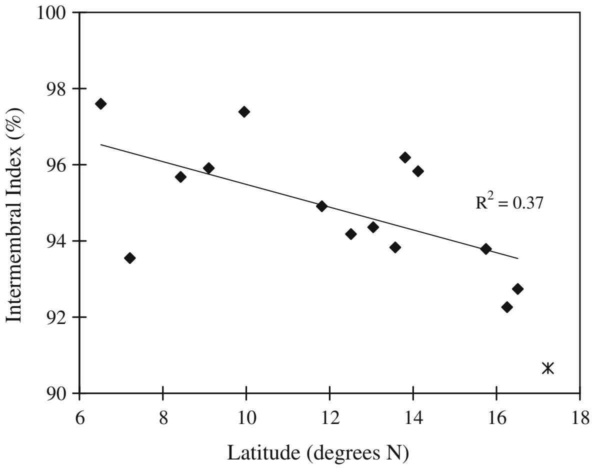
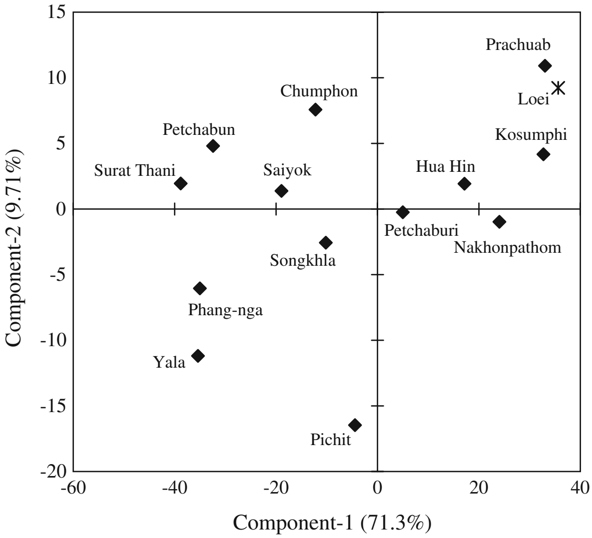


Fig. 4 Geographical variation of the intermembral index in female Thai long-tailed (solid diamonds) and rhesus macaques (*). Regression line for long-tailed macaques is superimposed.

Fig. 5 Scatterplot of the first (size) and second (limb proportion) component scores of the principal component analysis in female long-tailed and rhesus macaques: solid diamonds for Thai long-tailed and * for Loei rhesus macaques.



connecting Yala macaques (the lower and left end) with Prachuab macaques (the upper and right end). Surat Thani, Petchabun, and Chumphon populations have relatively longer limbs. Other populations occur on or near the trend line. The datum point for Loei rhesus macaques is also close to the trend line for long-tailed macaques.

Body Color Variation

We pooled the data for body color in males and females because it does not differ significantly between the sexes.

Lightness The coefficient of correlation between lightness and latitude is significant and high for many body parts (Fig. 6). The highest coefficient is for the back (R^2= 0.74, $p < 0.05$), and even the lowest one —for the crown— is significant (R^2=0.32, $p < 0.05$). The face, thigh (lateral), and waist exhibit higher coefficients of regression (inclination): 1.53, 1.12, and 0.93, respectively. Therefore, the body parts clearly reveal a geographical cline; the southernmost population, Yala has the darkest face and thigh (L^*=34.5 and 36.3, respectively), and the northernmost population, Kosumphi, has the lightest face and thigh (L^*=51.1 and 48.4, respectively). Thus, Gloger's rule, expressing the relationship between latitude of habitat and the lightness of the body color of animals, is applicable to the Thai long-tailed macaques.

However, there are some deviants from the geographical trends. We evaluated the degree of deviation from the geographical trend via the difference of lightness estimated from the regression equation and observation, standardized by the estimate and multiplied by 100: [(observed value – estimate)/estimate] × 100%.

The Songkhla population tend to be lighter than the estimate and the deviation is positive and somewhat large at some body sites such as the crown (8.4% of the degree of deviation), waist (9.6%), hand (10.7%), and foot (10.8%). The deviation in the Saiyok population is negative and large at body sites such as the waist (–9.1%) and foot (–5.0%).

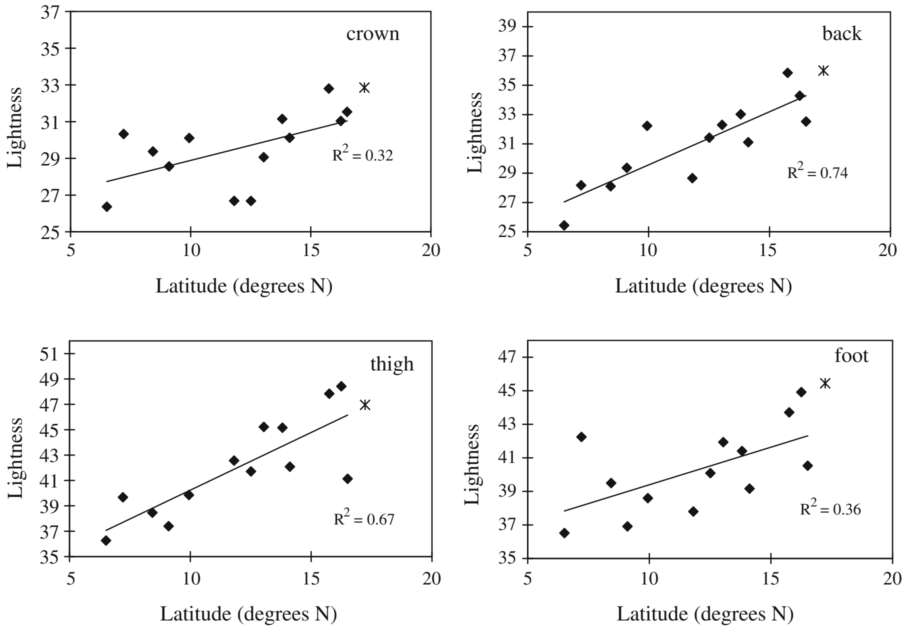


Fig. 6 Geographical variation of the lightness (L^*) of body color at the crown, back, thigh, and foot in long-tailed and rhesus macaques. Solid diamonds are for Thai long-tailed macaques and * for Loei rhesus macaques.

The data points for Loei rhesus macaques (Fig. 6) are close to the trends of Thai long-tailed macaques, though the crown (5.1%) and posterior thigh (–6.9%) of the former deviate substantially. Unlike long-tailed macaques, mature rhesus macaques have glabrous sexual skin on the posterior thigh, which is poorly developed in long-tailed macaques.

In general, the body color profiles of lightness (Fig. 7) appear to be similar among the populations, though lightness as a whole differs between populations. The crown and back are the darkest of all body sites. The color becomes darker distally in the forelimbs. The waist is lighter than the back, and the thigh is as light as the arm. The leg is lighter than the thigh and foot. The face is as light as or darker than the foot, with the exception of the Kosumphi long-tailed and Loei rhesus macaques. The posterior thigh is considerably lighter than other body areas because it is covered by whitish hairs similar to those covering the belly.

The lightness profile of Loei rhesus macaques is almost the same as that of Kosumphi long-tailed macaques and parallels that of the other long-tailed macaque populations.

In the color profile, there is a difference among populations in the contrast between the crown and back. The difference in contrast, ($L^*_{\text{crown}} - L^*_{\text{back}}$), is statistically significant between the populations. The contrast is positive, i.e., the crown is lighter than the back, in 3 southern populations —Yala, Songkhla, and Phang-nga (range: 0.69–1.18, Fig. 8)— whereas it is negative in the other 2 southern populations: Surat Thani (–0.58) and Chumphon (–2.03). The contrasts in all 10 northern populations are negative (range: –1.58 to –4.47). The contrast appears to

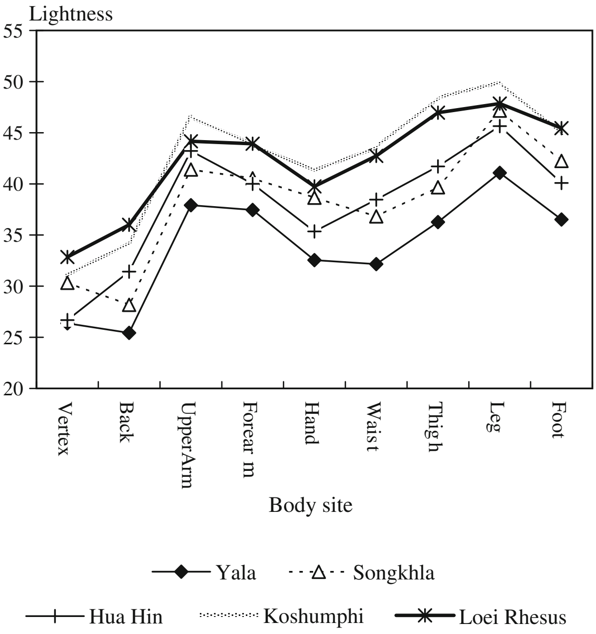


Fig. 7 Body color profiles of lightness (L^*) in long-tailed and rhesus macaques.

be clinal. Thus, a crown darker than the back appears to be a specific trait of the northern sample, whereas a lighter crown appears to be a trait of the southern one. However, different inclinations of the clinal variation between lightness of the crown and back produced the dichotomous difference between the 2 samples. Because the regressions for the crown and back with respect to latitude are significant, the contrast (subtraction) correlates with latitude (R^2=0.59). The Hua Hin and Pichit populations exhibit significant deviations from the trend, with a stronger negative contrast in the former, and no contrast in the latter. Loei rhesus macaques follow the trend of northern long-tailed macaques, i.e., the crown is darker than the back.

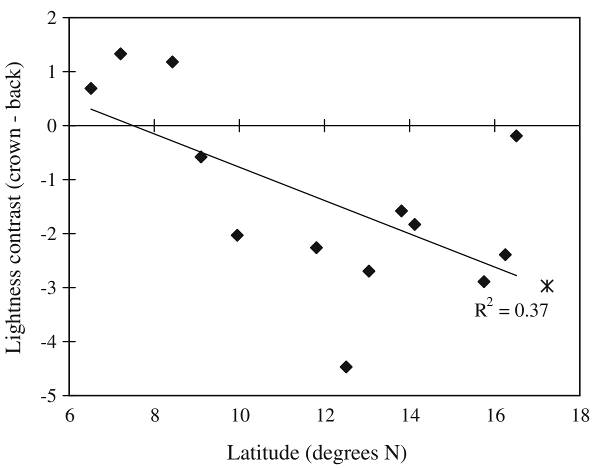


Fig. 8 Contrast in lightness (L^*) between the crown and back. Solid diamonds for long-tailed macaques and * for rhesus macaques.

Hue of green-red (a)* The hue of green-red (*a** value) is weak, ranging between 0 and 5. It does not correlate with latitude with respect to the back and crown (R^2= 0.03) and correlates positively for the foot (R^2=0.35), hand (R^2=0.23), posterior thigh (R^2=0.44), and face (R^2=0.58). There are nonsignificant differences in color profiles of *a** values between populations. However, sporadic variation occurs in some populations: a negative deviation at the arm, forearm, hand, and leg in the Saiyok population; a negative deviation at the waist, thigh, and leg in the Nakhonpathom population; and a positive deviation at the arm, forearm, hand, thigh, leg, and foot in the Phang-nga population.

Loei rhesus macaques exhibit no specific *a** value. Many of their body sites are comparable with those of long-tailed macaques, except at the waist and thigh, which exhibited positive deviations from the trend. However, rhesus macaques have greater *a** values at the posterior thigh, where the skin reddens with reproductive maturation.

Hue of blue-yellow (b)* The major component (hue) of chroma in the long-tailed macaques is blue-yellow (*b**). The *b** values at various body sites of Thai long-tailed macaques correlate strongly with latitude (Fig. 9), particularly for the face (R^2=0.78), and the inclination of regression is also high (coefficient of regression=0.79). There is a high correlation in the lower half of the body, including the foot (R^2=0.70), waist (R^2=0.63), thigh (R^2=0.57), and leg (R^2=0.55). Conversely, the *b** value at the crown does not significantly correlate with latitude ($R^2 < 0.1$). Positive deviants from the trend occur in the Saiyok population at the arm, forearm, hand, leg, and posterior thigh; in the Phang-nga population at the arm, forearm, hand, thigh, leg, foot, face, and posterior thigh; and in the Pichit population at the crown and back.

Loei rhesus macaques had larger *b** values than those of long-tailed macaques in the lower half of the body at the waist, thigh, leg, and foot, and smaller values in the upper half of the body at the back, arm, and forearm. Thus, rhesus macaques exhibit strongly contrasted body color with respect to yellow hue between the upper and lower halves of the body (a bipartite color pattern; Fooden 2000). The crown is more yellowish than those of long-tailed macaques.

The contrast of *b** values between the thigh and back exhibits a significant geographical variation between the 2 groups of Thai long-tailed macaques (Fig. 10). Southern populations, with the exception of the Phang-nga population, exhibit a negative contrast (less yellowish at the thigh), whereas the northern populations tend to exhibit a positive contrast (more yellowish at the thigh). Exclusion of the Phang-nga population from the comparison greatly improved the correlation (R^2), from 0.36 to 0.69. However, as shown by the geographical variation in the northern sample, it is possible that the contrast of yellow hue does not represent a geographical cline but instead a gap between the northern and southern samples. The coefficient of correlation in each group is not significant ($R^2 < 0.05$). The contrast between the thigh and back in Loei rhesus macaques (5.45) is considerably higher than that in any of the Thai long-tailed macaque populations.

Body Color Pattern

We applied factor analysis to the data of *L**, *a**, and *b** values for all body sites. One factor is sufficient to explain all the variance in color data (p<0.01). The factor

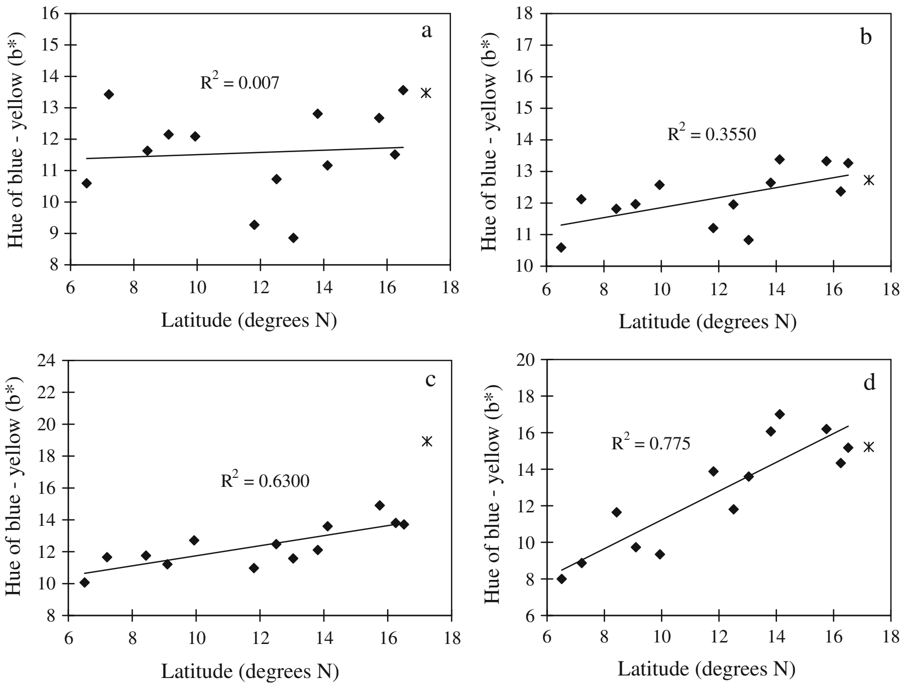


Fig. 9 Geographical variation of the blue-yellow hue (b^*) in long-tailed and rhesus macaques: **(a)** crown; **(b)** back; **(c)** waist; and **(d)** face. Diamonds for Thai long-tailed macaques and * for Loei rhesus macaques.

loadings of a^* values were large for the back, crown, forearm, waist, thigh, and leg, and those of L^* values were large for the thigh and back. The factor loadings of the L^* values for the foot, leg, waist, and crown, and the b^* values for the foot and hand are small (<0.4), indicating that the values are influenced by sporadically higher values in a few populations, such as the Saiyok and Phang-nga.

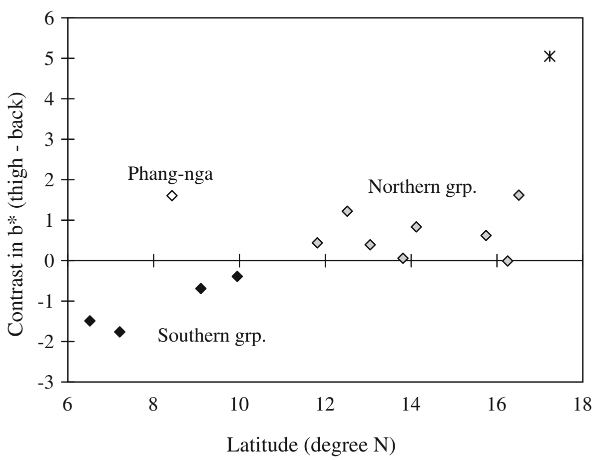


Fig. 10 Contrast in blue-yellow hue (b^*) between the thigh (lateral aspect) and back. Diamonds for long-tailed macaques: solid diamonds for troops of the southern sample, excepting the outlier (Phang-nga, open diamond), gray diamonds for troops of the northern sample, and * for Loei rhesus macaques.

The geographical trend in the factor score with latitude is significant (Fig. 11; R^2=0.49), i.e., the body color of the northernmost populations —Pichit, Kosumphi, and Pechabun (16.5–15.8°N)— is lighter and more vivid, whereas the body color of the southernmost populations, e.g., Yala (6.5°N), is darker and less vivid. There are significant positive deviants from this trend in the Phang-nga and Saiyok populations. Excluding the deviants greatly improves the coefficient of correlation (R^2=0.87), as shown by the regression line superimposed in Fig. 11.

The data point for Loei rhesus macaques positively deviates from the trend line of long-tailed macaques, reflecting the fact that they exhibit a distinctively different pattern from any of the long-tailed macaque populations, i.e., a bipartite color pattern.

Discussion

Morphological differences between the northern and southern long-tailed macaques and the hybridization between long-tailed and rhesus macaques

Macaca fascicularis fascicularis are widely distributed in Southeast Asia (Hamada *et al*. 2006), and are separated into northern and southern groups at the Isthmus of Kra by morphological and genetic traits (Darga *et al*. 1975; Fooden 1995; Melnick and Kidd 1985; Tosi *et al*. 2000, 2002, 2003). Fooden (1995, 2000) and Tosi *et al*. (2002) suggested that the distinctive characteristics of the northern long-tailed macaques were produced by interspecific introgression with parapatrically distributed rhesus macaques. Though Smith *et al.* (2007) noted no DNA sequence in long-tailed macaques close to those in rhesus macaques, they used few long-tailed macaque samples from the Indochina Peninsula. Fooden (2000) considered macaques distributed at the boundary areas ranging over 15–17°N in the eastern half of the Indochina Peninsula, i.e., in Thailand, Laos, and Vietnam also to be hybrids with long-tailed macaques.

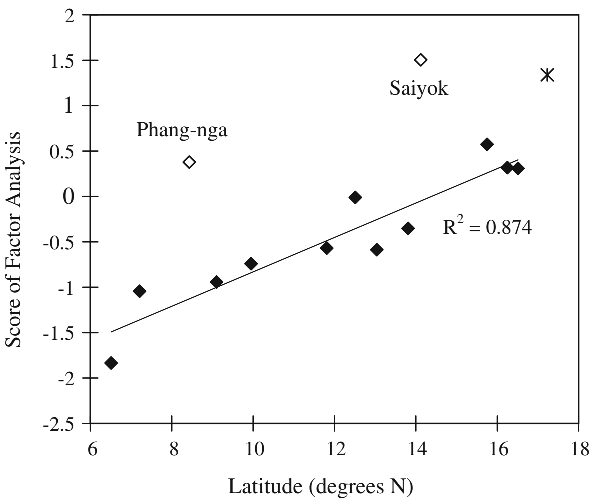


Fig. 11 Geographical variation in the scores of the factor analysis with the latitude in long-tailed (diamonds) and rhesus macaques (*). Two troops of long-tailed macaques, Phang-nga and Saiyok (open diamonds), appear to be outliers.

Researchers have not thoroughly examined the variation, particularly morphological, between local populations to test the hybridization model. One could also consider a climatic model, wherein morphological and body color traits are under strong environmental influence, including climate or related habitat conditions, which produce geographical variations in body size, body proportion, and body color that conform to the zoogeographical rules of Bergman, Allen, and Gloger.

With the exception of relative tail length and yellow hue contrast, Thai long-tailed macaques exhibit no morphological and body color variation that support the hybridization model. Fooden (1995, 1997) reported that there are geographical trends (clines) in body size among *Macaca fascicularis fascicularis*. According to Fooden (1995), in the south, the size increases from the equator northwards until *ca.* 10°N, corresponding to the Isthmus of Kra, conforming to Bergman's rule. In contrast, the size decreases with increasing latitude from north of the Isthmus to the northern limit of the range. He also reported that the body sizes of southern rhesus macaques followed the trend in the northern long-tailed macaques (Fooden 1995). According to Fooden (1995), the trend in the northern long-tailed macaques is not explained by the clinal climate but instead by hybridization, i.e., the populations experienced introgression from rhesus macaques proportional to the distance from the boundary zone. However, our findings do not support such trends in long-tailed macaques and rhesus macaques (Fig. 2).

The body proportions exhibited latitudinal variations in long-tailed macaques (intermembral index, Fig. 4). The results of principal component analysis also revealed that the variation of relative limb length is geographically clinal (Fig. 5). The Loei rhesus population followed both trends. The clinal variations in limb proportion may imply adaptation to the locomotor substrate (arboreality and terrestriality; Fleagle 1999) that varies with latitude (climate).

The proportion of the facial length (upper facial height) is one of the few traits distinguishing long-tailed macaques (with relatively longer faces) from rhesus macaques (Fooden 2000). However, Thai long-tailed macaques exhibit no geographical pattern in relative facial length, and the northernmost long-tailed macaque populations, e.g., Kosumphi and Pichit, have considerably longer faces than those of Loei rhesus macaques.

Long-tailed and rhesus macaques have specific body color patterns, which are expected to be useful to test the hybridization model. Thai long-tailed macaques and Loei rhesus macaques have similar lightness profiles (L^* value, Fig. 7), and lightness as a whole exhibits a geographical cline conforming to Gloger's rule (Fig. 6; Fooden 1995).

Researchers have regarded the lightness contrast between the crown and back as a trait separating the southern population with positive contrast (the crown is lighter than the back) from the northern population with negative contrast (darker crown; Fooden 1995). Because the lightness contrast in rhesus macaques is close to that in the latter group, it might support the hybridization model. However, we demonstrated that the lightness contrast is clinal and continuous in Thai long-tailed macaques (Figs. 6, 7 and 8). The lightness at each body site in long-tailed macaques correlates with latitude, and the inclination of the regression between L^* and latitude differs according to body site. The differences produce the clinal variation in the contrast, and at *ca.* 8°N, the contrast value turns from positive to negative.

The geographical trend also occurs in body color pattern deduced by factor analysis (Fig. 11), in which the southern populations of long-tailed macaques have darker and less vivid color than that of the northern populations. Loei rhesus macaques have a lighter and more vivid color than estimated from the trend in Thai long-tailed macaques.

One cannot attribute geographical variation in relative tail length (RTL) and yellow hue contrast only to the climatic cline; however, one can attribute it to hybridization. The variation in relative tail length in Thai *Macaca fascicularis fascicularis* exhibits a clear gap between the southern and northern populations. Though it exhibits a negative trend (Fig. 3, $R^2 = 0.785$) as a whole, which conforms to Allen's rule, the southern population have tails that are significantly longer (RTL > 125%) than those of the northern populations (RTL < 120%), and there is no significant correlation between RTL and latitude within each group ($R^2 < 0.05$). The southern rhesus macaques have longer tails (*ca.* 55% in RTL) than their conspecifics in China (*ca.* 30%) and India (*ca.* 45%; Hamada *et al.* 2006).

The yellow hue contrast between the thigh and back helps to separate the northern populations from the southern populations (Fig. 10). The contrast is negative in the southern long-tailed macaques, i.e., the thigh is less yellowish than the back, and positive in the northern sample; however, the variation within each sample does not exhibit a cline. Loei rhesus macaques have a greater contrast than that of any of the northern long-tailed macaques.

With the same focal long-tailed macaques as in our study, Malaivijitnond *et al.* (2007a) found that northern females have a strikingly different sex skin swelling pattern than that of the southern females. They also reported that the frequencies of human ABO blood groups in Thai long-tailed and rhesus macaque populations also suggest hybridization (Malaivijitnond *et al.* 2007b).

Our study revealed that the tail length and yellow hue contrast differences between the northern and southern long-tailed macaques are not great. This is also true for Loei rhesus macaques in comparison with their northern (China and its vicinity) or western (India and its vicinity) counterparts. Therefore, the hybridization is probably restricted. The variation of the 2 traits in northern populations is restricted, suggesting that the population size of the ancestors from which the traits were acquired might have been small. This may have facilitated the replacement of the Y-chromosomal gene haplotype of the Indochinese long-tailed macaques with that of rhesus macaques (Tosi *et al.* 2002), and also accounts for the observation that Laotian long-tailed macaques exhibit no intermediate trait within or among populations (Duckworth *et al.* 1999). The refugia during periods of a glacially cooler and arid climate, as assumed for various primate species in Asia (Eudey 1980; Jablonski 1993), are candidate locations for long-tailed macaques to obtain hybrid traits. The population accordingly acquired fixed traits before dispersing to the postglacial range.

However, the extent of introgression appears variable among localities in the Indochina Peninsula. Long-tailed macaques from Vietnam, which are assumed to be hybrids, tend to have considerably shorter tails (Fooden 1995). In particular, the ones in the Sontra Peninsula on the outskirts of Da Nang City in Vietnam (16.1°N, 108.2°E) have very short tails (van Peenen *et al.* 1971). Researchers consider refugia to have been present in the Indochina Peninsula in such mountainous areas as the Truongson Mountains (Annamite cordillera) in the east (Eudey 1980; Meijaard and Croves

2006), the Phu Khieo Mountains (Koenig *et al*. 2004) in the center, and Dawna Range in the west (including the Huay Kha Khaeng Wildlife Sanctuary; Eudey 1980). Further study is necessary to determine the location of the refugia in which the northern Thai long-tailed macaques received introgression.

After the postglacial dispersion, local populations of the northern long-tailed macaques would have acquired secondary variation in various traits due to global environmental conditions, specific adaptation to the new habitats, or genetic drift. The body size of the ancestors of the northern populations would have been as large as those of present-day populations in Prachuab, Hua Hin, or Kosumphi, and the other populations of the northern group would have become smaller.

The southern rhesus macaques have also experienced a partial genetic influence from long-tailed macaques in the acquisition of a hybrid trait of longer tail (Fooden 1964, 2000). However, because researchers have not examined the variability in southern rhesus macaques, it is not possible to deduce their history from our findings.

Diversity in Thai long-tailed Macaques and Their Conservation

We found that each of the local populations of long-tailed macaques maintains considerable diversity in morphology and body color. For example, the Phang-nga and Saiyok populations exhibit a distinctive red hue, and the Pichit population has relatively short limbs. The populations in Sumatra and the nearby Malay Peninsula (south of 10°N) tend to have a higher erythrism index (reddish body color; Fooden 1995). In addition to morphological uniqueness, they also exhibit unique behaviors, which are socially transmitted from generation to generation, such as the oyster-cracking behavior in the Laem Son populations (Malaivijitnond *et al*. 2007c) and dental-floss behavior in the Lopburi population (Watanabe *et al*. 2007). Though our focal population live in or close to human settlements, provisioned (Aggimarangsee 1992) and more or less isolated from neighboring populations, they still maintain traits unique enough to be conserved. Conservation efforts are directed mostly to populations inhabiting national parks, wildlife sanctuaries, or reserves; however, efforts should also be made to conserve local populations living close to human settlements.

Acknowledgments We thank Dilok Yanklin, Chalis Mungsuwa, Anu Kulaboot, Rilaphon Wongsrisai, and Nontakorn Urasopon for their help during the field study. We thank the monks at temples and authorities of recreational parks who permitted us to conduct research and offered much help. The Thailand Research Fund (grant RSA/02/2545 and RMU4880019), Chulalongkorn University (Grant for Primate Research Unit, to S. Malaivijitnond), the Japanese Society for the Promotion of Science (No. 1645017), and the 21st Century COE Program Formation of a Strategic Base for the Multidisciplinary Study of Biodiversity (to Y. Hamada) from the Ministry of Education, Culture, and Scientific Techniques, Japan provided funding for the study.

References

Aggimarangsee, N. (1992). Survey for semi-tame colonies of Macaques in Thailand. *Natural History Bulletin of the Siam Society*, *40*, 103–166.

Darga, L. L., Goodman, M., Weiss, M. L., Moore, G. W., Prychodko, W., Dene, H., *et al*. (1975). Molecular systematics and clinal variation in macaques. In G. L. Markert (Ed.), *Isozymes IV genetics and evolution* (pp. 797–812). New York: Academic Press.

Delson, E. (1980). Fossil macaques, phylectic relationships and scenario of deployment. In D. G. Lindburg (Ed.), *The Macaques: Studies in ecology, behavior and evolution* (pp. 10–29). New York: Van Nostrand Reinhold.
Duckworth, J. W., Salter, R. E., & Khounboline, K. (compilers). (1999). Wildlife in Lao PDR: 1999 Status Report. IUCN–The World Conservation Union/Wildlife Conservation Society/Centre for Protected Areas and Watershed Management, Vientiane, 275 pp.
Eudey, A. A. (1980). Pleistocene glacial phenomena and the evolution of Asian macaques. In D. G. Lindburg (Ed.), *The Macaques: Studies in Ecology, Behavior and Evolution* (pp. 52–83). New York: Van Nostrand Reinhold.
Fleagle, J. G. (1999). *Primate Adaptation and Evolution* (p. 596, 2nd ed.). San Diego: Academic Press.
Fooden, J. (1964). Rhesus and crab-eating macaques: Intergradation in Thailand. *Science*, *143*, 363–362. doi:10.1126/science.143.3604.363.
Fooden, J. (1976). Provisional classification and key to living species of macaques (Primates: Macaca). *Folia Primatologica*, *25*, 225–236.
Fooden, J. (1980). Classification and distribution of living macaques (*Macaca* Lacépède, 1799). In D. G. Lindburg (Ed.), *The Macaques: Studies in Ecology, Behavior and Evolution* (pp. 1–9). New York: Van Nostrand Reinhold.
Fooden, J. (1995). Systematic review of Southeast Asian longtail macaques, *Macaca fasciculari*s (Raffles, [1821]). *Fieldiana Zoology*, *81*, 1–206.
Fooden, J. (1997). Tail length variation *in Macaca fascicularis* and *M. mulatta*. *Primates*, *38*, 221–231. doi:10.1007/BF02381611.
Fooden, J. (2000). Systematic review of the rhesus macaque, *Macaca mulatta* (Zimmermann, 1780). *Fieldiana Zoology*, *96*, 1–180.
Fooden, J., & Albrecht, G. H. (1999). Tail length variation in fascicularis-group macaques (Cercopithecidae: *Macaca*). *International Journal of Primatology*, *20*, 431–440. doi:10.1023/A:1020556922189.
Groves, C. (2001). *Primate Taxonomy* p. 350. Washington: Smithsonian Institution Press.
Hamada, Y. (1982). Longitudinal somatometrical study on the growth patterns of newborn Japanese monkeys. *Primates*, *23*, 542–557. doi:10.1007/BF02373965.
Hamada, Y., Hadi, I., Urasopon, N., & Malaivijitnond, S. (2005a). Preliminary report on the recent status of golden long-tailed macaques (*Macaca fascicularis*) at the Kosumpee Forest Park, Maha Sarakham Province, Thailand. *Primates*, *46*, 269–273. doi:10.1007/s10329-005-0126-z.
Hamada, Y., Urasopon, N., Hadi, I., & Malaivijitnond, S. (2006). Body size and proportions and pelage color of free-ranging *Macaca mulatta* from a zone of hybridization in Northeastern Thailand. *International Journal of Primatology*, *27*, 497–513. doi:10.1007/s10764-006-9033-4.
Hamada, Y., Watanabe, T., Chatani, K., Hayakawa, S., & Iwamoto, M. (2005b). Morphometrical comparison between Indian- and Chinese-derived rhesus macaques (*Macaca mulatta*). *Anthropological Science*, *113*, 183–188. doi:10.1537/ase.03104.
Hamada, Y., Watanabe, T., Takenaka, O., Suryobroto, B., & Kawamoto, Y. (1988). Morphological studies of the Sulawesi macaques: I. Phyletic analysis of body color. *Primates*, *29*, 65–80. doi:10.1007/BF02380850.
Hayasaka, K., Fujii, K., & Horai, S. (1996). Molecular phylogeny of macaques: Implications of nucleotide sequences from an 896-base pair region of mitochondrial DNA. *Molecular Biology and Evolution*, *13*, 1044–1053.
Iwamoto, M. (1972). Morphological studies of *Macaca fuscata*: VI. Somatometry. *Primates*, *12*, 151–174. doi:10.1007/BF01730392.
Jablonski, N. G. (1993). Quaternary environments and the evolution of primates in East Asia, with notes on two new specimens of fossil Cercopithecidae from China. *Folia Primatologica*, *60*, 118–132.
Koenig, A., Larney, E., Kretiyutanon, K., & Borries, C. (2004). The primates of Phu Khieo Wildlife Sanctuary. *American Journal of Physical Anthropology*, (Supplement 38), 127.
Malaivijitnond, S., Hamada, Y., Suryobroto, B., & Takenaka, O. (2007a). Female long-tailed macaques with scrotum-like structure. *American Journal of Primatology*, *69*, 721–735. doi:10.1002/ajp.20380.
Malaivijitnond, S., Hamada, Y., Varavudhi, P., & Takenaka, O. (2005). The current distribution and status of macaques in Thailand. *Natural History Journal of Chula University*, (Supplement 1), 35–45.
Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007c). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*, 227–233. doi:10.1002/ajp.20342.

Malaivijitnond, S., Sae-Low, W., & Hamada, Y. (2007b). The human-ABO blood groups of free-ranging long-tailed macaques (*Macaca fascicularis*) and parapatric rhesus macaques (*M. mulatta*) in Thailand. *Journal of Medical Primatology*. doi:10.1111/j.1600-0684.2007.00223.x.

Meijaard, E., & Croves, C. P. (2006). The geography of mammals and rivers in mainland Southeast Asia. In S. M. Lehman, & J. G. Fleagle (Eds.), *Primate Biogeography*: *Progress and Prospects* (pp. 305–329). New York: Springer.

Melnick, D. J., & Kidd, K. K. (1985). Genetic and evolutionary relationships among Asian macaques. *International Journal of Primatology*, *6*, 123–160. doi:10.1007/BF02693650.

Nwe, D. T., San, A. M., Min, N. W. W., Thu, M. K., Oi, T., & Hamada, Y. (2005). Species diversity and distribution of primates in Myanmar. *Natural History Journal of Chula University*, (Supplement 1), 47–53.

Smith, D. G., McDonough, J. M., & George, D. A. (2007). Mitochondrial DNA variation within and among regional populations of longtail macaques (*Macaca fascicularis*) in relation to other species of the *fascicularis* group of macaques. *American Journal of Primatology*, *69*, 182–198. doi:10.1002/ajp.20337.

Tosi, A. J., Morales, J. C., & Melnick, D. J. (2000). Comparison of Y chromosome and mtDNA phylogenies leads to unique inferences of macaque evolutionary history. *Molecular Phylogenetics and Evolution*, *17*, 133–144. doi:10.1006/mpev.2000.0834.

Tosi, A. J., Morales, J. C., & Melnick, D. J. (2002). Y-chromosome and mitochondrial markers in *Macaca fascicularis* indicate introgression with Indochinese *M. mulatta* and a biogeographic barrier in the Isthmus of Kra. *International Journal of Primatology*, *23*, 161–178. doi:10.1023/A:1013258109954.

Tosi, A. J., Morales, J. C., & Melnick, D. J. (2003). Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. *Evolution; International Journal of Organic Evolution*, *57*, 1419–1435.

Van Peenen, P. F. D., Light, H., & Duncan, J. F. (1971). Observations on mammals of Mt. Sontra, South Vietnam. *Mammalia*, *35*, 126–143.

Watanabe, K., Urasopon, N., & Malaivijitnond, S. (2007). Long-tailed macaques use human hair as dental floss. *American Journal of Primatology*, *69*, 1–5. doi:10.1002/ajp.20403.