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AUTHOR(S):

Chatani, Kaoru

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Locomotion in Adult Japanese Macaques and Comparison with That in the Long-Tailed Macaques

KAORU CHATANI

Primate Research Institute, Kyoto University,
Inuyama, Aichi, 484-8506 Japan
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Abstract I discuss locomotor behavior of adult Japanese macaques as well as the age in which it is attained. Male and female Japanese macaques are typical quadrupeds in both terrestrial and arboreal settings. They used quadrupedal walking most frequently. The age of maturation of terrestrial locomotion is eight years of age at the latest for both sexes. But the age of maturation of arboreal locomotion seems to be ten years of age in females and later in males. I compared locomotor behavior of adult Japanese macaques with that of adult male long-tailed macaques reported by Cant (1988). Both species of macaque adopt quadrupedal movements most frequently. However, there are subtle differences between male and female Japanese macaques as well as between Japanese macaques and male long-tailed macaques. Female Japanese macaques seldom adopt vertical moving and leaping. Male Japanese macaques use leaping more frequently but seldom engage in vertical moving. Male long-tailed macaques comparatively often adopt vertical moving and leaping. Averaged and maximum leaping distances are shorter in Japanese macaques than in long-tailed macaques. The difference of the body weight between Japanese macaques and long-tailed macaques seemingly affects distance covered by each leap rather than its frequency and the share of leaping among the total traveling distance.

Key words Japanese macaques, Locomotion, Positional behavior

Introduction

Primates have diverse locomotor repertoires. Each taxon has a characteristic locomotor repertoire and characteristic morphologies related to locomotion. Therefore comparison among species is important to investigate the adaptive radiation of Primates. Many field researchers have qualitatively and quantitatively studied adult locomotion in Primates. Locomotion of Japanese macaques has been studied by many researchers who used experimental methods and observed free-ranging groups. However, locomotion in adult Japanese macaques has not previously been studied quantitatively. So it is valuable to study quantitatively locomotion of adults.

In Japanese macaques, it is generally said that males mature at eight to nine years of age and females at seven to eight years of age. But each morphology has its own growth pattern and all patterns are not the same (Hamada 1994; Nakatsukasa 1996). So it is difficult to determine the age of locomotor maturation.

The genus *Macaca* has the widest distribution of any of the non-human primates (Napier *et al.* 1985; Fleagle 1988). It is important to investigate the adaptive radiation of

this genus in order to compare *Macaca* species. Cant (1988) and Cannon *et al.* (1994) quantitatively studied locomotion of *Macaca fascicularis*. A step in investigating the adaptive radiation of *Macaca* is to compare the locomotions of *Macaca fuscata* and *Macaca fascicularis*.

Japanese macaques and long-tailed macaques fall into the same group among the four groups which occur in the genus *Macaca*. (Fooden 1976). They are closely related to each other phylogenetically. But they are very different in body weight. Based on the list arranged by Plavcan *et al.* (1997), body weights of adult Japanese macaques were 11.7 kg to 11.0 kg for males and 9.1 kg to 9.2 kg for females. In contrast to Japanese macaques, body weights of adult long-tailed macaques were 4.16 to 6.2 kg for males and 3.12 to 4.54 kg for females. It has been suggested that body weight is one of the most effective constraints on locomotion (Napier 1967, 1972; Grand 1972; Taylor *et al.* 1972; Cartmill 1974; Fleagle 1980; Fleagle *et al.* 1980; Cant 1992; Doran 1993; Hunt 1994). A small animal is usually expected to use leaping more frequently than a large animal. In contrast, Gebo *et al.* (1995) said, "body size is a poor indicator of how often these species (cercopithecids) leap during travel". From this point of view, it is interesting to discuss how body weight affects locomotor behavior of Japanese macaques and long-tailed macaques, which are closely related to each other but have very different body weights.

In this paper, I present the locomotion of adult Japanese macaques and discuss the age of maturation of locomotion, after which I compare locomotion of adult Japanese macaques with that of adult male long-tailed macaques, which I obtained from Cant (1988), then discuss characteristics of locomotion of Japanese macaques, followed by a discussion of the effect of body weight on leaping.

Subjects and Methods

The quantitative data analyzed here are the same as those described in Chatani (2003). Macaques of eight years of age or above were studied and analyzed here (Table 1), because "most growth terminates at approximately eight years of age" (Hamada 1994, p. 66).

The mean numbers of Percentages of Use of each Locomotor type (PULs) of males of 8 years and over, PULs of females of 8 years and over, PULs of males of 9 years of age and PULs of females of 10 years of age and over were calculated separately for discussing the age of maturation of locomotion.

For comparison with long tailed macaques, PULs of each locomotor type was calculated by reference to Table 1 of Cant's paper (1988, p. 32), whose data were of the adult males. The overwhelming majority of locomotor behavior recorded by him was arboreal. For this reason, I compared only arboreal locomotor behavior of Japanese macaques with that of long-tailed macaques.

Locomotor modes classified by Cant were different from those used in Chatani (2003). For quantitative comparison, the locomotor modes were collapsed into six types as follows: "quadrupedal moving", "leaping", "dropping", "vertical moving", "bipedal mov-

ing" and "suspensory moving". Cant's modes were categorized as follows: "quadrupedalism" and "pronograde clambering" fell into "quadrupedal moving"; "leaping" stayed as "leaping"; "dropping" remained as "dropping"; "vertical climbing" and "vertical clambering" fell into "vertical moving"; "bipedalism" became "bipedal moving". Suspending locomotor behavior was not mentioned. Locomotor modes in Chatani (2003) were categorized as follows: "quadrupedal walking", "quadrupedal running" and "bridging" fell into "quadrupedal moving"; "leaping" remained as "leaping"; "dropping" stayed as "dropping"; "quadrupedal climbing", "clinging locomotion" and "scramble round a support" fell into "vertical climbing"; "bipedal locomotion" became "bipedal moving"; "suspensory locomotion" became "suspensory moving". "Vertical climbing" and "vertical clambering" of Cant were locomotor modes on the top of supports angled at 67.5°, which differs from my definition (50°). But here I disregard the difference. Cant presented proportions of use of all locomotor modes in travel, foraging and feeding individually. Here I gather them into one. The PUL of each locomotor mode was calculated for comparison.

Results

1. Terrestrial locomotion in adult Japanese macaques

Results are shown in Table 1-A and Fig. 1-A. All individuals used quadrupedal walking (QW) most frequently in the terrestrial locomotor mode. PUL of QW for each individual was more than 75%. All males used QW more than 76.9%. PUL of QW in males of eight years old or above is 80.9%, that in males of nine years old or above is 81.0%. Hotei, a ten-year-old male, used QW most frequently in all males, 86.1%. Kihada, an eight-year-old male, used QW second most frequently, 80.8%. Ebisu and Shitadashi, nine-year-old males, used QW 79.9 and 76.9%, respectively. All females used QW more than 77.6%. PUL of QW in females of eight years old or above is 83.0%, that in females nine years old or above is 83.3%. Goishi, a fifteen-year-old female, used QW most frequently in all individuals, 92.7%. Mika, an eight-year-old female, used QW second most frequently, 85.7%. Kiri, a nine-year-old female, and Ine, a ten-year-old female, used QW more than 83%. Megane, an eight-year-old female, and Kuuko and Yoru, ten-year-old females, used QW more than 77%.

All individuals used quadrupedal running (QR) the next most frequently. PUL of QR for each individual was more than 6%. All males used QR more than 11.4%. PUL of QR in males of eight years old or above is 16.9%, that in males of nine years old or above is 17.6%. Shitadashi, a nine-year-old male, used QR most frequently in all males, 22.1%. Ebisu, a nine-year-old male, used QR second most frequently, 19.3%. Kihada, an eight-year-old male, and Hotei, a ten-year-old male, used QR 14.8 and 11.4%, respectively. All females used QR more than 6.3%. PUL of QR in females of eight years old or above is 13.3%, that in females nine years old or above is 13.0%. Goishi, a fifteen-year-old female, used QR least frequently in all individuals, 6.3%. But all other females used QR more than 10%. Yoru, a ten-year-old female, used QR most frequently in all females, 19.4%. Ine, a ten-year-old female, used QR second most frequently, 15.0%. PUL of QR in the

Table 1-A. Percentage of distances moved during each locomotor behavior (terrestrial) in adult Japanese macaques.

Name	Sex	Age (Year)	Percentage of Use of Each Locomotion Type											Total			
			Quadrupedal walk	Quadrupedal run	Bridge	Leap	Drop	Quadrupedal climb	Clinging locomotion	Scramble round support	Bipedal locomotion	Suspensory locomotion	Rolling		Swim		
Kihada	m	8	80.8	14.8	0	2.5	0	0.9	0	0	0	0	0	0	0	0	100
Ebisu	m	9	79.9	19.3	0	0.3	0	0.3	0	0	0.2	0	0	0	0	0	100
Shitadashi	m	9	76.9	22.1	0	0.9	0	<0.05	0	0	0	0.1	0	0	0	0	100
Hotei	m	10	86.1	11.4	0	0.6	0	1.9	0	0	0	0	0	0	0	0	100
Megane	f	8	78.4	14.5	0	0.5	0.1	0.4	0	0	0	6.0	0	0.1	0	0	100
Mika	f	8	85.7	13.7	0	<0.05	0	<0.05	0	0	0	0.6	0	0	0	0	100
Kiri	f	9	83.9	13.5	0	0.1	0	1.4	0	0	0	1.0	0	0	0.1	0	100
Ine	f	10	84.3	15.0	0	0.5	0	0.1	0	0	0	0.1	0	0	0	0	100
Kuuko	f	10	78.1	10.9	0	0.7	0.2	0.3	0	0	0	9.8	0	0	<0.05	0	100
Yoru	f	10	77.6	19.4	0	2.7	0	0.1	0	0	0	0.2	0	0	0	0	100
Goishi	f	15	92.7	6.3	0	0.7	0	<0.05	0	0	0	0.3	0	0	0	0	100
Average	m	8≤	80.9	16.9	0	1.1	0	1.0	0	0	0.1	<0.05	0	0	0	0	100
Average	f	8≤	83.0	13.3	0	0.7	<0.05	0.3	0	0	0	2.6	0	<0.05	0	<0.05	100
Average	m	9≤	81.0	17.6	0	0.6	0	0.7	0	0	0.1	<0.05	0	0	0	0	100
Average	f	9≤	83.3	13.0	0	0.9	<0.05	0.4	0	0	0	2.3	0	0	<0.05	0	100

Table 1-B. Percentage of distances moved during each locomotor behavior (arboreal) in adult Japanese macaque.

Name	Sex	Age (Year)	Percentage of Use of Each Locomotion Type										Total
			Quadrupedal walk	Quadrupedal run	Bridge	Leap	Drop	Quadrupedal climb	Clinging locomotion	Scramble around support	Bipedal locomotion	Suspensory locomotion	
Kihada	m	8	68.9	11.6	<0.05	9.6	4.2	5.4	<0.05	0.3	<0.05	0	100
Ebisu	m	9	63.8	19.4	<0.05	12.5	1.1	3.1	<0.05	0.1	<0.05	0	100
Shitadashi	m	9	76.9	11.3	<0.05	7.6	2.0	2.0	<0.05	0.2	<0.05	0	100
Megane	f	8	70.1	5.0	0.5	8.1	3.6	11.3	<0.05	0.7	0.7	0	100
Ine	f	10	83.6	12.0	1.0	0.4	1.1	1.5	<0.05	0.4	<0.05	0	100
Kuuko	f	10	92.3	3.0	0.9	0.3	1.3	2.0	<0.05	0.2	<0.05	0	100
Yoru	f	10	94.4	5.0	<0.05	<0.05	0.1	0.4	<0.05	0.1	<0.05	0	100
Goishi	f	15	72.2	7.0	0.3	5.0	0.1	1.8	3.9	9.7	<0.05	0	100
Average	m	8 ≤	69.9	14.1	<0.05	9.9	2.4	3.5	<0.05	0.2	<0.05	0	100
Average	f	8 ≤	82.5	6.4	0.5	2.8	1.2	3.4	0.8	2.2	0.1	0	100
Average	m	9	70.4	15.4	<0.05	10.1	1.6	2.6	<0.05	0.2	<0.05	0	100
Average	f	10 ≤	85.6	6.8	0.6	1.4	0.7	1.4	1.0	2.6	<0.05	0	100

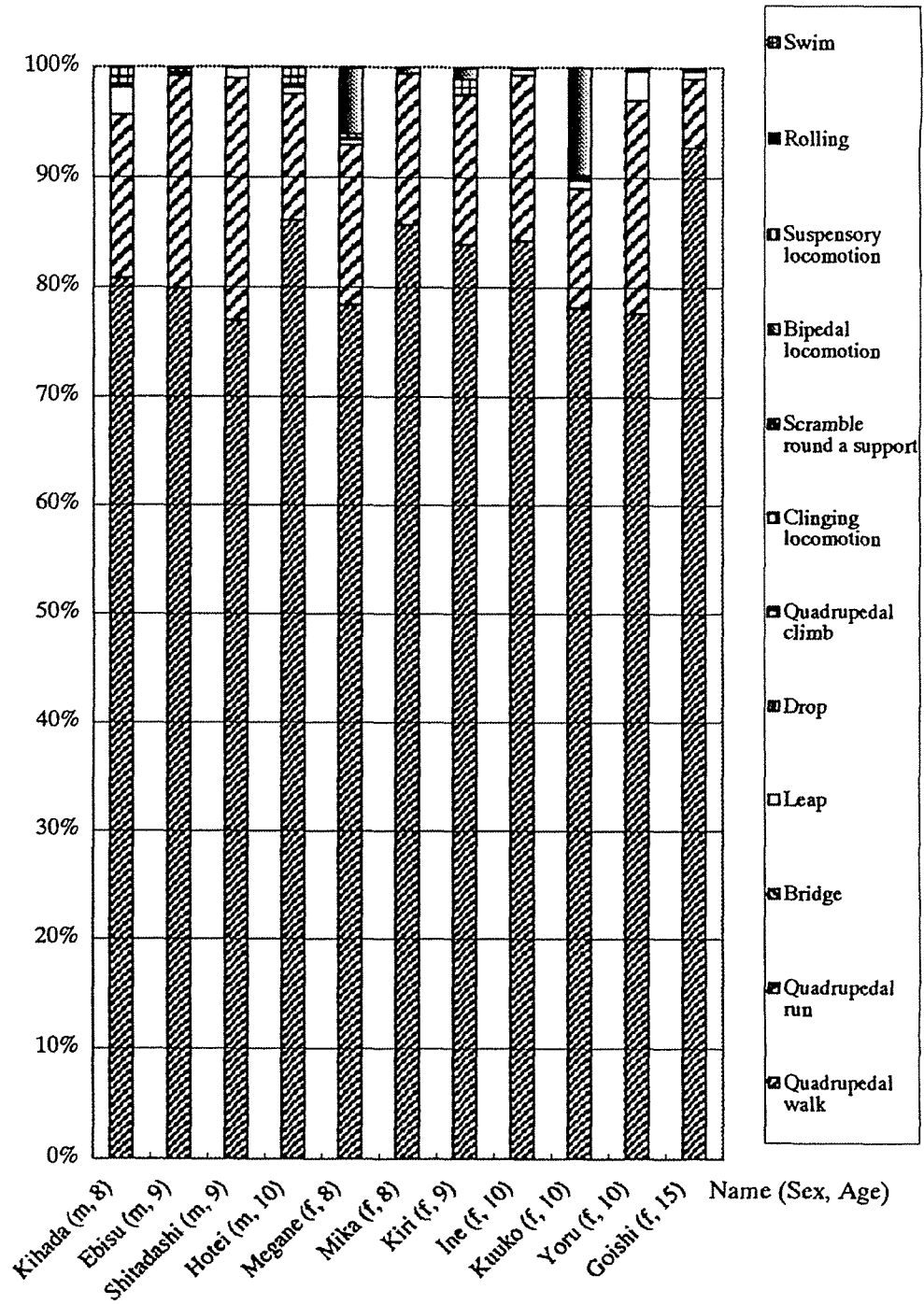


Fig. 1-A. Proportion of use of different locomotor modes (terrestrial).

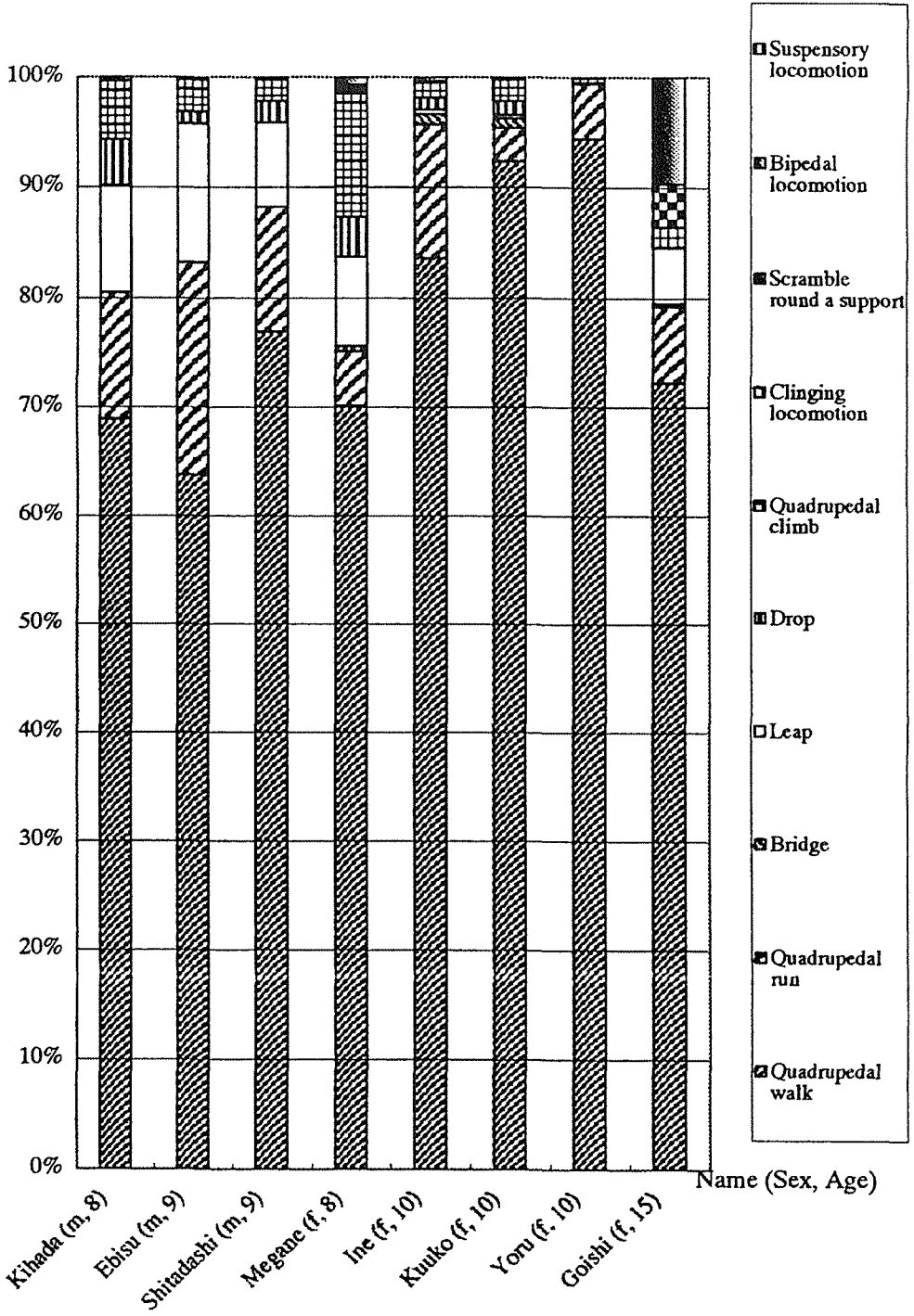


Fig. 1-B. Proportion of use of different locomotor modes (arboreal).

other females accounted for from 10.9 to 14.5%.

The total PUL of QW and QR of each individual was more than 89%. All individuals except Megane and Kuuko used QW and QR more than 95%.

Bridging (BG), clinging locomotion (CL) and suspensory locomotion (SU) were not used.

Leaping (LP) was used less than 5% by all individuals. All males used LP less than 3%. PUL of LP in males of eight years old or above is 1.1%, that in males of nine years old or above is 0.6%. Kihada, an eight-year-old male, used LP most frequently in all males, 2.5%. Shitadashi, a nine-year-old male, Hotei, a ten-year-old male, and Ebisu, a nine-year-old male, used LP 0.9, 0.6 and 0.9%, respectively. All females used LP less than 3%. PUL of LP in females of eight years old or above is 0.7%, that in females nine years old or above is 0.9%. Yoru, a ten-year-old female, used LP least frequently in all individuals, 2.7%. Kuuko, a ten-year-old female, and Goishi, a fifteen-year-old female, used LP 0.7%. Megane, an eight-year-old female, and Ine, a ten-year-old female, used LP 0.5%. Mika, an eight-year-old female, and Kiri, a nine-year-old female used LP less than 0.05%.

Dropping (DR) was seldom used. PUL of DR in males of eight years old or above and that in males of nine years old or above are 0%. PUL of DR in females of eight years old or above and that in females nine years old or above are less than 0.05%. Megane, an eight-year-old female, and Kuuko, a ten-year-old female, used DR 0.1 and 0.2%, respectively. But all other individuals did not use DR.

Quadrupedal climbing (QC) was used less than 2% by all individuals. All males used QC less than 2%. PUL of QC in males of eight years old or above is 1.0%, that in males of nine years old or above is 0.7%. Kihada, an eight-year-old male, and Hotei, a ten-year-old male, used QC most frequently in all males, 1.9%. Ebisu, a nine-year-old male, used QC 0.3%. Shitadashi, a nine-year-old male, used QC less than 0.05%. All females used QC less than 1.5%. PUL of QC in females of eight years old or above is 0.3%, that in females nine years old or above is 0.4%. Kiri, a nine-year-old female, used QC most frequently in all females, 1.4%. Megane, an eight-year-old female, and Kuuko, a ten-year-old female, used QC 0.4, 0.3%, respectively. Ine, a ten-year-old female, and Yoru, a ten-year-old female, used QC 0.1%. Mika, an eight-year-old female, and Goishi, a fifteen-year-old female, used QC less than 0.05%.

Scrambling round a support (SC) was seldom used. PUL of SC in males of eight years old or above and that in males of nine years old or above are 0.1%. Ebisu, a nine-year-old male, used SC 0.2%. All other males did not use SC. All females did not use SC.

Bipedal locomotion (BI) was seldom used. PUL of BI in males of eight years old or above and that in males of nine years old or above are less than 0.05%. Shitadashi, a nine-year-old male, used BI 0.1%. All other males did not use BI. All females used BI less than 10%. PUL of BI in females of eight years old or above is 2.6%, that in females nine years old or above is 2.3%. Kuuko, a ten-year-old female, used BI most frequently in all females, 9.8%. Ine, a ten-year-old female, used BI second most frequently, 6.0%. Kiri, a nine-year-old female, Mika, an eight-year-old female, used BI 1.0 and 0.6%, respectively. Goishi, a fifteen-year-old female, and Yoru, a ten-year-old female, used BI 0.3 and 0.2%, respectively.

Rolling (RO) was seldom used. All males and all females except Megane, an eight-year-old female, did not use RO. PUL of RO in females of eight years old or above is less than 0.05%. Megane, an eight-year-old female, used RO 0.1%.

Swimming (SW) was seldom used, too. All males and all females except Kiri, a nine-year-old female, and Kuuko, a ten-year-old female, did not use SW. PUL of SW in females of eight years old or above and that in females of nine years old or above are less than 0.05%. Kiri, a nine-year-old female, used SW 0.1%. Kuuko, a ten-year-old female, used SW less than 0.05%.

2. Arboreal locomotion in adult Japanese macaques

Results are shown in Table 1-B and Fig. 1-B. All individuals used quadrupedal walking (QW) most frequently in the arboreal locomotor mode. PUL of QW for each individual was more than 60%. All males used QW more than 63.8%. PUL of QW in males of eight years old or above is 69.9%, that in males of nine years old or above is 70.4%. Shitadashi, a nine-year-old male, used QW most frequently in all three males, 76.9%. Kihada, an eight-year-old male, and Ebisu, a nine-year-old male used QW 68.9 and 63.8%, respectively. All females used QW more than 70.1%. PUL of QW in females of eight years old or above is 82.5%, that in females nine years old or above is 85.6%. Yoru and Kuuko, ten-year-old females, used QW more than 90% (94.4 and 92.3, respectively). Ine, a ten-year-old female, used QW 83.6%. Goishi, a fifteen-year-old female, and Megane, an eight-year-old female, used QW 72.2 and 70.1%.

Many individuals used quadrupedal running (QR) the next most frequently. PUL of QR for each individual was more than 3.0%. All males used QR more than 11.3%. PUL of QR in males of eight years old or above is 14.1%, that in males of nine years old or above is 15.4%. Ebisu, a nine-year-old male, used QR most frequently in all males, 19.4%. Kihada, an eight-year-old male, and Shitadashi, a nine-year-old male, used QR 11.6 and 11.3%, respectively. All females used QR more than 3.0%. PUL of QR in females of eight years old or above is 6.4%, that in females nine years old or above is 6.3%. Ine, a ten-year-old female, used QR most frequently, 12.0%. Goishi, a fifteen-year-old female, used QR second most frequently, 7.0%. Both Megane, an eight-year-old female, and Yoru, a ten-year-old female, used QR 5.0%. Kuuko, a ten-year-old female, used QR 3.0%.

Bridging (BG) was seldom used. All male used BG less than 0.05%. Therefore, both PUL of BG in males of eight years old or above and that in males of nine years old or above are less than 0.05%. All females used BG less than 1.0%. PUL of BG in females of eight years old or above is 0.5% and that in females nine years old or above is 0.6%. Ine, a ten-year-old female, used BG most frequently, 1.0%. Kuuko, a ten-year-old female, used BG second most frequently, 0.9%. Megane, an eight-year-old female, and Goishi, a fifteen-year-old female, used BG 0.5 and 0.3%, respectively. Yoru, a ten-year-old female, used QR less than 0.05%.

Leaping (LP) was used less than 12.5% by all individuals. All males used LP less than 12.5%. PUL of LP in males of eight years old or above is 9.9%, that in males of nine years old or above is 10.1%. Ebisu, a nine-year-old male, used LP most frequently in all males, 12.5%. Kihada, an eight-year-old male, and Shitadashi, a nine-year-old male, used

LP 9.6 and 7.6%, respectively. All females used LP less than 8.1%. PUL of LP in females of eight years old or above is 2.8%, that in females nine years old or above is 1.4%. Megane, an eight-year-old female, used LP most frequently in all females, 8.1%. Goishi, a fifteen-year-old female, used LP second most frequently, 5.0%. Ine and Kuuko, ten-year-old females, used LP 0.4 and 0.3%, respectively. Yoru, a ten-year-old female, used LP less than 0.05%.

Dropping (DR) was used less than 4.2% by all individuals. All males used DR less than 4.2%. PUL of LP in males of eight years old or above is 2.4%, that in males of nine years old or above is 1.6%. Kihada, an eight-year-old male, used DR most frequently in all three males, 4.2%. Shitadashi, a nine-year-old male, and Ebisu, a nine-year-old males, used DR. 2.0 and 1.1%, respectively. All females used DR less than 3.6%. PUL of DR in females of eight years old or above is 1.2%, that in females nine years old or above is 0.7%. Megane, an eight-year-old female, used DR most frequently in all females, 3.6%. Kuuko and Ine, ten-year-old females, used DR 1.3 and 1.1%, respectively. Both Yoru, a ten-year-old female, and Goishi, a fifteen-year-old female, used DR at 0.1%.

Quadrupedal climbing (QC) was used less than 11.3% by all individuals. All males used QC less than 5.4%. PUL of QC in males of eight years old or above is 3.5%, that in males of nine years old or above is 2.6%. Kihada, an eight-year-old male, used QC most frequently in all males, 5.4%. Ebisu, a nine-year-old male, and Shitadashi, a nine-year-old male, used QC 3.1 and 2.0%. All females used QC less than 11.3%. PUL of QC in females of eight years old or above is 3.4%, that in females nine years old or above is 1.4%. Megane, an eight-year-old female, used QC most frequently in all females, 11.3%. Kuuko, a ten-year-old female, and Goishi, a fifteen-year-old female, used QC 2.0 and 1.8%, respectively. Ine and Yoru, ten-year-old females, used QC 1.5 and 0.4%, respectively.

Clinging locomotion (CL) was seldom used. All males used CL less than 0.05%. Therefore, PUL of CL in males of eight years old or above and that in males of nine years old or above are less than 0.05%. All females except Goishi, a fifteen-year-old female, used CL less than 0.05%. PUL of CL in females of eight years old or above and that in females nine years old or above are 0.8 and 1.0%, respectively. Goishi, a fifteen-year-old female, used CL 3.9%.

Scrambling round a support (SC) was seldom used. All males used SC less than 0.05%. Therefore, PUL of SC in males of eight years old or above and that in males of nine years old or above are less than 0.05%. All females except Megane, an eight-year-old female, used SC less than 0.05%. PUL of SC in females of eight years old or above is 0.1% and that in females nine years old or above is less than 0.05%. Megane, an eight-year-old female, used SC 3.9%.

Bipedal locomotion (BI) was used not so frequently. All individuals used BI less than 10%. All males used BI less than 0.3%. PUL of BI in males of eight years old or above and that in males of nine years old or above are 0.2%. Kihada, an eight-year-old male, used BI most frequently in all three males, 0.3%. Shitadashi and Ebisu, nine-year-old males, used BI 0.2 and 0.1%, respectively. All females except Goishi, a fifteen-year-old female, used BI less than 1.0%. PUL of BI in females of eight years old or above is 2.2%, that in females nine years old or above is 2.6%. Goishi used BI most frequently in all females,

9.7%. Megane, an eight-year-old female, and Ine, a ten-year-old female, used BI 0.7 and 0.4%, respectively. Kuuko and Yoru, ten-year-old females, used BI 0.2 and 0.1%, respectively.

Suspensory locomotion (SU) was not used.

The total PUL of QW and QR of each individual was more than 89%. All individuals except Megane and Kuuko used QW and QR more than 95%.

Differences among individuals in the trees were greater than those on the ground. All individuals also used quadrupedal walking (QW) most frequently in arboreal locomotor mode. PUL of QW for each individual was more than 60%. QR, LP, QC, CL and BI were often used. Their PULs were different among individuals. All individuals used QR more than 3%. All individuals except three 10-year-old females used LP more than 5%. QC was used more than 11% by Megane, an 8-year-old female, but was used 0.4% by Yoru, a 10-year-old female. CL was used around 4% by Goishi, but was seldom used by other macaques. BG was rarely used, some individuals did not use BG. DR was used more than BG, but it was seldom used. DR was employed more than 4% by Kihada, an 8-year-old male, which used DR most frequently. SC was rarely used by any of the individuals, except Megane. BI was not used frequently by any individuals except Goishi, a female 15 years old. Goishi used BI nearly 10%. SU was not used.

Females employed QW and BG more than males (see average values in Table 1-B). Males employed QR, LP and DR more than females. Males used QC slightly more than females. Females used CL and BI slightly more than males, but these average values were affected by PULs of only one female, Goishi.

Discussion

1. Locomotion of adult Japanese macaques

All Japanese macaques used QW most frequently both on the ground and in the trees. On the ground, QR was used the next most frequently, the sum of PULs of QW and QR was more than 90%. In the trees, the second locomotor behavior differed among individuals. But the sum of PULs of QW and QR was more than 75%. These results suggest that the Japanese macaque is a typical quadruped in both terrestrial and arboreal settings. In the trees, adult Japanese macaques may sometimes use LP, DR and QC but seldom use BG, CL, SC and SU. QC is the quadrupedal behavior on substrata. Almost all LP and DR were employed by adults on the substrata, but neither under supports nor the side of supports; i.e. taking off and landing posture were quadrupedal standing. These results also indicate that the Japanese macaque is a quadruped.

2. Age of maturation of locomotion

The number of individuals in this study is small, so an accurate estimate of age of maturation cannot be given. More individuals should be observed, but I would like to present a hypothesis. On the ground, the proportions of locomotor behavior in all individuals were not very different, except BI values. So, terrestrial locomotion may continue

Table 2. Percentage of distances moved during each locomotor behavior in adult Japanese macaques and adult male long-tailed macaques Data of long-tailed macaques from Cant (1988). These values are calculated for comparison.

Species	Sex	Age	Percentage of Use of Each Locomotion Type					
			Qadrupedal	Leaping	Drop	Vertical	Bipedal	Suspensory
<i>M. fuscata</i>	m	8yrs≤	84.0	9.9	2.4	3.5	0.2	0
	f	8yrs≤	89.5	2.8	1.2	4.3	2.2	0
	m	9yrs	85.7	10.1	1.6	2.5	0.2	0
	f	10yrs≤	92.9	1.4	0.7	2.4	2.6	0
<i>M. fascicularis</i>	m	adult	84.1	7.9	0.4	7.5	0.1	0

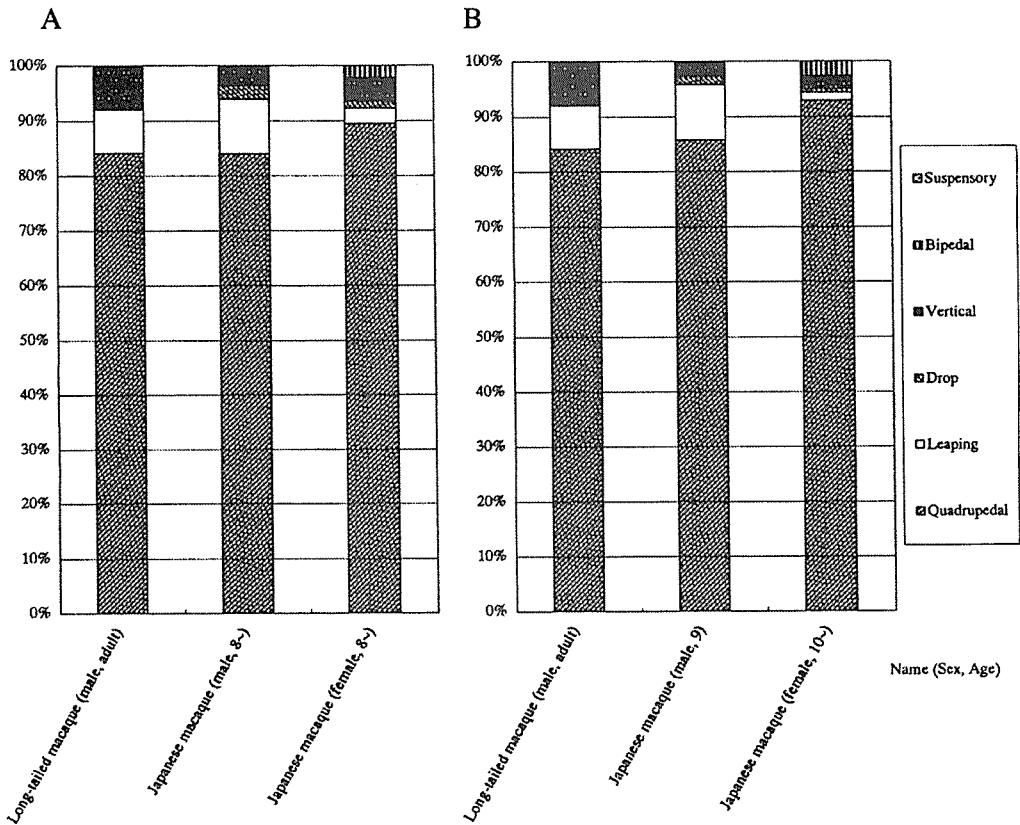


Fig. 2. A) Proportions of use of different locomotor modes of two macaques (arboreal, in the case of Japanese macaques 8 years old or above). **B)** Proportions of use of different locomotor modes of two macaques (arboreal, in the case of Japanese macaques 9 years old or above).

to mature until at least eight years of age.

In the trees, proportions in locomotor behavior of all female individuals 10 years old or above seem to have similar patterns except BI. So, female arboreal locomotion may have continued to mature until ten years of age. The proportions in males were varied, so it is likely that male locomotion may still be somewhat immature at 9 years of age. In Hamada's diagrams (1994, pp. 64-65), in many morphologies related to locomotion, the maturation of males seems to occur later than that of females. This suggests that locomotor maturation in males occurs later than that of females. It is also likely that locomotion of males differs from that of females. To get a more reliable estimate, further quantitative data is needed.

3. Comparison with long-tailed macaques

PULs of both species are shown in Table 2, Fig. 2-A (Japanese macaques ≥ 8 years of age) and Fig. 2-B (Japanese macaques ≥ 9 years of age). General proportions of both species were similar to one another. Both species used quadrupedal moving most frequently (more than 80%), which indicates that the genus *Macaca* is a quadruped.

The difference among male long-tailed macaques and male and female Japanese macaques is as follows. Leaping and vertical moving were used frequently by the long-tailed macaque. Male Japanese macaques used leaping frequently, but vertical moving less frequently than the long-tailed macaque. Female Japanese macaques used leaping and vertical moving less than long-tailed macaques. Male Japanese macaques used dropping more than long-tailed macaques. Bipedal movement was used by only one female Japanese macaque, and thus bipedal movement is not a characteristic arboreal locomotor mode in female Japanese macaques. Moreover, this locomotion was mostly composed of scooting and squatting walking. Since it is possible that Cant's definition of bipedalism did not include such locomotor modes, the comparison of bipedal movement may be misleading.

Japanese macaques and long-tailed macaques are typical quadrupeds. But male long-tailed macaques differ from male and female Japanese macaques in other locomotor behaviors. Among the three groups, quadrupedalism was practiced most frequently by female Japanese macaques, while frequency of quadrupedalism in male Japanese macaques is similar to that in male long-tailed macaques. It may be possible that the similarity between males of the two species and individuality of female Japanese macaques is related to sex differences.

However, male Japanese macaques used leaping and dropping more and vertical moving less than long-tailed macaques. These differences are discussed later.

4. Relation between leaping and body weight

In these three groups, the body weight of male Japanese macaques is the greatest and that of male long-tailed macaques is the least. If body weight affects frequency of leaping, it would not be expected that out of the three groups, male Japanese macaques would use it most frequently. This result is similar to that of Gebo *et al.* (1995). However, it is expected that frequency of leaping in female Japanese macaques is less than in male long-

tailed macaques. The male Japanese macaques analyzed here might be a little too young to be regarded as adults, and did not exhibit adult locomotor pattern. But they were apparently larger than females analyzed here in trunk length and trunk breadth, so the body weight of males was greater than that of females.

In male macaques of both species, it is indicated that PUL of leaping does not depend solely on body weight. Factors related to leaping are not only body weight, but also the extensors of hindlimbs for powerful take off, the joint structures for absorption of energy of impact and so on. Differences in these morphologies between the two species of macaques may affect the frequency of leaping.

I discussed only PUL of leaping so far, without considering the distance which the macaque leaped. The mean leaping distance of long-tailed macaques was 2.2 m (Cant 1988), and the median gap width where long-tailed macaque leapt was 1.5 m (Cannon *et al.* 1994). In contrast the mean leaping distances among Japanese macaques were 0.97 m and 1.03 m for males and females, respectively. The longest leap made by a male long-tailed macaque observed by Cannon *et al.* was more than 6m, but the longest leap made by an adult Japanese macaque that I have observed was about 2m for both sexes. According to these results, difference in body weight rather than frequency and PUL may affect differences in mean value and maximum value of leaping distance directly.

If the numbers of leaping bouts of the two species are the same, PUL would be larger in a species which has a longer leaping distance, than the other species which has a shorter leaping distance. If PULs of leaping of the two species were the same and their mean leaping distances were different, the numbers of their leaping bouts would differ from each other. Male Japanese macaques have a large PUL value and a shorter leaping distance than male long-tailed macaques, which is why Japanese macaques have more leaping bouts than long-tailed macaques. It is suggested that frequency, (how many times per hour an animal uses leaping), is not affected by body weight. But what affects the frequency of leaping (numbers of leaping bouts) cannot be solved here.

Usually it is expected that smaller animals use more leaping, larger animals use less leaping and more vertical moving. But PUL of vertical moving was not greater in the two sexes of Japanese macaque than in male long-tailed macaques (Table 2). Female Japanese macaques seldom used leaping. Thus, it is suggested that female Japanese macaques tend to use quadrupedal movement on horizontal or semi-horizontal supports instead of using vertical moving and leaping. Male Japanese macaques seldom used vertical moving, but used more leaping bouts in which distances leapt were short. Male long-tailed macaques used vertical moving and leaping rather frequently. Leaping was not common but distances covered were long. Male Japanese macaques may use short leaps many times to avoid vertical moving. Male long-tailed macaques may infrequently use long distance leaping and tend to use vertical moving more frequently than Japanese macaques. Long-tailed macaques may be more adapted to discontinuous arboreal settings than Japanese macaque.

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