Current Zoology

动 物 学 报

Volume 56 Number 2 Apr. 2010 www.currentzoology.org

Institute of Zoology, Chinese Academy of Sciences
China Zoological Society

Current Zoology

(Formerly Acta Zoologica Sinica)

Vol. 56 No. 2 Apr. 2010

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Cover: M. F. JAMAN et al. examined feeding behaviors of Japanese macaques in a forested enclosure. The macaques utilized a diverse range of plant species and spent 47% of their time feeding on plant foods, although they were provisioned with adequate amount of monkey chow to meet their basic nutritional requirements. Interestingly, the monkeys displayed this adaptive feeding behavior within only 16 months of their introduction into a forested enclosure for the first time. This study revealed great behavioral flexibility on the part of these monkeys to adjust to their new environment. See M. F. JAMAN et al., pp 198–208. Photo by M. F. JAMAN.

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Current Zoology Volume 56 Number 2 Apr. 2010

100-Top Journal in China

Current Zoology

ADDRESS OF EDITORIAL OFFICE Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

SUPERVISED by Chinese Academy of Sciences

PUBLISHED by Editorial Office, CURRENT ZOOLOGY. Tel.: +86 10 64807091; email: zool@ioz.ac.cn

PRINTED by Kexin Printing House

ISSN 1674-5507

CN 11-5794/Q

国内邮发代号: 2-497

国外发行代号 (Code No.):Q59

定价：75.00 元

Current Zoology 56 (2): 190–197, 2010

Early development of peer dominance relationships in a captive group of Japanese macaques *Macaca fuscata*

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Abstract We studied early development of peer dominance relationships in a captive group of Japanese macaques *Macaca fuscata fuscata* at the Primate Research Institute of Kyoto University. This study aims to give detailed descriptions on characteristic patterns of maternal rank acquisition from infant to juvenile. Focal subjects were 22 young monkeys belonging to three cohorts born in 2002, 2003 and 2005. Data were collected with a total 2130 sessions of 30-minute continuous recording of focal subjects combined with all occurrence-sampling methods. The onset of aggressive behavior varied per cohort and was delayed in cohorts with fewer close-aged associates. More than 60% of dyadic combinations in agonistic interactions between peers were unidirectional throughout the study period. Although some bidirectional interactions could have involved unstable relationships between particular individuals, most of the bidirectional interactions included a few continuous series of alternating one-sided interactions. A linear order could be found among peers from the first appearance of aggressive behavior, and nearly 90% of those dyads were concordant with that of their mother's rank order. Young males were responsible for most of the dominance relations that would not be predicted based on their mother's rank. These results suggest that infant monkeys may recognize their own social status relative to their opponent's before onset of aggressive behavior and adjust themselves into the matrilineal rank system accordingly [*Current Zoology* 56 (2): 190–197, 2010].

Key words Aggressive behavior, Dominance relationship, Early development, Japanese macaque

It has been well documented that individuals of many group-living primates are organized in a dominance hierarchy; that is, the directions of aggression / submission are mostly fixed among group members (de Waal and Luttrell, 1985; Kawamura, 1958; Koyama, 1967). Such dominance order is usually linear and stable over fairly long period in most species (Angst, 1975; Kawai, 1958; Koyama, 1967; Missakian, 1972; Mori et al., 1989; Silk et al., 1981). Dominance order may serve as devices to manage conflict between individuals and reduce the risk of physical fighting (Aureli and de Waal, 2000; Preuschoft and van Schaik, 2000). Female Japanese macaques socially inherit their maternal dominance rank (Kawai, 1958; Kawamura, 1958; Koyama, 1967; Kutsukake 2000; Mori et al., 1989). Maternal rank inheritance has also been recognized in other species of Cercopithecines; e.g., rhesus monkeys (Berman, 1980, 2004; Missakian, 1972), long-tailed macaques (Angst, 1975), bonnet macaques (Silk et al., 1981), barbary macaques (Paul and Kuester, 1987), vervet monkeys (Horrocks and Hunte, 1983), and yellow baboons (Walters, 1980). However, early characteristic patterns of dominance relationships remained unclear, which may prevent us from understanding the mechanism of maternal rank inheritance.

The process of maternal rank inheritance has been the topic of studies in some species for the last three decades; for example, Japanese macaques (Chapais and Gauthier, 1993; Koyama, 1985; Nakamichi, 1996; Norikoshi, 1974), rhesus macaques (Berman, 1980), yellow baboons (Walters, 1980), and vervet monkeys (Horrocks and Hunte, 1983). Most studies reported that a clear dominance order among peers could be found in the early developmental stages. A linear rank order could be observed among peer Japanese macaques at the age of one year (Koyama, 1967). Chapais and Gauthier (1993) made a detailed study of a confined group of Japanese macaques at the University of Montreal, and reported that most dyads among peers (80%) were performed unidirectionally from the onset of agonistic interaction at six months of age, though there were some exceptional cases that could be caused by the support of adult

Received Oct. 11, 2009; accepted Jan. 28, 2009

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males. Berman (1980), who studied a larger group of semi-free ranging rhesus macaques, indicated that 77% of the dyadic interactions between peers conformed to the rank order of their mothers at 27 to 30 weeks of age; however, this number was lower (58%) during the earlier developmental stages (11 to 22 weeks of age). The dominance order among peer vervet monkeys may occur soon after the infants begin to interact agonistically with other individuals, usually before they reach 7 to 10 months of age (Horrock and Hunte, 1983). Thus, it was apparent that monkeys established dominance relationships at a very early developmental stage, when they first started to perform aggressive interactions.

However, few details of the appearance of interaction patterns and its variation according rank acquisition are available, perhaps because of the paucity of data due to infrequent agonistic interactions in the early stage of infant life. The degree of stability and linearity of interactions, and eventual inheritance of rank from their mothers and other related variables have yet to be ascertained. Previous studies focused mostly on female infants and paid less attention to male infants, perhaps because males are not at the core of the macaque social group (e.g., Kawamura, 1958; Kawai, 1958; Kutsukake, 2000; Mori et al., 1989; Takahata, 1991). It is known that male infants interact relatively freely with others away from their mothers (Nakamichi, 1989, 1996). If sexual differences in rank acquisition are present, it may offer important insights for a better understanding of the developmental process of maternal rank acquisition.

In order to understand the process of maternal rank inheritance we should first provide detailed descriptions on stability, linearity and its inheritability from early development of social relationships among infants. Here, we investigated the early development of peer dominance relationships within three cohorts, and analyzed its characteristic patterns. The objectives of this study are to describe 1) when and how the onset of agonistic interactions occurs within different cohorts, 2) how dominance relationships are settled by infant peers, 3) when and how the linearity among peers is established, 4) how maternal ranks relates with peer rank, and 5) sex differences during early development of dominance relationships.

1 Methods and Materials

1.1 Subjects

The study was carried out on a group of Japanese macaques in captivity at the Primate Research Institute (PRI), Kyoto University, introduced from Takahama, Fukui Prefecture, Japan, in 1970 and 1971. The monkeys were maintained in a rectangular, 960 m^2 open-air enclosure with sides measuring approximately 21, 30, 31, and 36 meters and surrounded by a 5 m-high concrete wall topped with an electric fence. Several sleeping huts, some climbing apparatus, a pool, and a shade tree were available. The monkeys were fed with monkey chow every morning (210 g per individual per day) and sweet potatoes two or three times a week (300 g per individual per week). Wheat, peanuts, and several kinds of fruits and vegetables were given occasionally. Water was available *ad libitum*.

All group members were born in the enclosure, and their matrilineal relationships were known. In October 2002, the group was composed of 52 monkeys, including 5 adult males (≥7 years of age), 3 sub-adult males (5 – 6 years of age), 4 juvenile males (1– 4 years of age), 6 infant males, 26 adult females (≥5 years of age), 1 sub-adult females (3.5 years of age), 4 juvenile females (1– 2 years of age) and 3 infant females. The focal subjects were born between May 13th and July 4th 2002 (Cohort I, six males and three females), between May 8th and August 2nd 2003 (Cohort II, four males and five females, of which one male died in June 2004), and between May 4th and June 14th 2005 (Cohort III, two males and three females).

The monkeys were reared with minimal artificial handling except for the periodic removal of some individuals. For colony management, most of the yearlings were removed every year in August or early October, and ordinarily only one male and two females among them were retained in the group. For observations, however, all yearlings of Cohort I remained in the group. In October 2004, three males of Cohort I were removed together with one male and two females of Cohort II. In 2004 nine infants were born, but two died soon after birth. Among the latter group, 5 were removed in August 2005 and only two male yearlings remained. As a consequence, monkeys of Cohort I and III had only a few one-year older juveniles (close-aged associates) for their social interactions, 3 and 2 respectively, whereas those of Cohort II had 9 close-aged associates. Apart from these periodic removals, as well as the temporary removal for medical treatment, and the natural death of individuals, the group was kept intact.

1.2 Data collection

Observations started in July 2002. During a 125-hour preliminary observation period, individual identification was carried out, as well as an assessment of the dominance hierarchy among group members. Data were col-

lected by 30-minute continuous recording of focal subjects, combined with all occurrence-sampling methods (Altmann, 1974). One observer using a pen and paper notebook collected data. Each focal subject was followed once or twice a week from a distance of 1–5 m. Focal subjects from each cohort were chosen randomly for each session, omitting any individual who had been previously sampled, in order to equalize number of sampling sessions among peers. The subject monkeys in Cohort I were observed for a total of 532 hours (1064 × 30-minute sessions) from September 2002 to January 2003 and from April 2003 to August 2004 (mean $\pm$ *SD*, 59.1 $\pm$ 0.69 hours/ individual). Those in Cohort II were observed for a total of 395 hours (790 × 30-minute sessions) from May 2003 to August 2004 (43.9 $\pm$ 6.29 hours/ individual) and those in Cohort III for a total of 138 hours (276 × 30-minute sessions) from October 2005 to February 2006 and from May to October 2006 (27.6 $\pm$ 0.55 hours/individual).

Additionally, aggressive interactions among other group members were also recorded during the course of observations whenever the interactants could be recognized. Since the enclosure was not very wide and the frequency of aggressive interactions was low, most of the evident interactions among group members were easily observed and could be accurately recorded. An additional 280 hours *ad libitum* observation was used to record interactions between adult females and other group members. The data obtained from these observations were also included in the analysis.

Aggression was defined as behavior displayed when one subject monkey acted toward another in order to cause physical injury or warn of immediate aggressive actions by facial and threat displays (Aureli and de Waal, 2000). We followed the behavioral categorization reported by Berman (1980), Chapais (1988) and Rizaldi and Watanabe (2008), which include various kinds of threats (staring, open-mouth threat, etc.) and attacks (lunging, chasing, slapping, grabbing, wrestling, biting, etc.). Submission was defined as behavior displayed when the recipient of aggression exhibited submissive indicators, such as grimacing, retreating, fleeing, and fear screaming.

1.3 Data analysis

Dominant and subordinate individuals were judged on the basis of the direction of submissive behavior, while the dominance rank order was deduced from the matrix of submissive interactions (Appleby, 1983; de Vries, 1995). Any aggressive interactions involving the intervention of a third party were excluded from the analysis of dominance. We counted absolute age of subject animals at the onset of submissive and aggressive behavior. The ages were compared within and between each cohort using a One-Way Analysis of Variance (ANOVA). One infant of Cohort II that died during the study was involved in only 12 submissive interactions, and these data were excluded from further analysis.

The submissive interactions performed within each peer dyad were arranged chronologically throughout the study period for each cohort. Those dyadic relationships were classified into two types: unidirectional and bidirectional dyads (Chapais and Gauthier, 1993). In unidirectional dyads, one individual consistently received submissive behavior from another during the entire study period, while bidirectional dyads contained relationships in which both individuals received submissive behavior alternately from one another, which indicate a change in their dominance relationship and/or an unstable relationship.

When unidirectional dyads involved more than four submissive interactions, the binomial probability (Sokal and Rohlf, 1995) can be significantly different from random occurrence ($P < 0.05$), as well as those involving more than six ($P < 0.01$) and more than nine ($P < 0.001$) interactions. For bidirectional dyads we used Runs test (Sokal and Rohlf, 1995) to examine whether the direction of submission was distributed significantly uniformly, or occurred in a random sequence. Whenever direction of submission has changed and continued to the next interactions with the same direction within a given dyad, we called those submissions uniformly distributed.

A *run* (*r*) is a sequence of submissive interactions. For instance, within a given dyad, supposed subject A submitted to B for a period of time, then A begun receiving submission thereafter. In such case we counted two *run*s as having occurred, as long as the direction of submission persisted till the end of study period. If submission again reversed, the number of *run*s would increase, one more *run* for each further reversal. The total number of submissions received by subject A (*n1*) and B (*n2*) and the number of *run*s (*r*) were compared to Runs test Table (Sokal and Rohlf, 1995) to check significant probability of submission patterns. If it was significantly uniform, it might indicate that a change of dominance rank occurred within the dyad and soon stabilized. Otherwise, we judged submission occurred in a random sequence and the dominance relationships were unstable.

To measure the linearity of dominance order among peer individuals, we calculated linearity indices using MatMan 1.1 (de Vries et al., 1993; de Vries, 1995) from all data sets for each cohort, although apparent rank changes between some peers could be detected during this period. Subsequently, we examined the dominance order in more detail for each month. The numbers of submissive interactions were not enough to delineate relationships among all subjects of each cohort, but the rank order among peer individuals could be deduced, with the exception of a few individuals who displayed no interactions. In this way, we counted circular triads that occurred among subjects of each cohort.

Subjects born to higher-ranking mothers (higher-born subject) were expected to be dominant over those born to lower-ranking mothers (lower-born subject); such cases were categorized as a pro-dyad and vice versa as a contra-dyad (Chapais and Gauthier, 1993). Pro- and contra-dyads were counted for each month from the submissive interactions observed among peers compared with the dominance order among their mothers. The ratio of pro- and contra-dyads was used for assessing how peer rank relationships were reflecting those among their mothers. All statistical tests were two-tailed unless otherwise specified. Data were expressed as means $\pm SD$.

2 Results

2.1 Age at the onset of aggressive behaviors

We observed 412, 212 and 123 submissive interactions among peers of Cohort I (n=36 dyads, mean 11.4$\pm$6.63 for each dyad), Cohort II (or 200 interactions when the infant dead in June 2004 was excluded, n=28 dyads, mean 7.14$\pm$3.38), and Cohort III (n=10 dyads, mean 12.3$\pm$4.64), respectively. Age of the focal subjects at the onset of aggressive behavior was significantly different per cohort (Fig. 1). Aggressive behavior first appeared at the mean ages of 12.8$\pm$2.61, 5.2$\pm$1.92 and 10.5$\pm$2.8 months in Cohorts I, II and III respectively (One-Way ANOVA, $F_{2, 20}$ = 27.356, n=23 individuals, P<0.001), while no difference was found in the appearance of first submissive behavior; at the mean ages of 4.4$\pm$0.97, 4.0$\pm$0.99 and 4.3 $\pm$0.95 months in Cohorts I, II and III respectively ($F_{2, 20}$ = 0.501, n=23, P=0.613). The order of births did not influence the onset of aggressive and submissive behavior within each cohort (Spearman's Rank Correlation Test, $r_s < 0.5$, $P > 0.05$ for all six tests within aggressive and submissive behavior of each cohort). All first submissive behavior was performed by infants to elder monkeys, while most of the first aggressive behavior was toward peer individuals.

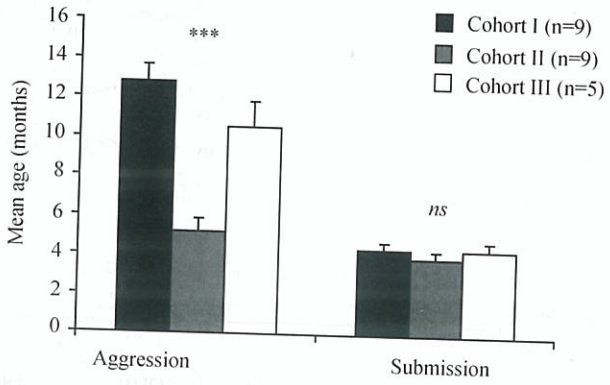

Fig. 1 Age of subject monkeys at the onset of aggressive and submissive interactions
Mean and SD are shown; One-way ANOVA; *** $P < 0.001$, *ns* = non-significant.

2.2 Stability of the dominance relationships

Most submissive interactions were consistent and conducted unidirectionally throughout the study period; 20 of 36 (56%) dyads in Cohort I, 17 of 28 (61%) dyads in Cohort II (the instances regarding the one infant male that died at 12 months of age were excluded), and 7 of 10 dyads in Cohort III (Fig. 2). This shows that nearly 60 percent of all dyadic interactions were performed unidirectionally in the earliest developmental stages, right from the time that first submissive behavior appeared among peers (10.3 $\pm$ 7.47, 6.6 $\pm$ 3.26, and 10.7 $\pm$ 2.50 interactions for each unidirectional dyad of Cohort I, II and III, respectively).

Bidirectional dyads involved several different patterns; for instance, 8 of 29 bidirectional dyads (27.5%) included only one submission reversal. Such dyadic patterns resembled unidirectional pattern (mean $\pm$ *SD*, 10.9 $\pm$ 4.6 interactions for each dyad). Among these, three were cases in which only the first interaction was the exception.

It was likely that, in many bidirectional dyadic interactions, submissive behavior occurred significantly uniformly, which was the case in 11 of the remaining 21 bidirectional interactions (8, 2 and 1 in Cohort I, II and III, respectively) (Runs Test, P<0.025, one-tailed). Nine of the remaining 10 dyads were also uniform but significance was not discerned, mostly due to few interactions. Only one dyad of *Tsuchi* and *Kazan* (males in Cohort I) showed frequent reversals with a random sequence in direction of submissive behavior during September 2003 to April 2004 (12 times).

Cohort I

	OKA	TOMO	TSUCHI	MIZU	KAZAN	Suigen	MURA	Shio	Jishin
OKA		5	20	24	16	7	27	8	7
TOMO			4/1	10/2	14/1	5	11	3	6
TSUCHI	-			13/5	17/8	2	6	8	1
MIZU	*	*ns*			18/1	7	20	4/2	15
KAZAN	-	*ns*	-			4/2	11/5	7/5	10/4
Suigen					-		13/3	4/6	8
MURA					*	*		10/2	5/5
Shio			-		*	*	*		5/5
Jishin					*ns*		*	*	

Cohort II

	Reiko	NATSU	OUJI	Otsu	KAGERO	Momo	Hime	Sarasa
Reiko		6/4	10/1	8/3	6/1	11	13	9
NATSU	*		6/1	3/2	4	6	10/1	8
OUJI	-	-		3/3	8	9	9	5
Otsu	*	-	-		3	2	3	3
KAGERO	-					7	11/1	5/3
Momo		-					-	9
Hime							-	
Sarasa								

Cohort III

	Mika	MIKI	Mina	KUMO	Ayu
Mika		11	21/3	10	7
MIKI			11	12	9
Mina	*			9/2	15
KUMO		-			11/2
Ayu			-		

Fig. 2 Matrix of submissive interactions among peers within each cohort

Numbers in the upper part of the diagonal line indicate the frequency of submissive interactions received by dominant (column) from subordinate individuals (row) during the entire study period. Integers indicate unidirectional interactions and fractions indicate bidirectional interactions; the numerator is the number of submissions received (columns) and the denominator is the number of submissions received (rows). Male subjects are shown in uppercase while females in lowercase. The degree of uniform in bidirectional dyads was shown in the lower part of the diagonal line; * $P <$ 0.025, *ns* = non-significant and - = insufficient data (Runs Test).

There were five cases in which the direction of submission changed shortly after the onset of aggressive behavior (less than one month), and subsequently stabilized, including the three interactions mentioned above. Out of these, three were cases in which initially lower-born older infants received submission from young higher-born infants (1 to 3 times), after which the direction changed. The differences in their ages were within 13 to 30 days. In the remaining two, the interaction patterns changed following the rank change of their mothers.

2.3 Linearity of the dominance relationships

The linearity index (h') for each cohort clearly indicated linear relationships among peer individuals, even though some rank changes among them occurred during the study periods; for Cohort I, h'= 0.85 in the period from May 2003 to January 2004 (P=0.0015), and 0.91 in the period from April to August 2004 (P= 0.0004); for Cohort II, h'=0.44 (P=0.2810) and 0.96 (P=0.0003) in each respective period, and for Cohort III, h' = 1.0 for the period from January to October 2006 (P =0.115). Cohort III included only five peers and so the linearity index was not statistically significant, but the number of unknown relationships was zero and linearity was obvious. In the earlier period, only a few interactions (23 between 14 peer combinations) in Cohort II were observed, which is why significant linearity could not be obtained.

After detailed assessments in each month, possible circular triads were found only once in each cohort for the entire month, and all of these circular triads were noticed during the course of rank changes of relevant individuals. The dominance order, then, became linear in the following months.

2.4 Inheritability of the dominance relationships

Most dyadic interactions between peers followed those between their mothers (pro-dyad): 89.5% in Cohort I, 87.8% in Cohort II and 94.4% in Cohort III (Fig. 3). No significant difference was found between cohorts (One-Way ANOVA, $F_{2,28} = 3.239$, n=31 months, $P > 0.05$). No significant correlation was found between occurrences of pro-dyads and age of the subjects (Spearman Rank Correlation Test, $r_s = -0.29$, 0.38 and -0.05, $P > 0.05$ for cohort I, II and III, respectively). Thus, higher-born infants were principally dominant over lower-born infants from the earliest period of their development.

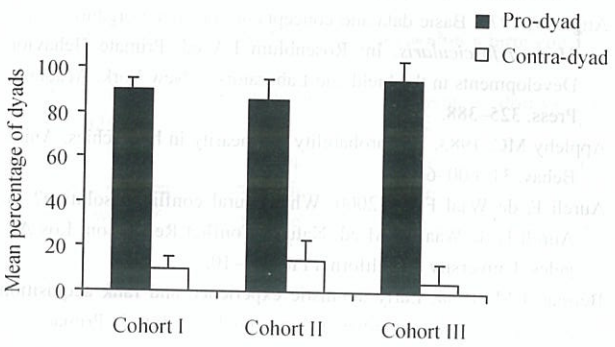

Fig. 3 Mean percentage of pro- and contra-dyads in each month (standard deviations are shown)
The data for Cohort I are for 14 months with 248 dyads, Cohort II for 9 months with 107 dyads, and Cohort III for 8 months with 54 dyads).

In the contra-dyads, *Kazan* (male in Cohort I) and *Reiko* (female in Cohort II) performed special roles; *Kazan* was involved in 11 dyads and *Reiko* in 6 dyads that formed 42% of contra-dyads in Cohort I (n=26) and 46% of those in Cohort II (n=13) respectively. They frequently approached and/or performed "head-flagging" toward the alpha or beta male as they requested support. The aggressive support by those high-ranked adult males was observed only when either *Kazan* or *Reiko* was hostile towards elder individuals.

2.5 Sexual differences during early development of the dominance relationships

It seemed that male infants often became dominant over female infants. Contra-dyad occurred significantly more often when male outranked female than vise versa (Chi-square for goodness of fit test, χ^2=16.667, df=1, P<0.001). From a total of 42 reversed relationships (contra-dyad) observed, 22 (52%) were cases in which lower-born males became dominant over higher-born females (11 dyads). In contrast, the instances that lower-born females became dominant over higher-born males were observed only twice (5%) within two dyads.

3 Discussion

Age of focal subjects at the onset of aggressive behavior varied between cohorts but did not differ for submissive behavior. This could be an effect of the number of close-aged associates available in the group before onset of aggressive behavior. A greater number of close-aged associates available for infants of Cohort II may have accelerated the earlier onset of aggressive behavior; they may have competed more often for the same interests compared to the other two cohorts (Koyama, 1985). This may not be applicable for submissive behavior, since ordinarily submission is displayed as a response to aggression of elder group members during the earliest developmental stages (Chapais and Gauthier, 1993; Berman, 1980).

It is noteworthy that about 90% of all dyadic interactions were performed in the same direction as those of the mothers. Thus, infants, may be aware of the relationships between their mothers as early as when they start to perform aggressive behavior, and may adjust their behavior according to the perceived social status of their opponents (Berman, 2004; Cheney and Seyfarth, 1999, 2004; Rizaldi and Watanabe, 2008; Seyfarth and Cheney, 2000). It was interesting that the onset of submissive and aggressive behavior occurred independently of their absolute age in each cohort. It may indicate that young monkeys could recognize the balance of power among group members even in the period before their onset of aggressive behavior, although it is difficult to ascertain the mechanism by which infants perceive their mothers' rank so early. Chapais and Gauthier (1993) suggested a fairly effective social learning process could function in the pre-initiative phase of rank acquisition. Such ability may be responsible for the variability in age of the onset of aggressive behavior between cohorts, and also simultaneous onsets within cohorts. Therefore, in infant monkeys trial and error may not be necessary for determining their own status among peers.

Although 40% of all observed dyads were bidirectional, many changes in the direction of submissive behavior might have occurred solely in accordance with changes among their mothers' status (Rizaldi and Watanabe, in prep). This was supported by the fact that many

bidirectional dyads were composed of some significantly uniform submission rather than occurring in a random sequence. It was not investigated systematically whether or not such a temporal reversal in the direction of submissive behavior among peers would decrease with increasing age in the subject group. However, those temporal reversals can still be found after they reach four years of age in some occasions (Rizaldi, personal observation). Thus, dominance relationships may involve some elasticity in their expression, according to, for instance, the temporal changes of an individual's physical condition.

Frequent random reversals in the direction of submissive behavior were found only in one dyad, between *Tsuchi* and *Kazan*. The unstable relationship between them continued for nine months, and a reversal occurred in most months (therefore, the circular triad was not counted though some individuals were ranked between them in several months), which might indicate an unfixed relationship between them. The status of *Tsuchi*'s mother was much higher (2^{nd}) than that of *Kazan*'s mother (8^{th}) among mothers of Cohort I. It was unknown why such a relationship could be found between these two individuals. *Kazan* often requested support from high-ranked males and his rank was higher than expected among his peers. This instance might indicate possible inter-individual variability in the process of stabilizing dominant relationships.

Male peers tended to acquire a higher rank than expected from their mothers, while this was rare among female peers. It was observed that the female infant, *Reiko*, also often requested the support of high-ranked males. She outranked a higher-born male infant for one month during the study period, but this soon reversed. Koyama (1985) and Nakamichi (1989, 1996) and Tartabini (1991) have reported that male infant Japanese macaques play more often with, and prefer to show closer proximity to same-aged or older males than female infants from the early developmental period onwards. In general, infant and juvenile males prefer rougher and more powerful play than females do, such as has been observed in savanna baboons (Owen, 1975; Pereira, 1989) and rhesus macaques (Symons, 1978). Male infants may be able to evaluate their power relative to others through rough play (Pellis and Pellis, 1997). It is also possible that female infants may more passively adjust themselves to their surrounding social conditions (Cheney and Seyfarth, 1999, 2004; Seyfarth and Cheney, 2000). Such differences in the attributes of males and females might contribute to differences in the characteristic of early rank acquisition.

Acknowledgements We are deeply indebted to the staff of the Human Modeling Research Center, Primate Research Institute, Kyoto University, Japan for their support and for giving us the opportunity to observe their monkeys during the course of the study. We thank Dr. Michael A. Huffman, Dr. Akio Mori, Dr. Chie Hashimoto, Dr. Hideki Sugiura, Dr. Hiroki Koda, and many other colleagues at the institute for their valuable comments and suggestions. We also wish to thank Dr. MA. Huffman and the Edanz Group Japan for help with polishing up the English. The first author was financially supported by JSPS (Japan Society for Promotion of Science) for manuscript preparation. This research complies with animal care regulations approved by The Committee of Research and Animal Welfare, PRI, Kyoto University, which meets the legal requirements of the Japanese Government.

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