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Diachronic Changes in the Dominance Relations of Adult Female Japanese Monkeys of the Arashiyama B Group

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INTRODUCTION

Most cercopithecoid species have a matrilineal social structure (Itani 1985). Males leave their natal social units and transfer into other social units, whereas females remain within the natal social units. Females are thus permanent residents and males are drifters.

Linear female rank orders are reported in many cercopithecoid species (*Macaca arctoides:* Estrada, Estrada, and Ervin 1977; *M. fascicularis:* Angst 1975; *M. radiata:* Koyama 1973; *M. sylvanus:* Taub 1980; *Cercopithecus aethiops;* Cheney, Lee, and Seyfarth 1981; *Papio cynocephalus:* Hausfater, Altmann, and Altmann 1982; *Presbytis entellus:* Hrdy and Hrdy 1976). However, there are few diachronic data on the rank order of female primates, except for two *Macaca* species, Japanese and rhesus monkeys.

Kawamura (1965) analyzed the rank order among female Japanese monkeys of the Minoo-B group, and pointed out two principles: one, the daughter is ranked after her mother, and two, between sisters, the younger is ranked higher than the older. The second principle is usually called "youngest ascendency". Koyama (1967, 1970) analyzed the female rank order of the Arashiyama groups, and confirmed Kawamura's hypotheses. Koyama also pointed out that a rank order existed among female kin groups, and that this had a great effect on the individual rank order. Sade (1967), Missakian (1972), and Chapais and Schulman (1980) found similar female rank orders in the Cayo Santiago rhesus monkeys.

In this report, the dominance relations among adult female Japanese monkeys of the Arashiyama B group are analyzed, and the diachronic changes in female rank order are discussed with particular reference to Kawamura's principles.

MATERIALS AND METHODS

The research was carried out on the Japanese monkeys *(Macaca fuscata fuscata)* of the Arashiyama B group, which had fissioned from the Arashiyama group in 1966 (Koyama 1970; Norikoshi and Koyama 1975). The monkeys have been provisioned and identified since 1954, and most maternal kin relations are known, except for a few male immigrants.

In the 1976 nonmating season from April to early October 1976, the group had about 210 monkeys, including eight adult males. The study subjects were 62 females who were 6.5 or more years old. Each female belonged to one of the ten kin groups descended from nine females who had been born before provisioning and a female born in 1955 but whose mother was unknown (table 1).

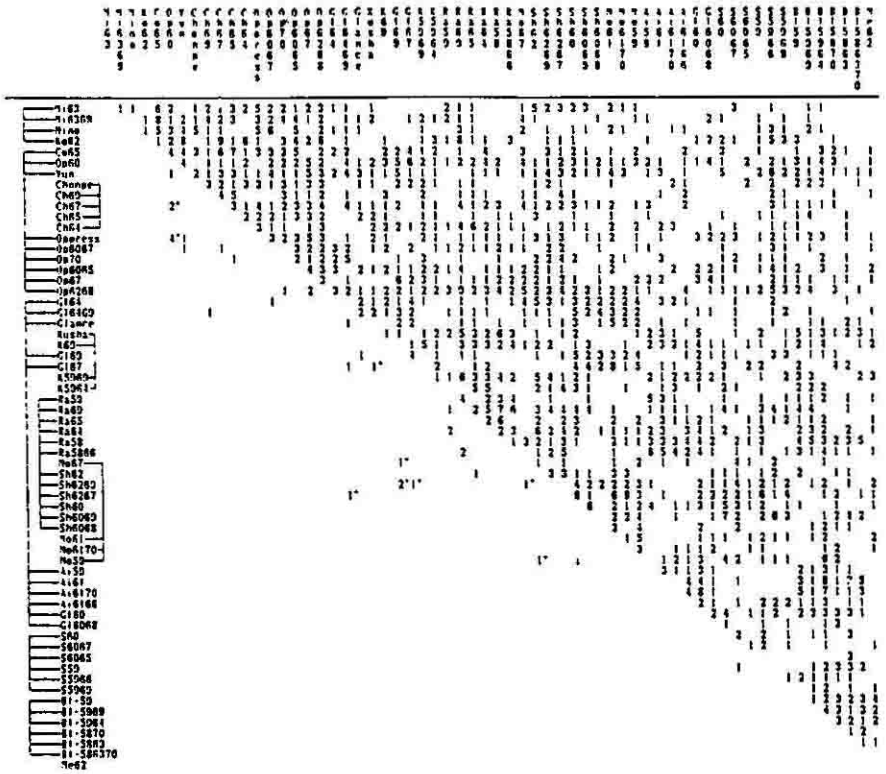
The park fed the monkeys five times a day, once every two hours. Each handful of wheat and maize was thrown on the ground at intervals of about 1.5–2 meters. The dominance relations between females were determined based on the approach-retreat episodes around the food. The dominance rank order was arranged based on these dyadic relations.

TABLE 1
FEMALE KIN GROUPS OF THE ARASHIYAMA B TROOP IN 1976

Kin Group	Rank Order in 1966	Number of Females ≥ 6.5 Years	Degrees of Consanguinity 1st	2d		3rd	4th	5th	Total
Kojiwa	1	4	2	2	(1)	1	1	—	6
Cooper	2	9	5	10	(7)	13	8	—	36
Chonpe	3	5	4	6	(6)	—	—	—	10
Kusha	4	4	1	3	(1)	2	—	—	6
Rakushi	5	12	5	13	(13)	18	26	4	66
Momo	6	4[a]	1	3	(3)	2	—	—	6
Ai	7	11	8	12	(10)	18	13	4	55
Shirayuki	8	6	4	3	(3)	4	4	—	15
Blanche	9	6	3	2	(2)	3	5	2	15
Me-62♀	10	1	—	—	–	—	—	—	—
Total		62	33	54	(46)	61	57	10	215

Note: Figures in parentheses represent sister dyads.
Degrees of consanguinity:
1st degree = mother-daughter
2d degree = sister-sister, grandmother-granddaughter
3rd degree = aunt-niece, great-grandmother-great-granddaughter
[a]One old female, Momo, was excluded, since she had become too infirm with age.

TABLE 2.
FEMALE RANK ORDER IN THE 1976 NON-MATING SEASON.



RESULTS

Female Rank Order

In the 1976 nonmating season, 2,433 approach-retreat episodes involving food were recorded for 1,168 dyads (61.8% of the possible dyads), which consisted of 161 kin and 1,007 nonkin dyads (table 2). Only one episode was recorded in 538 dyads, and two or more episodes in 630 dyads.

Of the 630 dyads in which multiple episodes occurred, one individual consistently supplanted the other in 611 dyads, one individual inconsistently

supplanted the other in 14 dyads (e.g., Op-60♀ supplanted Yun four times, and was supplanted by Yun once; table 2), and the episodes ended inconclusively in five dyads. Kin dyads rather than nonkin dyads accounted for most of the unstable dominance relations. That is, of the 19 inconsistent dyads, 13 were kin dyads (12% of the 111 kin dyads in which multiple episodes occurred) and six were nonkin dyads (1.2% of the 519 nonkin dyads). This difference is significant ($p < 0.001$, Fisher's exact probability test).

The 62 females can be arranged into an almost linear rank order (table 2). Only nine dyads showed exceptions to linear ranking, and were triadic relationships. These are marked with asterisks in table 2. Out of these nine dyads, eight dyads involved females who had risen in rank.

Dominance Relations between Mothers and Daughters

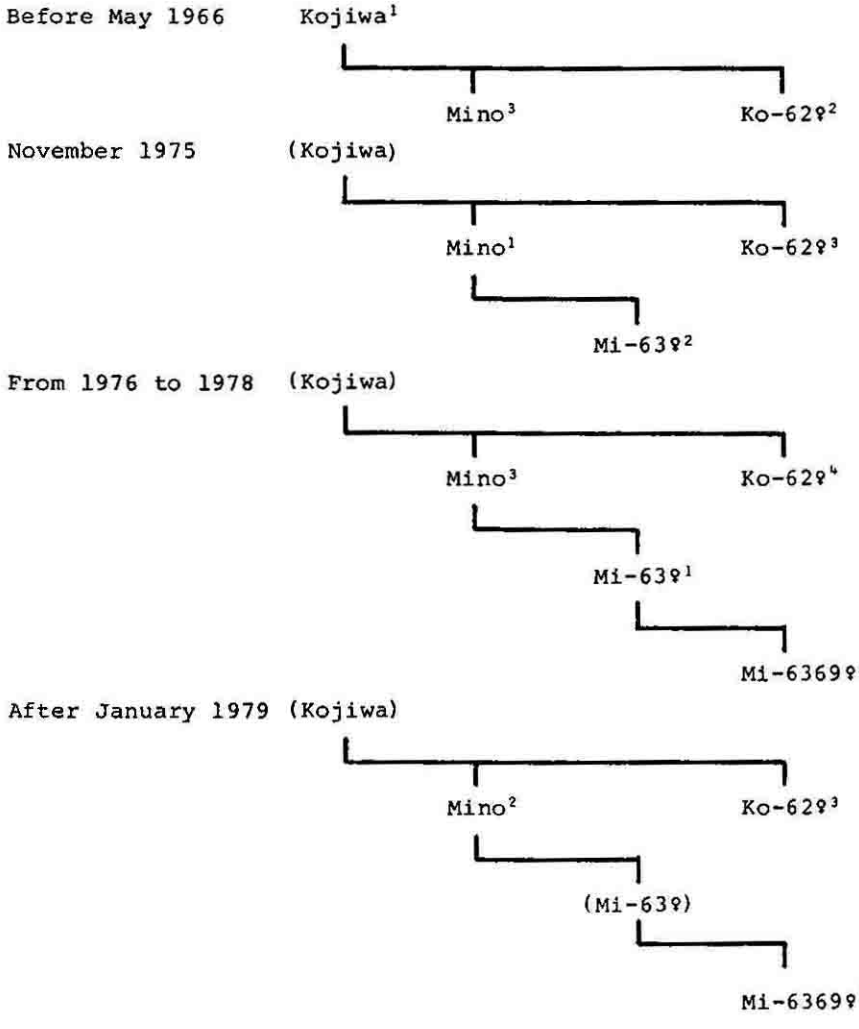
In general, mothers were dominant to their daughters. Of the 33 mother-daughter dyads, the mother was ranked higher than the daughter in 26 dyads, the daughter was ranked higher than the mother in three dyads, and the dominance relations were unknown in four dyads. In the case of one triadic relationship, the daughter, Op-60♀, was dominant to Yun and Ch-69♀, who were ranked higher than her mother, Oppress; thus, Op-60♀ was defined to be ranked higher than Oppress, although Oppress unilaterally supplanted Op-60♀ (table 2).

The senility of the mother may cause rank reversals. Momo, who was estimated to be 27 or more years old and was excluded from the study subjects, had trouble walking and was dominated by her daughter, Mo-67♀. Momo was inactive and observed to supplant only low-ranking females. In contrast, another old female, Kusha, who was estimated to be 24 or more years old but who was still in good health, dominated her daughter. Of the 11 mothers who were 20–22 years old, nine still dominated their daughters.

Nakamichi (1984) pointed out that in 1983 old females of the Arashiyama B group (23–29 years old) showed no marked decline in rank, although some of them were subordinate to their daughters. He reported that Oppress (29 years old) was subordinate to one of four daughters, and Glance (28 years old) was subordinate to three of five daughters. Perhaps physical decline results in some rank reversals between the mothers and daughters, after the mothers become 25 or more years old.

Although most dominance relations between mothers and daughters were stable, among the females of the first-ranking Kojiwa kin group, the first daughters superseded their mothers in rank and became alpha-females for three generations (fig. 1). First, in the 1965–66 mating season, Kojiwa was attacked by her first daughter, Mino, and became subordinate to Mino in May 1966 (Koyama 1970). Simultaneously, Mino superseded her younger

FIGURE 1.
THE CHANGES OF RANK ORDER AMONG THE FEMALES OF KOJIWA KIN GROUPS. NUMERALS SHOW THE RANKS.



sister, Ko-62♀ in rank. Kojiwa's age was unknown, and Mino was nine years old. In June 1966, the Arashiyama group split into Arashiyama A and B groups, and Mino became the alpha-female of the latter group.

Second, in the 1975–76 mating season, Mino (then 18 years old) was superseded in rank by her first daughter, Mi-63♀ (12 years old), without aggressive interactions between them, and Mi-63♀ became the alpha-

female. Third, in January 1979, Mi-63♀ (then 16 years old) was severely attacked and badly wounded by Mi-6369♀ and Mi-636974♀. Later, Mi-63♀ was found drowned in a pool in the park, and Mi-6369♀ became the alpha-female (Nakata, unpublished data; Iwatayama Natural Park 1984).

When Mino and Mi-63♀ were superseded in rank by their daughters, they were not very old ($\bar{x}$ = 17 years). All of these rank reversals took place during the mating season when tensions are heightened. Perhaps the rank reversals among the Kojiwa kin group females did not result from senility, but from social factors (e.g., competition for the alpha-female position; Gouzoules 1980).

Dominance Relations between Sisters

As Kawamura (1965) and Koyama (1967) pointed out, the younger sister tended to dominate the older, although the converse was not unusual. Of the 46 sister dyads, the younger ranked higher than the older in 32 dyads, and older ranked higher than the younger in 12 dyads. The dominance relations were unknown in the remaining two dyads.

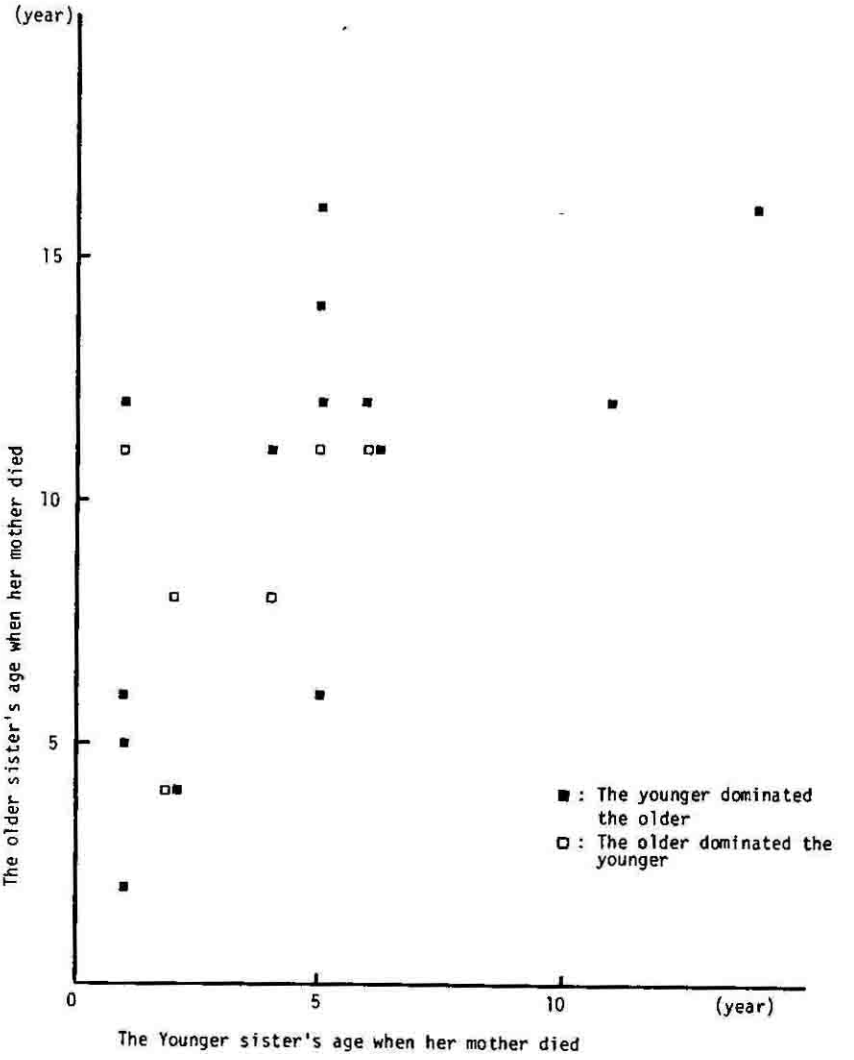
By contrast to that reported for *Papio cynocephalus* (Hausfater, Altmann, and Altmann 1982), age differences between sisters did not always affect their dominance relations. The mean age difference in the 32 dyads in which the younger dominated the older was 4.5 ± 2.9 years, and that of the 12 dyads in which the older dominated the younger was 5.5 ± 2.4 years. There is no significant difference between them (Mann-Whitney U test, $z = 1.30$, $p > 0.05$).

The rank reversal between the mother and daughter directly affected the dominance relations between the daughters. Mino, Mi-63♀, Op-60♀, and G1-64♀, who superseded their mothers in rank, also ranked higher than all of their younger sisters (for example, Mino > Ko-62♀).

In seven of the 46 sister dyads, the dominance relations were studied in 1966 (Koyama 1970). At that time the younger ranked higher than the older in six dyads, and the older ranked higher in one dyad. In the latter case (Ai-59♀ > Ai-61♀), their mother had died in 1963, and perhaps Ai-61♀ did not receive enough support from her mother to become dominant to Ai-59♀ (Koyama, personal communication). In 1976, Ai-59♀ continued to rank higher than Ai-61♀, and Glance had superseded Ai-59♀ and Ai-61♀ in rank. Glance had a long-term affinitive relation (peculiar-proximate relation or PPR) with a high-ranking male, Rh-59♂, and frequently stayed near him (Takahata 1982). Perhaps the proximity effect from Rh-59♂ affected their dominance relations.

The dominance relation between Ai-59♀ and Ai-61♀ suggests that the mother's death may affect the relation between the daughters. However, the older sister ranked higher in five of the 23 dyads in which the mothers were

FIGURE 2.
THE SISTERS' AGES WHEN THEIR MOTHERS DIED AND THEIR DOMINANT-SUBORDINATE RELATIONS.



still present, and in seven of the 21 dyads in which the mothers were absent. This difference is not significant ($x^2 = 0.74$). In the latter cases, there was no consistent correlation between the sisters' ages when their mothers died and their dominance relations (fig. 2).

Dominance Relations between Related Females Other than Mother-daughter and Sister Dyads

As Kawamura (1965) pointed out, the dominance relations between related females other than mother-daughter and sister dyads can be predicted from Kawamura's two principles; for example, a female should be ranked lower than her grandmother, mother's younger sisters, mother's younger sisters' daughters, and her younger sisters' daughters, and should be ranked higher than her mother's older sisters, mother's older sisters' daughters, and her older sisters' daughters.

Of the 136 dyads, the dominance relations corresponded with that expected from Kawamura's principles in 97 dyads, did not do so in 32 dyads, and were unknown in seven dyads. Of the 32 dyads that deviated from the expected relations, 28 cases resulted from the rank reversals between the mothers and daughters, or deviations from the principle of youngest ascendency.

For example, Mi-63♀, Op-60♀, and G1-64♀, who had superseded their mothers in rank, had four adult daughters. One daughter, G1-6469♀ was dominant to her grandmother, Glance, and to her mother's younger sisters, G1-67♀ and G1-69♀. Op-6065♀ and Op-6067♀ were subordinate to their grandmother, Oppress, but dominant to their mother's younger sisters in three dyads (e.g., Op-6067♀ > Op-70♀), and subordinate in only one dyad (Op-70♀ > Op-6065♀). The dominance relation was unknown in another grandmother-granddaughter dyad, Mino and Mi-6369♀.

Similarly, the females who ranked higher than their younger sisters also ranked higher than the younger sisters' daughters in all four dyads (e.g., Glance > Ai-6170♀). Their daughters also tended to be ranked higher than their mothers' younger sisters (in 12 of the 15 dyads; G1-69♀ > Ai-61♀), and their mothers' younger sisters' daughters (in six of the eight dyads; e.g., G1-69♀ > Ai-6166♀).

Rank Order among Female Kin Groups and Diachronic Changes from 1964 to 1976

Related females tended to occupy adjacent ranks, except in the Ai kin group (table 2). If the Ai kin group is divided into two groups, Glance (G1-64♀, G1-6469♀, Glance, G1-69♀, and G1-67♀) and Ai (Ai-59♀, Ai-61♀, Ai-6170♀, Ai-6166♀, G1-60♀, and G1-6068♀), an almost linear rank order existed among 11 female groups, in descending order of dominance, Kojiwa, Cooper, Chonpe, Glance, Kusha, Rakushi, Momo, Ai, Shirayuki, Blanche, and Me-62♀ groups. In 1976, there was no significant correlation between the ranks and the number of adult females who belonged to each group ($r = -0.375$, $p > 0.05$; the Cooper and Chonpe kin groups are

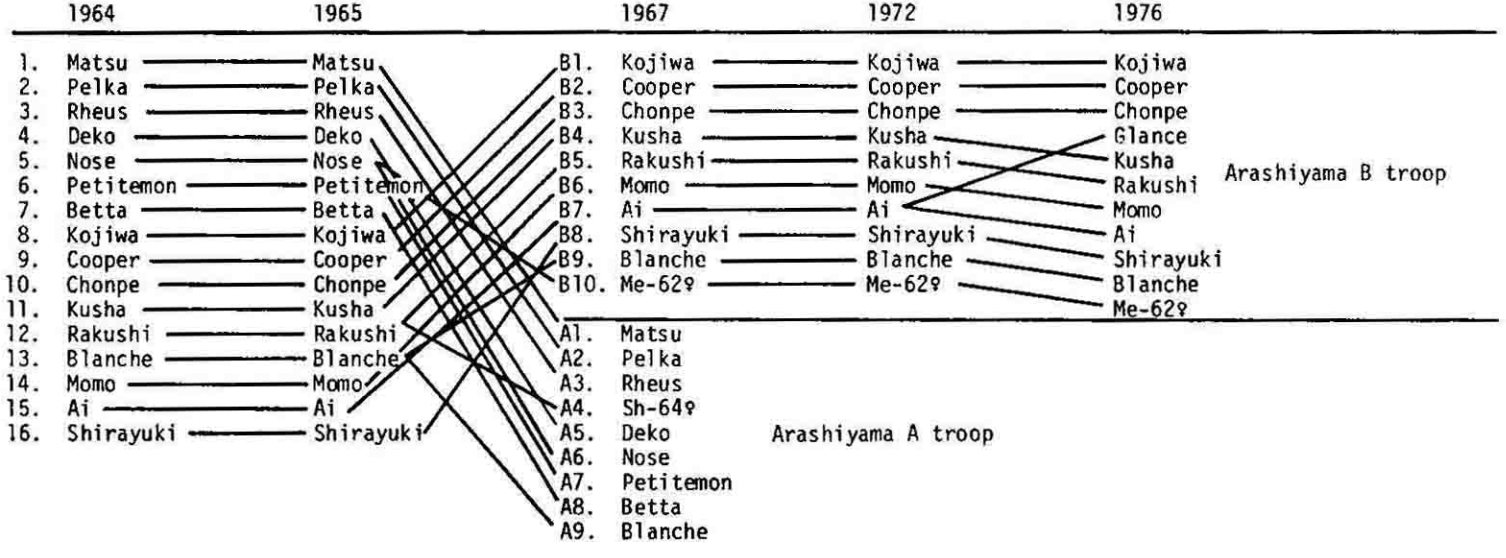
put into one group, based on Koyama's [1967, 1970] conclusion that they are related).

Figure 3 shows the diachronic changes in the dominance rank order among female kin groups from 1964 to 1976. In 1964, Koyama (1967) found there existed a linear rank order among 16 kin groups, in descending order of dominance, Matsu, Pelka, Rheus, Deko, Nose, Petitemon, Betta, Kojiwa, Cooper, Chonpe, Kusha, Rakushi, Blanche, Momo, Ai, and Shirayuki. However, in the 1965–66 mating season, Mino formed a consort relation with the first-ranking male, Zola, who was believed to have been related to the Matsu, Pelka, and Rheus kin groups (Koyama 1970). Mino kept a close relationship with Zola in the 1966 nonmating season, and superseded Kojiwa in rank. Simultaneously, the females who had been lower-ranking females than Mino began to associate with Mino and Zola, and gradually formed an independent group. They "challenged" the high-ranking females led by the second-ranking male, Ao, and became dominant. The first-ranking Matsu kin group fell to ninth-ranking, and the eighth-ranking Kojiwa kin group rose to the first-ranking. Eventually, a troop fission took place in June 1966 (fig. 3).

In the Arashiyama B group, the dominance rank order among kin groups has been stable from 1966 to 1976, except for the rise of the Glance group females who superseded the females of the Kusha, Rakushi, and Momo kin groups. In 66 of the 966 unrelated dyads in which approach-retreat episodes were observed in 1976, the dominance relations did not correspond with those expected from the dominance rank order of 1966. Of these dyads, the Glance group accounted for 63 dyads, and Mo-67♀ and Mo-59♀ for three dyads. In a few dyads, the females of the Kusha, Rakushi, and Momo kin groups still dominated these "upwardly mobile females", forming triadic relationships. For example, G1-6469♀ dominated Sh-62♀ who dominated Sh-6269♀, and Sh-6269♀ dominated G1-6469♀ (table 2).

The rise of the Glance group may have resulted from the proximity effect of Rh-59♂. In the 1976 nonmating season, all females of the Glance group stayed near Rh-59♂, and followed him with high frequency. By contrast, the Ai group females, including Glance's first daughter and granddaughter, G1-60♀ and G1-6068♀, did not have any relation with Rh-59♂, and their ranks did not change at all. Interestingly, few affiliative interactions occurred between the Glance group and G1-60♀ and G1-6068♀. The rank differences and the relationships with adult males had separated them (G1-60♀ and G1-6068♀ had affinitive relations with fifth-ranking K-63♂; Takahata 1982). However, most affinitive relations with adult males had few influences on the basic rank order among females, and the rise of the Glance group might be an exceptional case.

FIGURE 3.
THE DIACHRONIC CHANGES OF THE DOMINANCE RANK ORDER AMONG FEMALE KIN-GROUPS IN THE ARASHIYAMA TROOPS FROM 1964 TO 1976.



The rise of the Glance group may have been a precipitant factor in the second troop fission in February 1978. In November 1977, the park set up a new feeding site about 100 meters west from the original one, and the females of the Kusha, Rakushi, and Ai groups, who had been superseded in rank by the Glance group, began to use only this site. Eventually 11 members of the Kusha kin group and two unrelated males left the troop, forming Arashiyama C troop (Takahata 1982).

Female Rank Order and Reproductive Success

There was no consistent correlation between female rank order and reproductive success in Arashiyama. Koyama (unpublished data) found that between 1954 and 1983 the average birth rate per year of the high-ranking females was 0.63, that of the mid-ranking females was 0.63, and that of the low-ranking females was 0.59.

DISCUSSION

Although Watanabe (1978) pointed out that the rank order among Japanese monkey females might be unstable under natural conditions, stable linear rank orders have been reported among the females of many cercopithecoid species, irrespective of captive, provisioned, or natural conditions (e.g., Cheney, Lee, and Seyfarth 1981; Hausfater, Altmann, and Altmann 1982). In Yaku Island, where natural groups of Japanese monkeys have been observed since the 1970s, the rank order among female kin groups of M troop first recorded in 1981 (Furuichi 1983) had not changed by 1988 (Takahata, unpublished data).

In the Arashiyama B group, there were only a few exceptions to the linear nature of the rank order among 62 females, and most exceptions were related to the "upwardly mobile females", as Silk, Samuels, and Rodman (1981) found in a *M. radiata* group. This suggests that their ability for mutual individual recognition is high. Apparently, the monkeys know their social relationships well.

In general, the dominance relations among related females followed the two principles found by Kawamura (1965). Most mothers dominated their adult daughters, as Kawai (1965), Koyama (1967), Missakian (1972), and Chapais (1986) pointed out. The present study suggests that the rank reversal between the mother and daughter may take place after the mother becomes 25 or more years old. It is noteworthy that among the females of the first-ranking Kojiwa kin group, the rank reversals between mothers and daughters occurred in three successive generations. Social factors rather than physical ones may have precipitated these rank reversals; for example,

the mother and daughter may have been competing for the alpha-female status, as Gouzoules (1980) reported in the Arashiyama West group.

As Kawamura (1965), Koyama (1967), Missakian (1972), Fujii (1983), and Chapais (1986) reported, younger sisters tended to dominante the older, although the reverse was not unusual. The deviations from the "principle of youngest ascendency" may be caused by many social factors; for example, the rank reversal between the mother and older sister, the mother's death when the younger sister is still very young, or the proximity effect from a high-ranking male with whom the older sister has a persistent affinitive relation.

The dominance relations between related females other than mother-daughter and sister dyads tended to correspond to those expected from Kawamura's two principles. Most cases that deviated from the expected relations may have resulted from the rank reversals between the mother and daughter, or deviation from the principle of youngest ascendency. In other words, the deviations in the mother-daughter and sister dyads inevitably cause other deviations in the grandmother-granddaughter dyads or the dyads in the third or more degrees of consanguinity, because the daughter is ranked after her mother, and this continues to hold true in subsequent generations.

In the Arashiyama B group, the dominance rank order between female kin groups changed very little between 1966 and 1976. Thus, the dominance relations between unrelated females were very conservative. This supports the idea that maternal rank directly influences overall dominance hierarchy, and may correspond to the so-called "nepotistic" female dominance system, as Datta (1983), Lee (1983), de Waal and Luttrell (1985), and Chapais (1986) found in rhesus *(M. mulatta)* and vervet monkey *(C. aethiops)* troops. In Arashiyama, the changes in the rank order among female kin groups may have been a precipitant factor in both the first and second group fissions, which happened in 1966 and 1978. Disorder in the rank order may make it difficult for females to coexist.

Although Drickamer (1974) and Dunbar and Dunbar (1977) reported a correlation between female rank order and reproductive success, there was no consistent correlation reported in vervets (Cheney, Lee, and Seyfarth 1981) and Arashiyama troops (Takahata 1980; Gouzoules, Gouzoules, and Fedigan 1982). The primary function of female rank order may not be competition for reproductive success, but rather to facilitate coexistence within a group. In a matrilineal society, such as in a Japanese monkey group, the female rank order may originate in the adult daughter's inhibition against superseding her mother. The present study showed that most adult daughters do not challenge their mothers, and that the rank reversals observed among the Kojiwa kin group females were rather exceptional cases.

This inhibition may support the maintenance of the dominance rank order and make possible the coexistence of a large number of females in the narrow social space of a single group. At times, some females may compete for higher ranks, but the resulting disorder in dominance relations may make it difficult for them to coexist, and thereby cause a group fission.

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