Chapter 4
Primate Social Behavior: Understanding the Social Relationships of Japanese Macaques

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Abstract For many years, a variety of primate species have been studied in the wild or in captivity in various academic fields, such as biology, ecology, anthropology, psychology, and medical and veterinary science. Japanese primatologists began a thorough investigation of wild Japanese macaques after World War II, when research on other wild primate species was rarely conducted. Thus, Japanese macaques are among the primate species whose social organizations and life histories in the wild can be clearly described. This chapter provides an overview of the research on social relationships of Japanese macaques. Firstly, the dominance relationships and matrilineal blood relationships of adult females in a group, the relationships of adult males in a group, and the social events in which both females and males take part, are described. Secondly, the mother-young offspring relationships and social development of immature individuals are discussed. Lastly, the behavioral characteristics of old individuals are summarized.

Keywords Dominance relationships • Mother-offspring relationships • Social development • Kawamura's rules • Alpha male • Social grooming • Alliance • Mating • Group division • Malformed infant • Dead infant • Grandmother hypothesis • Aging

4.1 Introduction

The common ancestor of all primates first split into two branches: nonhuman primates and humans. Is this correct or not?

The answer is negative. The common ancestor of primates including humans appeared on the earth approximately 55 million years ago (Martin 1990). The common ancestor first split into two branches: prosimians and simians (Fig. 4.1). The common ancestor of the New World monkeys, now inhabiting Central and

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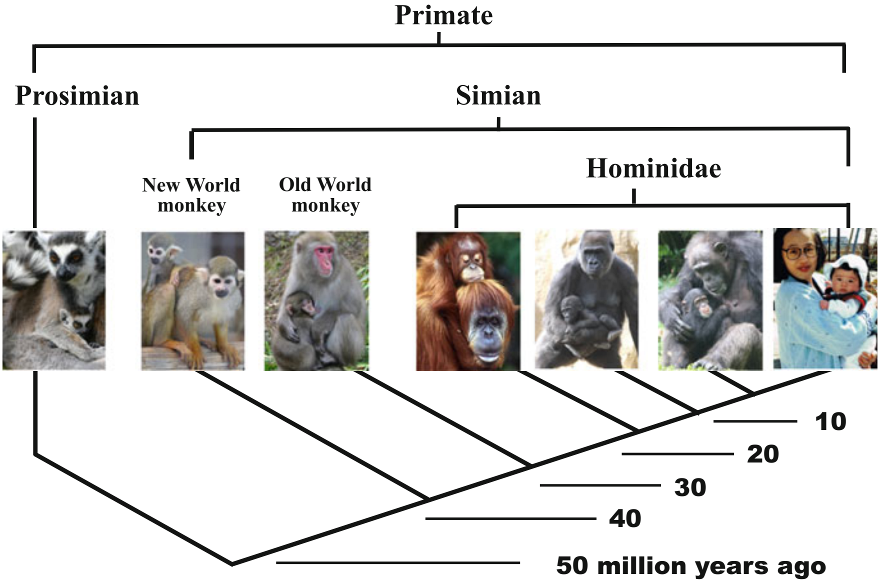


Fig. 4.1 A phylogenetic tree of primates including humans. Species are from *left* to *right*: ring-tailed lemur (*Lemur catta*), squirrel monkey (*Saimiri sciureus*), Japanese macaque (*Macaca fuscata*), orangutan (*Pongo pygmaeus*), gorilla (*Gorilla gorilla*), chimpanzee (*Pan troglodytes*), and human (*Homo sapiens*)

South America, diverged from the common ancestor of simians, and then the common ancestor of the Old World monkeys, now inhabiting Africa and Asia, diverged. The common ancestors of lesser apes and great apes, such as orangutans, gorillas, and chimpanzees, diverged from the common ancestor of the Old World monkeys. The common ancestor of chimpanzees and humans diverged about 7 million years ago, and they share 98 % of DNA (Dunbar and Barrett 2000).

At present, more than 300 nonhuman primate species live on the earth. The smallest species, rufous (or brown) mouse lemur (*Microcebus rufus*), weighs as little as less than 100 g, and the largest species, gorilla (*Gorilla gorilla*), can weigh as much as more than 150 kg (Dunbar and Barrett 2000; Rowe 1996). While some prosimian species and orangutans live a solitary life, most primates form social groups, varying in size and composition. Major forms of primate social groups are the following: a monogamous group (*pair-bond*) comprises one adult male and one adult female; a *polyandrous* group comprises one adult female and two or more adult males with whom she is mated; a *one-male* group comprises one adult male, several adult females, and their immature offspring; and a *multi-male, multi-female* group comprises two or more adult males, adult females, and their immature offspring (Boyd and Silk 2000).

While most primates inhabit the tropical or semi-tropical regions of Africa, Asia, Central America, and South America, Japanese macaques (*Macaca fuscata*) primarily inhabit the temperate regions. There are also some Japanese macaques at the southern limit of their range, and they are distributed in subtropical evergreen broad-leaved forests, such as in Yakushima Island, Kagoshima Prefecture. Other Japanese macaques are found in the northern Japan, where the temperature drops below −20 °C and the snow is several meters deep in the winter (Hanya 2010). It is because of these northern-dwelling macaques that Japanese macaques are widely referred to as ‘snow monkeys.’ The northern limit of Japanese macaque distribution, Shimokita Peninsula in Aomori Prefecture, is in fact the northern limit of all living nonhuman primate species.

Japanese macaques form multi-male, multi-female groups. The number of adult males in each group is much smaller than that of adult females, because most males leave their natal group upon maturity, while females usually remain in their natal group throughout their life. Most females experience their first birth at 5–7 years of age, give birth every 2–3 years thereafter, and die in the early 20s. Only a small number of females survive to be older than 25 years of age (Itoigawa et al. 1992).

For many years, a variety of primate species have been studied in the wild or in captivity in various academic fields, such as biology, ecology, anthropology, psychology, and medical and veterinary science. Japanese primatologists began a thorough investigation of wild Japanese macaques after World War II, when research on other wild primate species was rarely conducted. Thus, Japanese macaques are among the primate species whose social organizations and life histories in the wild can be clearly described. The descriptions depended greatly on the two methods, provisioning and individual identification, which Japanese primatologists used to observe wild groups of Japanese macaques for the first time.

When researchers began observing wild macaques in the early 1950s, the macaques were not easy to observe, because they were very shy, easily got frightened, and quickly fled, whenever they encountered people. Past hunting was responsible for their shyness and tendency to avoid humans (Yamagiwa 2010). To promote research (and tourism), then, researchers, with the help from local people, attempted to habituate monkeys. The attempt consisted in provisioning monkeys with artificial food; they received sweet potato, wheat, and soybeans in the foothills of a mountain in their home range. Monkeys started approaching the feeding site to eat the provisioned food and spending more time near the feeding site during the day (Fig. 4.2). Researchers spent long time with monkeys at close range after successful provisioning. As a result, they became able to identify each individual monkey by its facial and body characteristics, with no need for any artificial markings like hair dyeing. Individual monkeys were then named (not numbered). Using the methods of provisioning and individual identification by name, various aspects of the social lives of Japanese macaque groups, such as group organization, social relationships among group members, mother-infant relationships, and social development, were revealed (see Yamagiwa 2010 for the research history of Japanese macaques by Japanese primatologists). Not only researchers but also tourists visit artificial feeding sites referred to as ‘wild monkey parks’ and watch monkeys at close range, although the number of wild monkey parks and tourists visiting them have recently decreased.

Fig. 4.2 Japanese macaques of the Katsuyama free-ranging, provisioned group (Maniwa City, Okayama Prefecture) picking up and eating wheat scattered around the feeding area (*left*). All the individuals in the group have been identified since 1958, the beginning of provisioning. A mother (formal name, *Be71'79*) is 27 years old and the oldest animal in the group at the time of the photograph. *Be71'79* is pictured sitting with her 8- and 10-year-old daughters (formal names, *Be71'79'98* and *Be71'79'96*, respectively), both holding their newborn infants (*left* and *right*, respectively)

Provisioning improved the nutritional condition of Japanese macaques by decreasing travel time and distance. It also raised their birth rate and longevity, and lowered their mortality rate (Yamagiwa 2010). As a result, the usual group size of provisioned Japanese macaques increased to more than 100 individuals. By contrast, the usual group size of non-provisioned wild Japanese macaques is less than 100. On the face of this contrast, some researchers after the mid-1970s suspected that non-provisioned wild groups might behave differently than monkeys at artificial feeding sites do. These researchers began to habituate Japanese macaques without provisioning. With considerable efforts, they succeeded at some field sites. Studies of Japanese macaques in their natural habitats provided interesting and important data which were indispensable for understanding Japanese macaques from a socioecological perspective. Differences between provisioned and non-provisioned wild groups were found in demography, foraging, nomadic activities, and social behaviors. However, the observed differences should not be considered to be completely separate but to be different points along a continuum. For this reason, it is useful for promoting understanding of the whole picture of the social lives of Japanese macaques to investigate both free-ranging non-provisioned and provisioned groups.

In this chapter, I describe social relationships of Japanese macaques. Firstly, I focus on the dominance relationships and matrilineal blood relationships of adult females in a group, the relationships of adult males in a group, and the social events in which both females and males take part. Secondly, I discuss the mother-young offspring relationships and social development of immature individuals. Lastly, I survey the behavioral characteristics of old individuals.

4.2 Social Relationships Among Adult Females

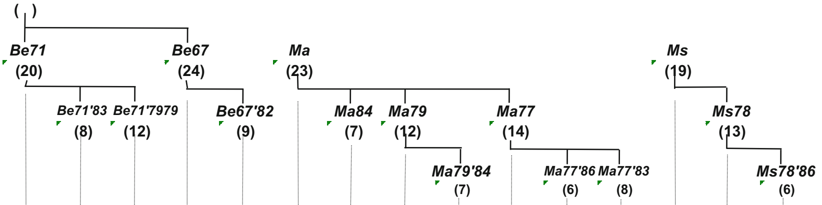
4.2.1 Dominance Relationships Among Adult Females

4.2.1.1 Kawamura's Rules

If you were to observe a social group of Japanese macaques for a while, you might witness the following episode: adult female A approaches adult female B who is just sitting on the ground, and B walks away from her seat. Which female do you think is dominant? In this case, female A is dominant to B. As in this example, if an individual successfully forces another individual to change its position just by approaching it, i.e., without displaying any obvious dominant behavior, such as gazing or opening the mouth, the approaching one is the dominant animal of the two. This type of social interaction is called 'supplanting.' If the approached one does not avoid the approaching one but shows a grimace at or turns its head away from the approaching one, the approaching one is the dominant one. Dominance relationships between two animals are also observed through unidirectional agonistic interactions in which an animal's aggressive behavior, e.g., threatening, is followed by another animal's subordinate behavior, e.g., bared-teeth grimace (Fig. 4.3). Dominance relationships can be observed in the food-dominance test for provisioned groups. For example, when a soybean is tossed between two animals, one animal takes and eats it, but the other remains sitting or moves away without trying to take the soybean. The soybean-taking animal is dominant.

Figure 4.4 shows the dominance matrix for 16 adult females, their blood-relationships through maternal lines, and ages in years when the data were recorded in a provisioned group at Katsuyama, Okayama Prefecture. For example, *Be71* is a female who was born to *Be* in 1971. *Be71'79* and *Be71'83* are *Be71*'s daughters born in 1979 and 1983, respectively, and thus are sisters 4 years apart in age. *Be71'79* is a niece of *Be67*, who is *Be71*'s older sister. The number within each cell indicates the total number of dominant behaviors that the individual in each row

Fig. 4.3 Facial expressions made by adult female Japanese macaques: open mouth threat face (*left*) and bared-teeth grimace (*right*)



	Be71	*Be71'83*	*Be71'79*	*Be67*	*Be67'82*	*Ma*	*Ma84*	*Ma79*	*Ma79'84*	*Ma77*	*Ma77'86*	*Ma77'83*	*Ms*	*Ms78*	*Ms78'86*
Be71		4	4	7	6	1	3	3	4	5	—	—	1	1	—
Be71'83	0		8	3	5	5	3	2	3	3	—	2	1	2	1
Be71'79	0	0		9	7	—	3	5	3	5	—	—	1	1	1
Be67	0	0	0		10	3	4	3	2	2	—	1	2	3	—
Be67'82	0	0	0	0		6	4	2	8	3	—	—	—	2	1
Ma	0	0	—	0	0		1	6	—	6	—	3	4	3	—
Ma84	0	0	0	0	0	0		3	5	8	1	7	3	1	2
Ma79	0	0	0	0	0	0	0		9	7	—	2	3	1	1
Ma79'84	0	0	0	0	0	—	0	0		1	3	3	2	2	1
Ma77	0	0	0	0	0	0	0	0	1		1	10	4	1	1
Ma77'86	—	—	—	—	—	—	0	—	0	0		2	—	—	1
Ma77'83	—	0	—	0	—	0	0	0	0	0	0		3	2	4
Ms	0	0	0	0	—	0	0	0	0	0	—	0		6	3
Ms78	0	0	0	0	0	0	0	0	0	0	—	0	0		2
Ms78'86	—	0	0	—	0	—	0	0	0	0	0	0	0	0	

Fig. 4.4 Dominant-subordinate matrix for 16 adult female Japanese macaques of three kin groups in the Katsuyama group and their blood-relationships traced through maternal lines. Rows and columns represent winners and losers of agonistic interactions, respectively. The *number* in *parentheses* indicates the age of each individual in years. The *number* in a cell indicates the observed number of dominant behaviors in each dyad, and the *dashes* indicate that no dominant-subordinate interactions are recorded. The *gray* areas indicate the results of agonistic conflicts between related females. For example, *Be71* (20 years old) was recorded to be dominant to her daughter *Be71'83* (8 years old) 4 times, but *Be71'83* was never recorded to be dominant to *Be71*. No dominant-subordinate interactions were recorded between *Be71* and the unrelated female *Ma77'86* (6 years old)

displayed toward the individual in each column. These behaviors include supplanting, agonistic interactions, and food-taking behaviors in food dominance tests. For example, the first three numbers in the first row are 4, 4, and 7. This means that *Be71* was recorded to be dominant to *Be71'83* four times, to *Be71'79* four times, and to *Be67* seven times. The first three numbers in the first column are 0. These numbers indicate that *Be71* was never recorded to be subordinate to any of these three females.

Before proceeding, it may be helpful to use the dominance interactions in Fig. 4.4 to find some of the rules or characteristics that govern the dominance relationships among these females.

If you examine the dominance relationships between mothers and daughters, you may find that mothers are dominant to daughters in all of the 11 mother-daughter dyads. If you examine the sister-sister dyads, you can see that younger siblings are dominant to older siblings in all of the 6 dyads. In this figure, all numbers greater than or equal to 2 are above the diagonal line, while all the numbers in the corresponding cells below the diagonal line are 0. This indicates that in the most dyads for which multiple episodes are recorded, one animal is consistently dominant to the other animal. Moreover, all the females in the *Be* kin group are dominant to the females of the *Ma* and *Ms* kin groups, and all the females in the *Ma* kin group are dominant to the females of *Ms* kin group. You might then surmise that the females of one kin group are collectively ranked above or below the females of other kin groups. You might also presume that the dominance rank order of the 16 females is almost linear, as there are no circular dominance relationships (i.e., it is not the case that individual A is dominant to B, B is dominant to C, and C is dominant to A).

Early in the history of Japanese primatology, Kawamura (1958) investigated the dominance relationships among 11 adult and young adult females in a provisioned group of 29 Japanese macaques. On the basis of his observations, Kawamura described two characteristics of the dominance relationships among adult females: (1) females are ranked just below their mothers, and (2) sisters are ranked in reverse age order, which is called 'the youngest ascendancy.' These two rules are called 'Kawamura's rules.' Although he did not state other findings clearly, Kawamura's data showed that one female was consistently dominant to another, that dominance rank order was almost linear, and that all females in one kin group were ranked collectively.

Kawamura's rules have been confirmed not only in other groups of Japanese macaques (as in Fig. 4.4), but also in groups of other macaque species and baboons similar to Japanese macaques. These species form multi-male, multi-female groups. Females stay in their natal groups throughout their life, while males usually leave their natal groups upon maturity. Note that the phenomenon of youngest ascendancy among sisters is controversial, because it has been confirmed in free-ranging, provisioned groups and in captive groups of Japanese macaques, but not in wild groups of Japanese macaques. This implies that youngest ascendancy might be a by-product of provisioning (see Hill and Okayasu 1995 or Kutsukake 2000 for the discussion).

4.2.1.2 Dominance Rank and Alliances

Alliance plays a determining role in female's acquisition and maintenance of a rank. Alliance is manifested when a third individual supports one of the two individuals in an agonistic interaction. Mothers tend to support their younger offspring in agonistic interactions between daughters. With support from the mother, a younger sibling, even if immature, behaves in a dominant manner toward her older sister when her mother is nearby. However, it may be difficult for a younger sibling to behave dominantly toward an older sibling when her mother is not nearby. Therefore, the dominance ranks of younger siblings relative to older siblings depend greatly on the mother. In other words, the ranks of younger siblings are regarded as *dependent ranks*, i.e., ranks dependent on their mother's support. However, younger siblings usually become consistently dominant toward older siblings before reaching young adulthood, regardless of their mother's presence in the vicinity. This means that before attaining adulthood, younger siblings can gain a *basic rank* relative to their older siblings (Kawai 1958).

Because mothers support daughters when they have agonistic interactions with others, young daughters can first gain a dependent rank and then gain a basic rank before they become mature. Females are more likely to give agonistic aid to their close relatives than to distant relatives, and they more often aid relatives than they do non-relatives. Therefore, an immature sister often becomes dominant to younger siblings after their mother's death, because they no longer have support from their mother. Younger siblings can gain a rank just below their older sibling, due to support from the older sibling. In cases where sisters lose their mother before they become adults, they usually fail to inherit their mother's rank within their kin group, but often succeed in inheriting their mother's rank relative to unrelated females, due to agonistic aids from related females, such as aunts.

As described above, alliance is more likely to occur between closely related individuals than between distantly related individuals; and it is more likely to occur between related individuals than between unrelated individuals. As a result, alliances serve to stabilize the dominance hierarchy among females. This is true not only for Japanese macaques (Watanabe 1979) but also for other monkey species, such as macaques and baboons (Cheney 1977; Bernstein and Ehardt 1985). In fact, 10–40 % of aggressive interactions among members of these species are polyadic (Deag 1977; Walters 1980).

Screams uttered by subordinates and threat calls uttered by dominants play a major role in the recruitment of allies (Cheney 1977; de Waal 1977; Gouzoules and Gouzoules 1989). This means, for example, that a mother may act agonistically toward her older daughter in response to recruiting behaviors, such as screams, displayed by her younger daughter. Unlike macaques and baboons, ring-tailed lemurs (*Lemur catta*), the prosimian primates that first diverged from the common ancestor of primates (see Fig. 4.1), have stable, non-linear dominance hierarchies among adult females. Daughters do not rank immediately below their mothers, and an older sister is not necessarily subordinate to her younger sisters. This dominance structure is probably related to the rarity of alliance. The lack of alliance may be due to the fact that the submissive call by a ring-tailed lemur is too short for supporters to recognize what has happened to the vocalizer and determine its location (Nakamichi and Koyama 1997). In other words, it is difficult for ring-tailed lemurs to form alliance because they do not emit calls or screams to effectively recruit support from allies against opponents, even though allies might provide support anyway. As a result, ring-tailed lemurs do not have linear dominance hierarchies even in a group of less than 10 adult females.

On the other hand, Japanese macaques often emit submissive calls (or threat calls) repeatedly. Calls are not only directed toward their opponents but also used to recruit potential allies (usually closely related individuals) against opponents. The abilities to recruit support from allies and to attract appropriate attention to agonistic interactions must be indispensable for maintaining dominance relationships and making complex social groups stable.

4.2.1.3 Dominance Relationships and Group Size

Kawamura (1958) reported that his rules were based on the observations of a small group including 11 adult females. It has been confirmed that dominance relationships conform to Kawamura's rules in groups of up to 50 adult females (Koyama 1967, 1970). In a group of 62 adult females, Kawamura's rules still apply, but deviations from the rules are relatively common (Takahata 1991). In some groups of approximately 70 adult females, the dominance rank order is almost linear, and the dominance relationships of nearly all adult female dyads are consistent. However, the dominance relationships of a few kin dyads do not adhere to Kawamura's rules, and some females rank separately from other members of their kin groups (Fig. 4.5). Kawamura's rules apply less often in middle- or low-ranking kin groups than in high-ranking groups. No linear dominance rank order has been found in very large groups including more than 100 adult females. However, it may still exist in high-ranking kin groups (Nakamichi et al. 1995a; Nakamichi and Yamada 2010).

The reason that dominance relationships are more likely to deviate from Kawamura's rules as group size increases is closely related to the fact that each member of a group identifies other members by both its own social interactions with them and observation of the interactions among them. As a group becomes larger, it becomes more difficult (or maybe, even impossible) for a member of the group to

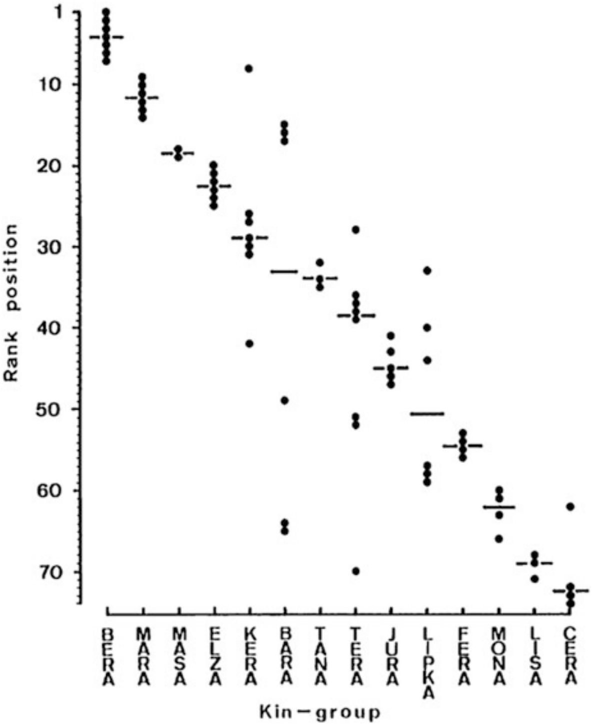


Fig. 4.5 Rank positions of females aged 6 or more years in the Katsuyama free-ranging, provisioned group of Japanese macaques. Each *dot* represents a female and her rank position among the 74 adult females. Each *horizontal bar* indicates the median rank position of a kin group. The kin groups are arranged in order of dominance rank, with the highest-ranking kin group listed on the *left* (From Nakamichi et al. 1995a, with permission of Wiley-Liss)

directly interact with most of the other members and to observe the interactions among them. Probably, by interacting with others and watching the interactions among them, an individual learns to identify others, understands its relationships with them, and understands the relationships among them. In a large group with more than 100 females, it is impossible for each group member to interact with all of the other group members and to learn the social relationships between them. The difficulty of interaction results in unstable dominance relationships in a large group (Nakamichi and Yamada 2010).

4.2.2 Social Grooming Among Adult Females

4.2.2.1 Functions of Grooming

In wild monkey parks, you can see monkeys grooming each other (i.e., social grooming, Fig. 4.6, left) and themselves (i.e., self-grooming, Fig. 4.6, right). Grooming is a common and frequently observed behavior of Japanese macaques and most other primate species.

Grooming behavior consists of manual or oral manipulation of the skin and fur (e.g., parting and stroking fur) and picking off things from the skin by hands or mouth. The functions of grooming in primates are presumed to be fur cleaning and the removal of ectoparasites. In fact, lice eggs comprise the majority (98.9 %) of what Japanese macaques eat during grooming (Tanaka and Takefushi 1993). Grooming has a social function besides its hygiene functions. Social grooming is presumed to be important for establishing, maintaining, and strengthening affiliative relationships with others. Grooming is also used to restore social relationships with others after agonistic interactions. Grooming in this context is considered

Fig. 4.6 Social grooming: a 13-year-old female grooms her 26-year-old mother (*left*). Self-grooming: a 26-year-old female grooms her left hind-leg (*right*)

to be useful for reducing the tension that has increased during agonistic interactions (Schino et al. 1988). In addition, grooming is considered to be a tradable commodity, and exchanged for reciprocal grooming or various kinds of social tolerance (Barrett et al. 1999). For example, in virtue of grooming a higher-ranking individual, a lower-ranking individual is allowed to remain near the higher-ranking individual even after grooming is completed. An individual may also be permitted access to a newborn infant by grooming its mother, and receive support from previously groomed individuals during agonistic interactions.

4.2.2.2 Distribution of Social Grooming Among Females

Grooming has various social functions. Generally, most females have grooming interactions with a relatively small subset of available females. Even in a large group with 50 or more adult females, the number of grooming partners is around 10 on average, and most females tend to devote more than 50 % of their grooming effort to a particular female grooming partner (Nakamichi and Shizawa 2003). Therefore, investigating the frequency with which individuals groom one another, i.e., the distribution of social grooming among group members, is useful for understanding the social organization of a group and the social intelligence of macaques.

As in other macaque species and baboons, social grooming among adult female Japanese macaques is kin biased and mainly directed up the hierarchy. Although related female dyads account for less than 10 % of all possible dyads in a group of Japanese macaques, about 50–70 % of grooming bouts among adult females occur among relatives; these results hold no matter what group they are in and what year grooming data is collected in (Ando 1982; Koyama 1991; Nakamichi and Shizawa 2003). This means that grooming tends to be kin biased at the group level but not at the individual level. It is not the case that all adult females groom related females more often than they do unrelated ones.

Analysis of grooming at the individual level reveals patterns that may be hidden in analysis at the group level. Most kin groups include at least one female who grooms unrelated females more often than she does related females. A similar pattern can be observed for the relationship between grooming and dominance. At the group level, approximately 70 % of grooming between unrelated females is directed up the hierarchy (Ando 1982; Koyama 1991). However, when grooming is analyzed at the dyad level, grooming is either directed down the hierarchy or well-balanced in 75 % of unrelated female dyads (Nakamichi and Shizawa 2003). These results indicate that while some individuals in a group show despotic behavioral tendencies, such as kin-biased grooming and grooming directed up the hierarchy, some other individuals show egalitarian behavioral tendencies, such as preferentially grooming unrelated or subordinate females. Egalitarian adult females may be important for increasing the integrity and cohesion of a large group because they may maintain or extend social networks with members of different kin groups.

4.2.2.3 Grooming Distribution and Cohesiveness Within Kin Groups

As described in Sect. 4.2.1, dominance relationships among adult females in a high-ranking kin group can be collectively ranked in accordance with Kawamura's rules. However, middle- and low-ranking kin groups include related dyads in which dominance relationships do not conform to Kawamura's rules and females tend to rank independently of other members of their kin groups (Nakamichi et al. 1995a). It is very important and interesting to determine why there are such differences in dominance relationship between high-ranking and lower-ranking kin groups. Here, I consider the relations between social grooming and dominance relationships within a kin group.

Figure 4.7a shows sociograms of grooming in the top ranking and middle-ranking kin groups in the Katsuyama group. Both of these kin groups include 8 adult females. In the top-ranking kin group, grooming interactions were observed in 21 of 28 possible dyads, while in the middle-ranking kin group, grooming interactions were observed in only 11 of 28 possible pairs. That is, the females of the top-ranking kin group distributed their grooming interactions among almost all available related females, while the females of the middle-ranking kin group tended to restrict their grooming interactions to a very small number of their relatives. The females of the top-ranking kin group maintained much stronger kin-group cohesiveness than those in the middle-ranking kin group do, by interacting with most of their relatives via social grooming. This strong cohesiveness among related females may account for why their collective ranking accords with the dominance relationships given by Kawamura's rules.

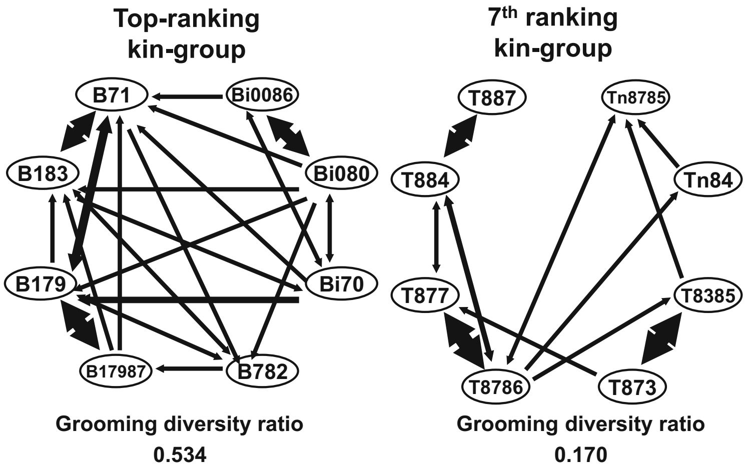


Fig. 4.7a Sociograms indicating the social grooming patterns among adult female relatives in the top-ranking kin group (*left*) and the middle-ranking kin group (*right*) of the Katsuyama group of Japanese macaques. The width of each *bar* corresponds to the number of observed grooming bouts. See Fig. 4.7b for grooming diversity ratio

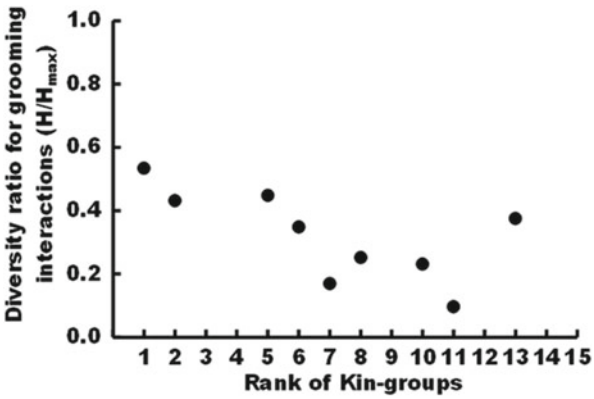


Fig. 4.7b The mean diversity ratio for grooming interactions among related females in kin groups consisting of 5 or more adult females. If a female had grooming interactions with all available related females equally, the ratio would be 1. If a female limited her grooming to a small subset of available related females, the ratio would approach 0 (Dunbar 1984). In comparison to the grooming interactions in lower-ranking kin groups, the grooming interactions of females in higher-ranking kin groups were more evenly spread among related females (From Nakamichi and Shizawa 2003, with permission of Springer)

4.2.2.4 Long-Term Grooming Relationships

The duration of grooming partnership is important for understanding macaque relationships, because females usually stay in their natal groups throughout their life and maintain affiliative relationships with some particular females, such as their relatives. Even though wild Japanese macaques have been observed for more than 50 years, data available for determining the duration of grooming partnership is unfortunately very limited. Nakamichi and Yamada (2007) compare the grooming interactions of 18 adult females in a free-ranging group of Japanese macaques with the data of the same females recorded 10 years earlier. These females engage in grooming interactions with some of the unrelated partners with whom they engaged in grooming interactions 10 years ago. This indicates that female Japanese macaques maintain grooming partnerships with the same females for at least 10 years. The 18 females also tend to engage in grooming interactions with some females related to their old grooming partners. The findings about kin-biased grooming tendencies, grooming directed up the hierarchy, and long-term grooming partnerships, indicate that female Japanese macaques are conservative with regard to grooming partner choice. On the other hand, they sometimes form grooming relationships with new partners, indicating that their social relationships can also be progressive and flexible.

4.2.3 *Special Food-Processing Behavior Performed by Some High- and Middle-Ranking Females*

Japanese macaques consume a wide variety of foods, such as leaves, buds, flowers, grass, and invertebrates, and do not have trouble processing most of these food items. Japanese macaques can easily consume most edible foods without using any difficult food-processing methods. They may process foods to make them more palatable (i.e., washing foods to remove the dirt). In the Katsuyama group, adult monkeys of both sexes, but not infants and juveniles, dig up grass roots in the winter and early spring when plants above the ground are scarce. Although most monkeys simply scrape the dirt from grass roots by their hands and eat them, some adult females pull 10–20 cm grass roots from the ground, carry them to the edge of the river, and wash them in the water before eating (Fig. 4.8, Nakamichi et al. 1998). The washing of sweet potatoes and wheat is often observed among Japanese macaques of a free-ranging, provisioned group on Koshima Island, Miyazaki Prefecture (Kawai 1965). Nakamichi et al. (1998) is the first report of Japanese macaque's washing the dirt from natural diets.

Females, when they wash grass roots, usually pull one root at a time and make a pile of several roots. They hold the pile of roots in one hand and carry it to a river, where they wash the roots by immersing them one at a time into the water. When macaques eat seeds from the ground, they normally pick up one seed at a time with one hand and eat it. It has rarely been observed that they pick up seeds with one hand, place them in the other hand, and subsequently consume several seeds at once. Some females carry several roots to the water at a time. This behavior may be considered to be very economical, and may reflect a relatively advanced cognitive ability that has not yet been examined in Japanese macaques (Nakamichi et al. 1998).

The grass root washing behavior is greatly related to dominance relationships among adult females. Less than 10 % of all adult females show root-washing

Fig. 4.8 Carrying and washing grass roots by adult females of the Katsuyama group of Japanese macaques. An adult female carrying several roots in one hand (*left*) and another adult female washing a root by rolling it along the surface of a flat rock at the edge of a river (from Nakamichi et al. 1998, with permission of Karger)

behavior. All the individuals that wash roots are high- or middle-ranking females; no adult males have been observed washing grass roots. It is very common for macaques to get food and eat it immediately. It is disadvantageous for low-ranking individuals to carry desirable foods because such behavior may increase the likelihood of an antagonistic response by high-ranking individuals (Nakamichi et al. 1998). Since digging up 10–20 cm grass roots from the ground can be a difficult task for immature Japanese macaques, they are unlikely to have the opportunity to wash grass roots. However, juveniles have sometimes been observed to watch their mothers washing and eating grass roots, and sometimes to pick up a half-eaten root to eat. It is probable that young adult females who have watched their mothers washing grass roots show similar behavior after they become mature enough to dig up grass roots without difficulty (Nakamichi and Yamada 2010). In fact, most females observed carrying and washing grass roots have at least one closely related female, e.g., a mother, who also carries and washes grass roots (Nakamichi et al. 1998). It is plausible that mothers transmit the ways of carrying and washing grass roots to their daughters but not to sons, in high- or middle-ranking kin groups. This tendency may be related to the fact that, as compared with juvenile males of the same age, older juvenile females spend more time with their mothers (Nakamichi 1989; Nakamichi and Yamada 2010).

4.3 Dominance Relationships Among Adult Males

4.3.1 Central and Peripheral Males

The number of adult males in a group of Japanese macaques is much smaller than the number of females, because males leave the group upon maturity. Thus, the ratio of adult males to adult females is less than 1. In a wild monkey park, there are usually a few adult males and much more adult females, with many juveniles and infants of both sexes. This is because only a limited number of adult males remain with adult females; whereas other adult males, most young adult, and older juvenile males tend to spend their time alone or with a few males. It has been recognized since the beginning of the research into wild Japanese macaques that their groups schematically have a concentric circle structure consisting of central and peripheral areas (Itani 1954). The central area includes a small number of adult males, many adult females, and their immature offspring. The peripheral area includes adult, young adult, and older juvenile males. Peripheral males, therefore, may have infrequent interaction with individuals in the central area.

Infant males remain in the central area with their mothers, but as they age, juvenile males tend to move from the central area to the peripheral area and spend much more time with similar-aged and/or young adult males (Nakamichi 1989). Most peripheral males eventually leave their natal group either by themselves or with other males. The move from the central to the peripheral area and eventual emigration of males contrast with the common tendency of females to stay in the central area throughout their lives. Males leave their natal group usually at 3–6 years of age and sometimes after reaching adulthood. Males of high-ranking kin groups tend to leave the groups when they are older and have a wider range of ages than those of less dominant kin groups (Itoigawa 1975; Kato 2001). Some adult males move farther than 20–30 km to enter a non-natal group (Hazama 1965). However, information regarding how males spend their time after leaving their natal group is still very limited. In free-ranging, provisioned groups, some males may remain in their natal group throughout their life.

4.3.2 Dominance Relationships Among Central Males

Adult males are easily identified in a group of Japanese macaques because they are a little larger than most adult females. It is easy to identify dominance relationships among males as well, by observing supplanting interactions between males: the supplanting male is dominant to the supplanted one. Moreover, unlike females, dominant males are likely to raise their tail while approaching subordinate males. This is a clear dominant behavior for male Japanese macaques (Fig. 4.9). Therefore, having the tail down may signal submissiveness. If a male that has been walking with his tail up lowers his tail just as he passes a sitting male, the walking male is subordinate to the sitting male.

In general, dominance relationships among central adult males are stable, and severe antagonism resulting in rank reversal has rarely been reported. A change in dominance rank among males usually occurs when a higher-ranking male suddenly disappears from the group, and, as a result, males who are subordinate to him rise in rank. This is also true for the change of the top-ranking (alpha) male. After the disappearance of an alpha male, it is very common for the former second-ranking (beta) male to become the new alpha male. On the other hand, when a male newly enters a group, it is common for him to be ranked at the bottom of the resident adult males (Itoigawa 1975, 1993). A newcomer male may acquire the top-ranking

Fig. 4.9 The second-ranking Japanese macaque male raises his tail (tail-up behavior) when approaching the third-ranking male, who keeps his face down

position if he enters a small group in which there are only a few males (Suzuki et al. 1998).

4.3.3 Change of Alpha Males

It is sometimes assumed that fully mature high-ranking males are physically superior to middle- or low-ranking males. This is sometimes but not always true. The following case illustrates how important psychological bonding with certain adult females is for maintaining the alpha male's dominance (Nakamichi et al. 1995b).

Rikinio was the 28-year-old alpha male of the Katsuyama free-ranging, provisioned group of Japanese macaques, showing the negative effects of aging, including a bent back, thin body, tooth loss, and relatively poor locomotor activity (Fig. 4.10). He remained the alpha male for 17 years, unusually long time, since 11 years of age. Two and a half months before his death, he suddenly began to drag his hind legs for an unknown reason. One month later, it became difficult for him to move with the group in the forest, and he stayed near the feeding site, not only during daytime but also at night. He interacted with group members only when the group was at the feeding site. However, he sometimes supplanted the beta male even after his locomotor ability decreased further, indicating that he was still dominant to the beta male (Fig. 4.10).

Nine days before his death, *Rikinio* was attacked (e.g., bitten) by the beta male four times. All the attacks occurred when *Rikinio* approached the beta male. *Rikinio* might have approached the beta male to confirm his dominance over the beta male (i.e., *Rikinio* tried to supplant the beta male). Instead of moving away from *Rikinio*, however, the beta male attacked him. In all the four attacks, the beta male made

Fig. 4.10 The first-ranking (alpha) male of the Katsuyama group of Japanese macaques, *Rikinio*, at 27 years of age. He lost three of four canine teeth, as well as some other teeth (*upper left*), and became thin and bent (*upper right*). When *Rikinio* approached the second-ranking (beta) male who was receiving grooming from an adult female (*lower left*), the second-ranking male quickly left, and then *Rikinio* received grooming from the same female (*lower right*)

aggressive sounds and bit *Rikinio*, and *Rikinio* screamed. The alpha female, *Pet* (her formal name *Be71*), rescued *Rikinio* at the fourth attack. She rushed in and acted aggressively toward the beta male. The beta male then stopped the attack and moved away. After this event, *Rikinio* sometimes approached the beta male and screamed at him when *Pet* was near *Rikinio*. *Pet* usually ran toward them and uttered aggressive sounds. Then *Rikinio*'s scream changed to aggressive sounds, and the beta male moved away from *Rikinio* and *Pet*. On the other hand, when he was not near *Pet*, he grimaced at the beta male with bared teeth (this is a typical submissive facial expression). These episodes indicate that *Rikinio* asked *Pet* to give him agonistic support, and he was able to remain dominant to the beta male only when he received her support.

Four days before his death, maggots had hatched in the bites on *Rikinio*'s back and his physical condition became much worse. When the beta male approached *Rikinio* who was sitting near *Pet*, *Rikinio* did not scream but grimaced at him, and *Pet* also grimaced him. Immediately after this event, the beta male mounted *Pet* three times. This change indicates that *Rikinio* was decisively outranked by the beta male.

Affiliation or psychological bonding with adult females and in particular with the alpha female allowed *Rikinio* to remain dominant over males who might otherwise outrank him. Adult males seem to recognize the significance of the alpha female. New alpha males of other groups, not just the one in the example above, have been observed to mount or attack the alpha female at the center of the group (Nakamichi 1999). It is rarely reported that other females than the alpha female are mounted or attacked by the new alpha male. Mounting or attacking the alpha female may be a ritualized display that functions to make the alpha female and other group members recognize the appearance of the new alpha male (Nakamichi et al. 1995b).

4.3.4 Changes in Dominance Rank Among Adult Males

Because the dominance rank change is rarely observed, it is interesting and important to describe an example of it. The following event was observed in a captive group of Japanese macaques. There were approximately 250 animals, including 16 adult males living in a 20 ha enclosure (Nakamichi, unpublished data). The third-ranking (gamma) male (18 years old) suddenly received vigorous challenges (e.g., biting and chasing repeatedly) from three middle-ranking (5th, 6th, and 7th ranking) adult males, and his rank went under them. A few days later, he was attacked by low-ranking males who joined the middle-ranking males in chasing him, and he was ranked at bottom. He rose in dominance rank again to a middle-position by receiving support from a middle-ranking male, one of those middle- and high-ranking males to which he attempted to maintain proximity.

This 18-year-old gamma male maintained relatively close proximity to the 17-year-old alpha male, and both of them had proximity to many adult females.

The affiliation between the two might have been useful for keeping their rank positions. The middle-ranking males' sudden attack on the gamma male happened 11 days before the death of the alpha male. They also attacked or threatened some of the adult females that surrounded the alpha and gamma males when resting or walking to forage. The middle-ranking males might have attacked these individuals to test the power of the alpha male. This is just one of the probable explanations.

It is very difficult to determine the factors that cause complicated social changes, such as dominance rank changes among adult males. This is because social changes tend to occur in a relatively short period, and they are very difficult to reproduce experimentally. The only way to collect detailed observational data on social changes is by observing behaviors of macaques in natural settings, however infrequent they are. Such data may lead to understanding of individual's social intelligence, which might otherwise be hidden.

4.4 Mating Behavior

While many primate species inhabiting the tropical regions give birth year-round, Japanese macaques mate and give birth in a certain time of year. The mating season includes 3–4 months in the fall and winter, and the birth season lasts for 3–4 months in the spring and summer. The gestation period is approximately 170–180 days. Females first come into heat and mate with males at 3.5 years of age, but rarely become pregnant at that age. Females usually give birth to their first offspring at 5–7 years of age.

Takahata and his colleagues (Takahata 1982a, b; Takahata et al. 2002) observed the Arashiyama free-ranging, provisioned group for 7 years and reported interesting findings about mating behaviors (Fig. 4.11). Their most salient finding is that individuals rarely mate with each other when they are closely related through maternal lines. Copulation between mother and son has not been observed, and that between siblings of different sexes has been observed only in one dyad. Copulations between uncle and niece and between aunt and nephew have been recorded. The number of the observed copulations, however, is much lower than the expected value. Copulations occur in more distantly related pairs as frequently as in unrelated pairs. This indicates that Japanese macaques avoid copulation in a close-kin dyad, i.e., within the third or less degree of relationship. They mate with more distant relatives as frequently as they do with unrelated individuals. This suggests that Japanese macaques have some mechanism by which they avoid mating with closely related individuals (inbreeding avoidance).

The mechanism by which Japanese macaques avoid inbreeding is probably based on their cognitive ability to memorize their relationships with others. Male offspring maintain relatively frequent interactions (including nurturing-nurtured relations) with their mothers during the first few years after birth. The interactions of male offspring with their mothers usually decrease with increasing age, and they are less frequent than the interactions of female offspring with their mothers are.

Fig. 4.11 A 12-year-old male is mounting an 18-year-old female in the Katsuyama group of Japanese macaques. The female was his mother's maternal cousin

Probably, the fact that siblings of different sexes suckle from the same teat in different years and have relatively frequent interactions with each other in immature days affects interactions among them in mature days. Frequent affiliative interactions at early stage of life may be responsible for male's psychological bonding with his mother or sisters. This psychological bonding or affiliative relationship may prevent a male from mating with his mother and sister. The reverse is also true. A mother and her daughters may avoid mating with her sons and their brothers, respectively, since frequent interactions occurred between her and her sons and between her offspring of different sexes when they were immature.

Similarly, when an adult male and an adult female maintain relatively frequent proximity to one another (peculiar-proximate relations) in the non-mating season, they tend to avoid mating (Takahata 1982a). Instead, they tend to mate with those with which they are not in frequent proximity. As Takahata (1982a) points out, Japanese macaques tend to select unfamiliar or unknown individuals as mating partners. In other words, psychological bonding or affinity greatly influences mating partner selection in Japanese macaques.

It might appear that higher-ranking males mate with females more frequently and sire more offspring than lower-ranking ones do. In a captive group of Japanese macaques, male dominance rank was positively correlated with the number of copulations with ejaculation, but was not related to the number of offspring (paternity can be determined by DNA analysis). This indicates that having a high rank among males may lead to a large number of opportunities for copulation, but not necessarily to a larger number of offspring (Inoue et al. 1991). Similar results have been reported for a free-ranging, provisioned group: peripheral males sire more infants than central males do (Inoue and Takenaka 2008).

4.5 Group Division

A group divides usually when food resources in the home range of the group are insufficient to meet the demands of all individuals of the group. Monkeys travel to a food patch and forage, and then move to another food patch. If many food patches in a group's home range are too small for all members to forage at the same time, it is more difficult for all group members to exploit these food patches, and agonistic interactions among some of them increase in order to make use of limited resources. This may cause some individuals of the group to travel independently of the other group members, leading to the loosening of group cohesion and social fragmentation. This is the beginning of group division. When a subgroup constantly travels and its membership is stable, group division is completed: the original group has divided into two groups. The home ranges of two groups are usually different, and one group may avoid the other group consistently whenever the two groups come into contact. As with the dominance relationship between individuals, a group is likely to be consistently dominant to a neighboring group.

The excessive increase in group size makes it difficult for individuals to interact with one another, not just to forage for themselves. Interactions among group members in general being less frequent may make their dominance relationships ambiguous. While this may increase agonistic interactions, they spend more time independently of one another, and then group division occurs. In other words, the increase in group size seems to be a primary cause of group division.

In addition, social conflicts among group members may cause group division (Koyama 1970). An example of this type of group division is described below (Itoigawa 1993, 1997).

The Katsuyama free-ranging, provisioned group of Japanese macaques consisting of 23 kin groups split into two groups: the main group and the branch group. The main group included one adult female of the 2nd-ranking kin group, most adult females of the 5th-ranking kin group, and all adult females of the 7th- through 23rd-ranking (bottom) kin groups. The branch group included all adult females of the 1st-, 3rd-, 4th-, and 6th-ranking kin groups, all but one adult females of the 2nd-ranking kin group, and one adult female of the 5th-ranking kin group. All infants but one joined the same group as their mothers did. An exceptional 1-year old female remained in the main group even after her mother switched to the branch group (Fig. 4.12).

Three years before the group division, two young adult males (8 and 5 years old) of the 1st-ranking kin group became the alpha and beta males, respectively. They acquired their dominance rank chiefly because of agonistic support from closely

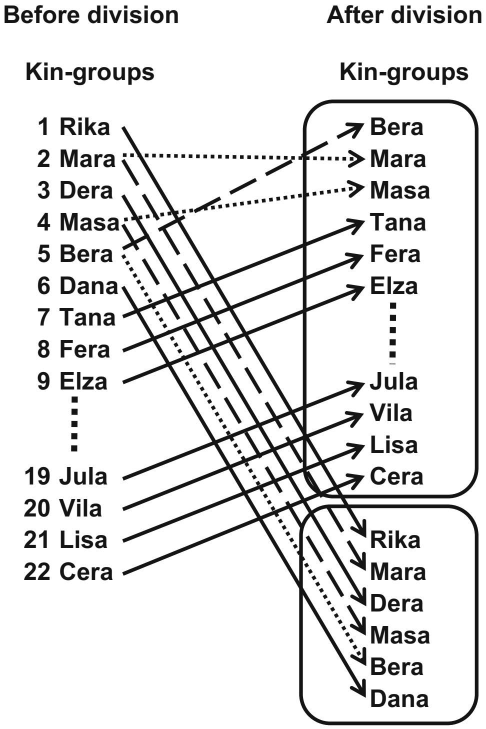


Fig. 4.12 Kin group composition of the free-ranging, provisioned Katsuyama group of Japanese macaques before and after group division in 1973 (based on Itoigawa 1993, 1997). *Solid lines* indicate that all individuals of a kin group became members of the same group at the time of division; *dotted lines* indicate that one or more members of a kin group became members of one group; and *dashed lines* indicate that the remaining large majority of the kin group become members of the other group

related females, including their mother and grandmother (the latter was the alpha female). A few adult females of the 5th-ranking kin group, by mating with the new alpha male, formed and maintained affiliative relationships with him after the mating season. They then started to behave aggressively toward adult females of the 1st-ranking kin group, especially the alpha male's mother and grandmother. This antagonistic behavior escalated and produced severe social conflicts between adult females of the high-ranking kin groups and those of the middle-ranking kin groups. The latter succeeded in expelling the former after repeated agonistic acts. The 5th-ranking kin group of the original group thus became the 1st-ranking kin group in the newly formed main group. Group members who had occupied high-ranking positions in the original group formed the branch group and began to travel through the new home range.

Group division is always caused by social changes in the original group, such as loosening of cohesion, social fragmentation, and instability of dominance relationships among group members. Such social changes are triggered by an increase in group size and social conflicts between subgroups of adult females. Indeed, adult females play the leading role in group division. Importantly, a group does not divide in a disorderly manner but along kin lines. The importance of relationships through maternal lines for the social lives of female Japanese macaques may be most saliently manifested in group division.

4.6 Mother-Immature Offspring Relationships

4.6.1 Cognition of Mother by Infant and Cognition of Infant by Mother

4.6.1.1 Precocial and Altricial Animals

Precocial birds, such as ducks, geese, and chicks, can walk soon after hatching, and hatchlings will follow the first moving object they see after hatching. This phenomenon is called ‘imprinting’ (Lorenz 1935). Since the first moving objects that hatchlings see are usually their mothers, imprinting is an indispensable mechanism by which precocial hatchlings identify their mothers and thus survive in the wild.

Goats are precocial, and stand and walk soon after birth. They show appropriate maternal behaviors, such as licking and permitting their kids to suckle, even when the kids are separated from them 5 min after birth and returned to them 2 h later. However, mothers do not accept kids that are separated from them immediately after birth (i.e., before they start to lick their kids) and returned to them 2 h later (Klopfer 1971). This shows that mother goats identify their kids in the first 5 min after birth in which they lick their kids.

In precocial birds and mammals, either mothers can identify their infants or infants can their mothers, soon after birth. By contrast, altricial birds and mammals are born too premature to walk, and need not identify mothers or infants soon after birth. Rather, they are assumed to be able to identify mothers or infants by the time infants become able to move independently.

Even though nonhuman primates cannot walk soon after birth, they are usually classified as precocial animals, because their infants are born with their eyes open and their body shapes are similar to adults’. In the majority of primate species, infants are born with grasping reflex, i.e., their fingers on four legs can flex in response to stimuli, allowing them to cling to their mothers’ belly or back immediately after birth, without any help from their mothers. Nonhuman primate infants tend to spend most of their time in contact with their mothers during the early stages of development, and as with altricial animal infants, they are presumed to be able to identify their mothers by the time they spend much time away from the mothers.

Infant Japanese macaques start to move by themselves by the end of the first week, albeit very clumsily. In the second month, the movements of infants become increasingly steady. At this time, infants increase the amount of time spent out of contact with their mothers and sometimes interact with other group members in the vicinity of their mothers, such as other infants and young juveniles. Two-month-old infants rarely move very far from their mothers. In the third month, as their locomotor skills develop, infants spend much less time in contact with their mothers and much more time independently. At this stage, infants begin to extend their social interactions with other group members (Itoigawa 1973; Nakamichi 1999, 2001). These developmental processes in infant Japanese macaques are similar to those in closely related species, such as rhesus macaques (Berman 1980).

4.6.1.2 Visual Recognition Between Mothers and Infants

The question here is when mothers and infants become able to discriminate between them and other group members. A pig-tailed macaque (*Macaca nemestrina*) mother is reported to discriminate her own infant from other infants by the end of the second week after giving birth (Jensen 1965). On the basis of this report, it may be deduced (but not experimentally determined) that Japanese macaque mothers can discriminate their own infants from other infants within a few weeks postpartum. In finding their infants in a group of two or more infants, macaque mothers may rely both on visual cues and on other cues, such as olfactory cues. Maestripieri (2001), after reviewing the substantial literature about mother-infant relationships in Old World and New World monkeys, concludes that mothers can discriminate between their offspring and other infants of the same sex and age within 3–4 weeks postpartum. Moreover, in primate species, lactating adult females often adopt an infant within 2–3 postpartum weeks. Experimental cross-fostering of infant rhesus monkeys has a high rate of success within the first 2 postpartum weeks. Maestripieri (2001) therefore remarks that in the early postpartum weeks, monkey mothers are in a maternal sensitive state in which they are highly motivated to take care of infants.

In order to assess the age at which infants discriminate their mothers from other adult females, Nakamichi and Yoshida (1986) conducted experiments with mother-infant pairs of captive Japanese macaques; infants were 12 weeks old or younger. In these experiments, 2 h after each infant was separated from its mother, it was allowed to approach four adult females: its mother and three unknown adult females. Each of them was placed in a small cage at a distance of 150 cm from the infant. Infants were forced to spend 2 h away from their mother before the beginning of an experiment, and not permitted to touch their mother directly during the experiment. Infants at 8–12 weeks of age, but not younger ones, approached and stayed in front of the cage of their mother much longer than they remained near the cages of the other adult females. This clearly demonstrates that the infant Japanese macaques at 8–12 weeks of age have acquired the ability to discriminate their mothers from other adult females. Infants tend to extend their social interactions with group members in the third month of age. The results of the experiments imply that visual recognition of mother precedes infant socialization.

4.6.1.3 Recognition of Infant Calls by Mothers

When observing monkeys at a wild monkey park, you may hear screams from a nearby thicket. You then see a female rush into the thicket and come out with her infant. After observing this scene, you would naturally think that the mother came to help her infant as soon as she heard the infant scream and that she was able to recognize the screams of her infant.

Playback experiments are useful for confirming the mother's ability to recognize infant calls. Shizawa et al. (2005) conducted playback experiments in a Japanese macaque group living in an open enclosure. They first collected the calls infants uttered when they lost sight of their mothers, and then played back the calls made by these infants and by other infants to the mothers. The results demonstrated that each mother was able to distinguish her own infant's calls from those of other infants when the infants were 4–6 months old. Japanese macaque infants after 3 months of age tend to leave their mother's sight much more often than they do earlier. Moreover, they tend to interact with group members much more often than before, thereby increasing the frequency of social encounters in which the infants may need agonistic support from their mothers. It is essential that their mothers correctly recognize the infant calls uttered to ask the mothers for help. Since Shizawa et al.'s (2005) experiments do not involve infants younger than 4 months old, it is possible that Japanese macaque mothers may recognize the calls of their own infants earlier. The age at which immature offspring are able to identify their mother's calls has not been identified.

4.6.2 Maternal Role in Infant Development of Locomotion and Foraging

4.6.2.1 Scaffolding

Japanese macaque newborns are able to cling with all four limbs at birth (see 6.1.1), but cannot walk at all for at least a few days. They are only able to stand by keeping the forearms straight and the hind legs bent at the knee. After infants are able to stand on all four legs with both elbows and knees straight, they begin to walk in a very clumsy manner. In the second and third weeks after birth, the following scene is sometimes observed: a mother puts her infant on the ground, leaves it a few meter away and exhibits lip-smacking, i.e., a friendly behavior of slightly opening and closing the lips several times at a relatively high speed. The infant then approaches the mother, keeping its eyes on her. When the infant reaches its mother, the mother holds it (Fig. 4.13). This suggests that the mother encourages her infant to walk by lip-smacking.

Scaffolding is a process of assistance that enables a human child to achieve a goal that would otherwise be beyond his or her abilities at a given stage of development (Wood et al. 1976). Parents' scaffolding is important for the development of competences in human children. Just as human mothers do, Japanese macaque mothers provide scaffolding for their infants, even though the infant's locomotor competence can develop with increasing age without maternal scaffolding. Scaffolding promotes mutual visual cognition between mother and infant, and strengthens the psychological bonding between them.

If a human mother demonstrates how to draw a circle with a crayon for her child, the child may mimic the mother's behavior and draw a circle, albeit clumsily. This is an instance of *active teaching*. Nonhuman primates rarely engage in active teaching. Even though monkeys of various species and great apes, such as gorillas

Fig. 4.13 Scaffolding by a Japanese macaque mother. (**a**) The mother encourages her 1–2-week-old male infant to walk independently by lip-smacking. (**b**) The mother lifts up her infant as he approaches her

and chimpanzees, have been studied for years, only one episode of active teaching has been reported: a chimpanzee mother in the wild demonstrated how to effectively crack a nut on an anvil stone with a stone hammer (Boesh 1991).

4.6.2.2 Acquisition of Food Repertoire by Infants

Without the opportunities of receiving active teaching, however, nonhuman infants learn important survival skills by observing their mothers and other group members. The acquisition of food repertoire is an example of this type of learning. Infant Japanese macaques start to lick or chew solid objects, such as grass, twigs, and even small stones, at around 2 weeks of age, and to eat foods in the second month after birth (Hiraiwa 1981). By observing infants and 1-year-old juveniles in a provisioned group of Japanese macaques, Ueno (2005) found that they were more likely to feed when other group members were feeding within 1 m of them than when these neighbors were not feeding. They also tended to eat the same items as their neighbors did. This tendency became more apparent with increasing age during the first 6 months and continued in the 2nd year. Because infants spend much more time with their mothers than with any other group members, mothers have the greatest influence on infant's food repertoire. In fact, mothers and their young offspring often co-feed in the wild (Fig. 4.14). Peers are influential as well, because same-aged young macaques spend a large amount of time playing, travelling, and resting together (Nakamichi 1989).

In addition, Tarnaud and Yamagiwa (2008) found that in a wild group of Japanese macaques, infants in the second half of the first year intensively observe elder group members engaging in plant and invertebrate foraging and learn what are edible for them. Juveniles in the second half of the second year do the same but less often. Intensive observation is defined as the act of turning the head toward the foraged food or the location of a foraging individual. The main target individual of intensive observation is the mother. These findings indicate that infants and juveniles build a similar food repertoire to neighbors' (mother and peers') by observing

Fig. 4.14 A 9-year-old Japanese macaque mother and her 10-month-old son are eating grass of the same species

their feeding behavior. Food repertoire is very often transmitted from mother to infant and less often from peer to peer, through the observation of feeding behaviors.

4.6.3 *Flexibility of Maternal Behaviors*

4.6.3.1 Maternal Responses to Infants with Congenitally Malformed Limbs

The clinging of infants to their mother has been hypothesized to be important for eliciting maternal care (Hansen 1966). However, experimental studies have cast doubt upon this hypothesis. For example, a macaque monkey mother carries and cradles her anesthetized infant (Rosenblum and Youngstein 1974); and a squirrel monkey mother carries her infant, even when its limbs are immobilized with masking tape (Rumbaugh 1965). These infants are only temporarily unable to cling. It has little implication for the question of how mothers behave toward infants that are unable to cling from birth. Maternal care might cease if infants were persistently unable to cling.

Since the 1950s, Japanese macaques with congenitally malformed limbs have been observed in free-ranging, provisioned groups in Japan. The number of such macaques has recently decreased near to zero in most free-ranging groups (Fig. 4.15). Unfortunately, the causes of limb malformations are largely unknown. The observations of severely malformed monkey infants (e.g., ones with no hands or feet) and their mothers provide an insight into the problem of whether monkey mothers continue maternal care for infants that cannot perform normal clinging behavior. Similarly, the observations are useful for determining how differently mothers of malformed infants behave than those of healthy infants do.

In a free-ranging, provisioned group of Japanese macaques on Awajishima Island, Hyogo Prefecture, mothers of several infants with congenital limb

Fig. 4.15 Japanese macaques with congenitally malformed limbs of the Awajishima group. A 1-year-old male with no hands is able to walk bipedally (*left*). A 9-month-old male infant with distorted feet and no hands is crawling on elbows and knees (*right*)

malformations cared for their infants so as to complement the infants' disabilities (Nakamichi 1986; Nakamichi et al. 1983a, b; Turner et al. 2005, 2012). The mothers carried their malformed infants in one hand and walked on the other three limbs. They cradled the infants in their forearm(s) and enabled the infants to suckle, because the infants, due to their limbs being malformed, were not able to keep their mother's nipple in their mouth on their own. This indicates that Japanese macaque mothers care for newborns, whether or not they have clinging ability. Infants with no cling ability requires more care than healthy infants do. Nevertheless, healthy and malformed infants have contact with their mothers and suckle for a similar length of time, at least in the first year after birth.

Malformed infants usually develop their own locomotor patterns that are appropriate for their limb malformations. Some infants with no hands walk on their hind limbs, and infants with four severely distorted limbs mainly crawl. As malformed infants age and develop their distinctive means of moving, they spend less time with their mothers and more time with other group members. They tend to spend time with adults or older female juveniles through such behaviors as passive body contact and receiving grooming. By contrast, healthy infants tend to interact with same-aged infants or juveniles that are older by 1 or 2 years, and travel and engage in social play with them. The restricted locomotor abilities of malformed infants often prohibit them from following healthy infants when they move quickly and widely, especially in the trees. Malformed infants usually approach, and if permitted, stay near adults that are less active than infants and juveniles. Adult group members generally behave tolerantly toward malformed infants. Not only do macaque mothers provide appropriate care for their disabled infants, but also other group members provide social support for them. Such maternal care and social support from other group members result in a 1-year survival in the wild of as many as 72 % of infants with congenital limb malformations; the corresponding value for healthy infants is 90 % (Nakamichi et al. 1997).

Mothers with limb malformations can provide appropriate care for their infants in the same ways as healthy mothers do. It is observed in at least one case that a mother with limb malformations is able to care for offspring that are disable to cling just as she is. A female named *Yuki* had normal feet but no hands, and acquired the skill to walk stably on her hind legs by the end of the 2nd year after birth. She gave birth to her first child at 6 years of age. Her first four children had congenital limb malformations, and therefore they had extremely limited or no clinging ability. However, *Yuki* was able to carry these infants in a special manner while walking bipedally: she held the infants to her belly or thigh using her stick-like forearm (Fig. 4.16). Two of her four offspring survived in the group for at least 2 years and the other two survived for 3 years and 6 months. Her 5th offspring was an healthy infant and able to cling with all four limbs. However, *Yuki* did not permit the infant to cling to her belly. Whenever the infant clung to her belly, she put her stick-like forearm between the infant and the belly and removed the infant. On the 4th day of the infant's birth, she abandoned it (Nobuhara, personal observation; Nakamichi 2002).

Yuki's 6th and 7th infants were both congenitally malformed. When the 7th infant clung to her with its normal hand, *Yuki* often attempted to refuse it. She then

Fig. 4.16 *Yuki*, an adult female with normal feet but no hands, and her severely malformed infant with no hands and distorted feet (*left*). *Yuki* walks bipedally while carrying the infant in a special manner (*right*) (Courtesy of T. Nobuhara)

gradually started to permit it to cling to her. After this, she permitted other healthy offspring to cling to her body.

The clinging ability has been considered to be essential for infant's survival and maternal care. Healthy mothers are usually able to take care of congenitally malformed infants that are not able to cling by their hands, as well as healthy infants with clinging abilities. Although *Yuki* lacked hands, she was able to develop her own infant-carrying pattern that was appropriate for both her disability and the disabilities of her offspring. However, she was not able to accept her first healthy child that was able to cling tightly to her body by its hands and feet. Disabled mothers who develop their own carrying patterns may not be able to quickly alter their patterns in order to care for infants with normal clinging abilities.

4.6.3.2 Maternal Responses to Dead Infants

It is important to determine whether monkey mothers abandon infants soon after death or maintain maternal behaviors toward dead infants, because the description of maternal behavior toward dead infants may reveal the aspects of the nature of nonhuman primate mothers that might otherwise be concealed.

It has been reported that a number of simian species, such as Japanese macaques, gorillas, and chimpanzees, carry infant corpses (see Fig. 4.1 for simian *vs.* prosimian, and Nakamichi et al. 1996 for a review). On the other hand, in prosimian species, no mothers have been reported to carry their dead infants, either in captivity or in the wild. Although wild ring-tailed lemur mothers do not carry their dead infants (Fig. 4.17), they have been observed to move back and forth between the dead infant that was left on the ground and the group on the day of the infant's death (Nakamichi et al. 1996). This behavior can be interpreted as follows: lemur mothers seek to stay not only with their dead infants but also with their group. However, it is difficult for lemur mothers to carry dead infants by hand. They then

Fig. 4.17 A ring-tailed lemur mother sitting and holding her dead infant in a clumsy manner (*left*). A Japanese macaque mother carrying her dead infant (*right*)

have a psychological conflict. They want to but cannot both stay near dead infants and remain with the group. It is assumed that the repeated movement between dead infants and the group is a means to resolve the psychological conflict. Although simian and prosimian mothers differ as to whether they carry their dead infants, they may not differ greatly in terms of maternal affection.

Simian mothers can avoid the psychological conflict between the desire to stay near their infants and the desire to stay near their group, because they are able to carry dead infants in their hands. There have been limited studies to address the questions: do all mothers carry their dead infants? How many days do mothers carry their dead infants? How do mothers behave toward their dead infants? How old must dead infants have been before mothers will refrain from carrying their bodies?

Sugiyama et al. (2009) analyzed the quantitative features of dead-infant-carrying behavior of Japanese macaque mothers in free-ranging, provisioned groups at Takasakiyama, Ohita Prefecture, based on data recorded over a 24-year period. They found that the dead-infant-carrying rate (dead-infant carrying cases to deaths within a year of birth) was as small as 10 %. In 26 % of all dead-infant-carrying cases, infants died on the day of birth, and in 78 % of the cases, infants died within 30 days of birth. In only 3 % of all dead-infant-carrying cases, infants died after 100 days of age. The oldest infant that was carried after death was 253 days old. Moreover, 28 %, 15 %, and 24 % of mothers abandoned carried infants within 1, 2, and 3 days of death, respectively. That is, 67 % of mothers abandoned their dead infants within 3 days of death. About 9 % of mothers carried their dead infants for more than a week after death. The longest carrying period was 17 days.

These findings indicate that dead-infant-carrying behavior is most likely to occur during the maternal sensitive period in the early postpartum weeks, during which mothers are highly motivated to take care of their infants (Maestripieri 2001). However, Sugiyama et al. (2009) reported that some mothers carried infants who died at 1 month of age or older, and Izawa (1987) observed that a wild Japanese macaque mother carried her 1-year old dead infant. Taking all these data together, it can be concluded that, whether or not they are in the maternal sensitive period, Japanese macaque mothers sometimes have strong attachment to infants, and carry them for a while even after death.

Even though Japanese macaque mothers may bond strongly with their infants, most mothers abandon their dead infants within a few days. According to Sugiyama et al. (2009), most corpses decompose rapidly due to hot and humid weather conditions. The corpses then smell bad and attract many flies, and this may lead mothers to abandon the corpses.

Rarely do group members other than mothers approach, touch, or sniff infant corpses. In contrast to the behavior of other group members, mothers carry and groom their dead infants. It has even been observed that they shoo flies that are circling or swarming the body of a dead infant even after the body has lost its original form (Nakamichi, personal observation). Moreover, it is difficult to find mothers behave toward dead infants in the way that can be interpreted as aversion (I never did). Therefore, decomposed corpses do not necessarily cause mothers to abandon their dead infants.

Mothers are likely to place dead infants on the ground and move away from them, when they feed on the feeding ground or forage for natural food in the vicinity of the feeding site. Mothers can very easily find dead infants left on the feeding ground, but not in the bushes. In fact, mothers have been observed to search for their dead infants in the bushes (Nakamichi, personal observations). When a mother cannot find her dead infant, her dead-infant-carrying behavior has to end unexpectedly. In other words, an explanation of mothers ceasing to carry dead infants is that they have lost sight of dead infants. This is just one of the probable explanations. Unfortunately, there is not enough data available to determine the factors responsible for mother's abandonment of dead infants.

Some mothers carry their stillborn, premature babies. A mother was observed to carry a hairless premature baby that was estimated to be approximately 90–100 gestation days old (the gestation period of a Japanese macaque is 170–180 days) (Nobuhara, personal communication). A parous mother was observed to lick and carry a hairless baby she gave birth to in a cage (Nakamichi, unpublished data). The hairless baby was different in appearance from a full-term newborn baby. These observations do not support the idea that mothers only carry infants who die after birth.

4.7 Social Developments of Immature and Adolescent Individuals

4.7.1 Relationships of Immature and Adolescent Males

In parallel with decreased time they spend with their mothers, infant Japanese macaques tend to increase their interactions with other group members, especially with age-mates (i.e., same-aged individuals). Japanese macaques have a birth season of 3–4 months in the spring and summer. As a result, infants have age-mates, and their locomotor abilities are very similar, even between sexes. They can interact with each other through social play and other behaviors. At the beginning in the 2nd year of life, however, clear differences between immature males and females appear and become important for partner selection (Nakamichi 1989).

Generally, younger juvenile males tend to spend time in the central area of the group. When they get older, they spend most of the time at the periphery of the group. That process is called 'peripheralization.' When juvenile males are 1 year old (i.e., in the 2nd year after birth), they live in the central area, and are very likely to maintain proximity to similar-aged males. When juvenile males are 2–4 years old and live at the periphery of the group, most of their social partners are similar-aged males. This is because older juveniles and young adult males occupy the peripheral area. The close relationships with similar-aged peers continue until males leave their natal group. There are many females of various age classes, many infant and younger juvenile males, and several adult males, in the central area. The preference of juvenile males for associating with individuals of the same sex and similar age appears in the 2nd year of life and precedes peripheralization (Nakamichi 1989). Juvenile males are not likely to change their social partners drastically in the process of peripheralization.

Nakamichi (1996) report that most immature males in the first 4 years of life tend to show a consistent preference for proximity (within 2 m) to certain same-sex individuals in their cohort that have dominance ranks adjacent to their own. Mothers with infants are likely to stay near each other, and sometimes interact in social grooming and other behaviors. Usually, such mothers are closely ranked individuals. The proximity relationships between mothers may provide the opportunity for their infant offspring to spend a large amount of time in proximity to each other. The proximity relationships thus formed may continue after infants grow and spend less time near their mothers. This suggests that the prolonged proximity relationships between immature males are largely a reflection of those between their mothers.

Most males leave their natal group upon maturity (i.e., 3–6 years of age; Itoigawa 1975). The frequency with which males are found at the periphery of the group or in the home range of the group gradually decreases until they leave the group. If males are not observed with their group for several months, they are considered to have left the group. However, the following questions have yet to be answered: what makes males leave the group, whether they leave with similar-aged males with whom they are closely associated throughout immaturity, and where and how they live after leaving the group.

4.7.2 Social Relationships of Immature and Adolescent Females

In contrast to immature males, immature females do not go through the process of peripheralization, and remain in the central area. They tend to maintain proximity to females of various ages and infants of both sexes that inhabit the central area of the group. Females maintain relationships with such individuals through various social behaviors from the 2nd year of age. For example, juvenile females tend to interact with infants by touching, grooming, and holding, and may also actively groom adult females (Nakamichi 1989).

As immature males do with closely ranked males, immature females tend to maintain prolonged proximity relationships with closely ranked females throughout the first 4 years, and such relationships are largely a reflection of the relationships between their mothers (Nakamichi 1996).

Most immature females have affiliative relationships with infants and females of various age classes in their group. However, the most frequent grooming occurs between mothers and their daughters (Koyama 1991; Nakamichi and Shizawa

2003), and agonistic alliances are most often formed by closely related females, and typically by mothers and their daughters (Watanabe 1979). These observations indicate that a female's most important social partner is her mother from immaturity to adulthood.

The loss of mother may have a great influence on young adult female's group social life. Yamada et al. (2005) observed the grooming relationships of 5–7-year-old adolescent orphan females and compared them with those of adolescent females with surviving mothers. Orphan females engaged in grooming interactions with other group members as much as females with mothers do. Sisters who lost their mother tended to develop grooming relationships with each other. Orphan females without sisters tended to develop grooming relationships with same-aged females and unrelated adult females. This study suggests that adolescent females have sufficient social abilities to overcome the loss of their mothers.

Most Japanese macaque females have the first pregnancy at 5 or 6 years of age, and their relationships with other group members may change after they produce their first offspring. A hypothesis, although there is not enough evidence to fully support it, is that newborns are attractive to some female group members, and this allows mothers with newborns to develop new social networks. The question of what social changes first childbirth give rise to may be investigated by observing young adult females who remain nulliparous and older than the average age of females at first childbirth. Katsu et al. (2013) observed young nulliparous adult females at 6–9 years of age and found that most of them maintained close relationships with their mothers. More specifically, most of them were observed to receive grooming from their mothers more frequently than the mothers do from them. That is, young adult female Japanese macaques may maintain close relationships with their mothers at least until first childbirth. Little data are available to examine whether or not young adult females change relationships with their mothers after first childbirth.

4.8 Aging

4.8.1 Physical Aging

Most Japanese macaques over 20 years of age develop physical declines: tooth loss, incomplete change from winter fur to summer fur, and a bent back. In addition to these changes, the vision of monkeys may become dim with age. Old monkeys may suffer from presbyopia and farsightedness. In grooming, young animals put their eyes close to the body part they are grooming and pick up small items, such as lice eggs. By contrast, some old animals tend to put their eyes away from the body part they are grooming. This is probably because old monkeys require a greater distance to bring an item into focus than young monkeys do (Fig. 4.18) (though no ophthalmological diagnosis of aged monkeys has been conducted). Moreover, locomotor

Fig. 4.18 Presbyopia in the Japanese macaque. At 21 years of age, this female (formal name, *Lipkira72'83*) grooms others, putting her eyes relatively close to the grooming fingers (*left*). At 25 years of age, the distance between her eyes and fingers is much greater than before, indicating a decrease in eyesight with age (*right*)

activities of monkeys tend to decline with increasing age: as they age, they are likely to spend more and more time sitting or lying motionlessly (Nakamichi 1984).

Reproductive abilities also decline with age. While the birth rate among 10–19-year-old Japanese macaques is as high as 50–65 %, the value decreases drastically with age after 20 years old, and approaches zero at 25–26 years of age (Itoigawa et al. 1992). The oldest recorded age at which a free-ranging, provisioned Japanese macaque female has given birth is 26 years (Itoigawa et al. 1992; Koyama et al. 1992). The average age of death for females in the Katsuyama group of Japanese macaques is 21.2 years (Itoigawa 1982). Based on these findings, female Japanese macaques older than 20 years of age can be regarded as aged.

4.8.2 Social Aging

Old age also affects social behavior of monkeys. Nakamichi (1984, 1991) observed a cross-section of Japanese macaque females ranging in age from 11 to 29 years in a free-ranging, provisioned Arashiyama group in Kyoto Prefecture. He also observed females of the same age in a group living in a 20-hactare open enclosure. The captive group was originally a branch group of the Arashiyama group that was transplanted to Texas, USA (Nakamichi 1984, 1991). Similar behavioral changes with increasing age were found in the two groups, even though their living conditions were different. As compared with younger females, older females, especially those over 25 years of age, tended to spend much less time in contact with or grooming other group members, and much more time alone. Moreover, old females tended to concentrate their social interactions on their youngest daughters. Some aged females were outranked by their adult daughters, but most showed no marked decline in rank. Other studies have shown that old age is more likely to affect the social interactions of low-ranking females than it does those of high-ranking females. Pavelka et al. (1991) found that high-ranking females in a captive group of Japanese macaques did not decrease social contact even when they were aged, while low-ranking ones did. Kato (1999) reported that old high-ranking females in the Katsuyama group of Japanese macaques maintained proximity to a larger number of unrelated adult females and immature individuals than old low-ranking females did. Nakamichi (2003) observed grooming interactions in the same group and found that the frequency of grooming bouts toward unrelated females decreased for both high- and low-ranking females with age, while the frequency of receiving grooming from unrelated adult females decreased with age for low-ranking females but not for high-ranking females. These results indicate the following: as they age, both high-and low-ranking females become more and more prone to select related individuals as recipients of grooming; and old high-ranking females, as opposed to old low-ranking females, remain as socially attractive as young high-ranking females and continue to receive grooming from others.

In extreme cases of social aging, old female Japanese macaques may leave the group. Some old females have been observed to leave a free-ranging, provisioned group, and to live alone for a few days or more (Nakamichi, unpublished data). It is unclear why they left the group. No information is available about how long they survived and how they spent their time alone.

The tendency toward social withdrawal and social dependency on related individuals becomes apparent with increasing age, especially for females over 20 years of age. Old high- and low-ranking individuals exhibit different social behaviors. Indeed, all females are different in terms of social factors, such as the number of adult daughters, their ages, and the number of grand offspring. Differences among old animals in both social environment and physical condition may cause different social behaviors. Therefore, the process of social aging should be described for each female, and special attention should be paid to idiosyncrasies.

4.8.3 Grandmother Hypothesis

One of the primary functions of social groups is to enhance reproductive efficiency. Therefore, almost all group members have reproductive abilities, or they are able to acquire them as they mature. Post-reproductive members do not usually stay in the group. Humans, unlike other species, usually remain in the group even after losing their reproductive abilities. The grandmother hypothesis is proposed to explain the evolutionary meaning behind the survival of post-reproductive women. According to the hypothesis, post-reproductive females can no longer produce their own offspring, but can contribute to the survival of their grandchildren. The survival of their grandchildren, in turn, increases the reproductive success of their offspring and thus their own inclusive fitness. Some studies provide empirical evidence that the grandmother hypothesis is true for humans (Hawkes et al. 1997; Mace 2000; see Fedigan and Pavelka 2007 for a review).

Fairbanks and McGuire (1986) report that young adult females with mothers, as compared with those without mothers, in captive groups of vervet monkeys (*Cercopithecus aethiops*), produce significantly more surviving offspring and have a lower level of infant mortality. This may be related to the tendency of grandmothers to stay near and take care of their infant grandchildren. The increased survival of infants living with grandmothers may also be related to the tendency of infants with grandmothers to be more independent of their mothers, as compared with infants without grandmothers (Fairbanks 1988a, b). However, it is not specified whether the grandmothers described in these studies are post-reproductive.

According to Takahata et al. (1995), Japanese macaque females at 20 years of age in a provisioned group have a post-reproductive lifespan of 4.5 years. This post-reproductive lifespan is defined as a time span in the following way: it is the sum of the time length between final parturition and disappearance from the group, (regarded as death) minus 1.5 years (the time length for an infant to become independent of its mother). However, there is no qualitative studies of the interactions of post-reproductive Japanese macaque grandmothers with their infant grandchildren. There are a few reported cases of social groups of nonhuman primates that support the grandmother hypothesis: for example, an old grandmother without dependent children (i.e., children who depend on her for care) continuously provides essential care for the survival of her dependent grandchild.

Nakamichi et al. (2010) is the first reported case to demonstrate the contribution of a grandmother to the survival of her grandchild. A 24-year-old grandmother provided essential care for the survival of her 2-month-old granddaughter; she held and carried the granddaughter for at least 6 days while the mother was temporarily absent from the group. The grandmother kept the granddaughter warm at night by holding her, but could not supply sufficient nutrition. She was too young to acquire food on her own, and would not have survived if her mother had been absent for a little more days. Another 23-year-old grandmother permitted the 14-month-old granddaughter to suck her nipples sometime within 6 weeks after her mother gave birth to a younger child. The grandmother started to produce milk within 1 month after the granddaughter's sucking acts were first observed. She also held and sometimes carried the granddaughter. Although 1-year-old Japanese macaque infants usually survive without maternal care, such as nursing and carrying, they suffer psychologically from the absence of maternal affection (Schino and Torisi 2001; Nakamichi et al. 2004). The grandmother satisfied the psychological need of the granddaughter by cuddling and carrying her and permitting her sucking behavior. The 1-year-old granddaughter could not have overcome her psychological distress without her grandmother's appropriate care.

These two cases show that old (but healthy) Japanese macaque females without dependent offspring can directly contribute to the survival of their physically and psychologically dependent granddaughters in the wild. This result accords with the grandmother hypothesis.

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Exercise

List the probable benefits and costs to individuals living in social groups.

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