# Chapter 11: Lifetime Social Development in Female Japanese Macaques

**Masayuki Nakamichi and Kazunori Yamada**

## 11.1 Introduction

In the majority of primate species, the infant is born with grasping extremities of all four limbs, allowing it to continue clinging to its mother's fur without support. Therefore, regardless of the mother's activity patterns, the infant is very likely to spend most of its time in contact with her in the early stages of development. In tandem with the development of locomotor abilities, the infant gradually increases the time spent away from her, thus extending its social milieu. Even after the infant is weaned from its mother, it still maintains a relationship with the mother throughout its immature days. These developmental changes in the mother–offspring relationship in the infant's immature days are universal among almost all primate species, including Japanese macaques (*Macaca fuscata*); behavioral differences between male and female infants, meanwhile, gradually increase with increasing age.

While most male Japanese macaques leave their natal groups upon maturity (Nishida 1966; Kato 2001), female Japanese macaques usually remain in their natal groups throughout their lives. Therefore, throughout their lives – which can be as long as 20 years or more (Itoigawa et al. 1992) – female Japanese macaques develop and maintain close, long-term relationships not only with females closely related to them through maternal lines but also with some unrelated females in the group (Nakamichi and Yamada 2007).

Among Japanese macaque populations inhabiting a variety of habitats, some intraspecific variations could be expected with respect to how females interact with group members, including their own offspring, throughout their lifetime development. For example, Johnson and Southwick (1984) reported that mother–infant

M. Nakamichi (✉)
Department of Ethology, Graduate School of Human Sciences, Osaka University,
1-2 Yamadaoka, Suita, Osaka 565-0871, Japan
e-mail: naka@hus.osaka-u.ac.jp

K. Yamada
Wildlife Research Center, Kyoto University, 2-24 Tanaka-sekiden-cho,
Sakyo, Kyoto 606-8203, Japan

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relationships in rhesus macaques (*Macaca mulatta*) did not differ across three different habitats in Nepal and India, whereas in savanna monkeys (*Cercopithecus aethiops*), the rate at which mothers rejected their infants differed between two habitats in Kenya, leading to a difference in interbirth intervals (Hauser and Fairbanks 1988). Unfortunately, few studies have directly focused on variations in behavioral responses to ecological conditions with respect to both infant social development and behavioral changes in adult females with increasing age in Japanese macaques.

The present chapter, therefore, focuses on describing lifetime social development of female Japanese macaques with respect to developmental stages such as infant (<1 year old), juvenile (between 1 year and the first estrus at around 3.5 years), adolescent (from the first estrus to the first birth at around 5–7 years), and adult (from the first birth to death), on the basis of behavioral studies conducted in several provisioned or wild groups (Fig. 11.1). Whenever possible, we address intraspecific variations in certain limited stages of development or some aspects of the females' social relationships.

## 11.2 Infants and Juveniles

### *11.2.1 Foraging*

Although Japanese macaque mothers continue to nurse their infants at least during the first year (Tanaka 1992), infant Japanese macaques begin to lick or chew solid objects (edible or inedible) such as stones, small clods, and twigs from as early as 2 weeks of age; they eat edible solid objects at 5 weeks of age (Hiraiwa 1981; Ueno 2005). They also begin to use the cheek pouches to store food temporarily from 8 to 10 weeks of age onward (Hasegawa and Hiraiwa 1980; Hiraiwa 1981). Few individual differences appear in the timing of each behavior related to solid food intake (Hiraiwa 1981).

Hasegawa and Hiraiwa (1980), who observed a provisioned group of Japanese macaques in Boso Peninsula, Chiba Prefecture, were the first to describe qualitatively the possibility that infants acquire the food repertoire from their mothers and other group members, on the basis of observations that an infant tried to eat the same object that its mother was eating and often nuzzled foraging macaques. The findings of Ueno (2005), who observed infants and 1-year-old juveniles longitudinally in a provisioned group in Arashiyama, Kyoto Prefecture, successfully exemplify the presence of the tendency toward synchronous feeding in infant and 1-year-old juvenile Japanese macaques: young macaques were very likely to not only show feeding behavior when their closest neighbors were feeding within 1 m of them much more frequently than when their neighbors were not, but also feed on the same food item. In particular, the tendency for infants to feed on the same items as their neighbors did became more apparent with increasing age, during the first 6 months after birth, and this tendency was maintained in 1-year-old juveniles. Such neighbors were mothers and peers. Tarnaud and Yamagiwa (2008), who

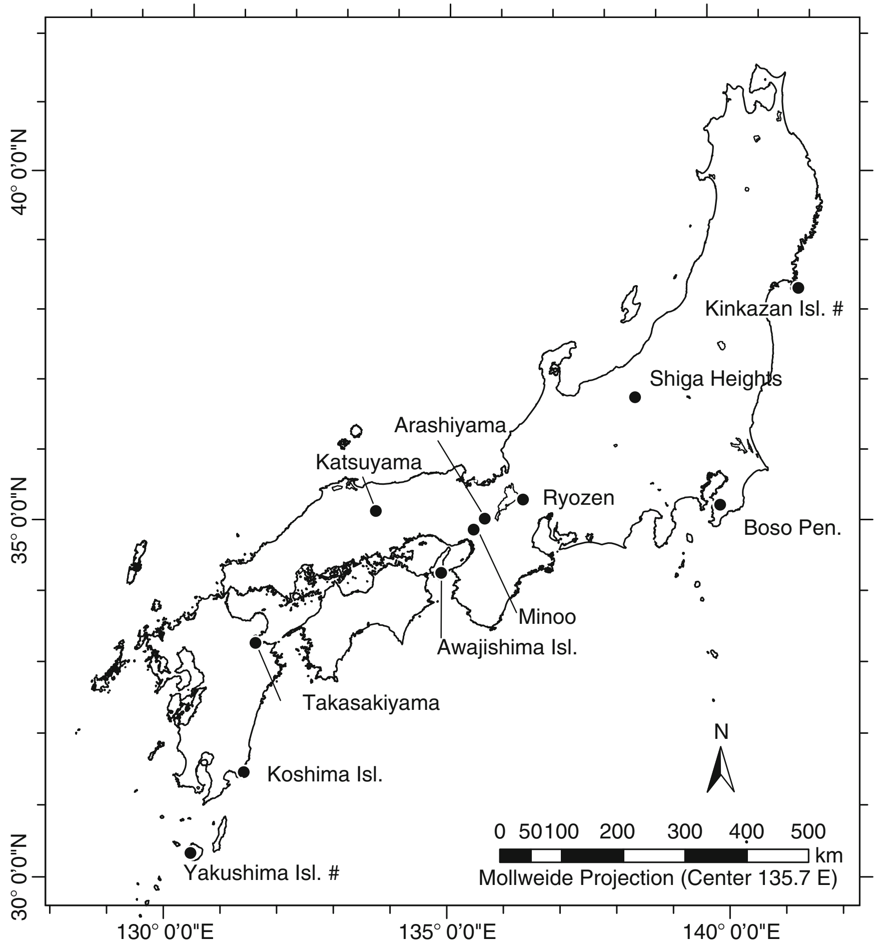

**Fig. 11.1** Japanese macaque study sites discussed in the present chapter. Site names marked with "#" indicate wild groups; those without "#" are provisioned groups. (The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2" by ESRI Japan Corporation, with permission)

observed wild groups of Japanese macaques on Yakushima Island, Kagoshima Prefecture, also found that intensive observations, defined as the act of turning the head toward the foraged food and/or location of a foraging individual, were directed by infants aged between 7 and 12 months and juveniles aged between 1.5 and 2 years toward elders engaging in plant and invertebrate foraging; additionally, such observations were more frequent in infants than in juveniles, and the vast majority of intensive observations were directed toward the mother. While it is apparent that mothers directly contribute to the survival of their infants through nursing, the findings by Ueno (2005) and Tarnaud and Yamagiwa (2008) show that mothers also provide the opportunity for their infants to acquire the repertoire of edible food items by permitting their infants to co-feed with them, which could lead to the social transmission of food-selection habits.

Close attention paid by young macaques toward their mothers or other elders is needed to acquire not only a large dietary repertoire but also the food-processing method. Although most adult macaques of both sexes within a provisioned group at Katsuyama, Okayama Prefecture, simply scraped dirt from grass roots with their hands as soon as they pulled the grass from the soil, and then ate it, some adult females carried grass roots to the river, where they washed the roots and then ate them (Nakamichi et al. 1998). They usually pulled one root at a time and set it aside to form a pile consisting of several roots, and they then carried the entire pile of roots to the river to wash and eat. The individuals who were seen performing this carrying and washing behavior consisted of several mothers and their adult daughters, all of whom belonged to high- and middle-ranking kin-groups. No adult males were recorded as carrying and washing grass roots. As immature macaques were rarely recorded as having dug roots as long as 10–20 cm, such tasks may be difficult for them; however, they were sometimes seen watching their mothers washing and eating the roots while sitting nearby and would pick up a half-eaten root to eat (Nakamichi et al. 1998). It is probable that young adult females who watched their mothers carry and wash grass roots when they were young begin to perform such behavior after they mature enough to pull grass roots out without any difficulty. In other words, the behavior of carrying and washing grass roots is likely to be transmitted from mothers to their daughters, and this tendency might be highly related to the fact that juvenile females spend much more time with their mothers than do juvenile males (Nakamichi 1989; see also Sect. 11.2.3).

Acquisition by the young of new behavioral patterns other than the aforementioned food-related behaviors, acquired by paying close attention to or intensively observing their elders, has also been reported with regard to louse egg-handling techniques during social grooming (Tanaka 1995, 1998; see also Chap. 9).

### *11.2.2 Infant Carriage by Mother*

As does nursing, infant carriage by the mother contributes directly to infant survival, because infants, particularly those under 6 months of age, do not always manage to follow the group members as they venture uphill and downhill into the forest, even though they develop locomotor abilities rapidly during the first few months after birth. According to Hiraiwa (1981), infants at 4 weeks of age begin to cling to the backs of their mothers, although there is a wide variation in this onset. Moreover, when the group was in progression, even 12-month-olds were carried dorsally on 40% of observed occasions.

Yamada and Nakamichi (under review) reported developmental changes in ventral and dorsal carriage by the mother and in the infant's following of its mother in the Katsuyama group. While ventral carriage was most frequently used in the first 4 months after birth, in the next 4-month period (i.e., 5–8 months of age), the occurrences of ventral carriage decreased drastically and those of dorsal carriage increased. In the third 4-month period, following by the infant occurred much more frequently than dorsal carriage; in the fourth 4-month period, the infant's following was still frequently observed, but dorsal carriage was rarely observed and no ventral carriage was observed near the feeding site. In the Katsuyama group, moreover, almost all infants around 12 months of age were found to be carried dorsally at least once a day while they remained near the feeding site, although mothers rarely carried their infants for long distances (Nakamichi, unpublished data). Moreover, some mothers in the Katsuyama group were recorded as carrying juveniles as old as 2 years dorsally, albeit infrequently (Nakamichi, unpublished data). Almost all infants around 12 months of age in the Arashiyama group were also found to be carried dorsally by their mothers (Sukino, personal communication); this was also the case in a provisioned group at Awajishima Island, Hyogo Prefecture (Yamada, unpublished data). More interestingly, some mothers in the Katsuyama group were recorded as carrying one infant ventrally while simultaneously carrying a 1-year-old offspring dorsally (Nakamichi et al. 2004); this was also seen in the Awajishima group (Nakamichi, unpublished data).

In combining these findings from the four provisioned groups, it is a general rule that although infant Japanese macaques around 12 months of age or older are old enough to move by themselves along with group members in mountainous areas, they still seek to ride on the backs of the mothers, albeit infrequently; this tendency indicates that infant Japanese macaques are very likely to be psychologically dependent on their mothers, even after acquiring independence from their mothers in terms of locomotor ability (Nakamichi and Yamada 2009). In other words, clinging to the mother's back allows them to satisfy psychological needs during stressful moments. In fact, when infants and young juveniles show "temper tantrum" behaviors, such as pressing the body to the ground and crying out toward their mothers nearby, they usually stop crying as soon as they are permitted to cling to their mothers' backs.

### *11.2.3 Relationships Between Immature Offspring and Their Mothers*

Some studies of Japanese macaques have examined certain factors that can influence the process by which infants become independent of their mothers with increasing age, including the infant's sex, mother's dominance, and mother's parity. These are well-known traditional factors (Berman 1984); here, we focus on the first two factors, while the third is examined later from the point of view of adult females (i.e., mothers) (see Sect. 11.4.1).

Itoigawa (1973) found that, in the Katsuyama group, female infants spent more time in contact with their mothers' ventral surface than male infants and were restrained and retrieved more frequently than male infants throughout the first

8 months of life. On the other hand, Suzuki et al. (1984), in studying the Arashiyama group, found no consistent differences in mother–infant contact between female and male infants during the first 6 months of life. Tanaka (1989) points out that an infant's sex rarely has a great influence on mother–infant interactions during the first 8 months, as seen in a provisioned group at Shiga Heights, Nagano Prefecture. Nakamichi (1989), who observed all infants of a birth cohort during the first 4 years of life in the Awajishima group, reports that the tendency for female infants to stay close to their mothers more frequently than male infants becomes apparent from the second half of the first year onward. Although male juveniles steadily decreased the time spent near their mothers throughout the first 4 years of life, female juveniles did not show such a decrease after the third year of life; instead, they maintained relatively frequent proximity to their mothers (Nakamichi 1989). Koyama (1991) also notes that at Arashiyama, female juveniles between 2 and 4 years of age groomed their mothers much more frequently than did male juveniles, while mothers groomed their daughters as often as their sons. These findings indicate that the difference in life-course between males who leave the natal group and females who remain in it become apparent in the early juvenile days in terms of their relationship with their mothers.

Some studies conducted on captive groups of macaques have shown that infants of low-ranking rhesus macaque mothers tend to spend more time in contact with and being restrained from their mothers more frequently than those of high-ranking mothers (White and Hinde 1975; Tartabini et al. 1980). However, clear differences in mother–infant interactions that accompany intimate physical contact, in terms of the mother's dominance rank, have not been reported in provisioned, free-ranging groups of Japanese macaques (Suzuki et al. 1984; Tanaka 1989). These findings from different free-ranging but provisioned groups of Japanese macaques indicate that infant sex and the mother's dominance rank might have much less influence on mother–infant interactions – at least under 1 year of age – than previously thought.

On the other hand, in provisioned situations where agonistic interactions occur relatively frequently among animals, often because of a scattering of highly preferred foods such as wheat and soybeans within a limited area or timeframe, immature females of high-ranking kin-groups more frequently remained with their mothers in the same feeding blocks to pick up wheat than those of middle- or low-ranking kin-groups, and this was also true for immature males (Imakawa 1988). These findings indicate that the higher a mother's dominance rank, the more effectively she serves as a secure "base" for her immature offspring of either sex, at least during feeding times (Imakawa 1988).

### *11.2.4 Relationships of Immature Females with Group Members Other than Mothers*

Initially, infant Japanese macaques are completely dependent on their mothers; however, they rapidly increase the amount of time they spend away from their mothers and thus extend their physical and social environments (Itoigawa 1973;

Hiraiwa 1981; Suzuki et al. 1984). Because the birth season of Japanese macaques is limited to a few months from spring to summer (Ando and Ukai 1983; Fooden and Aimi 2003), individual differences in the development of motor skills among infants of the same cohort are rarely apparent. As a result, infants usually begin to extend interactions with each other from around the second month of life onward (Suzuki et al. 1984); throughout the first year of life, they also spend much more time with same-aged infants than with older individuals other than their mothers (Nakamichi 1989). On the basis of social interactions, including social play, among infants in the Arashiyama group, Norikoshi (1974) found that the ranks of infants as young as 12 weeks of age were parallel to those of their mothers. Suzuki et al. (1984) confirm that there is a similar but clearer tendency among infants at the age of 6 months within the same group.

In the Awajishima group, juvenile females aged 2–4 years maintained roughly equal proximity to female group members of various age differences from their own (i.e., immature to adult females) and to infants of both sexes; juvenile males, meanwhile, maintained frequent proximity to males of the same and similar ages (Nakamichi 1989). Moreover, juveniles of both sexes in the Awajishima group showed a consistent preference for proximity within their cohort to certain same sex individuals whose dominance ranks were immediately adjacent to their own throughout the first 4 years of life; such proximity-based relationships between peers of the same sex largely reflected those between their mothers (Nakamichi 1996).

The characteristics for social relationships of immature macaques in the Awajishima group, which were depicted by proximity data, have been witnessed in some other groups of Japanese macaques through actual interactions such as play. At both Arashiyama (Koyama 1985) and Katsuyama (Imakawa 1990; Koyama 1998), females tended to play with individuals of the same age and same sex before the age of 2 years, but thereafter, they tended to play with younger macaques of both sexes; meanwhile, males tended to select individuals of the same age and same sex as play partners in their immature days, with a tendency to decrease frequency of play and decrease the number of play partners with increasing age, regardless of sexes. The tendency for female juveniles to stay near younger individuals, in particular, infants and 1-year-olds of either sex, was also found in a provisioned group in Koshima Islet, Miyazaki Prefecture (Hayaki 1983). Juvenile females in the same group were also reported to have relatively frequent grooming interactions with other juveniles of different ages (Mori 1974).

At Katsuyama, infant-handling, that is, carrying and holding young that are not one's own offspring, was mostly displayed by older juvenile females aged 3 and 4 years (96% of all observed caretaking events); infants under 1 year of age were the most frequent targets of infant-handling (90%) (Imakawa 1993). At Koshima, infant-handling performed by 3- to 5-year-old females accounted for as little as 22% of all caretaking events, while 1-year-old juveniles most frequently (44%) displayed this behavior; 85% of the target animals were infants (Mori 1986). At Boso, 2-year-old females displayed infant-handling most frequently, followed by 3-year-old females and then 1-year-old ones (Hiraiwa 1981). In the captive group at Roma Zoo, juvenile females (aged 1–3 years) and nulliparous adolescent females (aged 4–7 years) displayed infant-handling most frequently (Schino et al. 2003). In contrast, neither adult females with maternal experience nor males showed much interest in the infants of other females. Therefore, the tendency for juvenile females to display infant-handling much more frequently than juvenile males or adult females is common across the different groups, but the age at which female juveniles most frequently display infant-handling differed among the groups.

In summary, across the four provisioned groups of Japanese macaques, juvenile females were inclined to maintain proximity-based relationships with group members who usually formed the center of the group; those females actually tended to interact with younger individuals through social play, grooming, and infant-handling, although still rarely maintaining affiliative relationships with adult females other than their mothers through actual interactions such as grooming. With regard to male juveniles, their inclination to interact with males of the same or similar age was apparent, even before the spatial shifts from the center to the periphery of the group.

These findings from different groups indicate that, without clear intraspecific variations, both female and male juvenile Japanese macaques begin to prepare for their respective adult roles as early as around the second year of life, at which time they are still very likely to maintain frequent proximity to their mothers (Nakamichi 1989). Note that among both female and male juveniles, the process of developing social relationships with other group members could be influenced by the presence or absence of older siblings, because juveniles could acquire more opportunities to interact with elder animals by way of their older siblings (Kojima 1996).

## 11.3 Social Relationships of Adolescent Females with Group Members

The life stage of adolescence is defined as the interval from the onset of puberty to the beginning of effective reproduction (Pereira and Altmann 1985). Therefore, it is difficult to categorize adolescent females with respect to age period, because Japanese macaque females begin to experience first ovulation – one of the internal signs of the onset of puberty – at around 3.5 years of age, but the actual age differs from female to female (Nigi 1982). The same is also true for the age at which females first give birth: it extends from as early as 4 years of age to over 10 years of age, and it greatly depends upon nutritional conditions (Watanabe et al. 1992). Here, whenever possible, we focus on how and with whom nulliparous females aged around 4 years or more socially interacted, compared to females experiencing their first births.

Kudo (1986) classifies adolescent females into three classes in terms of their social interactions with group members: (1) sociable females who have grooming interactions with a relatively larger number of unrelated females, who tend to groom high-ranking females and/or females with an infant or juvenile more frequently than other females; (2) kin-orienting females who concentrate their social interactions on their own close female relatives; and (3) unsociable females who tend to spend little time interacting with group members. Moreover, regardless of typology, each adolescent female had a particular grooming partner who was also an adolescent, but such grooming relationships were likely to disappear after one of the pair gave birth to her first infant. On the basis of these observations at Koshima, Kudo (1986) concludes that the social relationships that each adolescent female formed and maintained with some females might disappear around the time of the first birth, and that new mothers had to reconstruct their social relationships with adult females with offspring. Some primiparous females at Katsuyama were found to interact more frequently with adult females, through affiliative behaviors such as grooming, after giving birth to the first infant, compared to before its birth (Nakamichi, unpublished data). This finding indicates that some young adult females become more social after having their first infant. Grewal (1980) also points out the differences in social interactions between nulliparous and primiparous females aged 4–7 years at Arashiyama.

Yamada et al. (2005) examined the grooming relationships of adolescent females at Katsuyama who had no experience of giving birth and ranged in age from 5 to 7 years, with a special interest in the influence of the loss of the mother on the social development of adolescent females. Although it was expected that the loss of the mother would force orphans to devote less time to grooming interactions than nulliparous adolescent females who still had mothers, orphans without sisters performed grooming interactions as frequently as non-orphans or orphans with sisters; this was because non-orphans maintained grooming interactions with their mothers whereas orphans acquired alternative grooming relationships with other group members. Orphans with sisters developed more grooming relationships with sisters, and orphans without sisters developed grooming interactions with same-aged females and unrelated adult females. Orphans without sisters also had a larger number of grooming partners than did non-orphans. On the basis of these findings, Yamada et al. (2005) concludes that adolescent females have enough social flexibility to develop a grooming network after losing their mothers; in such cases, a lack of close relatives such as mothers and sisters might accelerate socialization among adolescent females.

Mori et al. (1977) report that at Koshima the dominance ranks of nulliparous females were usually lower than those predicted by Kawamura's rules (see Sect. 11.4.3); however, after experiencing the first birth, young adult females tended to acquire the dominance ranks predicted by Kawamura's rules. Because dominance relationships among infants at 12 months of age are parallel to those among their mothers (Koyama 1970; see also Sect. 11.2.4), it is probable that dominance relationsships among same- or similar-aged juvenile females are also parallel to those among their mothers; however, such juvenile females may be still too young to be integrated into dominance relationships among adult females. To stabilize maternal rank inheritance among adult females, it may be necessary for young adult females first to experience a first birth.

The loss of the mother imposes a disadvantage on the daughter, namely, the failure to inherit the mother's dominance rank (Hasegawa and Hiraiwa 1980;

Takahata 1991; Nakamichi et al. 1995a; Kutsukake 2000). On the other hand, the loss of the mother may otherwise benefit orphaned females. Itoigawa (2001) reports that at Katsuyama, two orphaned sisters of a middle-ranking kin-group rose in rank with support from the alpha male, eventually leading to a group fission, in which one group comprising the two orphaned sisters, their relatives, members of other middle- and low-ranking kin-groups, and central high-ranking males became dominant to the other group that comprised females of high-ranking kin groups. In addition, the birth rate of the kin-group of the two orphaned sisters increased. Clearly, adolescent females have great flexibility in the socialization process, allowing some orphaned females to overcome the disadvantage of losing the mother.

## 11.4 Fully Adult Females

### *11.4.1 Maternal Behavior*

Most female Japanese macaques experience their first parturition at the age of 5 to 7 years, with only small differences across provisioned groups (Itoigawa et al. 1992; Koyama et al. 1992; Watanabe et al. 1992). Several studies report differences in maternal behaviors between primiparous and multiparous mothers. Nakamichi et al. (2004) report inappropriate maternal behaviors by a 9-year-old primiparous mother at Katsuyama toward her neonate directly after parturition. Near the feeding site, the primiparous mother was found not to perform maternal behaviors such as licking the neonate’s fur and eating the placenta, although most mothers appropriately perform these behaviors directly after parturition (Nakamichi et al. 1992, 2004; Turner et al. 2010). The mother did not permit her neonate to cling to her; instead, she carried it, holding its trunk with one or both hands. The following day, however, she carried her infant ventrally and nursed it appropriately, as the other mothers did. These observations suggest that some primiparous females may show inappropriate maternal behavior toward their neonates, even within free-ranging groups, but they are very likely to change their maternal behavior quickly so that their neonates can survive (Nakamichi et al. 2004).

Nonetheless, it is a common observation that maternal attitudes toward their infants could differ between primiparous and multiparous mothers, within the normal range. Tanaka (1989) reports that at Shiga Heights a mother’s parity has a great influence on mother–infant interactions. According to Suzuki et al. (1984), compared to multiparous mothers, primiparous mothers tend to spend more time in constant contact with their infants throughout the first 6 months of life, and are also more likely to perform not only protective behaviors such as restraining and retrieving infants but also negative behaviors such as pushing and biting infants, during the first 2 to 3 months of life. These actions indicate that primiparous mothers are very likely to be ambivalent or unstable in terms of maternal behavior. Hiraiwa (1981) also describes inappropriate infant-handling by primiparous mothers at Boso, such as holding an infant upside-down; it is probable that such inadequate or awkward infant-handling by primiparous mothers could result in a lowered infant survival rate. In fact, at Ryozen, Shiga Prefecture, the rate of infant mortality during the first year after birth for primiparous mothers was much higher than that for multiparous mothers (30.0% and 6.8%, respectively; Sugiyama and Ohsawa 1982); the same was also true for the Katsuyama group (12.6% and 9.7%, respectively; Itoigawa et al. 1992). Note that at Boso, the corresponding value for young orphaned mothers who had lost their mothers before reaching adulthood was much higher than that for primiparous mothers who had not (45.5% and 0%, respectively; Hiraiwa 1981).

These findings on mother–infant interactions from different free-ranging but provisioned groups of Japanese macaques indicate that a mother's parity has a great influence on maternal behavior, at least during the first several months of infant life; this holds true across different groups, but a mother's dominance and infant sex do not (see Sect. 11.2.4). However, some studies conducted on rhesus macaques may provide us with another story about maternal behaviors.

Maternal styles that can be characterized by the frequency of certain maternal behaviors, such as higher rejection rate, could bear a greater decisive influence on mother–infant relationships within the normal range. For example, Berman (1990), who observed free-ranging rhesus macaques on Cayo Santiago, reports that the rejection rates for individual mothers were consistent from infant to infant and similar to those of their own mothers, indicating that each female had her own maternal style and that it tended to be transmitted across generations. It is probable that individual females could display higher protectiveness toward their first-born infant than their second- or later-born infants, even within their own maternal style. Therefore, apparent behavioral differences in mother–infant relationships in terms of the mother's parity could appear when we compare two groups of primiparous and multiparous mothers. These findings could also be true for Japanese macaques. Similar to rhesus macaque females, Japanese macaque females are expected to have their own maternal style, with a common tendency for females to display more a protective maternal attitude toward their first offspring within their own maternal style.

Even though each macaque female has her own maternal style, each also has enough flexibility to adapt her caretaking behavior appropriately toward her infants. For example, Japanese macaque mothers were successfully providing appropriate care to infants with congenital limb malformations that resulted in impaired clinging ability (Nakamichi et al. 1983, 1997; Turner et al. 2005). Moreover, a female who had to walk bipedally because of her severely malformed forearms was able to care for her infants (Nakamichi 2002).

### *11.4.2 Infant Mortality and Maternal Responses to Dead Infants*

While infant survival in a free-ranging context is largely influenced by environmental conditions such as food abundance and climate (Izawa 2009), the quality and quantity of care for infants as provided by their mothers could naturally influence infant survival. Therefore, examining infant mortality across different groups may be useful in determining intergroup differences in mothers' caretaking behaviors. This is also true for interbirth interval, because frequent rejections by the mother of her infant can accelerate the weaning process, leading to shorter interbirth intervals (Fairbanks and McGuire 1987).

As shown in Table 11.1, no clear differences were found in the infant mortality and interbirth intervals among three provisioned groups in Arashiyama, Katsuyama, and Awajishima: at all sites, those values were approximately 10% and 1.5 years, respectively. These findings correspond to there being no clear differences in mother–infant relationships across the provisioned groups. On the other hand, the rates of infant mortality for the wild populations were higher than those in the provisioned groups (Table 11.1); this difference is primarily caused by food scarcity among wild populations compared to provisioned groups. Therefore, it is expected that the caretaking behaviors of mothers are quantitatively and/or qualitatively different between wild and provisioned groups. However, behavioral observations of mother–infant pairs in the wild have been so limited that we cannot posit the presence or absence of any such differences between them.

The carriage of a dead infant by its mother seems to be a common observation among almost all researchers of Japanese macaques. This behavior is also observed among other simian primates, both in the wild and in captivity (Nakamichi et al. 1996). However, neither detailed behavioral nor demographical data on the carriage of a dead infant have been available, even for provisioned groups of Japanese macaques. Recently, however, Sugiyama et al. (2009) have reported as many as 157 cases of mothers carrying dead infants in more than 24 years of observation among provisioned groups at Takasakiyama, Oita Prefecture. Generally, 28% of infants who died within 30 days of birth were carried, whereas the corresponding value for infants who died after 1 month of life was as low as 4%, indicating that mothers were more likely to carry their dead infants when the infants died within 1 month of birth.

According to Maestripieri (2001), most cases of infant adoption occurred within the first 2–3 postpartum weeks; he also found that cross-fostering that had been conducted experimentally within the first 2 postpartum weeks had a high probability of success, and that mothers were able to distinguish their offspring from other infants within 3–4 weeks postpartum. On the basis of this evidence, Maestripieri (2001) concludes that the early postpartum weeks comprise the maternal sensitive period, during which mothers are highly motivated to care for their infants. Such enhanced postparturition maternal motivation may be prompted by neuroendocrinal changes related to late pregnancy, parturition, and lactation (Maestripieri 2001). The finding that, regardless of their ages, macaque mothers carried their dead infants most frequently when the infants died within 1 month of birth (Sugiyama et al. 2009), may support the presence of a maternal sensitive period. However, it should be noted that not all mothers necessarily carry their dead infants; among all dead infants, the overall rate of maternal carriage is only 15% (Sugiyama et al. 2009), which seems much lower than generally thought. Moreover, some mothers carried infants who died at around 1 year of age (Izawa 1987; Sugiyama et al. 2009).

**Table 11.1** Infant mortality within 1 year (%), and interbirth interval (years) in provisioned and wild groups of Japanese macaques

| Location | Arashiyama | Katsuyama | Awajishima | Ryozen | Ryozen | Yakushima | Kinkazan |
|---|---|---|---|---|---|---|---|
| Condition | Provisioned | Provisioned | Provisioned | Provisioned | After provisioning was stopped | Wild | Wild |
| Infant mortality within 1 year (%) | 10.3 | 10.2 | 10.0[a] | 18.1[b] | 27.3[b] | 25.0 | 22.7 |
| Interbirth interval (year)[c] | 1.46 | 1.58 | – | – | – | 2.24 | 2.37 |
| Source | Koyama et al. (1992) | Itoigawa et al. (1992) | Nakamichi et al. (1997) | Sugiyama and Ohsawa (1982) | Sugiyama and Ohsawa (1982) | Takahata et al. (1998) | Takahata et al. (1998) |

[a] Infants with congenital limb malformations were excluded

[b] The values did not include male infants

[c] Average interbirth interval following surviving infants

Therefore, the carrying of a dead infant might be related not only to the neuroendocrinal state of the mother within the first postpartum month but also to idiosyncratic factors such as maternal style.

### *11.4.3 Dominance Relationships Among Adult Females*

Kawamura (1958), who observed a provisioned group consisting of 29 animals at Minoo, Osaka Prefecture, in 1958, found that among 11 females over 3 years of age, a mother was dominant to her daughter in six of seven mother–daughter dyads, and that younger sisters were dominant to their older sisters in all four sister–sister dyads (Table 11.2). On the basis of these findings, Kawamura first posited two rules about dominance relationships among adult female Japanese macaques: (1) females acquire the rank just below that of their respective mothers, and (2) sisters rank in inverse order of age. These two principles have been referred to as “Kawamura’s rules.” Moreover, he noted that all individuals of one kin-group were collectively ranked above or below individuals of other kin-groups. He was unsure whether his two rules were necessarily applicable to groups much larger than the Minoo group, but Koyama (1967, 1970) confirmed the applicability of Kawamura’s rules to the Arashiyama group, which included as many as 50 adult females (Table 11.2). Twelve years after Koyama’s studies (1967, 1970), Takahata (1988, 1991) again confirmed that the dominance relationships among 62 adult females of the Arashiyama group largely followed Kawamura’s two rules, although deviations were not rare (Table 11.2).

When groups are a little larger than those just mentioned, intragroup differences in dominance relationships among adult females become apparent. In both the Katsuyama group (Nakamichi et al. 1995a) and the Shiga Heights group, which included 74 and 69 adult females, respectively (Kutsukake 2000), the dominance rank order was almost linear, and one female demonstrated constant dominance over the other female in almost all adult female dyads. On the other hand, there were not a few kin dyads whose dominance relationships did not adhere to Kawamura’s rules; they were found in middle- and low-ranking kin-groups, but rarely in high-ranking kin-groups. Moreover, females of high-ranking kin-groups were collectively ranked within their kin-groups, whereas females of middle- and low-ranking kin-groups were ranked separately from members of their own kin-groups. These differences in dominance relationships among adult females, between high-ranking kin-groups and middle- and low-ranking kin-groups, can be caused by differences in cohesiveness among female relatives, which can in turn be assessed in terms of behaviors such as social grooming. In fact, the grooming interactions of females in high-ranking kin-groups at Katsuyama were more evenly spread among related females, while females in middle- and low-ranking kin-groups tended to concentrate in a very small subset of related females (Nakamichi and Shizawa 2003). That is, females of high-ranking kin-groups, each of whom is very likely to interact with most of her female relatives via social grooming, maintained a highly cohesive matrilineal unit that could lead to stable dominance relationships among them, thus following Kawamura's rules. On the other hand, most females in middle- and low-ranking kin-groups limited their grooming to a few of their relatives, which could lead to weak kin-group cohesiveness; in turn, rank reversals between related females could easily occur, contrary to Kawamura's rules.

Two years after the study by Nakamichi et al. (1995a), a strongly linear dominance rank order was still confirmed in the same group at Katsuyama, which included 85 adult females (Nakamichi and Shizawa 2003). However, another 2 years later, when the number of adult females increased to 107, a group fission occurred, producing one main and two branched groups. Before the fission, many circular dominance relationships among females appeared in middle- and low-ranking females, indicating the disappearance of a linear dominance rank order, whereas a perfectly linear dominance rank order from the 1st to the 41st ranked female was confirmed (Nakamichi 1998).

In two groups at Takasakiyama – A and B, which contained 308 and 85 adult females, respectively – many female dyads showed indefinite or unstable dominance relationships, and no linear dominance rank orders were observed among the adult females of either group (Mori 1977).

In combining these findings on dominance relationships among adult females across Japanese macaque groups that vary in size from small to extra large, it is apparent that dominance relationships among adult females are strongly influenced by group size (see Table 11.2). In groups comprising 50 or fewer adult females, dominance relationships adhere almost perfectly to Kawamura's rules: one female is consistently dominant to the other in almost all dyads, females are collectively ranked within their kin-groups, and a clearly linear dominance rank order is apparent. However, as the number of adult females in a group increases, the number of dyads whose dominance relationships do not follow Kawamura's rules tends to increase. In groups including as many as 70 to 80 adult females, dominance relationships similar to those in smaller groups are still maintained in high-ranking kin-groups, whereas females in middle- and low-ranking kin-groups, whose dominance relationships with their female relatives tend to deviate from those expected from Kawamura's rules, were ranked separately from members of their own kin-groups. In much larger groups, a linear dominance rank order is not found, and dominance relationships remain unstable in many dyads.

These changes in dominance relationships among adult females, relative to an increase in group size, could be associated with how often females can interact with most other females in a group and the cognitive ability of Japanese macaques. Because the number of individuals that females often see or with which they directly interact can be limited, it is impossible for those in a large group not only to have frequent interactions with most other females but also to understand the social relationships between most other females; this limitation leads to difficulties in identifying all group members and confirming dominance relationships between themselves and other females, thus resulting in unstable dominance relationships among adult females. This difficulty may be the case with groups that have around 100 or more adult females.

**Table 11.2** Dominance relationships among adult females in different provisioned or wild groups of different populations

| Location | Minoo | Koshima | Awajishima | Arashiyama | | Shiga Heights | Katsuyama |
|---|---|---|---|---|---|---|---|
| Wild/provisioned | Provisioned | Provisioned | Provisioned | Provisioned | | Provisioned | Provisioned |
| The start of provisioning | 1956 | 1952 | 1967 | 1954 | | 1962 | 1958 |
| Group name | Minoo-B | Koshima | Awajishima | Arashiyama | Arashiyama-B | Shiga A-1 | Katsuyama-A |
| Observed year | 1958 | 1970 | 1979–1980 | 1964 | 1976 | 1998 | 1990–1991 |
| Group size | 29 | – | 145+ | 125 | About 230 | 199–218 | 215 |
| Number of adult females | 11 | 23 | 49 | 50 | 62 | 69 | 74 |
| Age in years of adult females | 4 | 5 | 5 | 4 | 6.5 | 6 | 6 |
| Dominance relationships | | | | | | | |
| Percent of dyads in which one individual consistently demonstrated dominance over the other | – | – | – | – | 97.0% | 98.9% | 99.2% |
| Linearity in dominance rank order | Yes | Yes | Yes | Yes | Yes | Yes | Yes |
| Percent of dyads in which mother is dominant to daughter | 85.70% | 83.30% | – | 100% | 89.70% | 87.10% | 88.30% |
| (Number of mother–daughter dyads) | ($n=7$) | ($n=6$) | – | ($n=60$) | ($n=29$) | ($n=31$) | ($n=21$) |
| Percent of dyads in which younger sister is dominant to elder sister | 100% | 84.60% | – | 100% | 72.70% | 72.20% | 75.00% |
| (Number of sister–sister dyads) | ($n=4$) | ($n=13$) | – | ($n=28$) | ($n=44$) | ($n=36$) | ($n=28$) |
| Collective ranking of related females | | | | | | | |
| High-ranking kin-groups | Perfect | High | – | Perfect | High | High | High |
| Middle- or low-ranking kin-groups | Perfect | High | – | Perfect | Partially dispersed | Low | Low |
| Source | Kawamura (1958) | Mori et al. (1977) | Nakamichi (1981) | Koyama (1967) | Takahata (1988) | Kutsukake (2000) | Nakamichi et al. (1995a) |

| Katsuyama | | Takasakiyama | | Yakushima | | | | Kinkazan |
|---|---|---|---|---|---|---|---|---|
| Provisioned | | Provisioned | | Wild | | | | Wild |
| 1958 | | 1952 | | – | – | – | - | - |
| Katsuyama-A | Katsuyama-A | Takasakiyama-B | Takasakiyama-A | P | M | Nina (A) | Kw | A |
| 1992–1993 | 1995 | 1973–1974 | 1973–1974 | 1987–1989 | 1980–1981 | 2001–2002 | 2002 | 2004 |
| 229 | – | 292 | 983 | 15–17 | 27 | 25 | 55 | – |
| 85 | 107 | 85 | 308 | 6 | 7 | 8 | 20 | 17 |
| 6 | 5 | – | – | | 6 | 4 | 4 | |
| 96.7% | – | – | – | – | – | 100.0% | 100.0% | 97.3% |
| Yes | Yes (high-ranking kin groups) | No | No | Yes | Yes | Yes | Yes | Yes |
| – | – | – | – | 100% | 100% | – | – | 100% |
| – | – | – | – | ($n=5$) | ($n=2$) | – | – | ($n = 4$) |
| – | – | – | – | 0% | 0% | – | – | 50% |
| – | – | – | – | ($n=4$) | ($n=3$) | – | – | ($n = 2$) |
| – | High | – | – | – | High | – | – | High |
| – | Low | – | – | – | High | – | – | High |
| Nakamichi and Shizawa (2003) | Nakamichi (1998) | Mori (1977) | Mori (1977) | Hill and Okayasu (1995) | Furuichi (1983) | Ventura et al. (2006) | Ventura et al. (2006) | Tsuji (2007) |

Note that, in contrast to Kawamura's second rule, older sisters were dominant to younger ones on Yakushima, even though the number of adult females in a group was often fewer than 20 (Furuichi 1983, 1986; Hill and Okayasu 1995). We discuss later the dominance relationships on Yakushima (Sect. 11.5; see also Chap. 12).

In most groups other than extra-large ones, dominance relationships among adult females are usually stable for a relatively long period (Itoigawa 1997), but changes in dominance ranks sometimes occur. When a female had a long-term affiliative relationship with a high-ranking male, she could outrank not only her mother and younger sisters but also other higher-ranking unrelated females (Takahata 1991; Itoigawa 2001). Note, however, that an affiliative relationship between a female and a high-ranking male does not always guarantee the female an increase in rank (Takahata 1991). Close relationships between an immature female and a high-ranking male, such as one that provides "paternal care," may lead to her acquisition, when she grows up, of a much higher dominance rank than that expected by Kawamura's rules (Fujii 1983). We recorded at Katsuyama the case of a female from a bottom-ranking kin-group who rose in rank to a middle-ranking position after having frequent grooming interactions with and agonistic support from some members of a middle-ranking kin-group (Nakamichi, unpublished obervations), but it does seem unusual for a female to raise her rank through such an affiliative relationship with unrelated higher-ranking females. Although a female usually rises in rank independently of her relatives (Mori et al. 1977), almost all female relatives raise their ranks collectively at times, which may result in a group fission (Koyama 1970; Oi 1988; Itoigawa 1993).

### 11.4.4 Grooming Relationships Among Adult Females

It has been a common observation that grooming is kin biased and mainly directed up the hierarchy in Japanese macaques. At Katsuyama, the percentage of grooming bouts occurring among relatives of the total number of bouts was 57.6% in 1966–1967, 63.3% in 1977–1978, and 64.9% in 1992–1993 (Oki and Maeda 1973; Ando 1982; Nakamichi and Shizawa 2003), respectively. The corresponding values were 67.9% at Arashiyama (Koyama 1991), and 65% and 92% in wild groups on Kinkazan Island and Yakushima, respectively (Takahashi and Furuichi 1998). These values indicate the tendency for grooming to be kin biased at a group level, but this does not necessarily mean that all individuals of the group preferentially groom relatives. Rather, a Japanese macaque group may include some females who have grooming interactions with unrelated females more frequently than with their related ones. In fact, when grooming bouts among 85 adult females belonging to 16 kin-groups at Katsuyama were analyzed at an individual level, the following were found: a larger number of females showed tendencies for grooming to be kin biased and to be directed up the hierarchy, whereas at least one female in most kin-groups had grooming interactions with unrelated females as often as or more than with related females; and there was also a tendency for grooming to be directed down the hierarchy or to be well balanced (Nakamichi and Shizawa 2003).

The Japanese macaque is categorized as a despotic species among *Macaca* species, in terms of its dominance styles (Matsumura 1999; Thierry 2000; see also Chap. 12). The findings that a large number of females of the Katsuyama group showed tendencies for grooming to be kin biased and directed up the hierarchy corresponded exactly to the fact that the Japanese macaque is despotic. On the other hand, another finding was that the group included some females who showed an egalitarian tendency: grooming was directed down the hierarchy or was well balanced, and it was directed toward unrelated females as often as or more often than toward related females. Females showing such an egalitarian tendency were limited to a small number in each kin-group, but their very presence could play a role in tying together different kin-groups, thus maintaining and promoting the integrity and cohesion of a large group (Nakamichi and Shizawa 2003; see also Topic 7 by Kutsukake).

Biological market theory considers grooming a tradable commodity that can be exchanged either for itself or for other goods, such as various kinds of social tolerance (Barrett et al. 1999). In fact, some studies provide evidence for temporal or short-term relationships between grooming and grooming (Muroyama 1991), or between grooming and other goods such as access to newborn infants (Muroyama 1994; Henzi and Barrett 2002) or a reduction in aggression (Schino et al. 2005). On the other hand, in some female dyads, grooming relationships have continued for years; some other ideas are needed to explain their existence. Nakamichi and Yamada (2007) analyzed the grooming interactions of 18 Japanese macaque adult females who were studied twice, 10 years apart, at Katsuyama. Most females had frequent grooming interactions with closely related females in each of the two observation years; at the same time, they maintained grooming interactions with a few of the same unrelated females in both the first and second observation years. Females tended to maintain long-term grooming relationships for years with unrelated females who were similar to themselves in terms of dominance rank and/or age. On the other hand, long-term grooming relationships were also observed in some dyads where dominance rank reversals occurred between the two females or the dominance rank difference between them was large. It might be difficult to explain the continuity of grooming relationships in these dyads by virtue of biological market theory (Nakamichi and Yamada 2007). Moreover, in some mother–adult daughter dyads in which a daughter outranked her mother, the two individuals continued to select each other as the most frequent grooming partner, both before and after the dominance rank reversal (Nakamichi, unpublished data). Along with biological market theory, therefore, we need to consider other concepts, such as long-term psychological bonding or friendly relationships, to fully understand the existence of long-term affiliative relationships among females.

An episode of social grooming usually includes two animals, one of which is a groomer and the other, a groomee; grooming episodes simultaneously involving three or more animals are much less likely to occur. For example, in the Katsuyama group, the percentage of grooming bouts involving three or more females of the total of all bouts is less than 5% (Nakamichi, unpublished data); this may be

**Fig. 11.2** A grooming group consisting of four adult females and one adult male (*right*), in the Awajishima group of Japanese macaques

because, when two animals simultaneously groom a third one, it is not easy for the subordinate of the two groomers to continue grooming her desired target (i.e., the groomee or the third animal) while maintaining proximity to the dominant who is also grooming the same desired target. However, in the Awajishima group, it may not be unusual to observe grooming interactions simultaneously involving three or more adult females, although quantitative grooming data are not available (Fig. 11.2; Nakamichi and Turner, personal observation). Relatively frequent occurrences of grooming bouts involving three or more individuals indicate that females on Awajishima are so tolerant that they can remain proximate or maintain contact with each other, even when their dominance relationships are clear (Nakamichi 1981).

## 11.5 Tolerance Trait for Female Social Relationships in Yakushima and Awajishima Groups

In this chapter, we describe the female social development of Japanese macaques from infancy to adulthood, on the basis of literature involving free-ranging and provisioned groups, or wild groups; in so doing, we paid attention to intraspecific differences, but we found neither qualitatively nor quantitatively large differences across different macaque groups inhabiting a variety of habitats, with the exceptions of the following two points.

First, at Yakushima, in contrast to Kawamura's second rule, among sisters, the older was dominant to the younger (Furuichi 1983, 1986; Hill and Okayasu 1995), and the grooming time from dominants to subordinates and from subordinates to dominants did not differ (Hanya et al. 2008; see also Ventura et al. 2006). However, other characteristics of female social relationships at Yakushima were largely similar to those in other populations: the dominance rank order was linear, the mother was dominant to her adult daughter(s), and grooming was kin biased (see Table 11.2;

Furuichi 1986). Second, at Awajishima, females showed high levels of gregariousness without frequent agonistic interactions (Koyama et al. 1981); grooming bouts simultaneously involving at least three animals may occur relatively frequently (Nakamichi and Turner, personal observation), while a linear dominance rank order among adult females was confirmed. Unfortunately, it cannot be confirmed whether dominance relationships followed Kawamura's rules, because known kin relationships among adult females were very limited in this group.

Nakagawa (see Chap. 12), who surveyed the literature on different populations of Japanese macaques, found that macaques at Yakushima and Awajishima were considered tolerant in terms of social relationships, compared to other populations; he also points out probable phylogenetic, genetic, and socioecological causes thereof (see also Topic 1). Here, we suggest possible causes for the lack of a "youngest ascendancy" at Yakushima and the tolerant behavioral tendency at Awajishima, both from a developmental aspect.

In "youngest ascendancy," a younger sister can acquire a dominant position over her sister(s) with her mother's support (Kawai 1958; Kawamura 1958). However, if the younger sister becomes independent of her mother at a very early age, it might be impossible for her to acquire a rank position over her older sisters for lack of maternal support. It is well known that Japanese macaque mothers carry infants as old as 12 months or more, at relatively low cost; clinging to the mother's back can allow older infants or younger juveniles to satisfy psychological needs during stressful moments. Therefore, dorsal carriage by mothers could prolong affiliative mother–young offspring relationships that otherwise weaken over time (Nakamichi and Yamada 2009). As discussed earlier (Sect. 11.2.2), the dorsal carriage of infants aged around 12 months or more is usually observed in most Japanese macaque populations; the exception is Yakushima, where infants in the second half of the first year of life were infrequently found to be carried dorsally by their mothers and those in the second year of life were least likely to be so carried (Tarnaud, unpublished data). The earlier independence of an infant from its mother at Yakushima has not been confirmed with quantitative data, in terms of dorsal carriage or other behavioral indices; nonetheless, this tendency would probably explain the lack of "youngest ascendancy" in this population.

From a few months of life onward, infants at Awajishima have sometimes been seen staying in the ventral area of a female other than their mothers, without receiving rejection-related behaviors (Nakamichi 1981; Yamada, unpublished data). In other words, females permit infants of other females to enter their own ventral area, and mothers also permit their infants to make contact with other females. These affiliative interactions between infants and adult females other than their mothers have not been reported in other Japanese macaque populations. The Awajishima group is well known for having high birth rates of congenitally malformed infants (Nakamichi et al. 1997; Turner et al. 2008). Malformed infants find it difficult to spend great amounts of time with other infants in active behaviors such as social play, because of limited locomotor abilities caused by severe limb malformations; instead, they are permitted to spend a great deal of time maintaining physical contact with adult group members. This contact could lead to a relatively higher survival rate among these malformed infants; it could also promote frequent interactions with older juvenile females, in the context of infant-handling (Nakamichi et al. 1983, 1997). Therefore, it may be common for infants at Awajishima to interact affiliatively with group members other than their mothers and for adult females to permit infants to do so. Such a behavioral pattern from the early stages of development can make it possible to develop the tolerance trait, as evidenced by high levels of gregariousness, a lack of agonistic interactions, and social grooming simultaneously involving three or more individuals.

## 11.6 Aged Females

At both Arashiyama (Koyama et al. 1992) and Katsuyama (Itoigawa et al. 1992), the birth rate of female Japanese macaques from around 20 years of age decreases drastically with age, down to nil at 25 to 26 years of age. Similar to the decline in reproductive ability with increasing age, Japanese macaque females aged over 20 years are also very likely to decrease their total time spent in social interactions with other group members and increase time spent alone, showing progressively increasing social isolation with increasing age; this is the case with both the Arashiyama (Nakamichi 1984) and Katsuyama (Kato 1999; Nakamichi 2003) groups. Moreover, such an age-dependent decline in social interaction can be influenced by dominance rank and kinship: females at Katsuyama were more likely to concentrate their grooming interactions on related females with increasing age, and this tendency was more apparent in low-ranking females (Nakamichi 2003). Mitani (1986) also reported that elderly matriarchs in a wild group at Yakushima tended to cease grooming interactions with unrelated females but still continued coo call exchanges with them. Therefore, progressively increasing social isolation with increasing age is observed in terms of visually overt behaviors that accompany tactile interactions such as grooming, but elderly individuals could maintain a level of sociability equal to that from their youth, using other channels that require much less energy, such as vocal interactions.

Decreases in rank or rank reversals may occur with old age. At Arashiyama, two elderly females (i.e., more than 25 years of age) who were in the postreproductive period were outranked by some of their adult daughters, whereas females more than 20 years of age and with immature offspring were not outranked by their daughters (Nakamichi 1984). At Katsuyama, a female maintained her alpha position among adult females until her death at 32 years of age, without being outranked by her mature daughters (Itoigawa, personal communication). Her youngest daughter, who inherited the alpha position at 16 years of age, maintained the alpha position for 16 years until her own death at 32 years of age; at the time of death, she had been nonreproductive for 11 years (Nakamichi, unpublished). The oldest individuals at Katsuyama were 32 years of age; most of the elderly Japanese macaque mothers could maintain their dominance over their daughters, so long as they were in a sufficiently healthy condition to guarantee a daily social life in a group.

According to the “grandmother hypothesis,” postreproductive females can improve the survival of their grandchildren; this in turn enhances the reproductive success of their children, and thus their own inclusive fitness (for a review, see Fedigan and Pavelka 2007). In humans, midlife termination of reproductive ability in females, which does not occur in association with the advanced deterioration of the organism, is universal. Further, in humans, there is sufficient evidence to suggest that postreproductive grandmothers play an important role in the survival of their grandchildren (see Fedigan and Pavelka 2007); in nonhuman primates, however, postreproductive grandmothers are very rare, and the applicability of the grandmother hypothesis to nonhuman primate females is controversial (Fedigan and Pavelka 2001, 2007). Nonetheless, Nakamichi et al. (2010) reports two cases in the Katsuyama group in which elderly grandmothers without dependent offspring played an active role in the survival of their physically and/or psychologically dependent grandchildren. In one case, a 24-year-old grandmother provided essential care (such as holding and carrying) that ensured the survival of her 2-month-old granddaughter for a 6-day period during which the mother had temporarily disappeared for unknown reasons. The grandmother allowed her granddaughter to hold her nipple in the mouth, although she could not produce milk.

In the second case, a 14-month-old granddaughter began suckling on her 23-year-old grandmother within 6 weeks of her mother giving birth to a younger sibling; milk production seemed to be induced in the grandmother within 1 month because of repeated suckling by the granddaughter. For at least 6 months, the grandmother exhibited various patterns of maternal behavior, including nursing of the granddaughter (Fig. 11.3). Most 1-year-old macaque infants cease touching their mothers’ nipples and reduce the amount of time that they spend in contact with their mothers after the birth of younger siblings, whereas some other 1-year-old infants with younger siblings display behavioral depression characterized by reduced activity (Schino and Troisi 2001). We also observed that after a younger

**Fig. 11.3** The grandmother (*left*, 23 years old) is holding her granddaughter (22 months old) while she nurses her. On the *right*, the mother, who is the grandmother’s daughter (12 years old), is nursing her 10-month-old infant

sibling was born, some 1-year-old juvenile Japanese macaques attempted to access their mothers' nipples (Yamada and Nakamichi, unpublished data); some even resumed nursing from their mothers if a newborn sibling died within 1 month of its birth (Nakamichi et al. 2004).

In the second case, the 1-year-old granddaughter frequently attempted nipple contact with her grandmother; the grandmother accepted almost all of these attempts, which led to the satisfaction of the granddaughter's psychological needs (Nakamichi et al. 2010). These results indicate that grandmothers who were probably postreproductive exhibited maternal care behaviors toward their dependent granddaughters and could thereby promote their survival. Nozaki (2009) also reports a case in which a grandmother without dependent offspring, who was not old but middle-aged, became the most frequent grooming partner of her orphaned 1-year-old granddaughter, although she did not perform maternal behaviors such as nursing and carrying.

Because it is very rare for a Japanese macaque female to become a postreproductive grandmother (Pavelka et al. 2002; see Takahata et al. 1998), these two cases might be exceptional. However, it is useful to record these rare or infrequent cases involving postreproductive females to test the "grandmother hypothesis" in terms of the degree to which grandmothers can provide sufficient maternal care to their grandchildren and to describe the flexible and idiosyncratic nature of lifetime social development among macaque females.

## 11.7 Future Research

To clarify lifetime social development among female Japanese macaques, we still need to acquire data that answer the following questions.

First, do mother–infant relationships influence infants' social relationships with group members? If so, in what ways and by how much does the maternal style of each mother influence immature female offspring in developing social relationships with group members – particularly with same- or similar-aged immature females, with some of whom they could continue interacting after maturation? It is well known that each macaque female has her own maternal style (Berman 1990), but it remains an open question whether individual differences in maternal style can lead to differences in social development among their infants.

Second, do young adult females exhibit great change in their social relationships upon giving birth to their first infants? As mentioned earlier (see Sect. 11.3), Kudo (1986) reports that after their first birth, young adult females tend to "reset" affiliative relationships with some group members that they had maintained until then and to form new ones with some other individuals. However, quantitative data on such social changes among young adult female Japanese macaques are rarely available. If the experience of the first birth can trigger an apparent change in a new mother's social relationships, we need to clarify what it is and how it benefits her.

Third is the most important task, but it is also an extremely difficult one: describing with whom and how each female interacts throughout her lifetime in her group, at least from young adulthood to old age. The present chapter mainly focused on relationships among adult females, while those between adult females and males were not addressed (see Topic 7). Takahata (1982) reports the existence of peculiar proximity relationships between some female and male Japanese macaques, and Nakamichi et al. (1995b) report that the alpha female plays a significant role in an aged alpha male's maintenance of his dominance. Moreover, Nakamichi and Yamada (2007) report that long-term grooming partnerships are often maintained for years, even between unrelated females. However, there is a dearth of sufficient quantitative data to evaluate the benefits to females of maintaining these long-term affiliative relationships, even although the existence of long-term affiliative relationships among female baboons and the adaptive significance for females have been reported (Silk et al. 2006a,b). Thus, we need to conduct longitudinal observations to exemplify with whom, how, and for how long each female maintains affiliative relationships, not only with females but also with males; we also need to examine how and with whom she forms new affiliative relationships upon losing her familiar social partners, while paying particular attention to rarely observed incidents among macaques living in complicated but well-organized groups.

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