

Chapter 12

Behavior and Social Dynamics of Rhesus Macaques on Cayo Santiago

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12.1 Introduction

Rhesus macaques are Asian primates with a current geographic distribution that encompasses many countries such as Afghanistan, India, Thailand, China, Pakistan, Bhutan, Burma, Nepal, Bangladesh, Laos, and Vietnam. They thrive in almost any type of habitat, including tropical forests, dry and semidesert regions, swamps, and mountains up to 4,000 m high. In some countries such as India, free-ranging rhesus macaques also live in highly populated urban areas including villages, towns, temples, and railway stations. Although rhesus macaques can be found in large numbers and, in many cases, are easily accessible for observations, studies of free-ranging rhesus macaques in Asia have mainly focused on population biology, demography, and geographic distribution and much less on behavior and ecology (e.g., Southwick and Siddiqi 1994).

Much of our knowledge of the behavior, life history, and social dynamics of rhesus macaques comes from studies of the population on Cayo Santiago, a small island off the coast of Puerto Rico. Clarence Ray Carpenter, an American biologist who established the rhesus monkey colony on Cayo Santiago in 1938, began studies of social and sexual behavior soon after the monkeys were transplanted onto the island (Carpenter 1942a, b), but such studies were suspended during World War II. Stuart Altmann, a Harvard graduate student supervised by E. O. Wilson, is credited with the resumption of behavioral studies on Cayo Santiago in the late 1950s and

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early 1960s. Studies by Altmann and later by Conaway, Koford, and Sade provided the first systematic description of rhesus macaque behavior and social organization (Altmann 1962; Conaway and Koford 1965; Koford 1965; Sade 1972). These researchers began to recognize and track individual monkeys to gather information on births, deaths, and migration and on patterns of spatial association, affiliation, and aggression. By identifying and studying individuals, they learned that rhesus macaque society was organized around male dispersal, female kinship, and dominance relationships. Continued observations of rhesus macaques on Cayo Santiago up to the present day have provided a detailed understanding of their behavior and social dynamics. The information provided by research conducted with this population has generally been confirmed and supplemented by behavioral studies conducted in other research facilities as well as by studies of free-ranging rhesus macaques in India, Nepal, Pakistan, and other Asian countries (e.g., Southwick et al. 1965, 1982, 1996; Neville 1968a, b; Mukherjee 1969; Teas et al. 1980, 1982; Pearl and Schulman 1983; Marriott 1988; Goldstein and Richard 1989).

The rhesus macaque population on Cayo Santiago, however, differs from other captive and free-ranging populations in some aspects of its structure and internal dynamics. Whether the unique characteristics of the Cayo Santiago population translate into differences in the behavior of individuals, or in within-group or between-group behavioral dynamics, is an issue that has not been systematically addressed.

In this chapter, we will first review and summarize our knowledge of the species-typical social organization and behavior of rhesus macaques, using information that appears to be consistent across different populations, environments, and geographic areas where rhesus macaques have been studied (see Maestriperi 2007, 2010). We will then examine the unique ecological and demographic characteristics of the Cayo Santiago population and discuss how these characteristics may result in differences in social dynamics and behavior between the Cayo Santiago macaques and their wild counterparts.

12.2 Species-Typical Social and Behavioral Characteristics of Rhesus Macaques

12.2.1 Social Organization and Life History

Rhesus macaques live in social groups composed of a few adult males and many adult females and their offspring. The adult females and immature individuals within a group belong to several different matriline, i.e., families of individuals related through the maternal line. The matrilineal structure of rhesus groups results from sex-specific patterns of dispersal and philopatry: males emigrate from their natal group at puberty and join a new group, whereas females remain in their natal groups throughout their lives (e.g., Lindburg 1971; Sade 1972). Within a matriline, there can be four to six overlapping generations of individuals. For example,

a 10-year-old female's mother, grandmother, great-grandmother, offspring, and grand offspring may simultaneously be present in a group. The adult males in the group are generally unrelated to all other adults because they immigrated by themselves from another group.

Males emigrate from their natal group around the time they reach puberty. In their natal group, young males receive increasing amounts of aggression from both resident adult males and adult females, particularly when they attempt to mate with females (e.g., Colvin 1986). Aggression and lack of opportunities for mating eventually result in emigration. Young males may also be sexually attracted to females from other groups. By emigrating from their natal group, rhesus males minimize the risk of inbreeding and maximize their chances of mating success. When rhesus males emigrate, they usually do so alone, although in some cases two brothers may emigrate together (e.g., Meikle and Vessey 1981). After spending several months, or even years, alone or as part of a small all-male group, rhesus males join a new group. They can stay in the new group for several years, after which they may leave and try to join another group (e.g., Drickamer and Vessey 1973).

The size and demographic composition of a rhesus macaque group are influenced by rates at which infants are born, their age-specific patterns of survival and mortality, the ages at which individuals begin and cease reproducing, how frequently they reproduce, and patterns of immigration and emigration. Male and female infants are generally born in equal numbers, although small deviations in the birth sex ratios can occasionally arise in relation to variations in local environmental conditions (Rawlins and Kessler 1986; Berman 1988). Infant mortality is generally high, especially for males (Hoffman et al. 2010). If infants survive their first year, however, their probability of mortality drops dramatically (Hoffman et al. 2010). Females reach puberty at 3–4 years of age, while males do so 6–12 months later. Both females and males continue growing after puberty, and adult body size is typically reached between 5 and 6 years of age. Post-pubertal females can reproduce once every year, every other year, or less frequently. Female reproductive rates typically decline with old age, but it is unclear whether menopause occurs (Hoffman et al. 2010). Males, at least in theory, can reproduce multiple times every year. Mating activity is concentrated in a 5–6 month period (mating season), while infants are born and raised by their mothers in a subsequent 5–6 month period (birth season) (Hoffman et al. 2008).

The maximum life span for rhesus macaques in captivity is 35 or 40 years but is much lower in free-ranging populations (see below). As with other mammals, males have higher mortality rates than females at any age (e.g., Sade 1980). Adult mortality is significantly affected by reproduction. In general, adult males are more likely to die during the mating season, whereas adult females are more likely to die during the birth season (Hoffman et al. 2008). Sex differences in seasonal patterns of mortality reflect the survival costs of reproduction, which differ for males and females in a sexually promiscuous species such as the rhesus macaque. Mating effort is the most costly aspect of reproduction for males, and pregnancy and lactation are the most costly aspects for females. Increased male mortality during the mating season likely results from high vulnerability to infectious diseases due to mating-related male–male aggression and wounding in conjunction with testosterone-induced suppression of the immune system (Hoffman et al. 2008). Increased female mortality

during the birth season may be the result of pregnancy or delivery complications, or due to pregnancy- and lactation-related energetic stress, psychosocial stress, and stress-related immunosuppression (Hoffman et al. 2008).

12.2.2 Dominance

Rhesus macaques are aggressive and xenophobic primates, who have a strong tendency to attack unfamiliar conspecifics (Maestriperi 2007). In general, the first fight between two individuals can establish a stable dominance relationship between them: the winner of the fight will be dominant and the loser will be subordinate. After dominance is established, the subordinate individual generally avoids the dominant or expresses fear and submission in his/her presence. The dominant attacks the subordinate occasionally, and this will maintain or reinforce the dominance relationship between them. In many cases, the dominant's aggression consists of ritualized threats, to which the subordinate responds with submissive signals (e.g., Bernstein and Ehardt 1985).

Every rhesus macaque has hierarchical relationships with every other individual in the group, and such relationships are generally transitive; that is, if individual A is dominant over B, and B is dominant over C, A is also dominant over C. As a result of these dominance relationships, all individuals within a group are ranked on a linear hierarchy, and the individual's position in the hierarchy is called dominance rank. The highest-ranking male and female are called the alpha male and the alpha female, respectively. The alpha male outranks all other individuals in the group, and the alpha female outranks all of the females and most of the males with the exception of the alpha male (e.g., Bernstein and Williams 1983).

Females maintain stable dominance ranks within their natal groups throughout their lives, whereas males lose their original rank when they leave their natal group at puberty and acquire a new rank when they join a new group. Males who have joined a new group are typically lower ranking than the other adult male residents in the group. They gradually work their way up the hierarchy by making alliances with powerful males and females (Manson 1998). Females who belong to the same matriline have similar dominance ranks. In particular, closely related females, such as mothers and daughters or pairs of sisters, occupy adjacent positions in the dominance hierarchy. Mothers typically remain dominant over all of their daughters throughout their lives, while sisters rank in reverse order of their age, such that young females dominate their old sisters and a female's youngest daughter typically is the most dominant of her female offspring (Chikazawa et al. 1979). In addition to individual ranks within a matriline, dominance relationships also exist between matrilines. Each group of rhesus macaques has a top-ranking matriline, a bottom-ranking matriline, and other matrilines that rank between them. High-ranking matrilines tend to be larger than low-ranking matrilines (e.g., Ehardt and Bernstein 1986).

The hierarchical relationships between individuals and between matrilines are ultimately determined by the mechanisms through which dominance rank is transmitted

across generations. These transmission mechanisms are not genetic, but social, and involve agonistic support given by mothers to their offspring (e.g., Bernstein and Williams 1983; Bernstein and Ehardt 1986; Datta 1986). Natal males acquire ranks from their mothers just as females do. Mothers consistently intervene on behalf of their immature offspring when offspring get into fights with other group members. When pairs of juveniles fight, the mothers of both juveniles intervene to support their offspring, and the outcome of the fight is ultimately determined by the relative ranks of the mothers. Since this process is repeated many times and with different individuals, offspring eventually acquire a dominance rank just below that of their mother (Datta 1986). Although juveniles are initially lower ranking than all adults within the group, juveniles will challenge every adult that ranks lower than their mother. With their mother's support, they will eventually outrank these individuals. Dominance relationships between sisters are also settled by maternal intervention, as mothers always support their younger daughters against their older sisters (Datta 1986). More specifically, young females are initially subordinate to their older sisters but, around the time of puberty, they outrank them with their mother's help (Datta 1986). Rank reversals between mothers and daughters, or between adult sisters, are possible but rare (Chikazawa et al. 1979). They are likely to occur between sisters if their mother dies before the youngest sister reaches maturity.

Agonistic support between relatives is used not only to transfer dominance rank to juveniles but also to help females maintain their rank in adulthood. Agonistic support between nonrelatives is less frequent but plays an important role in social dynamics, particularly for males. Adult males rise in rank through the formation of coalitions with unrelated males or females (Datta 1986; Manson 1998; Higham and Maestriperi 2011). Furthermore, both adult males and females maintain and reinforce their status by intervening on behalf of unrelated individuals whenever these individuals attack males or females that are lower ranking than themselves. Agonistic support is solicited with scream vocalizations, particular facial expressions (raised eyebrows and eye movements), and body postures (tail raising and hindquarter presentation) (Gouzoules et al. 1984). Agonistic support is also obtained in exchange for grooming behavior, as grooming a higher-ranking individual for extended periods of time increases the probability of receiving tolerance and agonistic support from this individual (Schino 2007).

12.2.3 *Affiliation*

The strength of social bonds between individuals in a rhesus macaque group is generally predicted by their kinship, sex, and age (e.g., Lindburg 1971). Measures of the strength of social bonds include the amount of time spent in close proximity, physical contact, or engaged in grooming behavior. The strongest social bonds are between mothers and infants. Mothers and juvenile daughters also have strong bonds, as do sisters and other closely related adult females. Males are strongly bonded to their mothers as infants and to other young or adult males as juveniles or

subadults. Adult males who have no family members in their group form temporary social bonds with females in estrus, in which spatial association and affiliation are accompanied by mating (Lindburg 1971). Adult males generally do not associate with their offspring or show paternal behavior.

Social grooming, or allogrooming, is the main affiliative behavior used by rhesus macaques to establish and cement social relationships with one another. Grooming involves slowly brushing the coat of another individual and removing skin parasites and other particles with the fingertips. Grooming serves a hygienic function and also relaxes the recipient. A rhesus macaque can request grooming from another individual by lip smacking to encourage the other individual to approach and then by lying down in front of the other, often exposing the part of the body that needs to be groomed. Grooming can last a few seconds, minutes, or, occasionally, over an hour. Compared to males, rhesus macaque females generally give and receive more grooming (Drickamer 1976). Infants receive a great deal of grooming from their mothers beginning on their first day of life, but they rarely groom their mothers or other individuals in the first 6–8 months of life. Rates of grooming performed increase with age in both males and females, but sex differences emerge during the first year of life when females start performing more grooming than males (Drickamer 1976). Juvenile females increasingly groom both older females and younger individuals, and grooming of males increases dramatically after puberty. Females continue to groom their female relatives, particularly their mothers and sisters, at high rates into adulthood, but after they give birth, a large fraction of their grooming is directed to their offspring. At 3–4 years of age, juvenile males seek out adult males and maintain one-sided grooming relationships with them (Drickamer 1976). Young males shift from grooming older males to grooming females after puberty and around the time of emigration; in other words, they mostly groom males prior to departure from their natal group, and they mostly groom females after immigration into a new group. Prior to emigration, males receive grooming mostly from their mothers, and after immigration they receive grooming from unrelated females that are potentially their sexual partners. Grooming between adult males is much less frequent than grooming between adult females, particularly during the mating season (Drickamer 1976).

12.2.4 Mating

During the mating season, females have estrus periods, which usually last 5–10 days, around the time of ovulation. Adolescent females exhibit exaggerated sexual swellings during estrus periods, whereas adult females advertise their fertility through a reddening of the facial and anogenital skin and through behavioral solicitations of copulation. During female estrus periods, male and female macaques form temporary social bonds called consortships, which include proximity maintenance, grooming, and repeated copulations (Gordon 1981; Wilson et al. 1982). The male and female follow each other around and spend a lot of time sitting next to and grooming each other; the female frequently solicits copulation by presenting her hindquarter

to the male and the male responds by mounting her. Consortships may last from several hours to a few days. Rhesus males need multiple mounts (about ten or more) to achieve ejaculation, although subordinate males can occasionally ejaculate after a single, very brief mount. During consortships, dominant males guard female partners to prevent other males from approaching and mounting them (Gordon 1981; Wilson et al. 1982). The alpha male, however, often disrupts the consortships of other males. When a consortship ends, a female can begin consorting with a different male. Females may consort and copulate with several different males within an estrus period or even on the same day. Males are sexually promiscuous as well, and adult males and females mate, on average, with a similar number of partners (Gordon 1981).

Despite this promiscuity, rhesus macaques do not mate indiscriminately, and pairings are not simply the result of intrasexual competition for mates. Instead, it is very likely that partner choice plays an important role in the formation of consortships and more generally in the occurrence of all mating activities. Mate choice, however, is a poorly understood phenomenon in rhesus macaques (Manson 1995). Kinship and familiarity are the variables whose effects on mate choice are perhaps best understood. Neither males nor females tend to be sexually attracted to genetically related individuals or to unrelated individuals who are very familiar to them. Young males who have not yet left their natal group become increasingly attracted to females from other groups and attempt to follow them. Similarly, females are attracted to novel males and may leave their group temporarily to consort with peripheral or extra-group males. Although females also mate with the alpha male and other unrelated males within their group, they typically do not mate with males with whom they have a strong affiliative relationship (“friendship”; Manson 1995). Furthermore, females seem to develop a sexual aversion for males that have been in their group for 3–4 years or longer. This could be a proximate factor promoting male departure from the natal group at puberty and further migration after a few years of residence in a group. Attraction to novel individuals and aversion to mating with relatives and friends are behavioral adaptations that function to minimize the risk of inbreeding (Manson and Perry 1993).

Another variable whose effects on mate choice are relatively well understood is age. In rhesus macaques, both males and females tend to mate preferentially with middle-aged individuals in their reproductive prime rather than with sexually mature adolescents or very old but still fertile individuals (Manson 1995). Effects of dominance rank on female or male mate choice are generally weaker than those of familiarity and age. Although in some cases both males and females have been observed to mate more frequently or have longer consortships with high-ranking partners, in other cases there seemed to be proximity and mating preferences for low-ranking individuals (Manson 1995).

12.2.5 Maternal Care and Life Span Development

Pregnancy in rhesus macaques lasts about 5.5 months. Females typically give birth to a single infant; twins are rare and their probability of survival is very low. Mothers

are the main caretakers of their offspring, receiving no help from the offspring's father or other family members (e.g., Hinde and Spencer-Booth 1967). Newborn infants spend a great deal of time nursing or sleeping on their mother's chest. For the first several months post-birth, mothers carry their infants ventrally or dorsally while they travel. During the time devoted to resting or social activities, however, infants spend increasing amounts of time out of physical contact with but in close proximity to their mothers. During this time, young infants explore the environment or play with other infants. Young infants also receive much attention and grooming from juvenile and adult females. Mothers may restrict and control their infants' activities by physically restraining them and by making contact with them frequently (e.g., Hinde and Spencer-Booth 1967).

During the first few weeks of infant life, mothers are almost entirely responsible for maintaining contact and proximity with their infants. For example, infants tend to break contact and walk away from their mothers, while mothers follow them and reestablish contact. During the second or third month of infant life, however, responsibility for maintaining contact and proximity shifts to infants (Hinde and Spencer-Booth 1967). Therefore, mothers frequently break contact and walk away from their infants, while infants follow their mothers and make contact with them. In addition to breaking contact with infants more and more often, mothers also increasingly reject their infants' attempts to make contact and gain access to the nipples (Hinde and Spencer-Booth 1967). In doing so, mothers encourage their infants' independence and reduce the energetic costs involved in carrying them around.

Although changes in maternal behavior in relation to infant age are observed in all mothers, individual mothers differ from one another in the frequency with which they cradle or groom their infants, make or break contact with them, or restrain or reject them. Individual differences in maternal behavior are consistent over time and across different infants (Hinde and Spencer-Booth 1971). These differences are accounted for by characteristics of the mothers (e.g., their age, previous maternal experience, dominance rank, and personality), those of their infants (e.g., age and sex), and those of the surrounding environment (e.g., availability of food, risk of predation, risk of aggression, and risk of infant kidnapping by conspecifics) (Hinde and Spencer-Booth 1971).

Infants begin eating solid food in the first few months of life and are generally weaned by the end of the first year. Six months after giving birth, mothers may resume their menstrual cyclicity, mate, and conceive again. Infants actively resist weaning by responding to maternal rejection with screams and tantrums. They also interfere with their mother's mating activity and, in some cases, successfully delay conception and the birth of a sibling (Simpson et al. 1981). High-ranking mothers often produce an infant every year, while low-ranking mothers may give birth only every other year (e.g., Gomendio 1990). These differences in reproductive rates may result from differences in maternal behavior, as high-ranking mothers generally reject their infants earlier and at higher rates than low-ranking mothers (Gomendio 1990). Limitation of suckling activity through maternal rejection reduces the length of lactational amenorrhea and increases the probability that the mother will conceive again during the mating season. The birth of a sibling accelerates

the acquisition of independence for a 1-year-old rhesus monkey. As they become more independent, young males spend increasing amounts of time in rough-and-tumble play with their peers, while young females become increasingly interested in exchanging grooming with older female relatives or in playing with infants.

The sex differences in behavior that emerge at the end of the first year of life, or earlier, become more marked in the second and third years of life, when young males affiliate mostly with same-age or older males, while females become more embedded in the social networks of their matriline (Hinde and Spencer-Booth 1967). In adulthood, male and female behavior is strongly affected by the alternation of the mating and the birth seasons. During the mating season, males have competitive and aggressive interactions with other males, while attempting to consort with estrous females. During the birth season, adult males spend much of their time alone, or occasionally affiliate with other males (Chapais 1986). Females maintain strong bonds with their female relatives throughout the year. During the mating season, they also spend time consorting with males, while during the birth season their attention is primarily focused on their own and other females' infants. As males get older, they experience a sharp decline in their mating and social activities and spend more and more time alone (Corr 2000). Old females become less attractive as mating and social partners, the size of their social networks becomes smaller, and they focus most of their attention on their closest relatives, particularly their immature offspring (Corr 2000).

12.3 Unique (or Potentially Unique) Characteristics of the Rhesus Macaque Population on Cayo Santiago Relative to Other Rhesus Populations

The description of rhesus macaque social organization, life history, and behavior provided in the previous sections of this chapter can be considered species typical and applies to rhesus groups and populations living in different geographic areas and environments. Particular populations of rhesus macaques, however, can exhibit unique social and behavioral characteristics as a result of the ecological characteristics of the habitat in which they live and their own particular demographic structure. Although the rhesus macaque population on Cayo Santiago probably shares some demographic similarities with the rhesus macaque populations that live in urban areas in Asia (e.g., in terms of size of groups and the impact of food provisioning on behavior; Singh 1969), the Cayo Santiago macaques probably differ from the forest-dwelling rhesus macaques in Asia in a number of ecological and demographic variables. Such differences can potentially translate into differences in social behavior at the individual and group level.

Assuming that the forests of India, Nepal, Pakistan, and other Asian countries in which rhesus macaques currently live represent the closest representation of the habitat in which these primates evolved, Cayo Santiago differs from this environment in three major ecological variables: food provisioning, absence of predators,

and restricted home ranges. Food provisioning and absence of predators are associated with reduced risk of mortality and increased longevity in the Cayo Santiago population. Although no data are available for wild rhesus macaques, studies of other wild cercopithecine monkeys have suggested that it is rare for adults to live beyond 10–15 years. Among the free-ranging rhesus macaques on Cayo Santiago, half of adult females die between 15 and 25 years of age, with the maximum life span being around 31 years (Hoffman et al. 2010; Maestripieri and Hoffman 2011). Although adult males on Cayo do not live as long as adult females, when compared to wild rhesus populations, the effects of food provisioning and the absence of predators on adult survival (Hill 1999) are likely to be even stronger for males than for females. In macaques and other cercopithecine monkeys, risk of mortality is especially high when males spend time alone, either while they migrate from one group to another in adolescence or when they are evicted from their new group later in life (e.g., Sugiyama 1976). Being alone is risky because of the difficulty of finding food and the increasing vulnerability to predation. On Cayo Santiago, where these risks are nonexistent, there are many more adult males in the population than there would be in the wild, and many more of these males spend time alone without a permanent affiliation with a group (Berard 1990). Even though many more males than females are culled from the Cayo Santiago population every year, the presence of supernumerary males still represents a significant alteration in the demographic structure of the population and exerts a potentially important influence on behavior (see below).

In addition to affecting mortality and demography, lack of predation and food provisioning, along with restricted home ranges, can also have more direct influences on behavior. In the wild, vigilance for predators is crucial for survival and may represent an important constraint on social activities (Cords 1995). The rhesus macaques on Cayo Santiago are probably much less vigilant for predators than their wild counterparts, and their social activities are much less disrupted by anti-predator alarm calls and the need for quick dispersion. Therefore, reduced vigilance associated with lack of predators on Cayo Santiago may result in greater amounts of time available for social interactions and, therefore, higher frequencies and longer durations of such interactions (e.g., Marriott 1988).

The rhesus macaque groups on Cayo Santiago have distinct home ranges on the island and travel along particular paths within these areas on a daily basis, just as wild macaques do. The home ranges of the Cayo Santiago macaques are much smaller than in the wild. Because of food provisioning and restricted home ranges, the Cayo Santiago macaques spend much less time traveling and foraging and more time resting and engaging in social interactions than their wild counterparts (Marriott 1988). Food provisioning and restricted home ranges on Cayo Santiago also result in more frequent encounters and displacements between groups and more frequent aggression (see also Hill 1999, for Japanese macaques).

Increased aggression, both between and within groups, is especially frequent during feeding times, inside and around the feeding corrals where the food is distributed. Although feeding times and locations can be excluded from

behavioral data collection, it has been suggested that feeding-related aggression in food-provisioned macaque populations affects the social interactions between group members outside of the feeding context (Hill 1999). For example, social relationships between adult males in food-provisioned macaque populations may generally be more tense and competitive (with low frequencies of affiliation and high frequencies of aggressive and submissive behavior) than in wild populations (Hill 1999). Although adult males on Cayo Santiago occasionally affiliate with one another, especially during the birth season (Chapais 1986; Hill 1986), it is possible that male–male affiliation is less prominent in this population than in wild rhesus populations. Tense and competitive relationships between adult males on Cayo Santiago may also explain why these males form coalitions against other males or females less often than is observed in wild populations of other macaque species (e.g., Barbary macaques; Widdig et al. 2000; but see Higham and Maestriperi 2011, for recent observations of male–male revolutionary coalitions on Cayo Santiago).

The behavior of adult males on Cayo Santiago may be different from that of their wild counterparts not only because of the high number of males and their competitive relationships but also because of differences in migration patterns. On Cayo Santiago, opportunities for male dispersal are limited, and some males remain and mate in their natal groups or return to their natal groups later in life. As a result, all groups in the population contain a few natal adult males, some of which belong to the dominant matriline and are therefore themselves high ranking (Chapais 1983). Although some studies have reported that mating between close kin, such as mothers and their adult sons, may occur, it is rare and generally less than expected by chance (Sade 1968; Manson and Perry 1993). As previously mentioned, females show strong sexual aversions to related males based on familiarity cues such as proximity, and these aversions are effective in preventing incest even in groups in which the natal adult males are sexually active.

Regardless of the occurrence of incestuous mating, the presence of some natal males within a group can potentially alter the social dynamics and the rank relationships between males and females, particularly in cases in which natal males are high ranking (Chapais 1983; but see Manson 1993). Since high-ranking natal males continue to receive support from their mothers and other family members, opportunities for other non-natal males to achieve high rank may be lower than if no natal males had been present. If high-ranking natal males support their mothers and other close relatives against others, this can also result in significant alterations in social dynamics within their matriline as well as in the dominance relations between matriline. One possible difference between the Cayo Santiago and wild populations concerns the acquisition of alpha male status. Studies of wild populations of long-tailed macaques have shown that adult males who have recently immigrated into a new group pursue one of two different strategies to try to achieve alpha status (van Noordwijk and van Schaik 1985, 1988, 2001). Some males challenge the alpha male directly at the time of immigration; if they defeat him, they inherit his status and take over the group. Males who pursue the second strategy enter the male dominance hierarchy in the new group at the bottom and slowly work their way up the

ranks. These two different strategies have been reported also for wild rhesus macaques in Asia (Neville 1968b; Lindburg 1971), although they are not as well documented in rhesus as in other species. In the Cayo Santiago rhesus population, however, there is no evidence of males pursuing the first strategy; males generally join the group at the bottom of the hierarchy and accept a “seniority system” in which a male’s rank is a function of how long he has resided in the group (Berard 1990; Manson 1998). Recently, however, middle-ranking rhesus males on Cayo Santiago have been observed to form multi-male coalitions that resulted in significant changes in the dominance hierarchy including the eviction of the alpha male from a group (Higham and Maestriperi 2011).

Differences in group and matriline size between the Cayo Santiago and other rhesus populations may be the source of potential differences in female social behavior. In the period 2005–2010, the Cayo Santiago population has consisted of 900–1000 individuals divided into only six groups, which range in size from 70 to 300 individuals. In addition, these groups contain only a few, very large matriline (e.g., group R, $n=280$, currently contains only three matriline). Clearly, groups and matriline are much larger on Cayo Santiago than in the wild, and this may have consequences for female behavior. For example, the influence of matrilineal kinship on the distribution of female grooming and agonistic support within the group may be greater on Cayo Santiago than in other wild populations. Early studies in Cayo Santiago evidenced differences in maternal behavior and in early social development in relation to matriline and group size (Berman 1983; Berman et al. 1997; see also Blomquist 2009). Mothers may be more or less permissive of their infants’ social interactions, depending on the extent to which they are surrounded by kin and enjoy their protection and support. Infants’ social interactions with others, in turn, may differ in the extent to which they are biased toward their kin, depending on maternal care received and the size of the matriline and group to which they belong.

Although the processes of rank acquisition and maintenance are likely to be similar in all rhesus macaque populations, the benefits and costs of being high ranking versus low ranking may differ in relation to demographic variables. In a group of 20–30 individuals with several small matriline, a female belonging to the second-highest-ranking matriline may have only three or four females above her in the hierarchy and receive relatively low rates of aggression. In a group of 120 individuals and only three matriline, however, a female belonging to the middle-ranking matriline may be outranked by 30 or 40 other females and receive as much aggression as a low-ranking female. In this group, rank can be beneficial only to females in the top-ranking matriline. Accordingly, on Cayo Santiago, middle- and low-ranking females have equally high cortisol responses to stress when compared to high-ranking females (Maestriperi and Hoffman 2011), suggesting that both middle- and low-ranking females experience chronic social stress due to the aggression received. Rank-related chronic stress results in accumulation of allostatic load especially during aging, suggesting that social variables can have potentially important effects on longevity, health, and reproduction toward the end of the life span (Maestriperi and Hoffman 2011).

12.4 Conclusions

Differences in ecological variables such as food provisioning, absence of predators, and restricted home ranges between the Cayo Santiago macaques and their wild counterparts are associated with differences in the demographic structure of the populations, which in turn, may affect social dynamics and behavior. In addition, the ecological characteristics of the Cayo Santiago population affect the time budgets of rhesus macaques and increase the time available for social activities with conspecifics. Consequently, the frequencies of affiliation, aggression, and other social interactions, both within and between groups, may be much higher on Cayo Santiago than among macaques living in Asian forests. Food provisioning in itself can be associated with increased between- and within-group aggression. The presence of supernumerary adult males on Cayo Santiago, their limited opportunities for dispersal, and the tense and competitive nature of male–male relationships may result in potential alterations in the patterns of mating behavior within groups and in the mechanisms by which adult males rise in rank. Finally, the large size of groups and matriline on Cayo Santiago may be associated with differences in female social networks, the benefits and costs of high versus low rank, and differences in maternal behavior and social development. Although Cayo Santiago represents in many ways an ideal site for studies of social dynamics and behavior, the unique ecological and demographic characteristics found on this island suggest that caution should be used when extrapolating findings from this population to other populations of the same or other primate species. The same caution should also be used in studies of other primate species, as differences between populations in predation pressure, food availability, or demographic structure could result in significant differences in behavior and social dynamics.

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