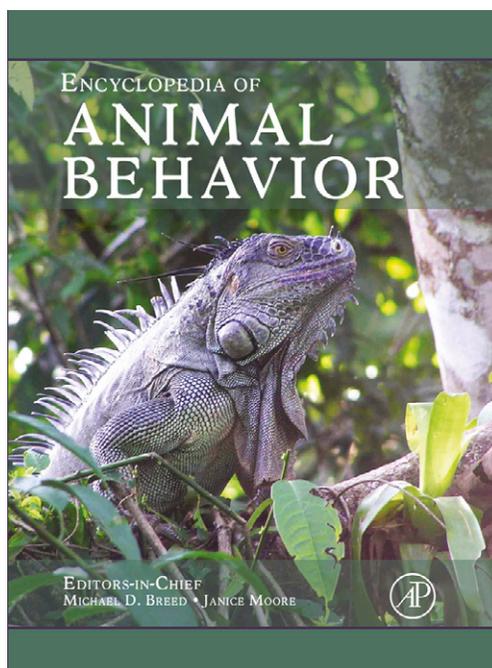


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## Rhesus Macaques

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The rhesus macaque (*Macaca mulatta*) is a medium-sized monkey. Adults are about half a meter tall and weigh between 5 and 8 kg. Males are about 5–10 cm taller and 2–3 kg heavier than females. Their bodies are covered with brown fur while their faces and rumps are pink or red and have no fur. Rhesus macaques are 1 of 19 species belonging to the genus *Macaca*. Macaques, in turn, belong to a large family of Old World monkeys called *Cercopithecidae*, which also includes baboons, mandrills, vervet monkeys, and many other African and Asian primates. Macaques originated in Africa and migrated to Europe when these two continents were still well connected by land bridges. From Europe, the macaques migrated eastward and into the Asian continent, where they differentiated into many species. The rhesus macaque and its close relatives – the Japanese macaque, the Taiwanese macaque, and the long-tailed macaque – are the most recent group of macaques to have evolved and colonized Asia. Rhesus macaques, in particular, have been very successful in this colonization process. Today wild rhesus macaques can be found almost anywhere throughout mainland Asia: Afghanistan, India, Thailand, China, Pakistan, Bhutan, Burma, Nepal, Bangladesh, Laos, and Vietnam. They are also found in almost any type of habitat, including tropical forests, dry and semidesert regions, swamps, and mountains up to 4000 m high. Rhesus macaques have been successful at displacing other macaque species from their native forest habitats as well as colonizing new habitats where no other macaques had gone before. According to some estimates, the rhesus macaque is the second most widespread primate species in the world after humans.

A key component of rhesus macaques' ecological success has been their ability to adapt to changes in the environment induced by people and to people themselves. In northern India, almost half the local population of rhesus macaques lives in villages, towns, temples, and railway stations. Most of the time, the monkeys just hang out on roadsides and in close contact with people. They have learned to raid crops, eat garbage, or steal food directly from people's kitchens. In addition to their omnivorous diet, the adaptability of rhesus macaques is also due to their resilience to stress and their ability to survive and reproduce in almost any environment. These characteristics have made the rhesus macaque the ideal laboratory primate for biomedical research.

After research laboratories throughout the United States imported hundreds of thousands of rhesus macaques from India, this country banned the export of these

primates in the 1970s. Although the United States and other countries continue to import rhesus macaques from China and other Asian countries, rhesus macaques are also actively bred in many research facilities in the United States. The best known breeding program for rhesus macaques was initiated in Puerto Rico in 1938, when a colony of rhesus macaques numbering several hundreds of individuals was established on Cayo Santiago, a 15.2-ha island 1 km off the southeastern coast of Puerto Rico. The monkeys, who were shipped to Puerto Rico directly from India, adjusted very well to the tropical climate of the Caribbean and began reproducing at high rates. The vegetation on the small island did not provide enough food for the monkeys, so they had to be fed with commercial monkey chow on a daily basis. Over the years, support for the colony has been provided by the US National Institutes of Health and by the University of Puerto Rico.

Studies of the behavior of rhesus macaques on Cayo Santiago began almost immediately following the establishment of the colony in 1938, but were soon suspended due to the 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 early 1960s. Studies by Altmann himself, and later Conaway, Koford, and Sade provided the first systematic description of rhesus macaque behavior and social organization. As researchers began, for the first time, to individually recognize the monkeys and gather information on births, deaths, migration, and patterns of spatial association, affiliation, and aggression, the importance of male dispersal, female kinship, and dominance as organizing factors for rhesus macaque society became apparent. 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 in Puerto Rico has been confirmed and supplemented by behavioral studies conducted in other research facilities such as the Sub-department of Animal Behaviour at the University of Cambridge, the Yerkes National Primate Research Center of Emory University, and the Wisconsin National Primate Research Center of the University of Wisconsin in Madison. Although studies of wild rhesus macaques in India, Pakistan, and other Asian countries have generally confirmed the findings obtained in research facilities, these field studies have been very few. Thus, the behavior of rhesus macaques in the wild remains generally understudied.

In the forests of India and Pakistan, rhesus macaques live in groups of 10–30 individuals, which include a few adult males and several adult females with their offspring. In urban areas in Asia and on the island of Cayo Santiago, social groups can include over 100 individuals. The adult females and immature individuals within a group belong to several different matriline, that is, families of individuals related through the maternal line. The matrilineal structure of rhesus groups results from the patterns of dispersal and philopatry characteristic of this species: males emigrate from their natal group at puberty and join a new group, whereas females remain in their natal groups throughout their lives. Within a matriline, at any point in time, there can be 4–6 overlapping generations of individuals, for example, a 10-year-old female with her mother, grandmother, sisters, aunts, cousins, offspring and grandoffspring, and nieces and nephews. The adult males in the group are generally unrelated to all other individuals because they immigrated by themselves from another group. On Cayo Santiago, however, groups sometimes include a few natal males who have reached adulthood in their natal group and have not yet emigrated.

The strength of social bonds between individuals in a rhesus group is generally predicted by their kinship, sex, and age. Strength of social bonds is generally expressed in amount of time spent in contact, close proximity, or engaged in grooming behavior. The strongest social bonds are between mothers and infants. Mothers and juvenile daughters also have strong bonds, as well as closely related adult females such as sisters. 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 the group form temporary social bonds with females in estrus, in which spatial association and affiliation are accompanied by mating. Adult males generally do not associate with their offspring or show paternal behavior.

Males emigrate from their natal group around the time they reach puberty (4–6 years of age). 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. 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 in other groups. When rhesus males emigrate, they usually do so alone, although rare cases of males emigrating with their brothers have been reported. 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 die alone, or try to join another group.

Rhesus macaques are aggressive and xenophobic primates who have a strong tendency to attack unfamiliar conspecifics. 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 will generally avoid the dominant, or express fear and submission in his/her presence. The dominant will attack the subordinate every now and then, to maintain or reinforce the dominance relationship between them. Every rhesus macaque has dominance relationships with every other individual in the group. Dominance relationships are generally transitive so that 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 dominance 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 is dominant over all other individuals in the group. The alpha female is dominant over all the females and males, with the exception of the alpha male and occasionally another or a few other adult males.

Females maintain stable dominance ranks within their natal groups throughout the lives, whereas males lose their ranks when they leave their natal group at puberty and acquire new ranks when they join a new group. Males who have joined a new group are typically lower ranking than all the other adult males resident in the group and gradually work their way up the hierarchy by making alliances with powerful males and females. 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 remain dominant over all of their daughters throughout their lives, while sisters rank in reverse order of their age so that young females dominate their old sisters, and a female's youngest daughter is the most dominant of her female offspring. In addition to individual ranks within a matriline, there are also dominance relationships between matriline, so that each group of rhesus macaques has a top-ranking matriline, and bottom-ranking matriline, and other matriline ranked in between them. High-ranking matriline tend to be larger than low-ranking matriline.

The hierarchical relationships between individuals and between matriline 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. Mothers consistently intervene on behalf of their offspring, when offspring get into fights with other group members. When two juveniles fight with each other, the mothers of both juveniles

intervene to support their offspring, and the outcome of the fight is ultimately determined by the relative rank 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 mothers. Although juveniles are initially lower ranking than all adults within the group, juveniles will challenge every adult that ranks lower than their mother, and 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. Rank reversals between mothers and daughters, or between sisters, are possible but rare. Young males acquire ranks from their mothers as females do, and maintain this rank as long as they remain in their natal group.

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. Adult males rise in ranks through the formation of coalitions with unrelated males or females. 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 lower ranking than themselves. Agonistic support is solicited with scream vocalizations, with particular facial expressions (raised eyebrows and eye movements), and with body postures (tail raising and hindquarter presentation). 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.

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 picking skin parasites and other particles with the fingertips. Grooming serves a hygienic function and also relaxes the recipient. A rhesus macaque can request to be groomed by another individual by lipsmacking and encouraging the other individual to approach, and then by lying down in front of the other and exposing the part of the body that needs to be groomed. Grooming can last a few seconds, minutes, or occasionally, over an hour. Rhesus macaque females generally give and receive more grooming than males do. Infants receive a great deal of grooming from their mothers beginning on their first day of life, but do not show any appreciable grooming activity in the first 6–8 months of life. Rates of grooming performed increase with age in both males and females and sex differences emerge in the first year of life when females start performing more grooming than males. 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 out and maintain one-sided grooming relationships with them. 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 and mostly limited to the nonmating season.

Both adult males and females use grooming behavior during their mating activities. 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). During the mating season, mating typically occurs in a 5–12-day period within a female's menstrual cycle. In rhesus macaques, exaggerated sexual swellings are exhibited only by adolescent females. Instead, 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 a temporary social bond called consortship, which includes proximity maintenance, repeated copulations, and grooming. Consortships may last from several hours to a few days. Rhesus males need multiple mounts (about 10 or more) to achieve ejaculation, although subordinate males can occasionally ejaculate after a single, very brief mount. During consortships, dominant males guard the females and prevent other males from approaching and mounting them. The alpha male, however, often disrupts the consortships of other males. When a consortship ends, a female can begin consorting with a different male, so that females can consort and copulate with several different males on a given day or estrus period. Some studies of rhesus macaques have reported that estrous females can shift partners 10 times in a period of 2 h, soliciting copulations from all the adult males in the group. Males are sexually promiscuous as well, and adult males and females mate, on average, with a similar number of partners. Despite this promiscuity, mating activities are not indiscriminate or random, or simply the result of competition for mating among individuals of the same sex. 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. Kinship

and familiarity are the variables whose effects on mate choice are perhaps best understood. Normally, rhesus macaque males do not breed in their natal group because they all emigrate at puberty. Mating between close relatives is infrequent also in situations where males achieve reproductive maturity in their natal groups and their mothers are still reproductively active. This is especially the case for the rhesus population on Cayo Santiago, where opportunities for male dispersal are limited, and some males remain and mate in the groups in which they were born, or return to their natal groups later in life. Many studies on Cayo Santiago have reported that mating between close kin, especially between mothers and their adult sons, is rare, and generally less than expected by chance. One common explanation for incest avoidance is that females develop sexual aversions to related males based on familiarity cues such as proximity. Consistent with this hypothesis, even individuals with no close relatives form affiliative relations with one set of individuals but mate with another. Rhesus macaque females generally do not mate with males with whom they have had an affiliative relationship. Females also 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. Several studies have also reported that females are attracted to novel males and leave their group temporarily to consort with peripheral or extra-group males. 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. Effects of dominance rank on female or male mate choice are generally weaker and often contradictory among studies. Although, in some studies, both males and females were reported to mate more frequently or have longer consorts with high-ranking partners, in others, individuals appeared to have proximity preferences for low-ranking individuals.

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 take care of their offspring on their own, with no help from the offspring's father, or other family members. Newborn infants spend a great deal of time nursing or sleeping on their mother's chest. Mothers carry their infants while they travel for several months. During time devoted to resting or social activities, however, infants spend increasing amounts of time out of contact but in close proximity to their mothers. During this time, young infants explore the environment or play with other infants. Young infants also receive a great deal of 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. 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. Therefore, mothers break contact and walk away from their infants frequently, while infants follow their mothers and make contact with them.

Mothers encourage their infants' independence by breaking contact with them frequently and physically rejecting their infants' attempts to make contact and gain access to the nipples. Individual mothers differ greatly 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. These differences are accounted for by characteristics of the mothers (e.g., her age, previous maternal experience, dominance rank, or personality), those of their infants (e.g., age or sex), and those of the surrounding environment (e.g., availability of food, risk of predation, risk of aggression, or infant kidnapping by other rhesus macaques).

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, and mate and conceive again. Infants actively resist weaning by responding to maternal rejection with screams and tantrums. Infants also interfere with their mother's mating activity and in some cases, successfully delay conception and the birth of a sibling. High-ranking mothers often produce an infant every year, while low-ranking mothers may give birth only every other year. These differences in reproductive rates may result from differences in maternal behavior, as high-ranking mothers reject their infants earlier and at higher rates than low-ranking mothers. 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 process of acquisition of independence for a 1-year-old rhesus monkey. Young males spend increasing amounts of time playing rough-and-tumble with their peers, while young females become increasingly interested in exchanging grooming with older female relatives or in playing with infants. Females reach puberty at 3–4 years of age, while males do so 6 or 12 months later. Both females and males continue growing after puberty and adult body size is typically reached at around 5 or 6 years of age. Maximum life span length for rhesus macaques in captivity is 35 or

40 years. Among the free-ranging rhesus macaques on Cayo Santiago, most individuals die between 15 and 20 years of age, despite abundance of food and lack of predators. In the wild, average age of death for adult rhesus macaques is probably 10 years. As with other mammals, males have higher mortality rates than females at any age. On Cayo Santiago, 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. Sex differences in seasonal patterns of mortality reflect the survival costs of reproduction and the fact that in a sexually promiscuous species such as the rhesus macaque, male reproductive effort is mainly expressed as mating effort, while female reproductive effort is expressed through pregnancy and lactation. Increased male mortality during the mating season mostly results from high vulnerability to infectious diseases due to male–male aggression and wounding in conjunction to suppression of the immune system associated with high levels of testosterone. Increased female mortality during the birth season may be the result of pregnancy or delivery complications, or energetic stress and immunosuppression associated with pregnancy and lactation. In the forests of India, rhesus macaques are probably vulnerable to predators such as tigers or large raptors. However, many ‘wild’ rhesus macaques currently live in areas without any natural predators, and in which the main threat is represented by humans. Given that some rhesus macaques recently attacked and caused the death of the Deputy Major of the city of New Delhi, in India, it is fair to say that rhesus macaques can be as dangerous to humans as humans are to them.

The common use of rhesus macaques in biomedical research and the availability of rhesus macaques in

research or breeding facilities such as Cayo Santiago Island in Puerto Rico, Morgan Island in North Carolina, or the NIH-funded National Primate Research Centers in the United States has made it possible to conduct extensive observational studies of this species and uncover many aspects of its behavior and social organization. Research with rhesus macaques has allowed scientists to understand many basic aspects of primate behavior, and animal behavior in general, such as dispersal and philopatry, altruistic and nepotistic behavior, aggression and submission, and dominance hierarchies. Studies of rhesus macaque behavior in research facilities peaked in the 1970s, but have become increasingly rare in the past 30 years. As a result, the rhesus macaque is currently one of the least studied primate species and some aspects of its behavior still remain unclear. This interesting primate species, however, still has much to contribute to the study and understanding of animal behavior. It is therefore hopeful that new generations of animal behaviorists will rediscover the rhesus macaque and address new questions about its behavior with renewed energy and enthusiasm.

*See also:* Animal Arithmetic; Chimpanzees; Monkeys and Prosimians: Social Learning.

### Further Reading

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