Pig-tailed macaque – *Macaca nemestrina* (Linnaeus, 1766)

Taxonomy

Kingdom – Animalia  
Phylum – Chordata  
Class – Mammalia  
Order – Primates  
Family – Cercopithecidae  
Genus – Macaca  
Species – nemestrina

The pig tailed macaque is part of a group of primates called the Old World monkeys, the Old World being Europe, Asia and Africa. Superficially, they are different from the apes in that most have tails, indeed the family name, Cercopithecidae, means ‘tailed ape’. They differ from the New World monkeys as their tails are never prehensile. The Old World monkeys are today indigenous to Africa and Asia, though the fossil record shows them to have inhabited Europe in the past. Aside from humans, the macaques are the most widespread primate genus, and there are currently 22 recognised species that fall within four phyletic groups.

The pig tailed macaque, *Macaca nemestrina*, is endemic to the subtropical forests of Brunei, North Western India, southern China, Laos, Cambodia, eastern Bangladesh, Indonesia, Myanmar, Malaysia, Borneo, Sumatra and Thailand. There are two distinct species of pig tailed macaque, the Southern, *Macaca nemestrina*, and the Northern, *Macaca leonina*, though little is known about the ecological or behavioural differences of the two species; indeed they used to be considered as sub-species. The differences in the geographical ranges of the two species are illustrated to the left. Where their ranges cross, for example in Thailand, there is some evidence of hybridisation of the species, though it seems that interbreeding in not common. The Southern pig tail is the only species that has been studied in the wild.

The Southern pig tail macaque has a white underside, with the rest of their fur being olive brown in colour. The fur on the top of their heads is very dark brown or black and grows in such a pattern that it gives the appearance of a depression here. The Northern pig tails are slightly different in their colouration, being slightly lighter in colour, with red streaks of fur on their face, from the corner of their eyes to the ear. The infants of the pig tail are born black, gaining the adult colouration pattern as they mature. Sexual dimorphism is shown in this species; males measure 495 – 564 mm with females
between 467 – 564mm, which is not greatly distinct. The males, however, have a bulkier frame and weigh substantially more; 6.2 – 14.5kgs compared to the females reaching between 4.7 – 10.9kgs. The teeth of the males, canines in particular, are much larger, which the male will utilise in aggressive encounters with other males, either in display or more rarely as weapons. The structure of the tail has given the pig tail its name; tails are short, less than the length of the body from head to rump. It is often bare, sometime covered sparsely with fur. The macaques generally carry their tails half erect, so they are curled around resembling that of a pig.

The preferred habitat of *Macaca nemestrina* is the lowland and hilly primary rainforests, though they are occasionally found in swamp and secondary forest. Rainforests where their numbers are highest are those that are undisturbed and intact. The pigtails coexist in their habitat with the long tail macaque, *Macaca fascicularis*, though the two groups rarely come into contact with each other, even sometimes being as close of 100 metres. This lack of overlap seems to occur due to the preference of different habitats. Pigtails are more terrestrial in their movements; they normally range in higher areas away from river, with the longtails occupying the opposing niches. Physique evolution of the two species reflects this adaptation to habitats with the long tails of *Macaca fascicularis* being important aids to their arboreal lifestyle, where the tail of a terrestrial monkey is somewhat redundant, hence the evolution of the pig-tail.

Habitats well suited to terrestrial-moving animals will have slight structural differences to those preferred by arboreal animals, such as less dense trees, less vines and therefore a clearer forest floor. This is very effective in keeping the animals separate, with neither species making any distinctive calls to announce their presence. The structure of the limbs and joints of *Macaca nemestrina* indicate a long adaptation to terrestrial locomotion, though they do sometimes travel through the trees. They tend to select the sturdier and horizontal supports when travelling through the trees. The Northern pigtails are slightly more arboreal than the Southern species.

Temperatures vary through the countries of habitation from as low as 4˚C in winter months in north eastern India to over 30˚C in more tropical countries. The pigtails also adapt to a range in altitudes, being found anywhere from sea level to above 2000 metres. The pigtails spread out over the landscape and cover a large area each day as they forage, and the home range of a troop can be anything between 0.6 and 8.28km². In areas of high population density, different groups can overlap each other by as much as 50%.

*Macaca nemestrina* live in large social groups, containing from anywhere between nine and 81 individuals. Complex social structures are adhered to within these groups, and relationships are maintained through a variety of behaviours including gestures, vocalisations and physical contact.
Groups are made up of a select few adult males, with one assuming dominance as the alpha. There is a linear structure of dominance, which is characteristic of macaque societies in general. Many adult females are present within a group, and it is structured according to matrilineal ranks. There is a structure of rank both within and between matrilines. Females remain within the group at maturity, and their rank is determined genetically; those born into a high ranking line will assume a position of high rank, and therefore power, within the group. To live in such a large group cohesively requires that strict hierarchies are adhered to, and conflict often threatens to destabilise social networks. Therefore methods are in place for controlling aggression and competition within the group.

Monkeys often get involved in each other’s fights, often to defend a member of kin, which is an example of inclusive fitness, or to form alliances with the hope of reciprocal altruism at some future point. However, *Macaca nemestrina* show signs of ‘policing’ within their societies, which is impartial interference in a fight within the group. Anderson (2005) studied a group of more than 80 individuals including four adult males and 25 adult females. He found antagonistic episodes took place at a rate of roughly 16 per hour, and in 66% of these, adults or subadults intervened. 71% of interventions were partial, probably for reasons discussed above. However, the remaining interventions were impartial. They were approached by taking up a position equidistant between the two aggressors, or attacking both simultaneously. In 42% of these policing incidents, the fight in question stopped after five seconds. The most effective, low cost interventions were attributable to three of the adult males and the most dominant female. Policing behaviour and its effectiveness are more predictable when in monkeys where power variance is low, for example in group members with a lower social rank. In individuals of higher rank, amongst whom power variance is high, policing is less effective. It is uncertain whether individuals obtain a higher rank and are therefore able to take on a policing role within the troop, or whether they express policing behaviour, which earns them a higher rank within the group. This third party policing stabilises social niches, and allows group members to interact with a larger, more diverse set of well connected partners (Flack, 2006). A lack of policing leads an increase in conflict frequency and severity, leading to more conservative social interactions and a less integrated society.

When in their large group, the spacing of the animals in not random, and aggression is the primary factor in determining proximity. Due to the large groups, *Macaca nemestrina* will often split into smaller groups of two to six monkeys, especially when foraging for food, to decrease direct competition between members of the group. Each of the sub groups keeps in regular contact through vocalisations. These sub groups are generally made up of macaques of similar age and sex.
Matrilineal kinship also has a significant effect on spatial relationships (Weigal, 1980). There is an attraction between members of the same sex to be in close proximity with one another, more so than that of rank or age. In Weigal’s (1980) study, pigtail males were attracted to those of a lower rank, and females to older group member, and with age usually comes a higher rank. It is suggested that the males avoid males of higher status; therefore there is a resultant gravitation towards lower ranked males. If the monkeys regularly approach, and choose to be in close proximity to, kin, this means they are more likely to be around members of the group who will offer regular grooming and who may aid in any agonistic encounters.

Much of the communication within the group is carried out through body language and facial gestures. Maestripieri (2005) studied gestural communication in three species of macaque. He observed most communication to revolve around issues of dominance and subordination. Gestures of bared teeth, present the genital region and smacking of the lips were directed up the hierarchy and were signals of submission. Touching the hips of another individual and mounting without sexual intent were gestures directed up the hierarchy. The ‘Pucker’ – when the macaques compress and protrude their lips and retract their eyebrows, forehead and ears – was the most frequent gesture observed in *Macaca nemestrina*, displayed by both males and females in a variety of social settings. It seems as though the ‘Pucker’ is used to coordinate and facilitate the occurrence of mating, grooming and interactions with infants. Whether directed at males or females, the ‘Pucker’ elicits very different responses. When a male makes this gesture towards an oestrus female, they often copulate directly following, whereas when directed towards another male, the recipient will generally retreat. An expression named by Maestripeiri as Eyebrows – the scalp and brow of the monkey retracted and the mouth open – was unique to the pigtails and was frequently exchanged between males in conjunction approach and retreat interactions, particularly when a male was offering support in an agonistic encounter. Pigtails also exhibit frequent bonding patterns and gesture, of which one is Eyebrows and a further being individuals embracing one another. The dynamics of the *Macaca nemestrina* social group are complex, and high levels of social tolerance seem to have led to the evolution of developed affiliative communication and bonding patterns.

Oi (1990) studied displays of aggression and dominance in a wild group of pigtail macaques. These animals are elusive and generally hard to study in the wild. The group studied was comprised of three adult males, fourteen adult females and numerous younger monkeys. Though aggression and agonistic displays were common, actual acts of violence were rare. Only 2.3% of agonistic encounters included biting, which seems to be the manifestation of the most intense aggression. These occurred mostly between females and juveniles, occasionally between females, though never between males. Though saying this, the highest frequency of agonistic interactions occurred between pairs of males. In 92.5%, the simple approach of an aggressor, sometimes with a threatening facial gesture, was enough to cause retreat of the opponent.
The males within the group dominate the females, and in the troop studied by Oi the two most dominant males attacked all the females at some point, where females and juveniles occasionally attacked two of the three dominant males. Juvenile and adolescent males will not be regarded as potential mates by the females, simply as competition for resources, therefore aggression between these dyads is common. The alpha male was never the recipient of any aggression, the second most dominant was rarely. There were three subsets of females within this group; a high, middle and lower ranking set. The adult males are at the top of the pyramid; within the group there were four adolescent males, two of which were dominant to some females and submissive to others, where the other two were submissive to all females. High ranking males seemed to show special concern of females in agonistic interactions. It was common for a third party to join such interactions, most frequently males were victims of these supported attacks, which were generally initiated by females or juveniles.

When exhibiting grooming behaviour, in 95.5% of bouts one or both partners were females. Grooming between females was unilateral, in contrast to mutual grooming exhibited by these monkeys in captivity. The majority of grooming was performed by subordinate females as a tool to strengthen relationships with higher ranking kin. All females who were groomed by a male showed signs of oestrus, and 85% of these episodes of intersexual grooming involved the two most dominant males. 8% of grooming took place after agonistic interactions, and in these instances the subordinate animal always groomed the dominant. Grooming among females much more frequently took place within each of the three subsets than between the groups. It was thought that the subsets represented groups of close kin; within the groups they had similar priority of access to food and often fed together, showing a high degree of tolerance of each other. As mentioned by Weigel (1980), these monkeys tend to gravitate towards kin.

Due to the matrilineal structure of the pigtail groups, the females to exhibit and maintain close bonds with one another. The males will emigrate from their group of birth around five or six years of age, therefore adolescent and adult males within a troop will not have been born there, so lack these ties of kinship that so bond the females. When joining a new group, the male will be at the lowest end of the hierarchy and will attempt to work his way up the scale, with his goal being to attain rank of alpha male. Should a male not successfully immigrate into another group, he will wander solitarily, or occasionally join with other roaming males, forming small groups. The males within a troop need developed diplomatic skills; while competing with fellow males for access to females, all the females for access to food, they must also be able to successfully coexist with them. This is achieved through policing, conciliatory grooming and the use of many gestures, which remove the need for potentially damaging physical violence. The alpha male also promotes a peaceful coexistence through expressions of tolerance towards subordinate members, an example of this being non-sexual mounting of an alpha by a subordinate. This tolerance may also ensure the cooperation of subordinate members in the defence of females against solitary males and predators.

*Macaca nemestrina* are not seasonal breeders and mating occurs throughout the year. The females reach sexual maturity at three years of age, and have the characteristic anogenital swelling during oestrus, which is much more pronounced that that of their counter species, *Macaca leonina*. Males reach sexual maturity a little later, at around 4.5 years. Females will mate with multiple males while in oestrus. If only one or two females are in oestrus at any given time, the top ranking males will monopolise the mating, and they are able to withhold access from lower ranking males. If a lower
male attempts mating, the dominant male will act aggressively towards both the male and the female taking part. It is only ever the adult males who seem to get involved in agonistic interactions over mates (Oi, 1990). Should many females come into season at the same time, lower ranking males have more opportunities to mate. Females do not seem to show a marked preference towards mating with those of a higher rather than a lower rank. There is no indication that a female experiences an increase in rank while she is in oestrus.

The gestation period in *Macaca nemestrina* is roughly 170 days, and during this time the pregnant females spends increasingly less time grooming others, shows a decrease in displays of aggression and a decrease in interest in sexual behaviour (Maestripieri, 1999). There is evidence that the likelihood of having offspring of a certain sex is influence by the rank of the female. Parental Investment Theory states that parents should invest more in offspring of the sex that is less costly to rear, provides higher fitness returns, or both. Pigtail macaque societies tend to have birth ratios slightly biased towards female offspring. Maestripieri (2002) noted within one group studied a birthing rate of 48.63% males. There was a significant difference in the birth sex ratios in relation to matrilineal rank; higher status matrines produced more daughters, where lower status produced more sons. In dominant matrines, daughters offer many benefits; they strengthen the kin group, increasing the power and therefore dominance of the matriline, and an increase in dominance is always desirable. However, they do take more investment; females remain in the family group, therefore are going to be a further source of competition for food and mates. They stay with their mothers for a longer period of time, nurse for longer, taking more of the female’s energy. These are expenses those females of lower rank cannot afford, and sons are more commonly produced who do not take as much of the female’s energy and who will leave the group after around four years. Females of a lower rank are also more likely to be attacked by higher ranking members of the group. This bias increased with the age of the monkeys. The inter-birth intervals were found to be longer after producing a female than a male, further suggesting that females are more costly to rear.

Infants are totally dependent on their mothers for the first year of life, and during the first month the young will rarely, if ever, break contact with the mother. Mothers care for their offspring without the aid of other individuals in the group, though within the group there is much interest shown towards infants, with higher ranking females sometimes grabbing infants of lower ranking mothers. As the infant ages, it will begin to explore the surroundings and gradually increase both the distance and time spent away from the mother, becoming more confident after the fifth week of life.

Pigtail macaques are highly frugivorous, with some researchers suggesting that up to 74% of their diet consists solely of fruit making them the most frugivorous of macaque species. They do also consume a wide variety of other foods, including insects, seeds, young leaves, leaf stems, even dirt
and fungus. Laksa (2000) demonstrated *Macaca nemestrina* to have a high sensitivity for maltose, which suggests that this carbohydrate is likely to add to the taste sensation when the animals feed on starchy plants. There are 104 genera of plants that these animals will eat, and many of these contain high amounts of starch. Therefore the preference and high sensitivity for maltose may be an evolutionary adaptation of its digestive system to the nutritional assessment of starchy plants. The macaques also possess cheek pouches in which they store food for the salivary predigestion of starch. Pigtails were also shown to prefer, or at least accept, higher levels of acidic tastants. This could help avoid competition with other frugivores for the most carbohydrate rich fruits. It also allows the macaque to take advantage of fruits which are nutritionally valuable, though perhaps not quite ripe; indeed these macaques have been observed eating unripe *ficus* fruits.

These macaques are listed as ‘vulnerable’ by IUCN, though are only on Appendix II of CITES. The major threats to this animal are through habitat loss and the hunting of the species. It is estimated that the wild population has declined by at least 20% over the last 10 years. This figure is based on a decrease in the possible areas of occupancy, the extent of their occurrence in the wild, quality of remaining habitat and levels of exploitation by humans. Pigtail macaques depend on primary rainforest for their habitat, therefore logging practises and conversion of forest into agricultural lands is a very serious threat. Even relatively small scale harvesting of products from a forest can significantly decrease the quality of the area. This macaque is killed for food by many tribes native to its range, and this greatly threatens the wild population. They are often illegally captured for supply to zoos, and are in high demand within the field of biomedical research, currently in particular for models for research on AIDS, and many other diseases.
References:


Oi, T (1990) Patterns of dominance and affiliation in wild pig-tailed macaques in West Sumatra. International Journal of Primatology vol 11, no 4
