THE EXPRESSION OF MALE INTEREST IN THE INFANT IN FIVE SPECIES OF MACAQUE¹

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Among most Old World monkeys, the infant elicits a high degree of interest and protective behavior from both males and females. The function of female interest is easily comprehended, as it is the mother who nurtures the infant and provides him with his first social interaction. The functions of male interest in the infant is at the outset less clear-cut, since the mating system and general social structure preclude the possibility of any special role such as "father" in the human sense of the word. Nonetheless, any pattern of behavior as ubiquitous and pronounced as male-infant attraction strongly suggests a function of adaptive significance. This paper will explore the forms this behavior takes in five closely related species of the genus Macaca: the rhesus, the bonnet, the Gibraltar, the crab-eating, and the Japanese macaques (Macaca mulatta, radiata, sylvania, irus, and fuscata, respectively). It will also set forth hypotheses to explain the functional significance of male interest in the young.

Expression of interest and protectiveness appears in males to varying degrees, depending on a variety of factors, among them the actual speciels, group traditions, dominance rank and individual personality. The Japanese have observed that some males simply are more interested in infants than others, regardless of other factors (Itani 1959:79). In the group of crab-eating macaques I have observed, one of the two mature males is obviously more tolerant of infants' advances than the other. In some species this pattern seems to be "neglected" in the wild state, probably for adaptive reasons, but the species will nonetheless exhibit the behavior under other conditions—in laboratories or in zoos (Harlow

and Harlow 1966:247). The intensity of the expression of male interest may vary over the course of the yearly cycle.

The expression of male interest may include holding, grooming, carrying, playing with, or sitting near the infant, but the basic expression of this interest is protective behavior. The amount of playing, grooming, intensive fostering and so forth varies from one macaque species to another, but in all groups studied, the male protects the young when they are threatened, augmenting the mother's protection. This protectiveness cannot be assumed to be a simple concommitant of living in a social group. In some other Old World species, such as the langurs, the male does not protect the young at all, and displays little interest in them. Among the macaques even the rhesus male, who in comparison to other macaque males does not often play, hold, groom, or carry infants, is nonetheless strongly protective when they are threatened. Macaque males which do not exhibit active interest in the infants are still tolerant of the infants under normal conditions. The langur male, in contrast, avoids all contact with the young.

Since males and infants relate to each other within the larger body of their society, their relations should be viewed in the context of the overall social structure. In macaque societies two types of organizational principles relate animals to one another. One principle is that of membership in a certain age/sex class comprised of groups of peer animals playing a specific role in the whole troop structure. Mature males form one of these classes; infants form another. The other principle is that of social sub-unit, in which animals relate to one another as individuals sharing close personal bonds. In this system infants and males associate together as individuals rather than as class members.

One very important relationship between individuals is that which can be called the maternal line grouping, and which has been reported for the rhesus, the Japanese, and the Gibraltar macaques. This association occurs between a female and her offspring, both young and adult,

and is characterized by a high rate of grooming, feeding together, and body contact. The dominance rank of a mother is accorded her offspring for a long period of their development by her backing them up in dominance interactions. Sade (1965:9) observed one rhesus male which continued to spend large amounts of time with his mother well after he was sexually mature. He spent more time grooming her during mating than he did grooming all the females with which he consorted. The mother also stood up for him in several dominance interactions, despite his age. The Japanese have reported a much higher rate of relaxed co-feeding, grooming, and general association among animals known to be siblings. This kinship affinity extends into adult relationships, and as a result even grandparent, aunt, and cousin affiliations may occur (Yamada 1963:51).

For this study the sibling relationship is especially significant. The mutual maternal relationship provides a context for intense and prolonged sibling contact. An adult male usually takes a greater interest in the offspring of his mother, sitting with them and grooming them much of the time. Some males have been seen carrying their mother's or older sister's infants (Koford 1963:151). Younger males especially tend to stay near their elder male siblings, and this may affect their status if their brother is a strong and dominant animal. 2 Shirek (personal communication) believes that some sort of lineage association existed in the group of crab-eating macaques she studied. As far as she could observe, this association was made up of females only. However, the processes involved in the social maturation of females (who never leave the nuclear area of the troop), make lineage relationships more discernible among females than among males. Since long term studies continue to report maternal relationships, this association appears to provide a major axis of social organization among the macaques.

The expression of male interest in the infant among the Japanese and Gibraltar macaques often takes a form which can be called male care.

This consists of intense male fostering of a specific infant, including carrying, grooming, playing, and strong protective behavior. It occurs during the birth season among the Japanese species (Itani 1959:72-73) and may occur all year around in the Gibraltar species (MacRoberts Ms.). It should be emphasized that this behavior does not in any way indicate biological paternity. In the macaque mating system, where a female may mate with several males on just one day of her fertile period, there is no way for the observer or even the monkeys themselves to tell which of the males is the real father of the resulting offspring. Male care is thus one facet of the social role played by the adult male, and connotes no biological role.

The Japanese groups, among which male care behavior occurs, show evidence that the most sociable and group-oriented males are the most intense practitioners of male care (Itani 1959:73). This behavior pattern may help a young male to gain access to the center of the troop, an area from which he is usually barred by the adult males. When a young male is carrying an infant, he is allowed to sit unmolested in the troop nucleus with the most dominant males and with the females with their infants (Itani 1959:85-86). With the recognition of the maternal relationship among both the Japanese and Gibraltar species (Yamada 1963; MacRoberts Ms.), there is some question as to whether some of the reported male care would not be better understood as care by a sibling (in this case brother). A male in a troop with maternal associations might be prone to select as his protected infant the young infant with which he has had a previous class association--his mother's or sister's offspring. In the groups studied by MacRoberts, females which were almost certainly related to younger animals showed fostering behavior identical to that of the males, which gives more credence to the theory that kinship influences the male's choice of protegé.

It should be stressed that this behavior is an elaboration of patterns such as temporary fostering which are typical of all macaques studied. The fact that paternal care occurs at different times of the yearly cycle in the two species exhibiting this behavior indicates that a general intensification of such behavior occurs at all times of the year and is not merely an isolated trait.

In the association of males as a class with infants as a class, the overall troop structure is important. In all the species adult males and infants are found in the central part of their troops. As a class, dominant males form a nucleus about which females and their infants cluster. Little is known about the ontogeny of infant interest in the male, but there is evidence that the infant's age plays an important role. Very young (four to eight weeks) Gibraltar macaques showed very little overt interest in their male patrons, who actually solicited their attention (Lahiri and Southwick 1966:259). In all others of the species noted, older infants (three to four months or older) take an active interest in getting close to the males. They often run up to dominant animals and hop around them, touching their faces if permitted. The macaque male is usually very tolerant of the infants and often has a group of them clustered about him, feeding and playing. The crab-eating macaques often play intensively with infants and let them feed with them when they keep the other animals away from the food. In this group, both males and young sought each other out for bouts of play. Mutual interest was very high but, as in other species, varied with individual monkeys (Shirek, personal communication). The extent of male attractiveness was emphasized for Japanese researchers when they located the body of a dead troop leader who had been very popular with infants by following a group of youngsters to an isolated spot where they had been gathering around the body and playing for several days after the male's death (Kawai 1960:228-29). Infants also associate with males who are in grooming or consort relations with their mothers. Sade (1966:70-71) saw one male temporarily protect an infant whose mother had died while in consort relations with the male.

About the nuclear group is a periphery of juvenile and sub-adult males which the rhesus and Japanese adult males do not allow into the center of the troop. In some less dominance-oriented species, such as the bonnet and the crab-eating monkey, this exclusion is less stringent, and the play pattern in males is intensified. Bonnet and crab-eating males will play with each other, with juveniles, and with infants, often joining play groups (Simonds 1965:190-92; Shirek, personal communication).

The adaptive significance of male interest in the infant involves two factors. One could be called the basic survival value, the other the social success value. The male macaque, with his greater size, strength, and large canines, is actually better able to protect the infant from overt attack (either by a predator or by a hostile troop member) than is the mother. The mother is also a protector, but is more important as a source of food and as a model for social behavior during the infant's early life.

To understand the relation of male interest to the social success of the infant, one must consider the functions of dominance. Dominance is the key to better feeding, to less chance of being injured by attack, and thus to better chance of sound health. It is often the key to a higher rate of reproduction. Any infant which is able to gain a high dominance status is better off in physical terms than one which is not so able. Infants, while physically incapable of establishing dominance by themselves, can derive dominance from other animals which have high status. The offspring of a dominant female derive her rank, thereby obtaining preferred food and possibly preferred shelter. In the captive group of crab-eating macaques which I have observed at the University of California Animal Behavior Station, the infant and two-year old daughter of the most dominant female have access to food denied to all other animals except their mother and the most dominant male. Dominant siblings may also act as sources of dominance for infants. The Japanese have observed the same sort of behavior among their groups (Yamada 1963:48).

In groups which exhibit male care, infants derive rank from their protectors. MacRoberts' groups had clear cases of both sorts of derived dominance, and its beneficial effects were obvious. Young animals which were not protected at all were the last to feed and were most frequently attacked by other troop members (MacRoberts Ms.).

The experience of being a dominant animal provides the infant with a valuable foundation for future dominant behavior as an adult. If both male and female take an active interest in an infant, the young monkey's chances of survival are very high. In addition, if both of these interested adults are dominant, the infant stands a very good chance of becoming a healthy, dominant, reproductively successful adult himself.

While this paper deals with the expression of male-infant behavior in macaques only, similar behavior patterns are found in other primates. Male baboons, especially the hamadryas, exhibit a behavior similar to the macaque fostering described here. Each adult male hamadryas maintains a small group of co-foraging females. He often recruits members for his group by adopting immature females and caring for them until they reach sexual maturity (Kummer and Kurt 1963). In other more trooporiented baboons, infants are attracted to males, who often monitor play groups and sometimes protect a sickly juvenile (DeVore and Hall 1965:86). Since baboons closely resemble macaques in both their morphology and their way of life, this parallelism is not surprising. Among the apes, Goodall (1963) has observed a high male tolerance of infants, combined with play and holding.

Emerging from a growing body of data is a picture of basic male interest in the infant. It is amply evident that males and infants are strongly attracted to each other both as individuals and as members of age/sex classes. The maternal association, which may well be genus-wide, fosters more intensive individual contacts. The general troop structure of dominance peer groups serves to relate males to infants as a class. These structural features provide the context for expression of male

interest through purely spatial factors. A male is most likely to express his protective behavior toward infants in his line or dominance peer group.

The channeling of male protective behavior may actually affect the evolution of a group's gene pool. A male who protects a sibling or a sibling's offspring is actually preserving a set of genes much like his own. A similar situation could result from protection of peer group infants. If it is the case that dominance is determined by some genetic factor, the protection by the male of an infant of similar genetic make-up may serve to foster selection for that trait. At any rate, male protection of an infant fosters at least a behavioral phenotype for dominance. While any one male cannot be considered the biological father of any one infant, it is clear that through the bond of mutual attraction and interest males play an important social role in the growth of a macaque infant.

NOTES

¹Judith Shirek Ellefson has provided me with much valuable information on the group of crab-eating macaques she observed in Singapore Botanical Gardens. I also obtained helpful data from a film of these animals which she presented at the 1966 annual meeting of the Kroeber Anthropological Society in Berkeley, California.

²This type of association has not been explicitly documented for the bonnet or crab-eating macaque, but there actually was no way in the comparatively short studies devoted to these species to distinguish this association from other forms of friendly associations.

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