



Social Structure, Infant Handling, and Mothering Styles in Group-Living Old World Monkeys

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I argue that in Old World monkeys, infant handling by individuals other than the mother is a heterogeneous phenomenon in structural and functional terms; species differences in maternal tolerance of infant handling are related to differences in the relative proportion of abusive to affiliative responses made to infants by adult females other than the mother; and infant handling by adult females is related to the species-typical social structure, with particular reference to social relationships among females and patterns of food competition. I apply the proposed relationship among social structure, infant handling, and mothering style to explain the observed variation in mothering styles between and within the subfamilies Colobinae and Cercopithecinae.

KEY WORDS: infant handling; mothering style; social relationships; cercopithecines; colobines; macaques.

INTRODUCTION

Studies of Old World monkeys in captivity and in the field have highlighted striking differences in mothering styles both within and among species, especially along the dimension of maternal restrictiveness/permissiveness of the infant and tolerance of infant handling by other individuals. Differences in mothering styles have been related to attributes of the mother–infant pair as well as to characteristics of the surrounding social

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and ecological environment (Nash and Wheeler, 1982; Berman, 1984; Higley and Suomi, 1986; Nicolson, 1987; Nicolson, 1991). Within species, mothering behavior appears to be influenced by the extent to which the social environment poses a risk to the infant, (e.g., by sociodemographic variables such as social density and group composition and maternal dominance rank), as well as by individual characteristics that may influence the perception of such a risk, e.g., maternal age and experience, temperament, or emotionality (Maestripieri, 1993d). Among species, differences in mothering styles have been related to differences in the species-typical social structure, but a controversy has arisen as to whether they are adaptive *per se* or whether they just represent byproducts of other adaptations or constraints (Thierry, 1990). Supporters of the adaptive hypothesis have argued that differences in maternal permissiveness are related to the patterns of agonistic dominance among females, as dominance relationships influence the ease with which mothers can retrieve their infants from other individuals (Rowell *et al.*, 1964; Hrdy, 1976; McKenna, 1979). According to this hypothesis, in despotic species characterized by strict dominance hierarchies, low-ranking mothers may be reluctant to surrender their infants to other individuals because of their inability to retrieve them. In contrast, in egalitarian species characterized by loose dominance hierarchies, mothers would be more confident in their ability to retrieve their infants from other individuals and therefore more permissive.

The hypothesis that species differences in mothering styles are related to status differences among females and relative ease of infant retrieval does not consider species differences in the pattern of interaction between infants and individuals other than the mother. However, to test this hypothesis properly, information about the nature of interactions between infants and other individuals, along with possible species differences, is necessary. In fact, if interactions with other individuals posed little or no risk to the infant and were highly beneficial to the infant or the mother or both, maternal intolerance of such interactions would be maladaptive. Likewise, if infant handling were riskier to the infant in egalitarian species than in despotic species, we might predict less permissive mothering in egalitarian species. It seems clear, then, that to understand the relationship between mothering style and social structure, we need to investigate infant interactions with others and their relationship with mothering style and social structure. Moreover, since differences in mothering style are likely to represent responses to differences in the risk (or perception of risk) posed by the social environment to the infant, we have to consider the hypothesis that species differences in mothering styles are specifically related to species differences in the quality of infant handling. Handling by other individuals, in fact, is the main source of infant risk in the social environ-

ment. Surprisingly, in spite of the amount of information currently available concerning both infant handling and variability in mothering styles, no serious attempt has been made to relate these two phenomena in a comprehensive explanatory framework. The failure to investigate the relationship between infant handling and mothering style is likely to be due to the confusion concerning the functional significance of infant handling and its consequences for the individuals involved. Moreover, infant handling is often confused with maternal tolerance of infant handling. For example, when infant handling is referred to as "relaxed and permissive allomaternal behavior" (McKenna, 1979), it is not clear whether the author is describing interactions between infants and nonmaternal individuals or maternal tolerance of such interactions. Indeed, four out of five major differences between the alloparental activities of the colobines and those of the cercopithecines listed by McKenna (1979) are likely to represent differences in mothering style rather than in the pattern of infant handling.

I aim to show that infant handling in Old World monkeys is a heterogeneous phenomenon in structural and functional terms, to develop a framework in which to explain how interspecific differences in mothering styles may be related to specific differences in the pattern of infant handling and in female social relationships, and to apply the framework to explain the observed interspecific variation in mothering styles in cercopithecine and colobine monkeys. Although some principles of the proposed relationship among social structure, infant handling, and mothering style have a general validity and may apply also to some New World monkeys and apes, I restrict the analysis to Old World monkeys because infant handling and mothering behavior have been especially investigated in these primates. While the general theory outlined here is consistent with what is known about the socioecology of social and maternal behavior in some Old World monkeys, further testing of specific predictions of the model is needed to more fully evaluate its validity and applicability to a wider range of species. Accordingly I further aim to provide directions for future research on socioecological influences on maternal behavior and infant development in primates.

INFANT HANDLING AS HETEROGENEOUS PHENOMENON

In nonhuman primates, interactions between infants and individuals other than the mother have been given many different names, such as infant passing, infant sharing, infant transfer, infant handling, allomaternal behavior, allomothering, aunting, kidnapping, babysitting, and play mothering. Although allomothering and aunting have probably been the terms

most commonly used, the neutral term infant handling should be preferred to these other terms. In fact, allomothering and aunting tend to imply an equation between interaction with infants and caregiving behavior, which may not always be warranted (Wasser and Barash, 1981). Interactions between infants and individuals other than the mother undoubtedly represent a complex phenomenon and the hypotheses concerning the function and evolution of infant handling are even more numerous than the terms to which this phenomenon has been referred (Table I). Almost all the hypotheses concerning the function of infant handling have been thoroughly examined by Vogel (1984), and the evidence for and against them gathered from data of infant handling in one species: the hanuman langur (*Presbytis entellus*). The hypotheses were grouped according to the potential benefits or costs of infant handling to the three individuals involved in the interaction, namely, the mother, the infant, and the third party. The main conclusions of his analyses were "(1) no unambiguous direct benefits to the infants can be evidenced, but the risks and the potential costs are high; (2) the mothers possibly receive a certain amount of direct benefits, but the indirect potential costs are high; and (3) only the complex category of allomothers seems to exhibit a rather positive benefit/cost balance" (Vogel, 1984). The main conclusion to be drawn, however, was that infant handling is a highly heterogeneous phenomenon for which no single functional explanation can be expected. In fact, individuals of all age/sex classes participate in infant handling but the frequencies and the nature of these interactions as well as the probable motivations of these individuals may be very different. As pointed out by Wasser (1983; Kohda, 1985; Nicolson, 1987), it is likely that most of the hypotheses advanced to explain infant handling apply in one form or another and that their relative importance varies according to the individuals involved. Nevertheless, infant handling has often been considered as a homogeneous phenomenon and even though specific predictions have been made and tested for different categories of individuals, the results have been invariably discussed relative to a single explanatory framework of infant handling, often rejecting one hypothesis in favor of another and alternately emphasizing its neutral (Quiatt, 1979; Scollay and DeBold, 1980), beneficial (McKenna, 1979; Fairbanks, 1990; Small, 1990; Stanford, 1992), or detrimental (Hrady, 1978; Silk, 1980; Wasser and Barash, 1981; Wasser, 1983; Sommer, 1989) effects.

Since speculations concerning infant handling have gone far beyond the information provided by empirical observations, I focus on only a few observations that have been reported consistently in a wide range of species to demonstrate the heterogeneous nature of infant handling. These observations are that (1) female primates of all ages interact more frequently with unrelated infants than males do; (2) juvenile and subadult females are

Table I. Hypotheses Advanced to Explain the Function and Evolution of Infant Handling

Hypothesis	Source ^a
(1) It is only a by-product of the selection for maternal behavior and has no specific function	Quiatt (1979), Scollay & De Bold (1980)
(2) It represents one instance of altruism evolved via kin selection or reciprocity	Riedman (1982)
(3) It provides inexperienced females with necessary maternal skills	Lancaster (1971)
(4) It allows mothers freedom to forage	Hrdy (1976)
(5) It allows other individuals to gather information about an infant	Hrdy (1977)
(6) It benefits the infant in times of danger when the group is dispersed and sudden locomotion is warranted	Hrdy (1976), Zucker & Kaplan (1981)
(7) It promotes the possibility of adoption if the mother dies	Jay (1963), Kriege & Lucas (1974)
(8) It provides immunity from aggression or a higher status to the individual handling the infant if she/he is subordinate to the mother	Cheney (1978)
(9) It confers a higher status to the infant when the handler is dominant to the mother	Kriege & Lucas (1974), Hrdy (1976)
(10) It benefits the social intelligence of the infant and the infant handler	Small (1990)
(11) When performed by a lactating female, it may favor the formation of bonds between her own infant and infants of high-ranking females	de Waal (1990)
(12) It inflicts indirect reproductive costs to the mother	Hrdy (1976), Wasser & Barash (1981)
(13) It provides indirect selection against abnormally poor or abnormally unrestrictive mothering	Quiatt (1979)
(14) It contributes to the group's cohesiveness and stability	Horwich & Manski (1975)

^aPapers in which the hypothesis has been advanced or discussed by authors.

usually the most frequent infant handlers; and (3) adult, multiparous females may handle roughly or attack alien infants, while showing appropriate and careful handling of their own infants.

In a number of species, although infant handling by males is observed, it occurs at far lower rates than among females (Chamove *et al.*, 1967; Spencer-Booth, 1970; Hrdy, 1976; Gibber and Goy, 1985). In females, interest in infants appears early before maturity and persists throughout their lifetime. For example, langur females begin infant handling when they are

as young as 3 months old (Hrdy, 1977; Scollay and De Bold, 1980) and aging vervet monkey females play a significant role in establishing and maintaining relationships with their infant grandoffspring (Fairbanks, 1988). In contrast to females, immature males seldom interact with unrelated infants except in play, and adult males generally avoid young infants (Walters, 1987). Exceptions to this pattern are found in male savanna baboons, which as adults, often form special protective relationships with infants (Altmann, 1980; Packer, 1980), and in male Barbary macaques and hamadryas baboons, which frequently handle infants as a means to mediate agonistic interactions with males or to form sexual bonds with females (Kummer, 1968; Deag and Crook, 1971). It is reasonable to argue that the difference between males and females in attraction to infants may be due to the female genetic and hormonal predisposition for maternal care (Coe, 1990). Stimuli such as the size of the infant at birth, its morphological features, and its motor patterns may have coevolved with maternal responsiveness and contribute to the formation of a strong bond between mother and infant (Hrdy, 1976). In other words, high responsiveness to infants may ensure that females will be good mothers. On this view, interest by females in unrelated infants may be just an outgrowth of interest in their own infants (Quiatt, 1979) and a large part of infant handling may have no specific function or adaptive value (I refer to this hypothesis as the null hypothesis).

Although the null hypothesis may certainly account for the difference between the sexes in the attraction to infants and frequency of infant handling, it is insufficient to explain why attraction to infants appears early in a female's life and why immature females of many species are often reported as the most frequent infant handlers (Riedman, 1983). In fact, to ensure proper care of the offspring, it would be sufficient for responsiveness to newborn young to appear at the beginning of reproductive activity, possibly triggered by physiological mechanisms related to pregnancy and parturition, as in some other mammals (Keverne, 1988). Therefore, an additional functional explanation seems to be necessary to account for the extreme interest in infants shown by immature females. The most suitable one is that the appearance of interest in infants early in the life of a primate female, long before the reproductive age, may be adaptive in all species in which the infant has a long period of dependence on the mother and maternal behavior needs to be learned by observation and practice—the learning-to-mother hypothesis (Lancaster, 1971). The early appearance of attraction to infants ensures that young females will spend enough time in contact with infants to acquire the skills necessary to raise their own offspring successfully during adulthood. The hypothesis that infant handling by immature females is adaptive is supported by the findings that mothering

skills improve with practice—older nulliparous females are more competent with infants than younger nulliparous are (Hrdy, 1977; Meaney *et al.*, 1990) and that females that have more experience in caretaking and carrying infants as juveniles are more likely to rear their first live-born infant successfully (Fairbanks, 1990; Hrdy, 1976; Riedman, 1982).

Another aspect of infant handling that is not explained by the null hypothesis concerns harassment of infants by reproductively experienced females. Even though inexperience and clumsiness may cause nulliparous females to handle an infant roughly, when adult, multiparous females cause distress to infants other than their own, while showing or having shown appropriate handling of their own infant, some intentionality in distressing or harming the infant must be inferred. Aggression toward infants involving slapping or biting may hardly be accounted for by inexperience, and adult, multiparous females are most commonly the performers of aggressive acts toward infants. For example, among langurs, multiparous females were abusive of infants more than twice as often as nulliparous females (Hrdy, 1977; 1978; Sommer, 1989). Similar observations have been reported in baboons (Altmann, 1980; Nicolson, 1987), rhesus, Japanese, and bonnet macaques (Rowell *et al.*, 1964; Silk, 1980; Hiraiwa, 1981; Maestripieri, 1993a). Among Japanese macaques, in particular, it was observed that “once a female had borne her own infant her frequency of alloparental care declined, and as she bore additional infants, she acted more and more aggressively toward the infants of other females” (Hiraiwa, 1981). It may be argued that since mothers themselves occasionally cause distress to or even attack their own infants, a behavior that has been referred to as “punishment” (Nicolson, 1987), harassment of infants by nonmaternal adult females may still be explained within the framework of maternal behavior and accounted for by the null hypothesis (Hrdy, 1977; Sommer, 1989). However, this is unlikely to be the case because distress caused by mothers to their own infants is almost invariably related to rejection and denial of access to the nipple (Nicolson, 1987). Rejection is virtually absent in the first month of the infant’s life and gradually increases thereafter (Nicolson, 1987). In contrast, distress or aggression toward infants by adult females is not related to rejection because adult females do not suckle infants other than their own (Nicolson 1987). It is most common in the first weeks of the infant’s life and declines thereafter [baboons (Wasser, 1983); rhesus macaques (Maestripieri, 1993c)]. It is obvious, then, that to explain harassment of infants by adult females, an explanation other than simple attraction to infants must be sought. The most suitable explanation is that harassment of alien infants by adult females is an indirect form of reproductive competition among females (Silk, 1980; Wasser and Barash, 1981; Wasser, 1983; Nicolson, 1987). In primates, as in many social mammals, female re-

productive success may be dramatically affected by the timing of a female's birth relative to others in her group and by the number of infants simultaneously present in the group. Therefore, if a female could detrimentally affect the competitive abilities of infants other than her own, she could thereby improve the relative competitive ability of her own offspring (Wasser and Barash, 1981). In particular, in species in which females are the resident sex, adult females may attempt to minimize the amount of competition they and their daughters will encounter in the future by limiting the number of unrelated females born and raised in their groups (Clark, 1978; Silk, 1983).

The hypothesis that harassment of alien infants is a form of reproductive competition among females relies on the validity of the assumption that harassment of infants is associated with a reduced probability of infant survival or future reproduction because of risk of death or suboptimal physical or psychosocial development due to injury or the physiological consequences of high stress. Evidence to support this assumption is inconclusive. The consequences of aggression toward infants may range from intimidation and distress to superficial injuries and serious wounds (Silk *et al.*, 1981). In bonnet macaques, aggression from adult females was associated with a reduced probability of survival in infants of low-ranking mothers (Silk, 1980). In captive vervet monkeys the average amount of infant carrying was not associated with infant mortality (Fairbanks, 1990). However, since infant carrying per se is not expected to reduce the probability of infant survival, these data remain difficult to interpret. The difficulty of demonstrating a relationship between harassment of infants and infant survival is associated with the scarcity of accurate longitudinal data. Moreover, in captivity, where these data are more likely to be available, the more serious consequences of interactions between infants and other individuals may be reduced by the safe environment and external intervention. The hypothesis, however, that harassment of alien infants is a form of reproductive competition among females is supported by some indirect evidence. This hypothesis, in fact, leads to some predictions that can be empirically tested. First, harassment of infants should be performed by pregnant females about to give birth or by mothers with newborn babies more frequently than by nulliparous females or multiparous females in other reproductive stages (Wasser and Barash, 1981). In fact, females in the former category have immediate competitive interests and are more likely to gain from such behavior than females in other reproductive stages. Second, harassment of infants should be directed especially toward unrelated infants, infants of the resident sex, and infants of low-ranking mothers. In fact, they will be the most likely future competitors of a female's own offspring and their harassment entails prospective benefits

associated with minimal costs because low-ranking mothers are unlikely to provide an adequate agonistic protection of their infants. The evidence available tends to support these predictions. For example, in macaques, aggression toward others' infants was shown more frequently by mothers with young than by any other category of individuals [rhesus (Rowell *et al.*, 1964; Spencer-Booth, 1968), Japanese macaques (Hiraiwa, 1981)], and in a number of species, adult females are more likely to harass unrelated female infants of low-ranking mothers than any other category of infants [langurs (Hrdy, 1976); macaques (Dittus, 1979; Silk *et al.*, 1981; Eaton *et al.*, 1985; Simpson and Simpson, 1985); baboons (Wasser, 1983); vervets (Horrocks and Hunte, 1983)].

The potentially detrimental consequences of interactions between infants and adult females are most apparent in one extreme form of infant handling: kidnapping. Long-lasting kidnappings have been reported both in captivity and in the field and some of these episodes ended with the death of the infant from starvation or dehydration [macaques (Bullerman, 1950; Furuya, cited by Itani, 1959; Kurland, 1977; Quiatt, 1979; McKenna, 1979; Maestriperi, 1993b), baboons (Strum, 1975; Altmann, 1980; Collins *et al.*, 1984; Shopland and Altmann, 1987; Brain, 1992), guenons (Bourlière *et al.*, 1970), langurs (Hrdy, 1978)]. Kidnappings are performed by both immature and adult females but the latter are less likely than the former to return the infant to its mother [in rhesus macaques (Maestriperi, 1993b)]. In fact, the majority of the reported cases of fatal kidnappings involved nonlactating adult females. Therefore, also long-lasting kidnapping performed by adult females can be considered evidence for reproductive competition among females (Shopland and Altmann, 1987).

In summary, three widely reported characteristics of infant handling, namely, the sex difference in attraction to infants, the extensive involvement of immature females in infant handling, and the instances of harassment of infants by adult females are best accounted for by three different hypotheses. This suggests that infant handling is not a homogeneous phenomenon and that its different components may vary across species and be related to the socioecological conditions in different ways.

SOCIAL STRUCTURE, INFANT HANDLING, AND MOTHERING STYLE

No concerted attempt has been made to relate infant handling to mothering style in a comprehensive explanatory framework. The only suggestion made in this sense was that if infant handling is just a by-product of maternal behavior, then "a logical extension of this argument is that, to

the extent that we see species differences in maternal behavior, we should see species differences in allomaternal behavior" (Caine and Mitchell, 1980). For example, in species in which mothers are more permissive, infant handling should be "less common or somehow less intense" (Caine and Mitchell, 1980). Unfortunately, both the premises and the conclusions of this suggestion seem to be incorrect. First, it is apparent that some aspects of infant handling cannot be explained as mere by-products of maternal behavior. Second, the assumption that maternal restrictiveness/permissiveness may be equated with interest in infants and that they can be compared to one another in terms of intensity does not seem warranted. Third, even if this assumption were correct, there is no indication that in species in which mothers are highly permissive of their own infants, (e.g., among langurs), females are less attracted to other infants. In contrast, in these species, infant handling is widespread and the mothers themselves are frequently involved in handling other females' infants (Hrdy, 1976).

Having argued that the category of infant handling is heterogeneous and includes interactions performed by different categories of individuals with different motivations and consequences for the individuals involved, a question arises as to which categories of interactions are most likely to be associated with specific differences in social structure and mothering styles. In species in which the development of the mother-infant relationship is substantially similar and the achievement of competent maternal skills is dependent to a similar extent on learning and practice with infants, no differences are expected in the general interest females of all ages have in infants or in the eagerness of immature females to handle infants. Since maternal restrictiveness represents a response to the potential risk posed by the social environment to the infant, and interactions with adult females are more likely to result in abuse of the infant than interactions with other categories of individuals are, differences in these interactions are most likely to affect the mothering style. Even though some interactions between immature females and infants may cause distress to the infant due to inexperience and clumsiness, no differences among species are expected in this regard. However, insofar as harassment of infants by adult females reflects reproductive competition among females and species differ in the intensity and pattern of competition among females, we may expect species differences in the extent to which interactions with adult females are risky to infants.

It is worth remarking that the fact that interactions with adult females are more likely to be harmful to the infant than interactions with immature females does not necessarily imply that, in general, interactions between adult females and infants are expected to be abusive. Instead, owing to their general attraction to infants, adult females are likely to display both

affiliative and abusive responses toward infants. Likewise, it cannot be ruled out that infant handling by adult females may actually benefit the mother, for example, by allowing her to shorten the interval to the birth of her next infant (Fairbanks, 1990). The relative balance of costs and benefits to the mother, however, and the relative occurrence of abusive to affiliative responses to infants, will depend on the pattern of competition and cooperation among females. In particular, since the mothering style is specifically affected by the potential danger to the infant, it may be predicted that differences in mothering styles will be related to the probability of the occurrence of abusive responses to infants by adult females.

In summary, species differences in the interest shown in infants by females of all ages are not necessarily to be expected, interactions with adult females are riskier to infants than interactions with immature females are, the former type of interactions and their consequences to the infant are more likely to vary across species than the latter, and species differences in mothering styles are likely to be associated with differences in the relative occurrence of abusive to affiliative responses toward infants by adult females.

Differences in infant handling by adult females may be associated with differences in female social relationships, in particular with reference to the pattern of female–female competition and cooperation. Several hypotheses have been proposed to explain species differences in female social relationships and some of them have also considered differences in mothering styles. Studies emphasizing the importance of dietary habits, dispersal, and intragroup inbreeding have implied that since folivorous primates tend to live in smaller groups, when they are monopolized by a single breeding male for a prolonged period and females do not transfer, females born in the troop will be related both matrilineally and patrilineally. As a consequence of high intragroup inbreeding, social relationships among females should be primarily cooperative and characterized, for example, by a high tolerance of infant handling (Hrdy, 1977; Wade, 1979; Gouzoules, 1984; Moore, 1992). The weakness of this explanation is that female dispersal is much more common among folivores than among species with other diets so that folivores may actually have a lower degree of intragroup inbreeding than, for example, frugivores (Moore, 1984, 1992; van Schaik, 1989). Moreover, as far as infant handling is concerned, the degree of inbreeding in itself may not be an important factor when resources are scarce and many infants are present. In that case, competition over food and the necessity to provide support of the offspring and other closely related kin may lead females to treat distantly related individuals and their close kin as unrelated individuals.

Studies emphasizing the effect of the species-typical dominance hierarchy on mothering style have implied that since intragroup competition is lower among folivores than among frugivores, in folivores female-female competition and status differences are reduced so that a mother's confidence in retrieving her infant from other females and her tolerance of infant handling should increase. One problem with this hypothesis is that it does not take into account possible species differences in the pattern of infant handling. A second objection is that the ease of infant retrieval seems to be relevant only for the risk posed to the infant by kidnapping. If infants are victims of harassment or aggression by other individuals, momentary handling can be as dangerous as prolonged kidnapping and ease of retrieval may not be an important issue.

The most comprehensive attempt to explain species differences in female social relationships in terms of patterns of competition/cooperation has been made by van Schaik (1989). He suggested that female social relationships primarily reflect competition for food and safety. Predation risk is the main pressure for living in groups and sets the lower limit to group size. The relative prevalence of scramble and contest food competition within and between groups related to the diet and size of food patches used sets the upper limit to group size and determines the characteristics of female dominance relationships and bonding as well as the pattern of dispersal and the genetic relatedness among females. Despotic and nepotistic relationships involving agonistic support of kin and displacement over food or aggression toward unrelated females and their kin are more likely to be found in frugivorous and omnivorous species than in folivorous species.

Differences in offspring survival are probably the most important component of variation in a female's reproductive success (Clutton-Brock, 1988), and offspring survival is strongly influenced by the quantity and quality of food that a female can acquire as well as by protection from the environment (Lee, 1987). Support and protection of a female's own offspring and displacement over food or active harassment of other females' offspring are likely to be a most effective means to compete in species with strong contest competition. Therefore, if van Schaik's (1989) model of female social relationships is extended to include patterns of infant handling, infant handling by adult females may be expected to involve a higher proportion of abusive interactions in species characterized by strong contest competition for food than in species characterized by weak contest competition or mainly scramble competition.

Even though infant mortality due to harassment or kidnapping by adult females may be negligible, the cost of infant loss to a female is so high that the potential risk posed by interactions with certain group members is likely to strongly affect the mothering style. Therefore, although the frequency of

abusive interactions with infants may be low compared to the total number of interactions, even slight differences in the proportion of abusive to affiliative interactions and in the severity of harassment are likely to give rise to marked differences in mothering styles. Since in some species the approach to infants by adult females is associated with a higher probability of harassment, the infant's proximity to and contact with these individuals will be perceived as hazardous by mothers, and mothers with young infants will show avoidance of these individuals and resistance to their attempts to interact with the infant. Indeed, the mere presence of these females may be perceived as a threat by the mothers and decrease their confidence in their surroundings so that a general shift in mothering style towards protectiveness and restrictiveness may be expected. In fact, adult females snatch young infants more easily when they are alone or are being handled by other individuals, especially immature females, than when they are held by their mothers [rhesus macaques (Maestriperi, 1993c)]. Therefore, when the potential risk posed by infant handling is higher, mothers are expected to limit their infants' freedom of movement and to display reduced tolerance of interactions between infants and any other individual. The above-outlined relationship among patterns of food competition, female dominance relationships, infant handling, and mothering style is summarized in Table II.

METHODOLOGICAL CONSIDERATIONS

Since the model predicts a relationship between mothering style and the relative occurrence of abusive to affiliative interactions between infants

Table II. Summary of the Proposed Relationship Among Patterns of Food Competition, Female Dominance Relationships, Characteristics of Infant Handling, and Mothering Style

Female dominance relationships	Pattern of food competition	
	Within-group scramble egalitarian-individualistic	Within-group contest despotic-nepotistic
Interest in infants by females of all ages	High	High
Proportion of abusive vs. affiliative responses made to infants by nonmaternal adult females	Low	High
Maternal tolerance of infant handling	High	Low

and adult females, accurate behavioral observations of mothering behavior and infant handling are needed to test the model properly. Differences in mothering behavior can be identified reliably. For example, marked individual or species differences in the rates of maternal restraint of the infant or resistance to attempts by other individuals to handle the infant have been reported (Hrdy, 1976; Altmann, 1980). Unfortunately, such accurate and reliable information is rarely available for infant handling. In most studies on infant handling, investigators have focused their attention on maternal reactions to infant handling and failed to report accurate behavioral descriptions of infant handling. Other studies have failed to discriminate between different individuals involved in infant handling and also the consequences of their interactions with infants. Individuals of all age/sex categories were sometimes collectively referred to a "aunts" or "nonmothers" and their interactions lumped in one category (Kohda, 1985). Likewise, interactions with infants often were not distinguished according to whether or not they caused distress to infants (Fairbanks, 1990; Small, 1990; Stanford, 1992). Therefore, we have to assume that in these analyses, behaviors such as carrying and grooming infants have been lumped with harassment of and aggression toward infants. Since infant handling has often been interpreted as a homogeneous phenomenon, even studies testing predictions derived from the competition hypothesis have used data concerning the totality of infant handling instead of focusing on abusive interactions only (Wasser, 1983; Sommer, 1989). To test the relationship between infant handling and mothering style proposed here, interactions with adult females must be distinguished from those with other categories of individuals, e.g., immature females or males of any age, and abusive interactions distinguished from affiliative interactions.

Another prediction of this model that needs to be tested with accurate behavioral observations is that species do not differ in the amount of interest shown in infants by females of all ages. In this regard, the frequency of approaches to mothers with newborn infants and attempts to touch and to handle the infant are likely to be a better indicator of interest in infants than the time spent by infants in proximity to or contact with individuals other than the mother. In fact, the latter measures are likely to reflect the extent to which infants are available for handling by other individuals, i.e., maternal tolerance of infant handling, rather than interest in infants. Therefore, although approaches to infants and attempts to handle them are not expected to vary among species, the time spent by infants in proximity to or contact with individuals other than the mother is likely to be lower in species where the risk of harassment by adult females is higher and mothers are more restrictive of their infants.

EVIDENCE IN SUPPORT OF THE MODEL

The ecological and behavioral differences between the Colobinae and the Cercopithecinae offer a good example for testing the proposed relationship among social structure, infant handling, and mothering style. Colobines are primarily folivores and *Presbytis* and *Colobus* have been proposed as examples of primates in which food competition is mainly by scramble and the social structure is egalitarian-individualistic (van Schaik, 1989). In contrast, most cercopithecines are characterized by within-group contest competition for food and their social structure is primarily despotic-nepotistic (van Schaik, 1989). Since colobine females are not expected to compete aggressively with females of their own group as much as cercopithecine females do, in colobines infant handling should be affiliative and mothering styles permissive to a greater extent than in cercopithecines. This may be the case even though female dispersal is more common and intra-group inbreeding is lower among colobines than among cercopithecines (Moore, 1992).

The basic pattern of maternal care is generally similar in colobine and cercopithecine monkeys. Mothers perform the greatest share of infant caretaking—feeding, thermoregulation, and protection against predators—and there is no evidence indicating that the importance of learning and experience in the acquisition of maternal competence differs among species (Nicolson, 1987, 1991). Interest in newborn infants by females other than the mother is typically high in both colobines and cercopithecines (McKenna, 1979) but there is a general consensus that colobine mothers are more permissive of infant handling than cercopithecine mothers are (Hill, 1972; Emerson, 1973; Horwich and Manski, 1975; Hrdy, 1976; McKenna, 1979; Kohda, 1985; Stanford, 1992). For example, colobine mothers may allow other females to handle their infants even shortly after birth and for a prolonged period of time (Jay, 1963; Hrdy, 1976; McKenna, 1979), while most cercopithecine mothers do not ordinarily surrender their infants to other individuals for several weeks after birth (Kohda, 1985). Among colobine monkeys, infant handling is believed to be primarily affiliative (Jay, 1963; Hrdy, 1976; McKenna, 1979; Kohda, 1985; Fimbel, 1992; Stanford, 1992). Nevertheless, when accurate observations were made, infants were often shown to experience distress and to be mistreated especially by adult females [langurs (Hrdy, 1977; 1978; Scollay and De Bold, 1980; Vogel, 1984; Sommer, 1989)]. As for colobines, in cercopithecines both affiliative—grooming, carrying, cuddling—and abusive—pulling and dragging—interactions between infants and females other than the mother can be observed. Unlike colobines, however, in which harassment of infants seems to result mainly from rough handling, cercopithecine infants, espe-

cially females, may be victims of aggression by adult females [macaques (Hiraiwa, 1981; Silk *et al.*, 1981; Maestriperi, 1993a), baboons (Wasser, 1983)]. For example, in bonnet macaques, Silk *et al.*, (1981) observed attacks on infants by adult females in which the former "sustained wounds that required medical treatment and extended periods of convalescence." Furthermore, the majority of long-lasting kidnappings which ended with the death of an infant from starvation or dehydration has been reported in cercopithecine monkeys [macaques (Furuya, cited by Itani, 1959; Quiatt, 1979; McKenna, 1979), baboons (Strum, 1975; Collins *et al.*, 1984; Brain, 1992; Shopland and Altmann, 1987), guenons (Bourlière *et al.*, 1970)]. Although studies involving direct comparisons are needed, the present evidence suggests that infant handling by adult females may be riskier to the infant among cercopithecines than among colobines and that differences in mothering styles may be related to differences in infant handling by adult females.

The hypothesis that differences in mothering styles may be associated with different patterns of infant handling seems to be confirmed also by the variability within subfamilies. Among colobines, for example, mothers among *Presbytis* spp. appear more permissive than mothers among *Colobus* spp. and *Nasalis larvatus* (Kohda, 1985). Interestingly, female *Nasalis* pull infants at a higher rate and are more reluctant to return them to their mothers than female *Presbytis* are (Kohda, 1985). Among cercopithecines, patas monkey (*Erythrocebus patas*) and vervet monkey (*Cercopithecus aethiops*) mothers allow other individuals to handle their infants at an earlier age than mothers among *Macaca* spp. and *Papio* spp. do. [patas (Hrdy, 1976; Chism, 1978; Zucker and Kaplan, 1981), vervets (Gartlan, 1969; Struhsaker, 1971)]. Among patas, infant handling by other females may include both affiliative and abusive components, but the overall pattern of interactions with infants was described as being affiliative and innocuous rather than detrimental, and the frequency of aggression directed toward other females' infants was low compared to the frequency of affiliative contacts (Chism, 1978; Zucker and Kaplan, 1981). Likewise, in vervet monkeys, active harassment of young infants has scarcely been reported (Lancaster, 1971; Struhsaker, 1971; Fairbanks, 1990). Aggression toward infants by unrelated adult females is absent for about the first 5 months of life and increases thereafter (Horrocks and Hunte, 1983). In contrast, maternal intolerance of infant handling and the occurrence of harassment of infants have been consistently reported among *Papio* spp. (Altmann, 1980; Wasser, 1983; Collins *et al.*, 1984) and *Macaca* spp.

Macaca seem to be particularly promising for investigating the relationship among social structure, infant handling, and mothering style. An increasing body of data has documented considerable differences in social

organization among macaque species. The differences have been summarized in terms of dominance style with some species (rhesus, Japanese, and probably also pigtail and longtail macaques) being more despotic and less socially tolerant than others [stumptail, bonnet, tonkean, and Barbary macaques (Thierry, 1985; Caldecott, 1986; de Waal and Luttrell, 1989; Thierry, 1990)]. Even though differences in social structure among macaque species have long been recognized (Lahiri and Southwick, 1966; Rosenblum and Kaufman, 1967), how these differences relate to ecological factors is still poorly understood (Caldecott, 1986).

Interestingly, preliminary studies indicated that differences in dominance styles may be matched by differences in mothering styles, particularly relative to maternal tolerance of interactions between infants and other individuals. In general, whereas rhesus, Japanese, pigtail, and longtail mothers restrict their infants for several weeks after birth [rhesus (Spencer-Booth, 1968) Japanese: (Hiraiwa, 1981), pigtail (Rosenblum and Kaufman, 1967, personal observation), longtail (Thierry, 1985)], tonkean, bonnet, Barbary, and stumptail mothers tolerate extensive interactions between their infants and other individuals from the first weeks of life [tonkean (Thierry, 1985), bonnet (Rosenblum and Kaufman, 1967); Barbary (Lahiri and Southwick, 1966; Small, 1990), stumptail (Gouzoules, 1975; personal observation)]. Even though the grouping of species into two broad categories of restrictive and permissive mothering may be initially useful, macaque mothering is likely to vary along a continuum with the rhesus probably being at the restrictive extreme.

Information concerning the characteristics of infant handling, especially with reference to the relative occurrence of affiliative to abusive interactions with infants, is scarce and cross-species comparisons can only be indirect. In all species, immature and adult females exhibit an extreme interest in newborn infants [rhesus (Rowell *et al.*, 1964; Spencer-Booth, 1968), Japanese (Hiraiwa, 1981; Ehardt, 1987), bonnet (Small, 1982), Barbary (Small, 1990), pigtail (personal observation), stumptail (Gouzoules, 1975; personal observation)]. In one study, immature female rhesus and bonnet macaques were reported to differ in interest in infants (Caine and Mitchell, 1980). Interest in infants, however, was measured by the time spent by these individuals in proximity to or contact with them. When interest in newborn infants was measured by the frequency of approaches to the mother-infant pair, no difference between rhesus and bonnets was found (Small, 1982). In Barbary macaques, infant handling by adult females appears to be primarily affiliative and aggression toward infants has not been reported (Lahiri and Southwick, 1966; Small, 1990). Adult stumptail females show a great deal of interest in the infant when it is on the mother but, during the first 2–3 months, make great efforts to avoid it when it is

off the mother and moving independently (Gouzoules, 1975; personal observation). During this period, harassment of infants is virtually nonexistent and interactions between adult females and infants involve only the females touching and grooming the infant (Gouzoules, 1975; Rhine and Hendy-Neely, 1978). After the third month some instances of harassment of infants occur (Gouzoules, 1975). This is in sharp contrast with the pattern of infant harassment in rhesus macaques. With the exception of adult males, other individuals do not show any avoidance of infants when they are off their mothers. The rate of harassment is especially high during the first 8 weeks of life and when the infant is away from its mother, that is, under conditions of the infant's maximal vulnerability (Maestriperi, 1993c). Rhesus mothers whose infants are harassed or attacked at high rates by other individuals are highly vigilant and restrictive (Simpson, 1988), and when maternal vigilance is reduced, e.g., during grooming time, the rate of harassment of infants increases dramatically (Maestriperi, 1993a). Aggression toward infants by adult females and maternal intolerance of infant handling have also been reported in another species at the despotic extreme, the Japanese macaque (Eaton, 1976; Hiraiwa, 1981). Paradoxically, however, the best documented evidence concerning aggression to infants comes from one of the more socially tolerant species, the bonnet macaque (Silk, 1980; Silk *et al.*, 1981). Clearly, to have a more precise picture of the differences among *Macaca* spp. studies involving direct comparisons among the species, using data collected with similar procedures, are needed.

CONCLUSION

My hypothesis suggests that in group-living Old World monkeys, species differences in mothering styles are directly related to differences in infant handling by individuals other than the mother, and both are influenced by the species-typical social structure. This hypothesis emphasizes the notion that the mothering style is related to the risk posed by the social environment to the infant. Perhaps because infant handling may include elements of the mother-infant bond, interactions with infants have often been equated with care and assumed to be invariable relative to the social and ecological conditions. In contrast, I emphasize that some interactions between nonmaternal individuals and infants can be considered by the same standard as social interactions between group members, and hence potential competitors for resources, and that part of infant handling is better understood within the framework of female social relationships.

The evidence currently available in support of the proposed relationship among social structure, infant handling, and mothering style must be

interpreted with caution, as it includes mostly indirect, qualitative comparisons among species. To test the proposed relationship between infant handling and mothering style, accurate behavioral observations concerning infant handling and maternal tolerance of infant handling are required. To test the proposed relationship between infant handling and social structure, qualitative differences in patterns of infant handling must be analyzed in the light of reliable information concerning the competitive regime of the species, e.g., in terms of relative strength of various components of food competition (van Schaik, 1989), and female social relationships, e.g., in terms of linearity and consistency of dominance relationships, occurrence of intragroup aggression, and grooming bonds.

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