



CAUSES AND CONSEQUENCES OF INFANT ABUSE AND NEGLECT IN MONKEYS

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ABSTRACT. *Recent studies of naturally occurring infant abuse and neglect in group-living monkeys have provided some insights into the potential causes and consequences of these phenomena. Infant abandonment by monkey mothers in suboptimal conditions for reproduction and parental investment suggests that neglect, at least in its most extreme forms, may be an adaptive behavior. In contrast, several lines of evidence indicate that infant physical abuse is a maladaptive form of aggression or parenting. Studying the natural occurrence of infant abuse in nonhuman primates can provide important information on the origin and maintenance of child maltreatment in human populations. © 2000 Elsevier Science Ltd. All rights reserved.*

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FROM AN EVOLUTIONARY PERSPECTIVE, aggression and violence between conspecifics may be adaptive or maladaptive. Aggression toward a conspecific is adaptive when it results in net reproductive benefits to the aggressor or his/her kin, such as increased reproductive opportunities or enhanced access to resources or status. Aggression toward a conspecific is maladaptive when it results in net reproductive costs to the aggressor or his/her kin, such as impaired ability to survive or reproduce. In human societies, some forms of aggression and violence toward conspecifics may reflect competition for resources and, therefore, have an adaptive function; however, they are nevertheless condemned by our societies' civil, moral, and religious norms. Other forms of aggression and violence are both maladaptive and condemned by societal norms. One putative example of such maladaptive violence is child abuse, particularly when directed toward one's biological offspring.

Similar to humans, animals show both adaptive and maladaptive aggression. Animal research, therefore, can be useful to understand why humans harm their conspecifics. Animal research could be particularly useful to understand maladaptive violence, because the causes of this phenomenon are often difficult to identify. For example, although a great deal of research has been conducted on child maltreatment in the last three decades, we are still far from understanding the etiology of this phenomenon.

Maladaptive aggression can be induced in animals by altering their species-typical physical and social environment. For example, when rhesus monkey (*Macaca mulatta*) infants are separated from their mothers at birth and raised under conditions of social deprivation, they tend to become hyperaggressive individuals during adulthood and females may become abusive mothers (Harlow & Seay, 1966; Ruppenthal, Arling, Harlow, Sackett, & Suomi, 1976; Suomi, 1978). Further, when macaque mothers are housed alone in a small cage, they may abuse their infants irrespective of their developmental history (Castell & Wilson, 1971; Jensen, Bobbitt, & Gordon, 1969; Negayama, 1981; Wolfheim, Jensen, & Bobbitt, 1970). One problem with this approach is that the alterations of the animal's environment are usually far more dramatic than those normally encountered by most humans during their lifetime. Therefore, the findings of animal research are difficult to generalize to humans. An alternative approach is to study the natural (i.e., not induced by humans) occurrence of maladaptive aggression in animals.

Although the behavior of free-ranging animals is generally well adapted to their environment, some behavioral pathologies may be expected to occur. Unfortunately, it is much easier to induce behavioral pathologies in animals with drastic alterations of their lifestyle than to investigate their natural occurrence. Perhaps for this reason, naturally occurring maladaptive aggression and violence in animals have rarely been studied. For example, although it has long been known that some monkey mothers living in undisturbed social groups in captivity or in the wild occasionally abuse their infants (Hiraiwa, 1981; Reite & Caine, 1983; Troisi, D'Amato, Fuccillo, & Scucchi, 1982), this phenomenon was not systematically investigated until recently. Recent studies of infant abuse and neglect in group-living Cercopithecine monkeys have provided some insight into the causes and consequences of this phenomenon. They have also highlighted a number of similarities between infant abuse in monkeys and child maltreatment, suggesting that the spontaneous occurrence of infant abuse in monkeys could represent a valid animal model for research on child maltreatment.

The aim of this article is to review the studies of naturally occurring infant abuse and neglect in group-living monkeys. Although infant neglect is not, strictly speaking, a form of aggressive or violent behavior, nevertheless, it might represent another pathological expression of maternal behavior and therefore it will be discussed along with abuse. The main focus of this article is on the possible causes and consequences of infant abuse and neglect in monkeys. The similarities and differences between the findings of primate and human research on infant abuse and neglect have been discussed elsewhere (Carroll & Maestriperi, 1998; Maestriperi & Carroll, 1998c).

DEFINITION OF INFANT ABUSE AND NEGLECT IN MONKEYS

One problem encountered in the study of naturally occurring behavioral pathologies in animals is how to identify maladaptive behavior. For example, although offspring neglect, abuse, or infanticide may look like a good example of maladaptive behavior, in some circumstances they may have an adaptive value. In other words, even if parents who neglect or abuse their young reduce their current fitness, they can nevertheless increase

their own future reproductive success. This may occur, for example, when the current offspring have a low probability of survival, and by neglecting or killing them, parents will increase their own chances of survival and future reproduction. A question then arises as to how to distinguish adaptive forms of offspring neglect and abuse from their maladaptive counterparts.

The most direct answer to this question would involve measuring the fitness costs and benefits of offspring neglect or abuse (e.g., the total number of offspring and grandoffspring produced by neglectful/abusive parents and nonneglectful/nonabusive parents during their lifetime). When this is not feasible, alternative strategies can be used. For example, in a study of naturally occurring infant abuse in rhesus macaques, Maestripieri (1998) argued that if abuse represented an adaptive reduction of maternal investment in the offspring, abuse should be accompanied by reduced effort in other aspects of maternal care such as nursing, carrying, or protecting the infant. Since in most cases, abusive macaque mothers score higher, rather than lower, than nonabusive mothers on measures of mother-infant contact and maternal protectiveness, this analysis suggests that infant abuse is, in most cases, a maladaptive behavior (Maestripieri, 1998; Maestripieri & Carroll, 1998b; Troisi, Aureli, Piovesan, & D'Amato, 1989; Troisi & D'Amato, 1984; but see Maestripieri, 1994). Therefore, the coexistence of harmful and nurturing behavior suggests the existence of a true pathological phenomenon.

The identification of infant abuse in monkeys is also relatively straightforward because most behavioral patterns of abuse are qualitatively different from any other behaviors in the maternal repertoire. Infant abuse among group-living monkeys takes the form of dragging the infant by its tail, pushing the infant against the ground, throwing the infant at a short distance, and other harmful behaviors such as stepping or sitting on the infant (Troisi & D'Amato, 1983). Most monkey mothers living in groups never display any of these behaviors at any time during the period of infant dependence (e.g., Hinde & Spencer-Booth, 1967). Specifically, although monkey mothers sometimes slap or bite their infants to discipline them or encourage their independence, the above-described patterns of behavior do not occur in this context.

The consequences of abuse may vary from infant distress to injury and death. Recent observations indicate that the severity of abuse is determined mainly by its frequency of occurrence and not by its physical patterns (Maestripieri & Carroll, 1998b), suggesting that mild and severe abuse are two facets of the same phenomenon. Preliminary data obtained in rhesus macaques also indicate that mildly abused infants have high baseline levels of cortisol and adreno-cortico-tropic-hormone (ACTH) long after the termination of abuse (D. Maestripieri and P. Plotsky, unpublished data), suggesting that abuse is a long-lasting stressful experience. Therefore, even if behavior patterns such as infant dragging or throwing do not necessarily result in injury or death, these patterns are likely to be maladaptive and therefore can be considered abuse.

The identification of infant neglect is more problematic than that of abuse. There are considerable quantitative differences in maternal care among monkey mothers of the same species and social group (Fairbanks, 1996), and although some mothers show minimal involvement in maternal care relative to others, it is difficult to establish that their behavior is detrimental to the infant. A more conservative approach used to identify neglect is to focus on abandonment (i.e., the complete cessation of maternal interactions with the infant). Because young infants are totally dependent on their mothers for nutrition, transport, and protection, abandonment usually results in infant death. Although abandonment, and possibly also less dramatic forms of neglect, are detrimental to the infant, this does not necessarily imply that they are maladaptive to the mother. In fact, unlike abuse, neglect and abandonment intrinsically reflect a reduction of maternal effort in rearing

the offspring and such reduced effort may be an adaptation to circumstances unfavorable to parental care. Some characteristics of infant abandonment in monkeys suggest that this, in fact, may be the case.

GENEALOGICAL AND DEMOGRAPHIC STUDIES OF INFANT ABUSE AND NEGLECT

Naturally occurring infant abuse and neglect in monkeys have been investigated with genealogical/demographic studies and with observational investigations. Maestriperi and co-workers investigated the occurrence of infant abuse and neglect in three large populations of rhesus macaques, pigtail macaques (*Macaca nemestrina*), and sooty mangabeys (*Cercocebus atys*) living at the Field Station of the Yerkes Regional Primate Research Center over a period of 30 years (Maestriperi & Carroll, 1998a; Maestriperi, Wallen, & Carroll, 1997a, 1997b). Population size ranged from almost 400 individuals in the pigtail macaques to over 3,000 individuals in the rhesus macaques. The analysis focused only on the most extreme forms of neglect and abuse, namely infant abandonment and abuse resulting in serious injury or death.

In all the three species, abuse and neglect did not occur together. For example, there was no evidence that an infant was first abused and then abandoned by its mother. Abusive mothers tended not to neglect their infants and neglectful mothers tended not to abuse them. In only a few cases, did mothers display both abuse and neglect, although with different infants. The proportion of infants that were abused varied considerably in the three species, ranging from 1.5% in rhesus macaques to 9.39% in pigtail macaques. Similarly, the proportion of neglected infants ranged from 0.4% in rhesus to 2.79% in pigtails. The proportion of mothers who abused their infants ranged from 2.53% in rhesus to 23.94% in pigtails, and the proportion of neglectful mothers ranged from 1.49% in rhesus to 15.49% in pigtails. Mangabeys had intermediate values between rhesus and pigtail macaques.

Because only severe forms of neglect and abuse were considered, the overall prevalence of abuse and neglect in these monkey populations is probably higher than reported and the relative prevalence of abuse versus neglect may be different as well. The reason for the different prevalence of abuse and neglect in the three species is not clear. It may be worth noting, however, that the pigtail and mangabey populations were probably more inbred than the rhesus population. Therefore, if abusive and neglectful behavior are, to some extent, genetically determined, their prevalence may be greater the higher the degree of inbreeding in the population.

In pigtail and rhesus macaques, infant abuse, but not neglect, tended to be concentrated in some matriline and never to occur in others, whereas among the mangabeys such a phenomenon was not observed. In the pigtails, the physical patterns of abuse differed among matriline as well; in some matriline abusive mothers mostly dragged or pushed their infants whereas in others mothers mostly roughly groomed or bit their infants. In all three species, abuse was especially common among closely related females such as mothers and daughters or sisters. For example, in one matriline of pigtail macaques, all the five abusive mothers were sisters. Although these findings suggest that infant abuse can be transmitted within families and across generations, there was little evidence that individuals that had been abused during infancy tended to become themselves abusive parents in adulthood. This, however, may have been an artifact of the data analysis for two reasons. First, if abusive mothers had been mildly abused during infancy, this informa-

tion was unlikely to be available, and second, only a minority of infants that were severely abused survived and were later reintroduced into the breeding population.

In all three species, infant abuse and neglect were associated with different demographic factors. Infant neglect was essentially limited to young mothers and newborn infants whereas infant abuse was unrelated to maternal parity or infant age. In all three species, neglectful mothers neglected only one of their offspring, typically the first, whereas most abusive mothers repeated abuse with successive offspring. In rhesus and pigtail macaques, infant birth order did not affect the probability of abuse whereas in the mangabeys, the birth order of severely abused infants was significantly higher than that of their siblings that survived without intervention. In other words, infants born late were more at risk of abuse than infants born early. Infant sex was not a risk factor for neglect or abuse in any species.

The findings obtained from rhesus macaques, pigtail macaques, and mangabeys concur with those of other studies and other species in suggesting that infant neglect and abuse may be different phenomena with independent causal factors. For example, in a large population of vervet monkeys (*Cercopithecus aethiops*) studied over a period of 10 years, infant abandonment or otherwise high levels of maternal rejection were most common among the youngest and the oldest females of low body weight (Fairbanks & McGuire, 1995). There was no evidence, however, that mothers that frequently rejected or abandoned their infants also physically abused them. Infant neglect and abuse tended to be associated with different demographic and environmental variables also in a study of rhesus macaques raised under conditions of social deprivation (Ruppenthal et al., 1976).

Altogether, these findings suggest that maternal age, lack of experience, or, in some cases, a poor health condition, can be risk factors for infant neglect but not for abuse. The primary risk factor for infant abuse appears to be genetic relatedness to another abusive individual. The frequent occurrence of infant neglect among very young or very old mothers or among mothers in poor health conditions suggests that neglecting or abandoning an infant may be an adaptive response. The probability of infant survival is generally low among very young or very old mothers for several reasons including lack of experience, reproductive dysfunction, and risk of disease or death. Therefore, whenever the chances of infant survival are especially low, very young mothers may be better off sacrificing their current offspring to invest more in their own growth and future reproduction. Similarly, it may be adaptive for very old mothers to channel all of their resources in assisting their previous offspring.

The distribution of infant abuse within families and across generations suggests this phenomenon may be transmitted in the population with experiential or genetic mechanisms, or both. Studies of rhesus macaques and vervet monkeys have shown that the parenting styles of individual females resemble those of their mothers and that similarities can be accounted for by direct experience of being mothered during infancy or by observational learning of interactions between the mother and younger siblings (Berman, 1990; Fairbanks, 1989). Thus, it is possible that patterns of abusive behavior could be transmitted from mothers to daughters with learning mechanisms similar to those underlying the intergenerational transmission of mothering styles. It is also possible, however, that closely related females share some biologically determined psychological and behavioral characteristics (see below) that put them at risk of displaying abusive behavior. The crucial experiment to assess the relative importance of experiential and biological influences on infant abuse will involve cross-fostering female infants between abusive and nonabusive mothers and studying their patterns of maternal care when they give birth to their own infants.

OBSERVATIONAL STUDIES OF INFANT ABUSE AND NEGLECT

Because infant abandonment usually occurs in the first hours or days of life and results in infant death, it is difficult to conduct quantitative observations of the behavior of mothers that abandon their infants. Observational studies of infant abuse in group-living macaques, however, further support the hypothesis that abuse and neglect are different phenomena. Abusive mothers rarely, if ever, abandon their infants, and observations of their behavior suggest that abuse is associated with maternal protectiveness and control rather than with indifference and neglect. Troisi et al. (1982) first reported the case of a group-living, wild-born Japanese macaque (*Macaca fuscata*) mother that had abused to death all of her infants. The abusive mother scored higher than control mothers in the tendency to make contact with and restrain her infant; abuse occurred when the infant attempted to break contact with her or failed to respond to her retrieval signals (Troisi & D'Amato, 1984). The administration of an anxiolytic drug (diazepam) to the abusive mother reduced both maternal protectiveness and infant abuse (Troisi & D'Amato, 1991). Troisi et al. (1989) reported the case of another mother living in the same colony of Japanese macaques who abused all of her three infants. Also in this case, infant abuse was associated with protective maternal care, but abuse was not as severe as to cause infant death. Based on these findings, Troisi and D'Amato (1994) emphasized separation anxiety and maternal possessiveness as possible determinants of infant abuse. Specifically, they argued that abusive mothers may be anxiously attached to their infants and react with violence to their infants' attempts to break contact with them.

In a recent observational study of infant abuse in rhesus macaques, abusive mothers differed from controls in a number of parenting style measures (Maestriperi, 1998). Abusive mothers spent a higher percentage of time in contact with their infants, initiated contact with them more often, and restrained them more often than control mothers. Abusive mothers also rejected their infants more often than controls. Therefore, based on a commonly used classification of parenting styles in monkeys (Fairbanks, 1996), abusive mothers could be classified as Controlling mothers because they scored high on measures of both protectiveness and rejection. The finding that abusive mothers have controlling parenting styles has also been reported in pigtail macaques (Maestriperi & Carroll, 1998b), thus further supporting the hypothesis that infant abuse reflects inappropriate attempts to control the infant's behavior. The parenting styles of abusive mothers were consistent with successive infants and both the frequency and the patterns with which they abused their infants in two consecutive years were highly correlated (Maestriperi, Tomaszycski, & Carroll, in press b). Thus, the behavioral data on infant abuse are consistent with the findings of the epidemiological studies indicated that abused infants' siblings are at high risk of abuse.

In rhesus macaques, abuse decreased with infant age and was not consistently associated with particular infant activities or external events (Maestriperi, 1998). In pigtail macaques, however, the most common events immediately preceding infant abuse were stressful events such as aggression, infant kidnapping, or extragroup disturbances (Maestriperi, 1994; Maestriperi & Carroll, 1998b). Abusive mothers were not more likely than controls to find themselves in such stressful situations, suggesting that they may be individuals particularly vulnerable to stress or with problems in emotion regulation. Data from rhesus macaques also suggest that an aggressive temperament and a low amount of social contact with other individuals may contribute to both controlling parenting styles and infant abuse (Maestriperi, 1998).

To date, most studies of infant abuse in monkeys have focused on maternal and environmental characteristics as possible predictors of abuse. To investigate the possibility that

some aspects of infant behavior triggered the occurrence of abuse, Maestripieri, Jovanovic, and Gouzoules (in press a) investigated infant crying in abused and nonabused rhesus monkey infants. Abused infants cried more than controls in the first 12 weeks of life, and this was true also when cries following abuse were excluded from the analysis (see also Seay, Alexander, & Harlow, 1964). The acoustic structure of some of the cries of abused infants was also different from that of controls. Specifically, their screams differed in call duration, call rate, and number of units per call, while their coos differed in the ending frequency of the call, the peak frequency of the basic and the highest harmonic, and the position of the peak frequency in the call. Although these findings may suggest that both the frequency and the acoustic properties of abused infants' cries may have been especially aversive to their mothers, alternative explanations are also plausible. Abusive mothers rejected their infants more frequently than controls and some of them showed a preference for carrying infants dorsally rather than ventrally, causing frequent infant crying. Thus, the high frequency of crying in abused infants is more likely to have resulted from the behavior of abusive mothers than from abused infants being fussy. Further, some of the differences in the acoustic structure of abused infants' cries were due to the fact that screams caused by abuse were acoustically different from those occurring in other contexts.

Aside from the differences in infant crying between abused and nonabused infants, there was little evidence of a causal relationship between crying and abuse. First, only less than 10% of all abuse events were immediately preceded by infant crying unrelated to abuse. Second, if infant crying per se had had an important role in triggering abuse, the frequency of abuse should have increased with infant age in parallel with the increase in infant crying. In contrast, the frequency of abuse decreased as infants grew older. Therefore, although infant cries may contribute to the maintenance of abuse (e.g., by increasing the probability of abuse being repeated) infant crying per se appears to have a negligible role in triggering abuse.

The findings concerning infant crying concur with other observations in indicating that infant characteristics play a minor role in the occurrence of infant abuse relative to maternal and environmental characteristics. For example, the fact that in many cases abuse begins as early as the first day of infant life argues against the hypothesis that abuse is triggered by infant behavior because monkey newborns are generally passive (Maestripieri, 1998). The fact that abusive mothers abuse most, if not all, of their successive infants also emphasizes the importance of maternal characteristics (Maestripieri et al., 1997a, 1997b; Maestripieri et al., in press b). On the other hand, since some infants are abused less severely than their siblings, it is possible that infant characteristics contribute to the occurrence of abuse in subtle ways that have not yet been investigated.

Abused and nonabused infants differ in aspects of their behavior other than crying; however, these differences are likely to be consequences, rather than causes, of abuse. In rhesus macaques, abused infants broke contact with their mothers less frequently than controls in the first 2 months of life (Maestripieri, 1998). This finding concurs with those previously reported for socially deprived rhesus macaques in suggesting that abuse increases the infants' tendency to cling to their mothers (Seay et al., 1964). In pigtail macaques, abused infants did not differ from controls in measures of making or breaking contact with their mothers, but they started playing with their peers later in life and, overall, played less often than controls (Maestripieri & Carroll, 1998b). Specifically, abused infants initiated social play less frequently than controls, although they received a similar number of play initiations from their peers. Again, these findings are consistent with those reported for rhesus infants abused by their socially deprived mothers (Seay et al., 1964), and suggest that the difference in play is more likely to represent a consequence rather than a determinant of abuse.

Observations of abused infants in group-living monkeys were generally concentrated in the first 3 months of life, when most of the abuse takes place. Therefore, the long-term consequences of abuse for social development are currently unknown. Female infants that are abused by their mothers may be likely to become abusive mothers themselves, but conclusive evidence demonstrating the occurrence of this phenomenon is still lacking. Studies of rhesus monkey infants abused by their socially deprived mothers showed that these infants were easily disturbed in novel settings and hyperaggressive with their peers in the second year of life (Seay et al., 1964). If these findings were replicated in group-living monkeys, they would provide important evidence that early abuse may be a determinant of subsequent behavioral alterations or pathologies.

CONCLUSIONS

Both animals and humans show various forms of adaptive and maladaptive aggression. Although adaptive and maladaptive aggression may be superficially similar, they should not be confused with each other. For example, in several species of primates and other animals, adult males kill the offspring of unrelated females to induce female estrous and increase their own opportunities for mating and reproduction (Hrdy, 1979). Although maternal abuse of offspring in primates may be superficially similar to male infanticide, it is likely to differ from it in both its causes and consequences.

Recent research on naturally occurring infant abuse and neglect in monkeys has improved our understanding of why some mothers maltreat their offspring. Perhaps the most consistent information provided by primate studies is that infant abuse and neglect appear to be different phenomena with different causal factors and, possibly also a different function. Infant neglect, at least in its most extreme forms, appears to be an adaptive response to circumstances unfavorable for parental care. In contrast, infant abuse is likely to be a naturally occurring behavioral pathology that brings no fitness benefits to monkey mothers. Longitudinal and observational studies of infant abuse points to three domains of determinants: genetic relatedness or close proximity to other abusive individuals, the mother's temperament, and environmental stress. The specific mechanisms operating within each of these three domains of determinants need to be clarified by further studies. Future studies should address the extent to which infant abuse reflects a specific dysfunction of the mechanisms regulating parental behavior or those more generally involved in the regulation of aggressive behavior. In this regard, the study of the neuropsychological aspects of abusive behavior could make an important contribution (see research with humans by Milner, 1991). Most of the evidence available to date suggests that the role played by infants in causing abuse is negligible. Some infant behavioral characteristics, however, such as the frequency and acoustic properties of their cries, may contribute to the expression of abusive behavior in individuals or environmental circumstances that are at risk for abuse.

The developmental consequences of infant abuse are only beginning to be investigated. In addition to risk of injury or death, infant abuse is likely to have negative consequences also for infant biobehavioral and social development. Preliminary data suggest that, similar to other forms of early stress, infant abuse could bring about long-lasting changes in the organism's responsiveness to stress. From the standpoint of social development, infant abuse appears to delay, at least temporarily, the development of infant independence from the mother and the formation of social relationships with other individuals. The longitudinal study of individuals that were abused by their mothers during infancy could

make a significant contribution to understanding how abuse is maintained and transmitted across individuals and generations.

Because of their low frequency of occurrence, the study of naturally occurring infant abuse and neglect in primates may require a higher investment of time and resources than similar phenomena experimentally induced by drastic alterations of the animals' environment or lifestyle. Moreover, infant abuse and neglect should be comparatively studied in different species to account for the possibility that differences in social organization affect the form with which these phenomena manifest themselves in primates. Such an investment, however, could be highly profitable because this research has the potential to provide important information on the origin and maintenance of one of the most pervasive and damaging forms of maladaptive behavior in primate and human populations.

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