



## Parent–Offspring Conflict in Primates

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*Parent–offspring conflict (POC) theory (Trivers, 1974) has stimulated controversy in evolutionary biology and behavioral ecology. The theory has been criticized by some primate behavioral researchers on both conceptual and empirical grounds. First, it has been argued that it would be more advantageous to mothers and offspring to agree over the allocation of parental investment and to cooperate rather than to disagree and engage in conflict. Second, some studies have provided data suggesting that primate mothers and offspring engage in behavioral conflict over the scheduling of their activities rather than parental investment. In reality, parent–offspring interactions are likely to involve both cooperation and conflict, and the hypothesis that mothers and infants squabble over the scheduling of their activities is not incompatible with POC theory. Furthermore, the predictions of POC theory are supported by a number of empirical studies of primates. POC theory has enhanced our understanding of the dynamics of parent–offspring relationships in many animal species, and it is very likely that future studies of primates will continue to benefit from using POC theory as an explanatory framework.*

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### PARENT–OFFSPRING CONFLICT THEORY

Trivers (1972) defined parental investment (PI) as any investment by the parent in an individual offspring that increases its chance of surviving and hence reproductive success at the cost of the parent's ability to invest in other offspring. In a seminal paper on the evolution of parent–offspring

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conflict (POC), Trivers (1974) argued that offspring are selected to demand more investment than parents are selected to give. In his view, the ensuing behavioral conflict over PI is caused by a genetic conflict of interests because whereas parents are equally related to all of their offspring and selected to balance investment among their current and future offspring, the offspring are only half related to their siblings and therefore are selected to demand investment from their parents even at their siblings' expense. Trivers (1974) argued that behavioral conflict between parents and offspring should occur over the termination of PI, with offspring demanding a longer investment period, as well as over the amount of investment to be provided at any time during the period of offspring dependence.

Trivers' POC theory has stimulated substantive controversy in behavioral and evolutionary biology (Mock and Forbes, 1992; Godfray, 1995; Stamps, 1980). After some initial skepticism about the theory's scientific validity (Alexander, 1974), subsequent theoretical models showed that POC can indeed evolve and be maintained in a population by natural selection (Parker and MacNair, 1978). Unfortunately, many of the models did not make specific predictions about the behavior of parents and offspring and therefore have been difficult to test (Godfray, 1995). Mock and Forbes (1992) pointed out that attempts to test POC theory empirically have also been hindered by the inherent difficulty of measuring PI, the flawed assumption that PI optima of parents and offspring are only determined by asymmetries in genetic relatedness, and the fact that only results showing that offspring win the conflict can constitute unambiguous demonstration of phenotypic POC because a parental win is the default result by virtue of the power asymmetry between parents and offspring.

Although mother-offspring behavioral conflict has been documented in a wide range of mammals and birds, some authors have warned against the risk of overinterpreting the behaviors (Godfray, 1995) or have explicitly questioned the notion that behavioral conflict reflects evolutionary conflict of interest (Altmann, 1980; Bateson, 1994). For example, Bateson (1994) argued that conflict between mother and offspring in many species of animals occurs at stages other than weaning, that offspring often appear to wean themselves, and that mothers and offspring monitor each other and act in the common interest rather than engaging in competition or conflict. In a reply to Bateson (1994), Svensson (1995) pointed out that even though mother and offspring monitor each other and often exchange mutually advantageous information, their optimal amount of PI may still differ. Therefore, neither the notion of mother-infant monitoring and cooperation nor the empirical findings cited by Bateson (1994) are necessarily incompatible with POC theory.

POC theory was stimulated by observations of intense behavioral conflict between parents and offspring in birds and primates (Trivers, 1985). The

offspring solicit resources from their parents in ways that appear energetically costly or that risk attracting predators. Furthermore, primate infants often engage in squabbles with their parents that may continue for a number of years. Although primates would appear to be ideal subjects to investigate POC theory empirically, most primate studies have actually challenged POC theory rather than supported it.

In this article, I re-evaluate the testing of POC theory with primate data by describing mother–infant behavioral conflict in different species and then reviewing studies of POC in relation to whether the researchers interpreted their findings as inconsistent or consistent with Trivers' theory.

### **MOTHER–OFFSPRING BEHAVIORAL CONFLICT IN PRIMATES**

Behavioral conflict occurs in most species of primates in which parent–offspring interactions have been carefully studied. Quantitative information about the phenomenon is limited for prosimians and New World monkeys (Ehrlich and MacBride, 1989; Gould, 1990; Ingram, 1977; Locke-Haydon and Chalmers, 1983). Behavioral conflict has been well documented in some species of Old World monkeys and apes.

Observations of maternal rejections and infant distress responses in langurs and baboons were reported by Jay (1963), DeVore (1963), and other field workers. In Jay's (1965) study, langur mothers alternated for weeks between rejecting their infants and allowing them to cling. A few mothers began to reject their infants after only 1 mo, whereas others females did not reject their infants until they resumed estrus. All females intensified their rejections when they returned to estrus. Like langurs, baboon mothers observed by DeVore (1963) increasingly rejected their infants upon resumption of estrus. Rejected infants gave loud cries and intensified their attempts to cling to their mothers and to nurse. Ransom and Rowell (1972) reported that some baboon mothers began rejections at postpartum week 10 whereas others did so at 35 weeks, when they resumed estrus. Rejection was occasionally accompanied by aggression. According to Nash (1978), maternal aggression in baboons occurred in 3 main contexts: weaning of suckling, resistance to the infant's riding, and mating activity. In her study, maternal aggression, rejection, and tantrums peaked at the same time and conflict was most intense in conjunction with the mother's mating activity. Unlike previous baboon researchers, Altmann (1980) mentioned no behavioral conflict occurring after the mother's resumption of estrus. Instead, she emphasized that mothers often rejected contact attempts made by the infants during foraging and, to a lesser extent, during travelling and resting. In macaques, maternal

rejections can begin as early as the first month of infant life and peak between 10 and 12 mo of age (Hinde and Spencer-Booth, 1967; Maestripieri, 1994a). The most common contexts for mother-infant behavioral conflict include travel (Johnson, 1986), feeding (Rosenblum and Sunderland, 1982), the formation of sleeping clusters (Hammerschmidt *et al.*, 1994) and the mother's resumption of mating (Berman *et al.*, 1993; Collinge, 1987; Gomendio, 1991; Worlein *et al.*, 1988).

Mother-infant behavioral conflicts in the great apes have been described as intense and prolonged. In orangutans, the first signs of conflict occurred at 5 mo of age and continued for several years; conflicts with older offspring often included violent screaming and aggression (Horr, 1977). Behavioral conflicts were most common during daytime feeding and at the time of nest building, particularly when mothers had newborn and ejected previous offspring from the nest. In chimpanzees, mother-infant conflicts occur during feeding, grooming, travelling, evening nesting, suckling, and mating (Clark, 1977; Goodall, 1968; Horvat and Kraemer, 1982; Pusey, 1983; van de Rijt-Plooij and Plooij, 1987; Yerkes and Tomilin, 1935). According to Clark (1977) and Horvat and Kraemer (1982), travel was the most distressful situation, whereas van de Rijt-Plooij and Plooij (1987) reported that conflict was most common in the context of suckling. Intense maternal aggression during the mother's mating activities was also reported by Clark (1977) and van de Rijt-Plooij and Plooij (1987). Clark (1977) reported that maternal rejections began 2–3 years before the cessation of suckling and intensified when mothers resumed estrus, when infants were *ca.* 3–4 years old. As weaning progressed, the infants displayed many elements of depression and during the final months of suckling, they regressed to infantile behaviors such as whimpering, ventral riding with the mother, and long periods of contact. During the final months of suckling, chimpanzee infants also increasingly groomed their mothers.

Mother-offspring behavioral conflict has also been documented by primate studies of mating harassment. In many species, two individuals engaged in copulation are often harassed by other individuals, which scream at, threaten, pull, or hit one or both mating individuals or attempt to interpose themselves physically between them. Infants and juveniles harass their mothers' attempts at mating in some species (Niemeyer and Anderson, 1983). A 3-year-old home-reared chimpanzee harassed her human fosterers during sexual intercourse (Niemeyer and Anderson, 1983). The literature on primate harassment of matings suggests that infants and juveniles may be successful in delaying the mother's conception and reproduction, and therefore that "much harassment by immature primates can ultimately be interpreted in terms of parent-offspring conflict" (Niemeyer and Anderson, 1983, p. 217).

## PRIMATOLOGICAL CHALLENGES TO POC THEORY

### Altmann's Timing Hypothesis

The first and perhaps most comprehensive primatological challenge to POC theory was posed by Altmann (1980), who questioned the notion that mother-infant behavioral conflict in primates necessarily reflects an underlying evolutionary conflict of interest over PI (investment hypothesis). She argued that maternal rejections and infant tantrums reflect instead a conditioning process by which mothers train their infants not to solicit access to the nipple at inconvenient times such as during feeding or walking (timing hypothesis).

Altmann (1980) noted that the relation between maternal activity and infant contact in yellow baboons changed over time. Specifically, during their first 4 mo, infants were more likely to be out of contact when their mothers were resting or grooming, and more likely to be in contact when their mothers were traveling. After 4 mo, however, infants were more likely to be in contact when their mothers were resting or grooming than when they were traveling. Since mother-infant conflict was first observed at 4 months, Altmann (1980) hypothesized that the contingency reversal may be causally related to behavioral conflict and that maternal rejections served to condition the infant to the appropriate time for contact and nursing rather than to encourage the infant's nutritional or locomotory independence per se. She argued that consistent with this hypothesis were "limited data on the time infants spent on the nipple, which indicate that 'nipple time' dropped rapidly over the first 4 months without rejection, decreased no more rapidly in the next few months" (p. 176). Thus, in her view, although maternal rejections initially resulted in infant distress and tantrums, infants soon learned to restructure their schedules so that they obtained care without interfering with their mother's maintenance activities.

Altmann (1980) also expressed some general concerns about the applicability of POC theory to primate behavior. First, she argued that some of the assumptions underlying theoretical models of POC may not be consistent with the characteristics of most primate mating systems, reproduction, and rates of maturation. She also argued that infant demands for extra care are likely to result in high cost/benefit ratios to both mothers and infants. Costs to the mothers may include immediate reduction in the chance of surviving or diminished ability to provide care for the current infant, reduced feeding efficiency, reduced attentiveness to predators, or inability to keep up with the group. Costs to the infants may include waste of energy, missing feeding opportunities, and increased vulnerability to predators. Since in most primates infant survival is, by definition, entirely contingent on maternal

survival (Pereira and Altmann, 1985), Altmann (1980) suggested that self-inflicted costs to the infant may be greater and play a more important role in parent–offspring relations than had previously been assumed. She therefore argued that because of these detrimental effects of infant demands for extra care, parent–offspring genetic conflict of interest may arise infrequently as a relevant variable in real life situations.

Altmann (1980) argued that behavioral conflict in primates may have evolved without genetic conflict of interest as a result of the infant's immaturity at birth, its long period of dependency, and the changing conditions under which parenting and development take place over a lifetime, including the fact that infants need to adjust their behavior to their mothers' changing activities. Thus, primate infants will learn that they can obtain a greater benefit by waiting to obtain more milk when the mother is resting than by fighting to be allowed the nipple when she is feeding. Providing additional care at rest time will cost the mother less, and so she will be more willing to provide it. Altmann (1980) concluded that genetic conflict of interest does not invariably lead to conflict at the behavioral level. Instead, cooperation and compromise are likely alternative behavioral resolutions of conflicts of interest. Indeed, among socially living animals, cooperation and compromise in parent–offspring interactions may form a useful developmental base for group organization and cohesion among adults and serve as a model for resolution of potential conflict situations among adults. In contrast, resolution by conflict may be more generally appropriate to more solitary and territorial species.

Altmann's (1980) behavioral observations and her insightful discussion of the costs and benefits of POC made an important contribution to our understanding of mother-infant relationships in primates. However, the costs of behavioral conflict in primates had not been overlooked by Trivers (1974, 1985). In fact, he pointed out that the costs of behavioral conflict and its inefficiency constitute the clearest argument in favor of the view that such conflict results from an underlying genetic conflict (Trivers, 1974). For example, he noted that weaning conflicts in baboons may last for weeks or months, involving daily competitive interactions and loud cries from the infant in a species otherwise strongly selected for silence. Accordingly, in his view, the persistence of mothers and infants in the conflict and the costs incurred by both were entirely consistent with POC theory.

Parents and offspring share half of their genes, and if taken to an extreme, their behavioral conflict could be detrimental to both of them. However, their optima for PI are likely to differ. Therefore, the notion that parents and offspring cooperate and compromise is not incompatible with the occurrence of conflict over PI. Likewise, the observation that monkey mothers increase the frequency of infant rejection during feeding does not necessarily

constitute evidence against POC theory. The mother's maintenance activities may be some of the proximate cues that precipitate behavioral conflict, and maternal rejections during feeding time may indeed result in a restructuring of suckling time. Such restructuring of time is compatible with POC theory. First, restructuring of time could be accompanied by changes in PI, as inferred from time spent suckling, even if such changes are only apparent after weeks or months of intense conflict. Second, changes in suckling time may not necessarily follow behavioral conflict unless the conflict is clearly resolved to the mother's or the infant's advantage. Finally, behavioral conflict may affect forms of PI other than milk transfer, such as infant carrying (Altmann and Samuels, 1992), infant protection (Maestripieri, 1994b), or infant thermoregulation (Schino and Troisi, 1998). Infants may also prevent their mothers from maintaining social relationships that are essential to their reproductive success in the long term (Dunbar and Dunbar, 1988). Thus, at every age of the infant, there may be several arenas of conflict with the mother (Simpson *et al.*, 1986). The time courses of conflicts over different goals may also differ, such as body contact during stationary social activity as opposed to body contact during travel (van de Rijt-Plooij and Plooij, 1987).

### **Macaque Studies That Failed to Support the Investment Hypothesis**

One of the first studies building upon Altmann's criticism of POC theory in relation to primate behavior was conducted with Japanese macaques by Worlein *et al.* (1988). Both maternal rejections and infant distress peaked when mothers resumed mating (between 21–28 weeks of infant age) and then fell to a lower level through the rest of the year. Ventral contact decreased steadily in the first 20 weeks but remained relatively stable from weeks 21 to 44, while the duration of contact bouts increased significantly at the peak of the mother's mating season. Infant grooming of their mothers also increased in weeks 21–28 and peaked at the time when mothers were most involved in mating. Worlein *et al.* (1988) argued that, in a weaning situation, an increase in maternal rejection should be accompanied by a decrease in ventral contact and an increase in infant independence. However, infant independence did not appear to be greatly affected by the mother's resumption of mating. They also pointed out that maternal investment as inferred from measures of maternal rejection dropped most sharply in the weeks before and during the mothers' mating season, though the infants were not nutritionally weaned until the following year. Therefore, Worlein *et al.* (1988) concluded that mothers were trying to reschedule infant suckling activity rather than encouraging their nutritional independence. In their view, the behavioral conflict during the mating season may have reflected a conflict of interest

over PI, but mothers and infants appeared to disagree about the mother's future reproduction rather than the infant's nutritional independence.

Despite the authors' interpretation of the data, Worlein *et al.* (1988) provided no direct evidence to support the timing hypothesis. Furthermore, the lack of a significant association between behavioral conflict and changes in mother-infant contact time may be interpreted as evidence against POC theory only if one assumes that conflict is always resolved to the mother's or the infant's advantage. Because maternal efforts to reduce contact can be matched by the infants' increased efforts to maintain contact, this may not always be the case. Worlein *et al.* (1988) were correct to argue that mother-infant conflict at the resumption of mating should not be considered a weaning conflict, if weaning is viewed as the transition from milk to solid food and the achievement of infant nutritional independence. However, if weaning is defined as a period characterized by a sharp drop in PI (Martin, 1982), then it is clear that conception is a significant stage of the weaning process because it is associated with increasing reallocation of maternal resources from her current to her future offspring. Thus, mother-infant conflict over the mother's opportunity to conceive future offspring is a crucial aspect of the conflict over weaning, and Worlein *et al.*'s (1988) findings are generally consistent with POC theory.

Gomendio (1991) attempted to replicate and to extend findings of Worlein *et al.* (1988), and her criticism of POC theory was more explicit. She observed rhesus macaque mother-infant pairs from the 4th to the 12th mo, i.e. the period that usually includes the mother's return to mating. Maternal rejections increased as a function of infant age, whereas the frequency with which infants gained access to the nipple decreased steadily. In the month in which mothers returned to estrus, there was an increase in both the number of maternal rejections and the number of infant attempts to gain access to the nipple compared to the previous month. Infant distress also peaked at the time when mothers returned to estrus. However, the overall frequency with which infants successfully gained access to the nipple did not change significantly. Thus, Gomendio (1991) concluded that the period of most intense behavioral conflict was not accompanied by changes in maternal investment.

Gomendio (1991) also showed that, throughout infant mo 4–12, mothers that conceived exhibited a higher number of rejections than mothers that did not conceive. Furthermore, infants of conceivers were less successful in making nipple contact than infants of nonconceivers were. When data were analyzed in relation to the time of first estrus, there was no significant difference between conceivers and nonconceivers in the number of maternal rejections, number of infant attempts to make nipple contact, and number of successful attempts in the month in which mothers returned to estrus or in the following 2 mo. Three mo after the first estrus, however, conceivers



had a higher number of rejections and their infants had a lower number of successful attempts to make nipple contact. Gomendio (1991) concluded that her findings challenged POC theory because (1) behavioral conflict did not arise as a result of mothers reducing suckling, and (2) mothers that failed to conceive did not have more demanding infants.

Gomendio's (1991) findings can be interpreted in different ways. First, the failure to detect changes in nipple contact in relation to estrus may have been an artifact of statistical analyses. In fact, comparisons between the same mother-infant pairs during the month of first estrus and the previous month were conducted with tests for unpaired samples instead of paired samples, thus introducing infant age and maternal characteristics as confounding variables in the analysis. Second, although Gomendio (1991, p. 1001) argued that "behavioural conflict, therefore, was not a consequence of mothers forcing a reduction in the frequency with which their infants got onto the nipple in order to be able to conceive, and infants resisting, as had been suggested," her findings are entirely consistent with this explanation. For example, she reported that at the time of the first estrus, both maternal rejections and suckling attempts increased in frequency, whereas over a longer period of time increased maternal rejections were associated with reduced contact and suckling. This finding is entirely consistent with other studies showing that maternal rejections result in a short-term increase in infant contact followed by a long-term decrease. Furthermore, her data showed that conceivers maintained higher levels of rejections in the months following their return to estrus, and their infants were significantly less successful in gaining nipple contact.

Gomendio (1991) argued that according to POC theory, differences between conceivers and nonconceivers should have resulted from the behavior of their infants, so that more demanding infants should have succeeded in obtaining more investment and inhibiting their mothers' reproduction. However, her data indicate that differences between conceivers and nonconceivers resulted from differences in maternal rather than in infant behavior, suggesting that they were the outcome of different maternal investment strategies. Although Gomendio's (1991) interpretation of the findings may be correct, it is not clear why her interpretation would challenge POC theory. The level of POC in which mothers are willing to engage depends on their investment strategies and is sensitive to variables such as her own resources, the probability of future reproduction, and the chance of offspring survival. Therefore, some of Gomendio's (1991) findings are more relevant to the issue of how POC is resolved than to the issue of whether or why POC occurs.

Gomendio's (1991) study was later replicated by Berman *et al.* (1993) using a population of rhesus macaques on Cayo Santiago. The comparison

of mother-infant interactions during the mother's first 4–9-day estrus period and a 5-week baseline period immediately preceding it showed that, during mother's estrus, infants spent significantly less time in all forms of bodily contact. In addition, mothers initiated fewer nipple contacts than they had done previously, though the rate of rejection also decreased. Infants dramatically increased contact-seeking and distress-related behavior, including both the total attempts to make nipple contact and the number of successful attempts.

Both before and during mother's estrus, younger infants had higher rates of suckling bouts and nipple contact than those of older infants. During estrus, younger infants had more frequent tantrums than older infants did, they spent more time on the nipple than previously, and their mothers initiated a larger proportion of nipple contacts. Mothers of young infants that threw many tantrums were responsive to them and allowed contact. The data suggest that, during estrus, younger infants won, at least temporarily, the behavioral conflict with their mothers. When differences in infant age were statistically controlled, it appeared that most infants that threw a lot of tantrums were successful in achieving high rates of nipple contact in spite of their mothers' frequent rejections. Mothers that conceived during their first estrus period had higher rejection rates and lower proportion of contact initiation than those that did not conceive. Conceivers also had lower rates of nipple contact and fewer nipple contacts per suckling bout than those of the other mothers, while their infants had higher rates of distress calls.

Some findings of the study of Berman *et al.* (1993) are difficult to interpret due to the high number of behavioral measures and correlations, some of which produced opposite results. For example, during estrus, frequency measures of contact increased while duration measures decreased; tantrums were positively correlated with increased contact whereas distress calls were negatively correlated with contact; conception was predicted by maternal rejection and contact initiation but was unrelated to rates of nipple contact and suckling bouts. Despite these inconsistencies, the study provided strong evidence that (1) maternal behavior during estrus affected nipple contact and probability of conception, (2) infant behavior changed during estrus and affected maternal behavior; and (3) maternal behavior during estrus was unrelated to baseline maternal behavior scores.

Berman *et al.* (1993) interpreted their findings as being consistent with Gomendio's (1991) conclusions and inconsistent with POC theory. However, whereas Gomendio (1991) concluded that behavioral conflict did not arise as a result of mothers reducing suckling, Berman *et al.* (1993) clearly showed that conflict was associated with maternal attempts to reduce suckling during estrus. Similarly, whereas Gomendio (1991) concluded that infant behavior failed to affect their mother's probability of conception, Berman

*et al.* (1993) showed that highly demanding infants were quite successful in achieving nipple contact and inhibiting their mother's reproduction. Thus, the findings of Berman *et al.* (1993) supported rather than challenged POC theory. Their study also provided suggestive evidence that POC is resolved in different ways depending on infant age and level of demand. Thus, individual differences in infant as well as maternal characteristics appear to be crucial variables affecting POC, and issues of conflict resolution should be explicitly considered by studies of POC in primates.

### **Contrasting the Investment and Timing Hypotheses**

One of most ambitious empirical challenges to POC theory in primates has been posed by Barrett *et al.* (1995), who argued that, for any particular period of POC, the investment and the timing hypotheses make opposite predictions. Accordingly, the investment hypothesis predicts that suckling time should decrease in a way that is independent of maternal activity, whereas the timing hypothesis predicts that suckling time should decrease more strongly during activities in which the presence of an infant is a hindrance. Furthermore, the investment hypothesis predicts that rejection behavior and weaning conflicts should be independent of maternal activity, whereas the timing hypothesis predicts that the occurrence of rejection and weaning conflicts should be biased towards activities in which the presence of an infant is a hindrance. Finally, the investment hypothesis predicts that the total amount of time spent suckling should decrease significantly over time, whereas the timing hypothesis predicts that the amount of time spent suckling should not change substantially.

Although the attempt of Barrett *et al.* (1995) to derive mutually exclusive and empirically testable predictions must be commended, their predictions may be useful to assess the validity of the timing hypothesis but are unlikely to provide evidence in favor of or against POC theory. Since the 2 hypotheses are mutually compatible, the investment hypothesis does not necessarily predict that decreased suckling time and behavioral conflict should occur independently of maternal activity. Moreover, the investment hypothesis would predict a decrease in suckling time only if the conflict of interest is clearly resolved to the mother's advantage and the maintenance of contact is primarily determined by her needs. Similarly, the timing hypothesis would predict that the amount of time spent suckling should not change substantially if mothers are successful in training their infants and rescheduling their demands for suckling. However, the assumption that mothers always win the conflict or that they are always successful in training their infants is not entirely justified.

Barrett *et al.* (1995) tested their predictions with data on maternal activities—feeding, moving, resting, and social interaction—and mother-infant distance—nipple contact, non-nipple ventral contact, non-ventral contact, and proximity—in gelada baboon mother-infant pairs. The probability of contact and nipple contact during maternal feeding and moving time decreased steadily over the first 7–9 mo. In contrast, the probability of contact and nipple contact during maternal resting and socializing time remained at relatively high levels throughout the study period. In particular, after mo 3–4, infant suckling bouts were more likely to occur when mothers were resting or socializing than when they were feeding or moving, a result in part due to the fact that infants >5 weeks old tended to be carried dorsally by their mothers during locomotion. Rejections were more frequent during feeding than during socializing, moving, or resting, and rejections increased steadily over time, peaking in mo 6 and 9. Finally, the time spent by infants in ventral contact, ventral contact and on-nipple, and ventral contact and off-nipple dropped rapidly and was reduced to zero by 5 mo, whereas the total time spent on the nipple showed a much more gradual decline over time. Gelada infants appear to spend a considerable part of their suckling time without being in ventral contact.

Barrett *et al.* (1995) argued that their findings strongly support the timing hypothesis and provide evidence that weaning conflicts in primates are disputes about scheduling access to milk rather than about the quantity of milk transferred to the infant because (1) infant contact and suckling were dependent on maternal activity, and (2) maternal rejections were most frequent during feeding time, i.e. the activity most likely to be disrupted by the presence of an infant. Accordingly, the most critical evidence in favor of the timing hypothesis vs. the investment hypothesis was provided by the developmental changes in various forms of infant contact. Barrett *et al.* (1995) argued that if nipple contact had been the source of conflict, then on-nipple time should have declined much more rapidly than off-nipple time regardless of the form of contact: ventral or non-ventral. This was clearly not the case. Conversely, if ventral contact was the source of conflict, e.g., because ventral contact is more disruptive of feeding, then ventral contact time should have declined more rapidly than non-ventral contact time regardless of nipple contact. Although data on non-ventral contact time were not shown or analyzed, it is unlikely that non-ventral contact time declined more rapidly than ventral-contact time since mothers shifted from ventral to dorsal carrying after week 5.

Since developmental changes in various forms of infant contact may not necessarily result from behavioral conflict, the relevance of these data to understand the source of mother-infant conflict is unclear. Measures of time spent in bodily contact or nipple contact are not necessarily useful to

understand behavioral conflict unless the responsibilities for making and breaking contact are clearly identified. For example, even though various forms of contact show different developmental changes, it is possible that mothers and infants contribute equally to the changes and that no conflict occurs (Hauser and Fairbanks, 1988). The only clear measure of behavioral conflict analyzed by Barrett *et al.* (1995) was the rate of maternal rejection. However, it provided the clearest evidence against, rather than in support of, the timing hypothesis. In fact, the timing hypothesis predicted that rejections should be strictly associated with time in ventral contact because ventral contact interferes with maternal feeding. The data of Barrett *et al.* (1995) clearly showed that all ventral contact was terminated by mo 5, whereas maternal rejections peaked in mo 6 and 9. Thus, although the study of Barrett *et al.* (1995) provided evidence that mothers rejected their infants more often during feeding than during other activities, it failed to provide evidence that maternal feeding was an important determinant of developmental changes in maternal rejection rates and, more generally, of behavioral conflict.

### **Infant Growth Rates, Infant Tantrums, and POC**

Lee (1996) recently argued that in order to understand primate weaning in relation to reproductive and life-history strategies, the issue of infant growth to a threshold weight is far more important than issues of evolutionary conflict of interest. Although Lee's (1987) earlier work on weaning was conceptually framed in terms of POC theory, her recent views are more consistent with those of Altmann (1980) and Bateson (1994). Thus, Lee (1996) maintained that, in the weaning process, mother and infant are not engaged in conflicts of interests, but instead in the process of resolving them. Therefore, she concluded that "new models of behavioral conflict during the weaning transition, which are dissociated from evolutionary conflicts of interest, may help us understand causality in the process of weaning" (p. 95). Although infant growth rates are certainly important to understand weaning, it is not clear why infant growth rates can provide an explanation for weaning independently from or alternatively to POC theory. In fact, infant growth itself may be a crucial element of the conflict of interest between mother and offspring. Furthermore, since Trivers' (1974) theory provides a framework to understand the functional significance of POC, models that address the proximate causation of behavioral conflict and weaning are not incompatible with POC theory.

The latest primatological challenge to POC theory has been posed by Barrett and Henzi (2000), with a study of mother-infant interactions and infant tantrums in free-ranging chacma baboons. They contrasted Bateson's (1994) and Trivers' (1974) views of parent–offspring dynamics and developed

some testable predictions from both models. According to Barrett and Henzi (2000), Bateson's (1994) view of parent-offspring interactions, which emphasizes honest signaling of need by the offspring and convergence between the PI optima of parent and offspring, predicts that (1) infants should achieve independence from their mothers spontaneously and without maternal intervention; (2) tantrums should occur as a response to environmental conditions that require the offspring to receive an increased level of PI; (3) tantrums should only be shown by infants that face increased risk of mortality without further PI; and (4) tantrums should result in increased PI. They tested the predictions against the following predictions derived from POC theory: (1) the frequency of tantrums should not be linked to habitat quality in a systematic fashion; (2) all infants should display tantrums at some point; (3) tantrums should occur during a period of decreasing PI.

The first prediction derived from Bateson's (1994) hypothesis seems to require evidence that mothers do not attempt to encourage infant independence or that their behavior is totally ineffective. This prediction is clearly not supported by most primate research. As for the other predictions, tantrums are not the primary means with which infants demand investment from their mothers, i.e., they are not the equivalent of chick food begging calls. Infants obtain milk from their mothers by making nipple contact and sucking. Contrarily, tantrums represent one of several infant responses to maternal rejection. Other responses include distress calls, following the mother, and attempting to make contact again. Infants that are not rejected by their mothers are not expected to throw tantrums, and absence of tantrums in itself cannot be used as evidence for or against POC theory. Insofar as there is a predictable relation between habitat quality and maternal rejections and between rejection and tantrums (Lee, 1987; Hauser and Fairbanks, 1988), Trivers' hypothesis should predict systematic covariation of habitat quality and infant tantrums. Furthermore, if both maternal rejections and infant tantrums are interpreted as honest signals of physical condition and both mother's and infant's condition covary with habitat quality (Hauser, 1993), then the relation between habitat quality and POC predicted by Bateson's (1994) hypothesis is the same as that predicted by POC theory. Finally, according to POC theory, expressions of behavioral conflict, such as infant tantrums, may be associated with periods of decreased PI, increased PI, or no change in PI, depending on how the conflict is resolved.

Barrett and Henzi (2000) observed 10 infants, ranging between 0 and 18 mo old, during a 12-mo study. Consistent with the typical developmental pattern of cercopithecine monkeys, time spent on the nipple decreased over the first 18 mo whereas time spent independently feeding increased. It is not clear how many mothers ever rejected their infants, but the behavior only occurred between ages 5 and 10 mo and the overall correlation

between rejection and nipple or feeding time over the 18 mo is nonsignificant. Barrett and Henzi (2000) interpreted the findings as “circumstantial support for Bateson’s (1994) argument regarding the convergence of investment optima” (p. 656). However, with such a small data set and a single correlation test, the analysis was not an effective investigation of the role of maternal rejection in the development of infant independence.

Barrett and Henzi (2000) reported that tantrums were only shown by 3 of the 10 infants and were too infrequent to be analyzed statistically. Two infants had tantrums during the summer months when habitat quality was low and suckling temporarily increased. The third infant had tantrums during a period of epidemic disease. Barrett and Henzi (2000) argued that their findings were contrary to the predictions of POC theory and consistent with Bateson’s (1994) hypothesis. However, both their data and their interpretation do not appear to be strong enough to warrant such conclusions. Moreover, the fact that a subset of infant tantrums were excluded from data analysis because they “seemed to be associated with the scheduling of infant access to the nipple . . . rather than with quantity of investment” (p. 649) is not justified.

Overall, the studies have raised important questions about the nature of mother-infant conflict in primates and have produced some interesting findings. However, such findings do not pose a fundamental challenge to Trivers’ (1974) hypothesis. Instead, in many cases, studies that were critical of POC theory actually provided evidence that is consistent with it. The finding that time spent in contact or suckling may not change during periods of intense behavioral conflict may be somewhat puzzling. Although it does not necessarily argue against POC theory, the theory would be supported if it could be demonstrated that infant suckling attempts or maternal rejections result in changes in contact time or suckling and that such changes affect the mother’s subsequent reproduction, which have in fact been demonstrated.

## **PRIMATE FINDINGS CONSISTENT WITH POC THEORY**

### **Effects of Maternal Rejections on Infant Behavior and Other Findings Consistent With the Investment Hypothesis**

The debates over whether mothers actively wean their infants or infants wean themselves and whether maternal rejections actually increase infant independence were already intense among primate researchers before POC theory. On one side of the debate, authors such as Hinde and Spencer-Booth (1967) showed a strong correlation between maternal rejection rates and reduction in infant contact seeking behavior, suggesting that mothers play an important role in infant independence and that their

rejections are successful. Conversely, other authors argued that even infants raised without their biological mothers eventually achieved some degree of motor, nutritional, and social independence and showed that maternal rejections caused an increase in the infant's attempts to make contact. Based on these findings, they argued that maternal rejections play a marginal role in infant independence and that infants basically wean themselves (Kaufman, 1974). The controversy was resolved by acknowledging that both mothers and infants play a role in the process of infant independence and that, while maternal rejections may be followed by a short-term increase in infant contact, they eventually result in a long-term decrease in contact (R. A. Hinde, personal communication, 1990).

This view is consistent with the observations reported in several primate studies. For example, in wild baboons, frequent maternal rejections were associated with a temporary intensification of contacts, followed by a long-term decrease in infant contacts (Nash, 1978). Infants that were rejected early and frequently by their mothers spent less time in contact whereas ones that were not rejected by their mothers suckled or rode to an unusually advanced age (Nash, 1978; Ransom and Rowell, 1972). In wild chimpanzees, when mothers resumed estrus and consorted with males, there was an abrupt increase in maternal rejections and a decline in mother-offspring association (Pusey, 1983). Similarly, van de Rijt-Plooij and Plooij (1987) reported that peaks in mother-infant behavioral conflict were associated with a shift in responsibility for making contact from mother to infant. Peaks in maternal rejections and aggression resulted in temporary intensification followed by reduction of time in contact. Indeed, van de Rijt-Plooij and Plooij (1987) pointed out that the overall decrease of time in contact as a function of age was characterized by periods of rapid decrease in contact time preceded by intense periods of mother-infant conflict and temporary regressions. They concluded that "aggressive prevention of nipple contact and ventral riding played a decisive role in the changing mother-infant interaction leading to reducing ventro-ventral contact" (van de Rijt-Plooij and Plooij, 1987; p. 35).

In rhesus macaques, high rates of maternal rejection are associated with higher probability of conception in the following mating season (Simpson *et al.*, 1981, 1986; Gomendio, 1991; Berman *et al.*, 1993). High maternal rejection and intense behavioral conflict can occur both in the first few months of infant life and when mothers resume estrus, and the two periods of conflict can have independent effects on a mother's probability of conception (Berman *et al.*, 1993). Although these findings do not provide direct evidence in favor of POC theory, they suggest that mother-infant interactions affect the mother's subsequent reproduction and that there is the potential for mothers and infants to engage in conflicts of interest over PI.



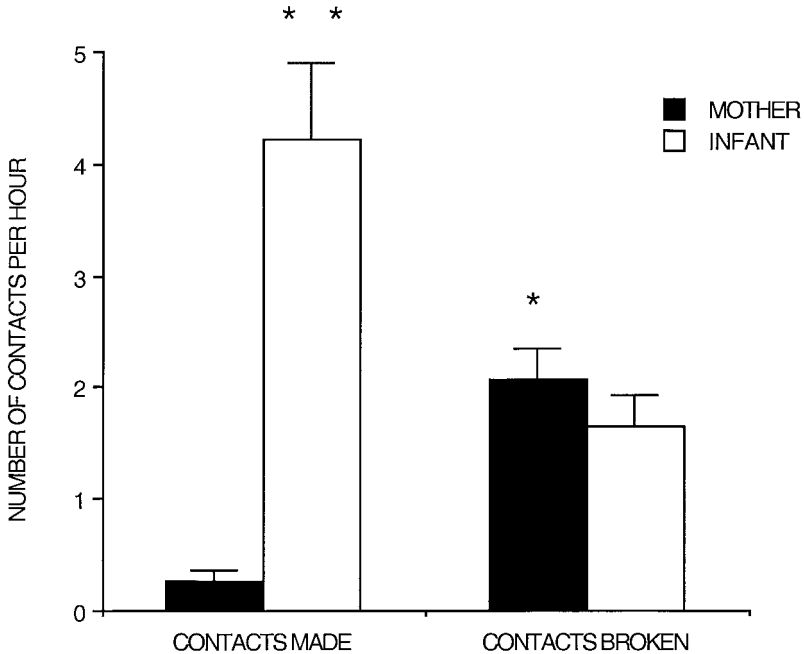


Fig. 1. Mean number of contacts made and broken by mothers and offspring.

The occurrence of mother-infant conflict over time spent in contact can be directly inferred from contact-making and breaking data (Fig. 1). During the mating season at the Field Station of the Yerkes Regional Primate Research Center, in 9 rhesus macaque mother-infant pairs, the number of contacts made by offspring is significantly higher than the number of contacts made by mothers (Student's *t*-test for paired samples:  $t = -5.47$ ,  $df = 8$ ,  $P < 0.001$ ), while the number of contacts broken by offspring is significantly lower than the number of contacts broken by mothers ( $t = 2.21$ ,  $df = 8$ ,  $P = 0.05$ ; Fig. 1). The data clearly suggest that offspring were more motivated than mothers to spend time in contact and that mothers resisted infant demands for contact.

According to Trivers (1974, 1985), the shift in responsibility for maintaining contact from mother to infant, which in rhesus macaques occurs at about 3 mo of infant age (Hinde and Atkinson, 1974), is also consistent with POC theory. In fact, the paradoxical finding that as the infant becomes increasingly active and independent, its initiative in maintaining proximity to the mother increases, is consistent with the notion that the change reflects the underlying tendency for POC to increase during the period of PI. Thus,

as the interests of mothers and infants increasingly diverge, infants must assume a greater role in obtaining investment from their mothers.

### **Variables Affecting the Intensity of POC**

Several studies on the influence of food availability or habitat quality on POC have produced findings consistent with POC theory. In vervets, Lee (1987) found that infant mortality peaked during periods of intense mother-infant conflict, and in particular at mating resumption. Since high infant mortality may have been due to low food availability, Lee (1987) argued that behavioral conflict at mating resumption occurs over what levels of lactation are sufficient to ensure infant survival and growth rather than over the mother's subsequent reproduction. Lee (1987, p. 419) found that before mating resumption, maternal rejections were associated with a reduction in suckling bout frequencies and concluded that "the onset of m-o conflict, as indicated by increased rates of rejection and decreased suckling success, was related to the abrupt seasonal decline in food quality. Mothers may have used this transition between high and low food quality as the proximate cue for initiating conflict. The effects of the onset of conflict were found in reduced suckling bout frequencies in subsequent months."

The influence of ecological variables on mother-infant conflict in vervets was also emphasized by Hauser and Fairbanks (1988), who compared data in captivity with those obtained in two different habitats in the field: a dry woodland habitat and a swamp habitat. Direct conflict was estimated by the rate at which mothers rejected infant attempts to make ventral contact and to suckle. They estimated indirect conflict by the relative contribution of mothers and infants to making and breaking ventral contact. Conflict was minimal when infants had approximately equal rates of making and breaking contact. As both infant attempts to make contact and mothers' attempts to break contact increased, they considered conflict to be increasing. They measured resolution of conflict by time in contact.

Contact made and broken by mothers was similar in the two field habitats. Infants in the swamp habitat made contact with their mothers more often than infants in the dry woodland habitat did, but in the former habitat infants were more likely to be rejected by their mothers than in the latter habitat, suggesting that mother-infant conflict was most intense in the swamp habitat. Mother-infant pairs in the dry woodland habitat spent more time in contact than dyads in the swamp habitat did in the first 3 mo, suggesting that conflict was resolved differently in the two habitats. Conflict was least intense in captivity, where rejections were rare and mother and infant played approximately equal roles in maintaining contact (Hauser and Fairbanks, 1988).

Hauser and Fairbanks (1988) argued that the level of mother-infant conflict in the field is affected by the interaction between food quality and interbirth intervals. When food quality is low, conflict is so great that a mother must either sacrifice her infant or jeopardize her own survival. When food quality is high, a mother should be able to satisfy her own and her infant's nutritional needs with little conflict. At intermediate levels of food quality and availability, the level of mother-infant conflict should be higher for females attempting to produce one offspring per year than for females attempting to produce one every two years. Thus, low levels of conflict in the dry woodland habitat are due to poor quality of food available and the fact that females are constrained to produce offspring every two years. In the swamp habitat where food quality is high, females produce offspring every year and conflict is more intense. In captivity where food is abundant, conflict is less intense than in the field.

The influence of habitat quality on the intensity of mother-infant conflict was also investigated by Lycett *et al.* (1998). They compared mother-infant interactions in mountain baboons that lived in a harsh habitat and were under strong environmental stress, with eastern African baboons that lived in a relatively high quality habitat. Consistent with the authors' predictions, mountain baboons appeared to exhibit higher levels of PI and less intense mother-infant conflict. In fact, nipple contact levels were higher, nutritional independence was reached later, weaning tantrums occurred at a lower rate, interbirth intervals were longer, and infant survival was higher among the mountain baboons than in the eastern African baboons. These findings contradict those obtained by Hauser and Fairbanks (1988) with vervets, which suggest that conflict is most intense under harsh conditions and may be, at least partly, accounted for by differences between baboons and vervets in their ability to modulate interbirth intervals (M. Pereira, personal communication, 2001).

### **Resolution of POC**

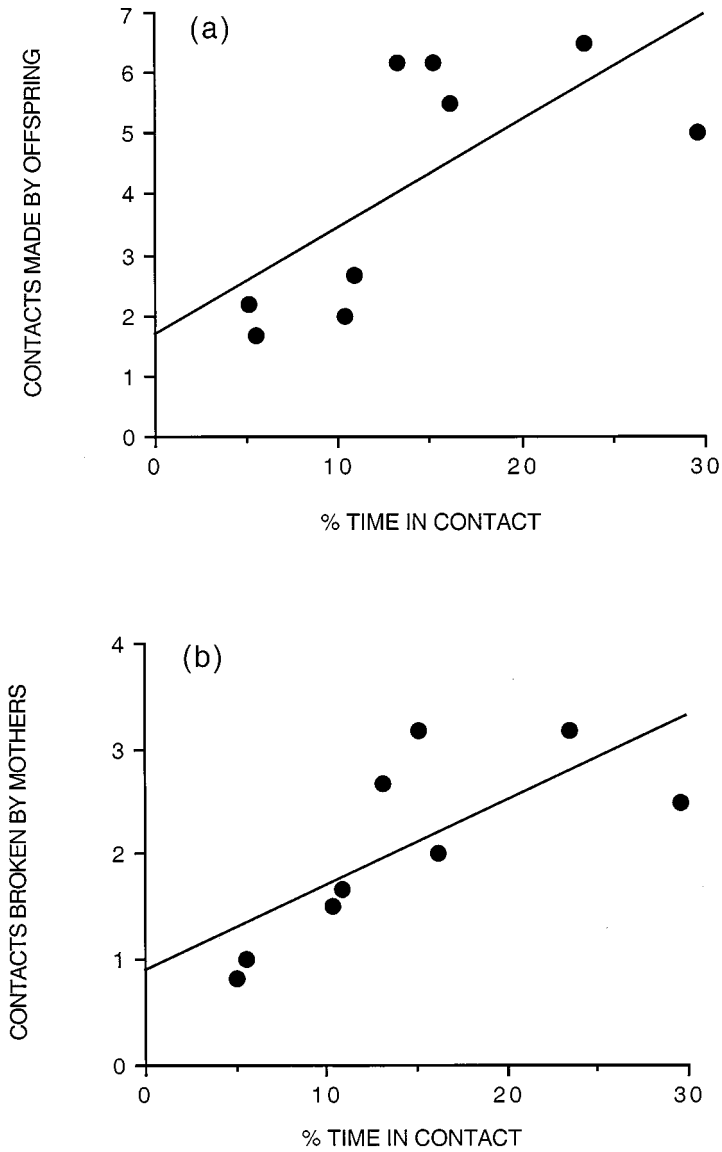
The studies of Hauser and Fairbanks (1988) and Lycett *et al.* (1998) suggest that the way POC is resolved may be more apparent if one compares different mother-infant dyads instead of interactions within the same dyads over time. In fact, the assessment of conflict resolution with longitudinal data can be complicated by the fact that maternal rejections may have different short-term vs long-term effects on infant behavior and by the fact that monkey mothers tend to be consistent in their behaviors towards their infants over time (Fairbanks, 1996). Thus, the investigation of variability in POC among mother-infant dyads is a promising area of primate research.

Using this approach, it is possible to infer how POC is resolved from data on contact-making, contact-breaking, and time spent in contact. Specifically, it may be argued that if infants win the conflict over time spent in contact, individual differences in contact time among different dyads should be positively correlated with the number of contacts made by infants. In contrast, if mothers win the conflict, individual differences in contact time among different dyads should be negatively correlated with the number of contacts broken by infants or with maternal rejections. Data from the rhesus macaque mating season suggest that the conflict is won by infants, at least temporarily. Fig. 2a shows that time spent in contact by 9 mother-infant pairs is positively correlated with the number of contacts made by offspring (Pearson's correlation:  $r = 0.69$ ,  $P < 0.05$ ) but not with the number of contacts made by mothers ( $r = -0.21$ , NS). The correlation between time in contact and number of contacts broken by mothers is also significant, but it is positive rather than negative ( $r = 0.74$ ,  $P < 0.05$ ; Fig. 2b). The correlation between time in contact and number of maternal rejections is also negative ( $r = 0.80$ ,  $P < 0.05$ ). The number of contacts made by offspring is positively correlated with both the number of contacts broken by mothers ( $r = 0.93$ ,  $P < 0.01$ ; Fig. 3a) and the number of maternal rejections ( $r = 0.74$ ,  $P < 0.05$ ; Fig. 3b). Thus, the more offspring demanded contact, the more their mothers broke contact with them and rejected them. Altogether, these findings suggest that maternal attempts to reduce time in contact with highly demanding offspring were largely unsuccessful. This is consistent with the observation that only 58% of all maternal rejections were successful in keeping the offspring out of contact for  $>1$  min.

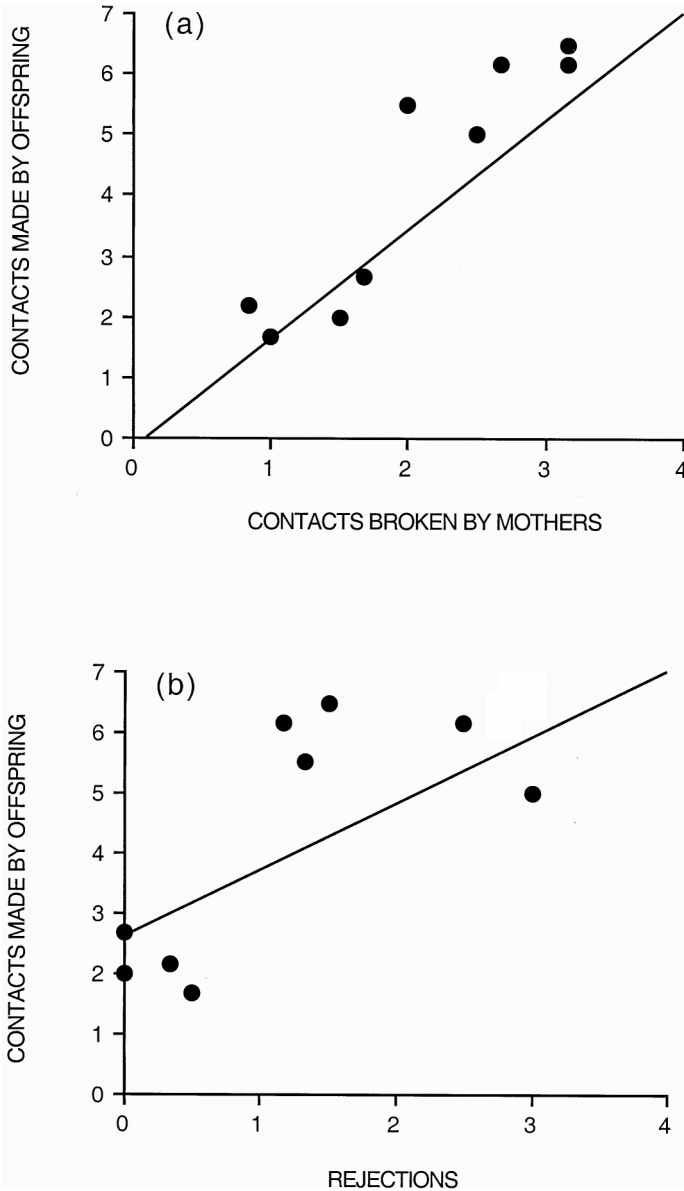
### Conflict Over Parental and Mating Effort

One may argue that the demonstration of behavioral conflict over time in contact does not necessarily provide evidence supporting POC theory because time in contact is not an accurate measure of PI. Time in contact is a poor indicator of milk transfer and therefore of milk-related maternal investment, though probably no worse than time on the nipple or frequency or duration of suckling (Cameron, 1998). However, time in contact can be considered a form of parental effort (Clutton-Brock, 1991). Thus, establishing that mothers and offspring are in conflict over parental effort rather than just over the scheduling of their activity can be an important step toward confirming the validity of POC theory in primates.

Mother-infant contact can bring about energetic demands on the mother in terms of infant carrying and thermoregulation (Altmann and Samuels, 1992; Schino and Troisi, 1998). For example, Schino and Troisi (1998) argued



**Fig. 2.** (a) Correlation between time in contact and number of contacts made by offspring. (b) Correlation between time in contact and number of contacts broken by mothers.



**Fig. 3.** (a) Correlation between number of contacts made by offspring and number of contacts broken by mothers. (b) Correlation between number of contacts made by offspring and number of maternal rejections.

that primate mothers and infants have different thermoregulatory needs because infants have a higher surface-to-volume ratio and therefore lose heat more rapidly than adults do. Therefore, infants may be more sensitive to low temperatures than their mothers are, and their different needs may give rise to behavioral conflict over time in contact. Consistent with this hypothesis, Schino and Troisi (1998) found that ambient temperature did not influence time spent in contact by Japanese macaque mothers and infants but affected their role in maintaining contact. Specifically, decreasing temperatures were associated with an increasing role played by infants in maintaining contact with their mothers and with more frequent maternal rejections.

In addition to conflict over parental effort, evidence of conflict over the mother's mating effort can also be consistent with POC theory. However, studies of macaques to determine whether infant interference with the mother's mating activity reduces her probability of conception have provided only circumstantial evidence in support of POC theory. In long-tailed macaques, infants were more likely to interfere with interactions between their mothers and adult males than with interactions between their mothers and adult females (Gore, 1986). Although mounts between mothers and adult males were never terminated as a result of infant intervention, adult males were more likely to be in proximity to mothers when their infants were absent than when they were present. Thus, the presence of infants may have acted as a deterrent against male interactions with their mothers. Moreover, both mothers and adult males reacted negatively, e.g., with rejection or aggression, to infant interference in their interactions. However, there was no correlation between the number of infant interferences and their mothers' subsequent interbirth intervals. Thus, although the behavioral conflicts between mothers and infants are consistent with POC theory, there is no evidence that infants were successful in delaying their mothers' reproduction.

In another study of Japanese macaques mothers increased rates of infant rejection during the mating season, and there are positive correlations between maternal rejection rates, infant distress responses, and infant attempts to make nipple contact with mothers (Collinge, 1987). Infant distress calls mostly followed rather than preceded rejections and, in more than half the cases, infants were able to regain contact with their mothers after being rejected. Although Collinge (1987) interpreted her findings from the perspective of POC theory, her study provided no information as to whether the time spent in contact by mother and infant, the mother's mating activities, or her probability of conception were affected by mother-infant behavioral conflict. However, Schino *et al.* (2001) provided compelling evidence that in Japanese macaques, the mating season is associated with a clear increase in

maternal rejections, decrease in the role played by mothers in maintaining contact and proximity, and overall decrease in time spent in ventroventral contact and proximity when compared with the periods before and after the mating season. The presence of an adult male near the mother, independently of consort activity, was associated with lower mother-infant proximity.

### **Maternal Responses to Infant Signals of Need**

The findings of longitudinal studies of maternal responsiveness to infant distress calls are generally consistent with POC theory. The hypothesis that offspring distress calls are honest signals of need (Godfray, 1991) predicts that primate infants emit distress calls only when it is strictly necessary. This hypothesis assumes that signals of need are costly and that offspring in good condition will not gain by simulating a high level of need (Godfray, 1991; Maynard Smith, 1991). Accordingly, primate mothers are expected to respond to offspring distress calls and to provide parental care to the best of their abilities.

In contrast to the honest signaling hypothesis, POC theory predicts that primate infants will emit distress calls more often than necessary. If distress calls are cheap signals, primate mothers should be unresponsive to some of the solicitations. However, if distress calls are costly and reduce infant fitness, they increase the value of extra resources to the offspring so that parents gain by investing more in them (Zahavi and Zahavi, 1997). Accordingly, infants may obtain more resources than mothers are selected to provide. Moreover, if parent-offspring interactions extend over a considerable period of time, parental care may have an effect on subsequent offspring solicitations so that the costs of additional investment to the parent may be offset by the reduction of subsequent offspring solicitations (Johnstone, 1996).

Consistent with POC theory, Hauser (1986) argued that primate mothers and infants go through cycles of interactions in which infants alternate between truthful and deceitful communication and mothers alternate between responsiveness and skepticism. Specifically, there should be an endless cycling of strategies with 4 different stages: (1) infant truthful-mother responsive; (2) infant deceitful-mother responsive; (3) infant deceitful-mother skeptical; (4) infant truthful-mother skeptical. Hauser (1993) investigated the rate of distress calls uttered by wild vervet infants during the first 4 mo and their effectiveness in obtaining access to the nipple or transport by the mother. Call rate was low and effectiveness was high early on. In weeks 8–10 there was a sharp increase in call rate and a substantial decrease in



effectiveness. For infants that survived, call rate decreased in weeks 12–16, whereas effectiveness increased. In contrast, for infants that died within the first year, call rate continued to increase and effectiveness stayed low. The observed association between increased call rate and decreased effectiveness in the first 10 weeks appeared to contradict the hypothesis of honest communication between parents and offspring, which predicts a positive correlation between call rate and allocation of care. In contrast, the changes in call rate and call effectiveness are consistent with the hypothesized alternation between truthful and deceitful communication. The differences between dyads with surviving and nonsurviving infants were tentatively accounted for in terms of habitat quality and maternal and infant condition.

The rate of distress calls emitted by captive stump-tailed macaque infants, like those of vervets, increased steadily with age, peaking in week 8 (Maestriperi, 1996). Maternal responsiveness to infant calls decreased linearly from 100% in weeks 2 and 3 to a minimum of 36.9% in week 8. The number of calls decreased in weeks 8–10 and increased again in weeks 10–12, whereas effectiveness followed an opposite pattern. The latency of retrieval increased linearly with infant age, suggesting that mothers waited increasingly longer periods before retrieving their infants as they grew older.

When taken together, the studies of mother-infant communication suggest that, consistent with POC theory, primate infants can be both honest and deceitful in the solicitation of parental care. Monkey mothers may use infant age and call rate as rules of thumb for responsiveness to distress signals, and both age and call rate may be reliable cues to whether calls are honest signals of need (Maestriperi and Call, 1996). Distress vocalizations are usually assumed to be costly to produce because of energy expenditure and increased probability of attracting predators (Godfray, 1991). However, the costs of these signals may be higher to younger infants than to older ones as, for example, the latter are more likely to escape a predator attack than the former. Therefore, distress calls by young infants are expected to be infrequent, limited to situations of real need, and associated with high maternal responsiveness (Berman *et al.*, 1993). As infants grow older and the costs of distress signals decrease, the latter are likely to become more frequent and increasingly used out of context, this being accompanied by reduced maternal responsiveness. Infants, in turn, may reduce call rates when effectiveness is low and begin another cycle of honest signaling. This interpretation of the dynamics of mother-infant relationships is compatible with the manipulative use of infant signals predicted by POC theory, but it also agrees with the view that mothers and infants monitor each other's responses and adjust their behavior accordingly (Altmann, 1980; Bateson, 1994).

## CONCLUSIONS

Parent-offspring behavioral conflict is widespread, intense, and often prolonged in many primate species. Although POC theory is not unequivocally supported by all primate research, it is premature to conclude that mother-offspring behavioral conflict does not reflect an underlying evolutionary conflict of interest over parental investment. Trivers' (1974) theory has enhanced our understanding of the dynamics of parent-offspring relationships in many animal species, and it is very likely that future studies of POC in primates will continue to benefit from using the theory as an explanatory framework. Such studies should consider that maternal behavior may have different short- vs. long-term effects on infant behavior, take into account the issue of how POC is resolved, investigate variation among different mother-infant dyads rather than just variation within the same dyads over time, and consider multiple measures of parental and mating effort as well as the dynamics of parent-offspring communication. Experimental studies on physiological aspects of maternal investment and stress along with physical and physiological indicators of infant growth and development are also needed. Furthermore, experimental studies manipulating variables such as availability of resources or maternal time budgets and investigating the effects of such manipulations on POC could be important contributions. Finally, POC needs to be further investigated and contrasted in seasonal vs nonseasonal primate species, as well as in species with and without alternative caregivers.

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