

Growing Up Cooperatively: Family Processes and Infant Care in Marmosets and Tamarins

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Abstract: *Parenting patterns range widely among human and nonhuman primates. Rarely do single mothers parent without help. Many female-bonded species have female relatives (grandmothers and aunts) to help with infant care. In other species both parents assist in infant care, or there is cooperative care where several group members work together to rear a single infant or litter. Cooperative care is relatively uncommon in primates, but is found in many birds and in some non-primate mammals such as wolves and meerkats. In primates, cooperative care is seen primarily in marmosets and tamarins, small monkeys from the New World. We first describe patterns of cooperative care of infants in cotton-top tamarins (*Saguinus oedipus*) and common marmosets (*Callithrix jacchus*). Then we examine the cooperative care family as a social system describing the mechanisms that maintain relationships among family members to maintain cooperative care. Human beings also require cooperative care due to the long duration of infancy and childhood, so we conclude with some speculations about how cooperative care benefits children and how research with cooperative care primates might help us to become more successful parents.*

Growing Up Cooperatively

Childcare in mammals is often studied and discussed only in the context of mother-infant interactions because mothers bear the costs of gestation and lactation. Occasionally there are studies on fathers and the role they play in infant care. Rarely is infant care and infant development studied in the context of families and the contributions that each family member might make to successful infant care. The animal models that are used to study parenting are typically species where mothers alone are responsible for all infant care (e.g., rats, Fleming, 1996; vervet monkeys, Fairbanks,

1996; rhesus macaques, Roma, Ruggiero, Schwandt, Higley, & Suomi, 2006). Yet a survey of primate parenting by field primatologists John Mitani and David Watts (1997) found a broad spectrum of infant care ranging from the solitary parenting of orangutan mothers; through female-bonded species such as baboons and macaques where female relatives assist in infant care and males defend groups; to biparental species such as titi monkeys where fathers are active participants in infant care; to the cooperative families of marmosets and tamarins, where not only fathers but older siblings play important roles in infant care and survival. Mitani and Watts (1997) noted that nonhuman primate species with greater infant care support for mothers have higher reproductive success (greater infant survival and shorter interbirth intervals) than those species where mothers must do more by themselves. In a recent book, *Parenting for Primates* (2005), Harriet Smith argues that primate parenting is energetically costly and is characterized by continuous attention to infant needs, by the importance of helpers for mothers, and by the learning of parenting skills.

Nowhere are Smith's three principles of primate parenting better illustrated than in the cooperatively breeding primates, marmosets and tamarins. However, few scientists studying human development are aware of these species and the causes and benefits of cooperative infant rearing that have been shown. Because most of the basic research on nonhuman primates has focused on species where mothers must do all of the infant care, there has been little attention given to primate models that might illustrate the importance of families in caring for human infants.

Here we first describe the broad patterns of cooperative infant care in mammals and follow with a description of cooperative care in marmosets and tamarins, the hypothesized reasons for the development of this system and the benefits to infants. Second, we examine the marmoset and tamarin family as a social system requiring coordination and cooperation as well as the deferral of reproduction by non-breeding helpers (i.e., alloparents). We conclude with a discussion of how research results from studies of cooperative care in nonhuman primates might have implications for informing appropriate infant care in our own species.

Cooperative Breeding

In many bird species and some mammals such as California mice, prairie voles, hamsters and titi monkeys, both fathers and mothers are actively involved in infant care. In biparental bird species, fathers and mothers take turns incubating eggs and, once eggs hatch, both parents are involved in nest guarding, thermoregulation, and providing food for the chicks. In mammals, mothers must provide all of the care during pregnancy and by nursing. However, fathers can play critical roles in defending the mother and infants, in retrieving infants that leave the nest, and in providing food and thermoregulation for mother and infants. A characteristic of biparental birds and mammals is a close social relationship between parents, often called a pair bond. Recent research using DNA fingerprinting indicates that some offspring of biparental birds are sired by males other than the one living with the mother, meaning that the relationship between mates is one of social monogamy rather than genetic monogamy.

In at least one biparental rodent, the California mouse, monogamy is both social and genetic. The male living with the mother sires all of the pups (Ribble, 1991).

Cooperative breeding species differ from biparental species in the importance of alloparents in assisting parents with infant care. Alloparents in cooperatively breeding species typically delay their own reproduction while assisting a breeding pair with their infants. This deferral of reproduction is often accompanied by a physiological suppression of fertility in at least one sex. Thus in pied kingfishers, sons are reproductively suppressed and unable to mate while in their natal group, although unrelated male alloparents are found and they are not reproductively suppressed (Reyer, Dittami, & Hall, 1986). In mammals such as wolves (Moehlman & Hofer, 1997; Asa, 1997), mongeese (Creel & Waser, 1997), meerkats (Griffin, Pemberton, Brotherton, Gaynor, & Clutton-Brock, 2003), naked mole rats (Lacey & Sherman, 1997; Faulkes & Abbott, 1997), and marmosets and tamarins, it is usually females that are reproductively suppressed—either not ovulating while in the presence of a reproductive female, or ovulating but not becoming pregnant.

Among monkeys and apes, the marmosets and tamarins have the most pronounced system of cooperative breeding. Field data on mustached tamarins (*Saguinus mystax*), (Garber, Moya, & Malaga, 1984) and on cotton-top tamarins (Savage, Snowdon, Giraldo, & Soto, 1996b) demonstrated that infant survival is directly related to the number of helpers present, reaching maximum survival in groups of five or more potential caretakers (parents plus three alloparents). Surprisingly, we have found similar results in our captive colony of cotton-top tamarins with group sizes of five or more having the greatest infant survival (Snowdon, 1996).

Why are helpers so important for cooperatively breeding species? First, cooperative breeding can maximize the reproductive output of a female. In marmosets and tamarins, mothers usually give birth to twins that weigh up to 20% of the mother's weight at birth. (Imagine a 130 pound woman giving birth to twins that weigh 13 pounds each at birth.) In captivity and in many field conditions, the reproductive female can become pregnant within two to four weeks postpartum and give birth to twins twice a year (tamarins: Ziegler, Bridson, Snowdon, & Eman, 1987; marmosets: Lunn & McNeilly, 1982). Thus, a female marmoset or tamarin can produce four infants a year, compared with one infant each year in baboons or macaques and one infant every four to five years in great apes.

Second, infant care by the father and by others relieves the female of the energetic burden of carrying infants. Infants that at birth weigh 20% of the mother's weight and become larger after that do represent significant energetic costs for those that carry them. Two studies of captive cotton-top tamarins, where the monkeys had more than adequate food resources and where the energetic costs of traveling through the trees in search of food and shelter were eliminated, have found that tamarin males lose up to 10% of their body weight during the most intensive period of infant care (Sanchez, Peleaz, Gil-Burmann, & Kaumanns, 1999; Achenbach & Snowdon, 2002). With increasing numbers of alloparents, the weight loss of any one carrier is reduced (Achenbach & Snowdon, 2002). In the wild, a weight loss of 10% would represent a significant energy stressor for males, and one can see immediately why multiple caregivers are critical. Another study of captive tamarins found that those carrying infants spent

significantly less time foraging, eating, moving, or engaging in social interactions (Price, 1992). Male marmosets and tamarins in captivity gain weight during their mate's pregnancy (Ziegler, Prudom, Schultz-Darken, Kurian, & Snowdon, 2006), which may prepare them for the subsequent weight loss that results from infant care.

Third, fathers and alloparents are important not only for carrying infants, but they also play a critical role in the weaning process. Food-sharing, either through direct offering of food to infants or through tolerating infants taking food, is common in all marmoset and tamarin species studied to date (Brown, Almond, & Van Bergen, 2004). In some species, adults have specific, intense forms of food-associated calls that appear to attract infant attention to food and to indicate that food is available. In captive cotton-top tamarin groups, infants have a higher probability of obtaining food from the adult when the adult produces these calls compared to when they do not (Roush & Snowdon, 2001; Joyce & Snowdon, 2007). In wild golden lion tamarins, adults use these infant-directed calls to lead juveniles toward hard to catch insect prey or to locations where juveniles can obtain insect prey (Rapaport & Ruiz-Miranda, 2002; Rapaport, 2006).

The functions of food sharing are hypothesized to supplement nutrition and/or to provide information to infants about novel foods. Studies of golden lion tamarins in captivity (Rapaport, 1999) indicate that food sharing is greater with foods novel to the infant or foods that are difficult to process. Field studies on the same species find that food sharing is used to help young locate and obtain hard to acquire animal prey, with adults doing less food sharing as infants and juveniles become more competent (Rapaport & Ruiz-Miranda, 2002, Rapaport, 2006). Since animal prey is highly nutritious, both nutritional and informational hypotheses are supported. The informational hypothesis has not been supported by studies on captive common marmosets where parents do not preferentially transfer novel foods with infants (Brown, Almond, & Bates, 2005). Regardless of whether food sharing has a nutritional or informational function, the net result is that food sharing may help infants complete the weaning process earlier than they might have without food sharing. Notably cotton-top tamarins begin food sharing with twins sooner than they do when they have singletons (which are less energetically demanding) and subsequently twins feed independently earlier than singletons (Joyce & Snowdon, 2007).

A final role played by fathers and helpers is in vigilance against predators (Caine, 1993). In wild cotton-top tamarin groups, individual animals took turns in carrying infants versus serving as sentinels. These roles changed frequently throughout the day (Savage, Snowdon, Giraldo, & Soto, 1996b).

For marmosets and tamarins, infant rearing is definitely a family affair. We have seen that infant survival is a function of having multiple caregivers. Caregivers incur significant costs as reflected by weight loss during the period of infant care and further through sharing high quality food with infants during the weaning process. Various family members take turns carrying infants, looking for food resources, and serving as sentinels for the family. Much of this is done by post-pubertal animals that, instead of reproducing themselves, are helping to care for infants not their own. The coordination of food finding, infant care, and vigilance requires a high degree of communication among group members. Furthermore, close social relationships are likely

to be critical, not only to maintain the pair bond between the two parents, but in preventing others from reproducing—while at the same time keeping those individuals within the group and functioning as alloparents. To understand the mechanisms of how cooperative breeding works, it is necessary to look at family dynamics.

Family Dynamics

Family dynamics in marmosets and tamarins can be separated into four types of relationships: adult-adult relationships both as partners and as parents, adult-alloparent relationships, sibling relationships, and infant-family relationships. First, it is essential that there is a close bond between the breeding adults before breeding begins and subsequently that there is close coordination during infant care. Second, the breeding adults face the problem of how to recruit others to serve as alloparents and to prevent these alloparents from reproducing while contributing to the survival of the infants. Third, one can expect potential sibling conflicts over access to infant care and over potential breeding opportunities should they occur. Finally, do infants have different relationships with different family members? How is infant development affected by cooperative rearing? We examine each of these dynamics in turn.

Parental Relationships as Mates

Since paternal investment in infant care is critical for infant survival in marmosets and tamarins, both parents should be careful in choosing a mate. A female needs some assurance that her mate will stay with her and be available to care for infants after they are born. A male needs to be confident that the infants he will help care for at considerable energetic costs are his own and not those of another male. This reasoning suggests that there should be caution by both sexes in mate choice and that established mates should have well-developed mechanisms for reassuring each other and maintaining trust.

However, we know relatively little about mate choice and initial pair formation from field studies because pair relationships are generally long lasting with changes occurring only with the death of one mate or following some environmental catastrophe. What information we do have suggests unexpectedly that mate choice may rarely be an option in the wild. Animals must find partners and mate opportunistically. If mate choice prior to pairing is limited, then there is an even greater need to have mechanisms to maintain the relationship after pairing. In wild cotton-top tamarins, we observed stable pair bonds over three consecutive years, but following a drought that left no surviving infants, animals changed partners, forming new breeding pairs, which were then stable for the three additional years of our study (Savage, Giraldo, Soto, & Snowdon, 1996a). Savage, Giraldo, Soto, and Snowdon (1996a) also observed that many subadult animals of both sexes left their groups. When animals could be located subsequently, none had yet become breeding adults, suggesting that dispersing tamarins cannot easily establish new breeding territories.

In wild common marmosets, Lazaro-Perea, Castro, Harrison, Arajau, Arruda, and Snowdon (2000) observed the deaths of breeding females in three groups. In one group, a new female from outside the study population appeared in the group within two weeks and subsequently became pregnant within two weeks of joining the group. In the other two groups, replacement of the breeding females was slower. The males (fathers and brothers) in each group began spending more time separated from the females (daughters), and after four months, the males formed new groups with females from outside the study population. The remaining females in each group formed a new group with males from outside the study population. Within a month of forming the new groups, all females gave birth. Since the gestation period is five months, these females became pregnant (presumably with unrelated males) soon after the death of the breeding female, their mother. The relative lack of new breeding opportunities and the rapidity with which other females become pregnant following the loss of a breeding female suggest that animals make the best of any breeding opportunities, reinforcing the hypothesis that mate choice may not be much of an option for wild marmosets and tamarins. This again emphasizes the importance of mechanisms to maintain relationships after pairing.

In captivity, high levels of sociosexual activity are seen in the first hours and days of formation of new pairs. Over successive weeks the high rates of sociosexual behavior decrease, although animals still mate on an average of at least once a day (Savage, Ziegler, & Snowdon, 1988). A characteristic that marmosets and tamarins share with humans is continuous receptivity (Converse, Carlson, Ziegler, & Snowdon, 1995). Animals mate throughout the ovulatory cycle and during pregnancy as well. Figure 1 illustrates the observed rates of mounting behavior (part of copulatory behavior) in 30 minute daily observations of four pairs of tamarins over several ovulatory cycles in the first year after pairing (Porter & Snowdon, 1997). Day 0 is the day of ovulation as determined by a peak in urinary excretion of luteinizing hormone (Ziegler, Bridson, Snowdon, & Eman, 1987). It should be obvious from the figure that there is no consistent relationship of mounting behavior with respect to ovulation in these newly formed pairs.

Frequent sexual behavior across the ovulatory cycle and during pregnancy may be one way in which adults maintain their relationship. Increased sexual behavior may also serve to reassure mates when the relationship is challenged. In two studies of mated pairs, we observed increased sexual behavior following a minor challenge to the relationship. Porter (1994) separated pairs for 30 minutes and then reunited them and observed them for another 30 minutes. The left two histograms in Figure 2 show baseline rates of mounting with a doubling of mounting rates following reunion after a brief separation. Ziegler, Epple, Snowdon, Porter, Belcher, and Kuederling (1993) transferred scents from a cycling female to several pairs of tamarins over the entire ovulatory cycle of the donor female. The behavior of the mates with each other was observed daily immediately following the scent transfer, and mounting behavior is shown in the right two histograms of Figure 2. The mounting rate in response to the odors of a novel female was equal to the mounting rate following brief separations, but the mounting rate doubled on the days when the donor female was ovulating. This suggests that pairs increase sexual behavior following the challenges of separation and

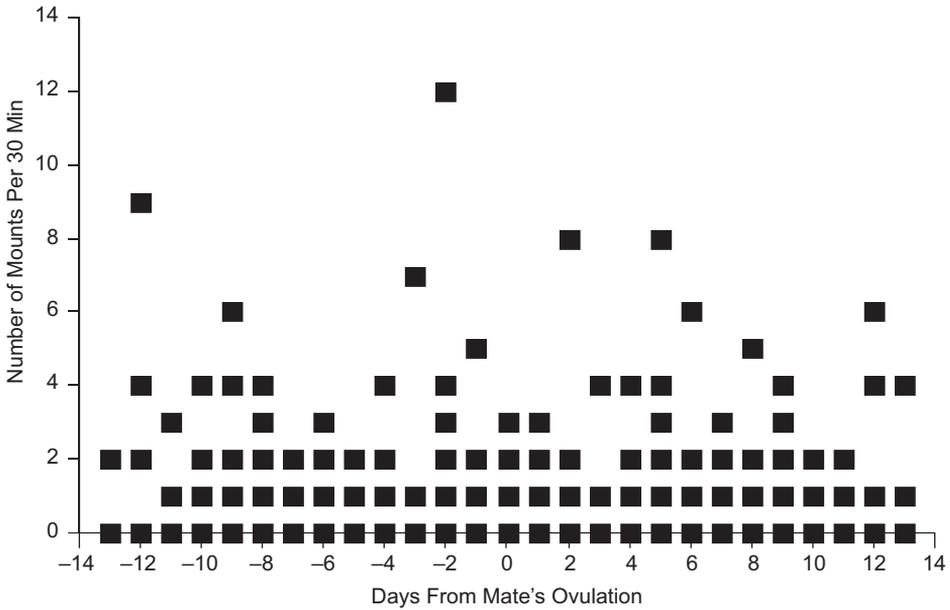


FIGURE 1. Mounting behavior by cotton-top tamarin males in relation to their mates' ovulation date. Day 0 is ovulation as determined by a peak in luteinizing hormone. Data are from four pairs studied over multiple ovulations in the first year after pair formation (from Porter & Snowdon, 1997).

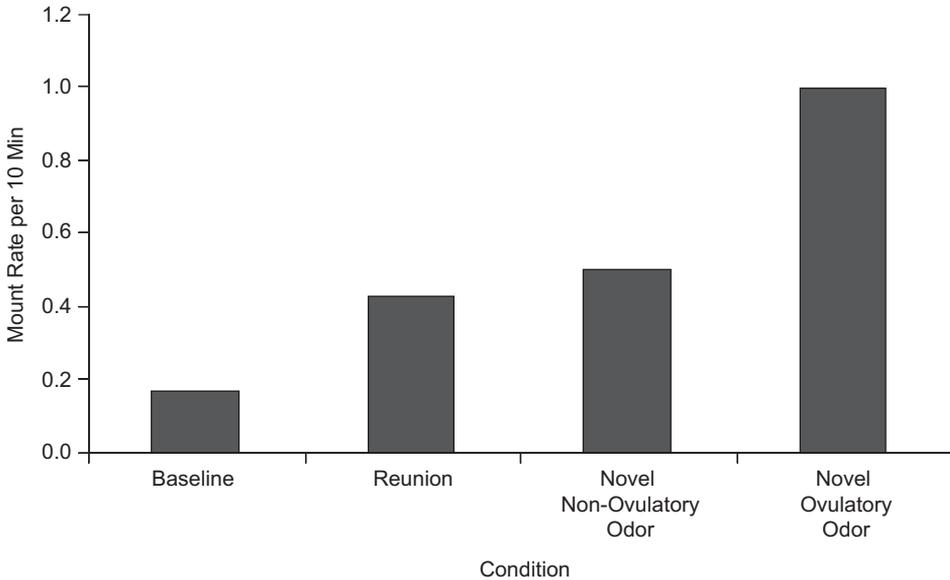


FIGURE 2. Male mounting behavior in baseline conditions, during reunion following a 30 minute separation, in response to an odor of a novel non-ovulating female and a novel ovulating female. (Adapted from Porter, 1994 and Zeigler et al., 1993).

following presentation of odors from a novel female, especially when the novel female is fertile. Males also displayed more frequent erections on days where the odors were from an ovulating novel female compared with other days in her cycle. In another study, females demonstrated an eight-fold increase in solicitation behavior when odors of a novel, reproductive female were presented (Washabaugh & Snowdon, 1998). These studies suggest that both sexes are responsive to olfactory cues from novel reproductive females. Increased sexual arousal in males coupled with increased proceptivity by females led to increased sexual behavior that appears to maintain and reinforce pair bonds in the face of threats to the relationship. Alternatively, males may be aroused by ovulatory odors in general and the increased responsiveness of the mate diverts the male's sexual interest to her.

Although both males and females have high stakes in maintaining relationships, one might argue that males, due to uncertainty of paternity and their energetic costs of infant care, might have a greater stake in relationship maintenance than females. In cotton-top tamarins, we have seen asymmetries in responses of males and females. In the brief separation-reunion tests described above, tamarins often give plaintive-sounding long calls during the period of separation. As shown in Figure 3, both sexes increased the rate of long calls during separation, but males gave these calls significantly more often than females (Porter 1994).

Another test of the strength of pair relationships involves presenting mated pairs with intruders. French and Snowdon (1981) presented paired cotton-top tamarins with intruders of both sexes. Males displayed high levels of aggression toward male intruders and females responded to female intruders with increased scent marking rather

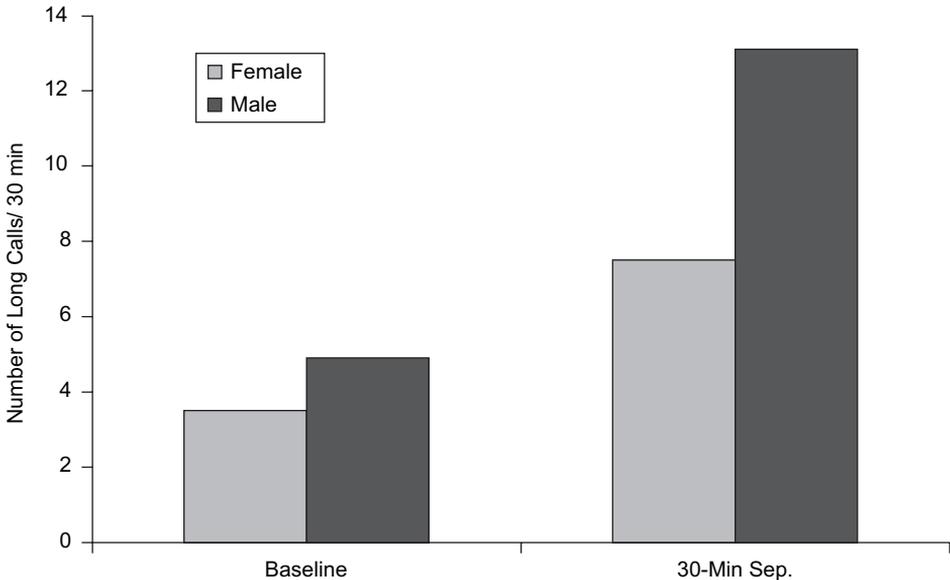


FIGURE 3. Mean number of long calls given by male and female cotton-top tamarins in baseline conditions and during a 30 minute separation from the mate. (Adapted from Porter, 1994).

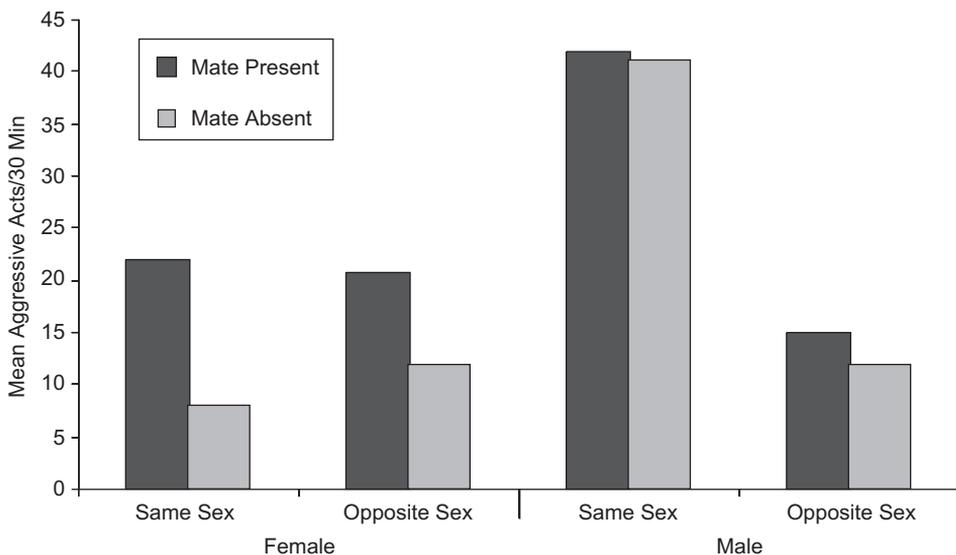


FIGURE 4. Mean number of aggressive acts directed toward same sex and opposite sex intruders by female and male cotton-top tamarins as a function of whether the mate was present or absent. (Adapted from Porter, 1994).

than aggression. In a subsequent intruder study, Porter (1994) presented males and females with intruders of both sexes, but also tested each animal alone as well as with its mate present. As in the French and Snowdon study (1981), females responded to other females with more scent marking than direct aggression. As shown in Figure 4, females responded with more aggression when their mate was present than when he was absent to both male and female intruders. Males, however, did not respond differently based on mate presence. Although they always responded more aggressively toward males than females, they showed as much aggression toward intruders when the mate was absent as when she was present. Males may be more responsible than females for ensuring the maintenance of the pair bond.

Another behavior often thought to be involved in maintaining relationships is grooming. In many nonhuman primates, subordinates groom more dominant animals. In cotton-top tamarins, we have found a striking asymmetry with breeding males grooming their mates more often than the reverse. The left histogram in Figure 5 shows that in 100% of 10 tamarin pairs, males groomed their mates more often than vice versa. In wild common marmosets, reproductive pairs also spent considerable time in grooming each other. Mates groomed each other more than 20% of observation time in focal samples (Lazaro-Perea, Arruda, & Snowdon, 2004). As with captive cotton-top tamarins, males groomed females more than vice versa in every single group (Figure 5 center histogram).

In summary, cotton-top tamarins engage in high rates of non-conceptive sex at the onset of a relationship and at lower but still daily rates throughout the relationship. The increased rate of non-conceptive sex following brief separations and in response to olfactory cues from novel females suggests that non-conceptive sex also is impor-

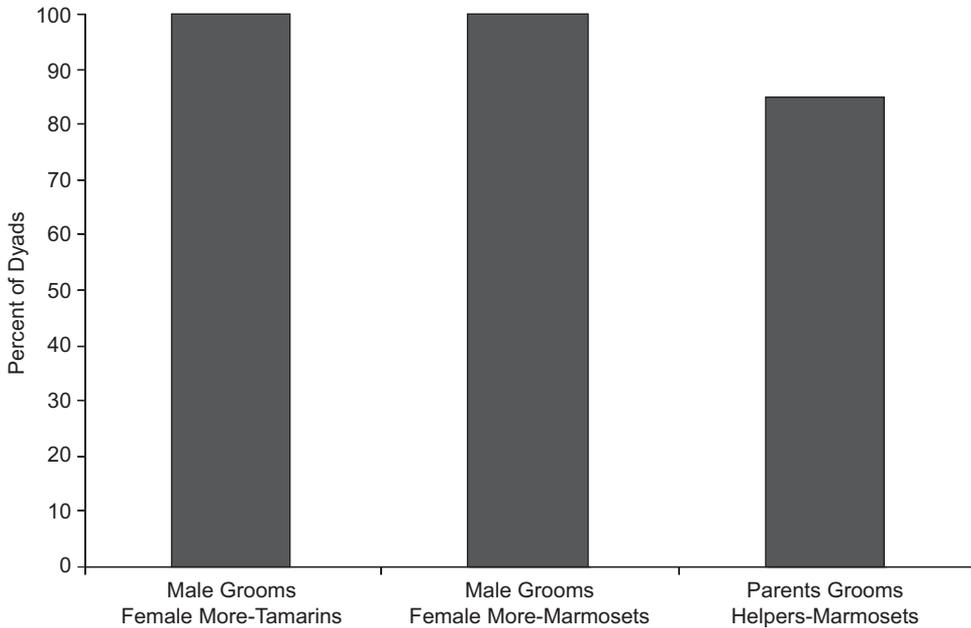


FIGURE 5. Percent of dyads in which males groom females more or adults groom helpers more. (Tamarin data adapted from Ziegler et al., 2004, marmoset data adapted from Lazaro-Perea et al., 2004).

tant to restore or reinforce relationships in the presence of some threat. Finally, there is a sexual asymmetry with males being more upset by separation than females, being aggressive toward intruders regardless of the presence or absence of the mate, and by males grooming females more often than their mates groom them. This grooming asymmetry is also seen in common marmosets. This asymmetry makes sense in the context of male uncertainty of paternity and the high costs including weight loss during infant care.

Other marmoset and tamarin species display somewhat different responses. In golden lion tamarins, intruder studies similar to those of French and Snowdon (1981) found that females were highly aggressive to other females, whereas males showed less aggression toward male intruders (French & Inglett, 1989). In wild populations, multiple females in the same group are pregnant at the same time and fertility suppression of females is much weaker than in cotton-top tamarins (Baker, Dietz, & Kleiman, 1993), suggesting a higher potential cost to breeding females by failing to keep unrelated females out of the group.

Intruder studies with common marmosets indicate that male responses are conditional on the presence of the female in contrast to the tamarin results. Evans (1983) and Anzenberger (1985) found that male marmosets courted novel females when tested in the absence of their mates, but were aggressive toward the same females when their mate was physically present or could be viewed behind a one-way mirror.

Following from these behavioral results, Ziegler, Schultz-Darken, Scott, Snowdon, and Ferris (2005) studied the responses of male common marmosets to the odors of

novel, ovulating females. Some males showed increased arousal to odors of novel, ovulating females including erections, and many males also had increased blood levels of testosterone within 30 minutes of the presentation of the odor. There was considerable variation among males and it was observed that the significant increase in testosterone was found only in single males and in paired males without infants. Fathers showed little behavioral interest and no testosterone increase to odors of novel females, suggesting that fatherhood inhibits the response to novel females.

However, in field studies of common marmosets, Lazaro-Perea (2001) observed nearly daily encounters between each of her focal groups and one of its neighboring groups. These territorial encounters included increased scent marking, long calling, lunges and fights, but Lazaro-Perea also observed frequent copulations between a male from one group and a female from the other group. These copulations primarily involved non-breeding members of the group although breeding males were also observed to copulate with neighbors. The breeding females, however, remained in the central part of the family's territory and did not engage in boundary conflicts or copulate with others. Females that engaged in extragroup copulations did not become pregnant, except when the breeding female in their group had died. Lazaro-Perea (2001) suggested that the extragroup copulations accompanying territorial conflicts allowed marmosets to assess their neighbors, detecting when a breeding position might be available, and possibly evaluating future mates.

Why do breeding male common marmosets court other females and engage in extra-group mating when cotton-top tamarin males do not? One possibility is that the costs of paternal care may be less in common marmosets than in tamarins. One study of male body weights in captive common marmosets after birth found no weight loss (Nievergelt & Martin, 1999) in contrast to the weight loss seen in cotton-top tamarins. However, in both species, males gain weight during their mate's pregnancy (Ziegler, Prudom, Schultz-Darken, Kurian, & Snowdon, 2006). Expression of male parental care appears to be more variable in marmosets than in tamarins (Zahed, Prudom, & Ziegler, in preparation; Zahed & Snowdon, in preparation). Thus, if male marmosets do not need to invest as much in infant care as tamarins, then their relationship with their mate may be more tentative.

Parental Relationships in Parenting

So far we have focused on the relationships that parents have with each other without consideration of infants, but how parents relate to each other in the context of infant care is equally of interest. Several studies have indicated hormonal changes in males during infant care. One of these hormones, prolactin, stimulates milk production in female mammals. Dixon and George (1982) first documented that serum prolactin levels increased in male marmosets when they were carrying infants. Mota, Franci, and Sousa (2006) replicated these results, finding elevated levels of prolactin in males when they were carrying infants, but not at other times postpartum. These results suggest that prolactin levels are a result of infant carrying. Almond, Brown, and Keverne (2006) gave experienced marmoset fathers cabergoline, a drug that is a

dopamine agonist, which has the effect of lowering prolactin concentration. There was no decrease in paternal behavior. Instead, males carried infants at the same rate as they had before. The treated males (compared to their non-treated control condition) showed increased interest in infants when they were not carrying them. These results taken together suggest that for experienced common marmoset fathers, prolactin is not necessary to cause paternal care and appears instead to increase as a result of infant care. If prolactin served as a social reinforcer (as seen in studies of human sexual behavior where prolactin levels are elevated at orgasm, see Krueger, Haake, Chereath, Knapp, Janssen, Exton, Schedlowski, & Hartmann, 2003), then an increase in prolactin during infant care may reward the father and keep him involved in infant care. Cabergoline suppression of prolactin reduced infant care responses when males were tested away from the influences of other family members (Ziegler & Prudom, unpublished data).

We found that male cotton-top tamarins displayed high levels of urinary prolactin during the period of infant care, with levels correlating with the amount of experience a male had as a father (Ziegler, Wegner, & Snowdon, 1996). Prolactin concentrations were higher in males that had more litters. Male prolactin levels postpartum were as high as those of lactating females (Ziegler, 2000). When we looked at prolactin levels in the two weeks prior to birth, we were surprised to find no differences between prepartum and postpartum prolactin levels. Do males anticipate the birth of infants and change hormone levels before infant birth? If they do, what cues does a male use to detect that his mate is pregnant?

We studied several males throughout the pregnancy of their mates and gathered hormonal samples two or three times each week (Ziegler, Washabaugh, & Snowdon, 2004). Half of the males were experienced with more than three sets of surviving offspring and the other half were first time fathers or had fathered a previous litter that had not survived. We monitored the males for several hormones: prolactin, estradiol, testosterone, dihydrotestosterone, cortisol, and corticosterone. We also monitored female hormonal changes throughout the cycle. At approximately the midpoint in pregnancy, the fetal adrenal gland begins to secrete glucocorticoids that we were able to detect in urine of the pregnant female. Within a week of the increase in glucocorticoid excretion in female urine, every experienced father displayed an increase in excreted corticosterone, and following that was a cascade of hormonal changes with experienced fathers developing elevated estradiol and testosterone levels not seen in less experienced fathers. All experienced males displayed elevated levels of prolactin by the midpoint of pregnancy, whereas the less experienced fathers displayed an increase in prolactin levels only in the month before infant birth.

What could be involved in this difference? It could be the behavior between mates, but we could find no consistent patterns of behavioral change in experienced pairs. However, the less experienced pairs spent increased time in contact and grooming behavior in the month before infant birth. Ziegler, Washabaugh, and Snowdon (2004) hypothesized that experienced males had learned to respond to cues produced by the pregnant mate, which initiated the pattern of hormonal changes whereas the less experienced males are not able to respond to these cues, but needed the increased affiliation in the month before birth to initiate hormonal changes.

However, the design of the study was confounded. Because female tamarins ovulate two to four weeks after birth, experienced fathers are still caring for the previous infants during the early stages of pregnancy, whereas less experienced fathers do not have infants. Can we separate the effects of infant presence from the potential cues from a pregnant female? We took experienced fathers and paired them with nulliparous females and then collected hormonal samples throughout the female's first pregnancy. These males had considerable experience through multiple pregnancies of a previous mate, but there were no infants present during the pregnancy of the new mate. These males did not show the early pregnancy increase in prolactin levels, suggesting that the elevated prolactin levels we had observed earlier were due to stimuli from the previous infants. The males demonstrated the increase in corticosterone within a week of the rise in the pregnant female, suggesting that the glucocorticoid increase is due to some cues from the mother or the fetuses (Almond, Ziegler, & Snowdon, in preparation). Since the increase in glucocorticoid secretion may be due to activation of the fetal adrenal gland, this could represent a communication system whereby the fetuses communicate through their mother to induce changes in their father's hormones to prepare for their birth. More research is needed to test this hypothesis.

The mother's tolerance of the father's involvement in infant care is critical. We have found great variability in the contribution of fathers and mothers to infant care in first time parents. Carrying by the mother can range from 20% to 80% of the time in the first weeks after birth. In the wild, we have also observed that first time mothers carried infants in more than 90% of the observations in the first two weeks, whereas experienced mothers more readily allowed others to carry their infants. First time parents typically have higher mortality of infants than more experienced parents (Snowdon, 1996), and this higher mortality may be due to lack of coordination between parents or to the unwillingness of first time mothers (or fathers) to share infant carrying with mates. In experienced parents with alloparents present, mothers typically carry infants only 15% of the time, contacting their infants only to nurse them (Ziegler, Widowski, Larson, & Snowdon, 1990).

Parent-Alloparent Relationships

As noted above, in both field and captive studies the presence of alloparents increases infant survival and reduces the energetic burden on both parents. The presence of non-reproductive helpers primarily affects the amount of effort that fathers invest in carrying infants (McGrew, 1988; Zahed & Snowdon, in preparation). To be effective alloparents, animals must not compete with the parents for reproduction. But why should an alloparent delay reproduction, and what are the dynamics of the relationships between parents and alloparents that recruit alloparents and prevent them from reproducing?

Across all cooperative care species, alloparents may gain both direct and indirect benefits from delaying reproduction. First, in most groups alloparents are the older siblings of the infants being cared for. Thus, alloparents are assisting in the survival of their own kin and increasing inclusive fitness. Second, several studies in marmosets and tamarins have shown that early experience caring for someone else's infants is

critical to becoming competent parents. Data from multiple colonies have documented very low reproductive success in tamarins with no previous experience in infant care (Epple, 1978; Tardif, Richter, & Carson, 1984; Johnson, Petto, & Sehgal, 1991). There is some debate over what is important about this experience (Tardif, 1997). Animals with no prior infant exposure display an interest in infant related cues and will retrieve a crying infant, but they display discomfort when an infant is on the back, often biting and pushing the infant off, only to retrieve it again. Third, infant care may be a passport for entry into a group and may improve an alloparent's subsequent breeding success if it makes that animal more likely to take over a future breeding vacancy or to court a mate more effectively. Thus, although an unrelated group member does not benefit from increased inclusive fitness, serving as an alloparent may improve future direct fitness by increasing the likelihood of subsequent mating and acquiring skills in infant care. Given the relative lack of breeding options available to wild marmosets and tamarins as discussed above, serving as a temporarily non-breeding alloparent may be the best option available (Snowdon & Cronin, in press).

We have presented some of the possible reasons why alloparents might benefit, but is there a role that parents play in regulating fertility and rewarding the behavior of non-reproductive alloparents so that they will remain as care providers? Studies of marmosets and tamarins have provided evidence that parents can control fertility in female offspring. In our colony of cotton-top tamarins, we have collected daily urine samples from subordinate females at a variety of ages over several months. In 31 of 31 females, there was no evidence of ovulation (Figure 6, left histogram). We hypothesized that odor cues from the reproductive female inhibited fertility in other females. In a scent transfer study, we found that females removed from the direct presence of a reproductive female, but receiving daily scent transfers from their mothers, delayed ovulation by at least a month after pairing, and they did not become pregnant during the 60 days of scent transfer. In contrast, control females receiving water blanks ovulated readily and became pregnant in as few as eight days after being paired (Savage, Ziegler, & Snowdon, 1988). However, cues from the reproductive female were not the only cues leading to inhibition. When we housed females with fathers or brothers away from the reproductive female, we observed no ovulation (Widowski, Ziegler, Elowson, & Snowdon, 1990). Only when females could see, hear, and smell novel males did they ovulate (Widowski, Porter, Ziegler, & Snowdon, 1992; see Figure 6 center and right histograms). Data from the field indicated that pregnancy in more than one female was rarely observed and only in groups where a novel male had entered prior to presumed conception. Thus for cotton-top tamarins, females are prevented from ovulating both by cues from the reproductive female and from familiar group males.

Male tamarins do not appear to be reproductively suppressed through either behavioral or hormonal mechanisms (Ginther, Ziegler, & Snowdon, 2001). Adult sons were studied while living in family groups and then three years later after becoming successful fathers with their own infants. These males showed no change in mean urinary levels of luteinizing hormone, testosterone, and dihydrotestosterone (Ginther, Ziegler, & Snowdon, 2001). Adult sons in families actually displayed as much sexual activity as when they were paired with a novel female, but sons in families directed most of their sexual activity toward siblings with the majority directed toward brothers (Ginther, Ziegler, & Snowdon, 2001). In some primate species development is sup-

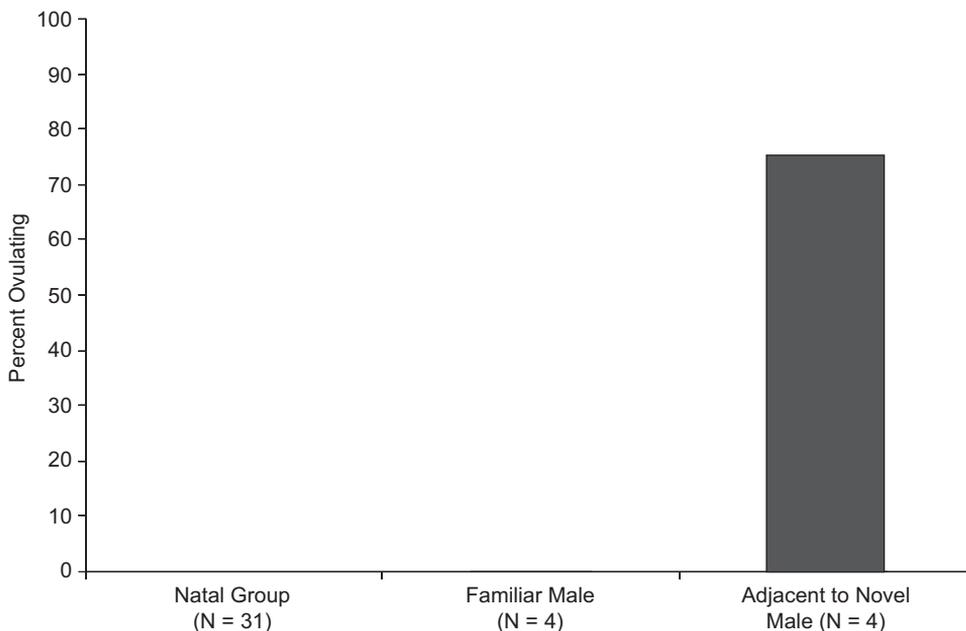


FIGURE 6. Percent of cotton-top tamarin females ovulating in natal group while living with their mother, when living without the mother but with a familiar, related male and when housed adjacent to a novel, unrelated male.

pressed in subordinate males or helpers. However, in a longitudinal study of development, sons achieved testicular size, body weight, and levels of reproductive hormones equal to those of experienced breeding fathers (Ginther, Washabaugh, & Snowdon, 2000; Ginther, Carlson, Ziegler, & Snowdon, 2002)

A somewhat different story emerges in common marmosets. At least one subordinate, post-pubertal female was observed to ovulate in about 50% of captive, family groups (Abbott, 1984; Ziegler & Sousa, 2002) although subordinate, ovulating females did not become pregnant. When peer groups were formed of multiple males and females, only one female ovulated (Saltzman, Schultz-Darken, & Abbott, 1997). Scent transfers from reproductive females to previously suppressed females also prevented these females from ovulating as in tamarins (Barrett, Abbott, & George, 1990). As noted above, subordinate female wild common marmosets often engage in extragroup copulations during territory interactions, but there was no evidence that any of these copulations resulted in pregnancy until after the death of the reproductive female (Lazaro-Perea, Castro, Harrison, Arajau, Arruda, & Snowdon, 2000). As with cotton-top tamarins, there was no evidence of male reproductive inhibition (Baker, Abbott, & Saltzman 1999).

More limited data from captive saddleback tamarins (*Saguinus fuscicollis*) (Epple & Katz, 1984) show that reproductive suppression also occurs and can be maintained by scents from reproductive females. Pygmy marmosets (*Cebuella pygmaea*) are similar to common marmosets with some females displaying ovulation at the same time

as the reproductive female but not becoming pregnant (Carlson, Ziegler, & Snowdon, 1997). Lion tamarin reproductive females and their daughters appear to display synchrony in patterns of estrogen secretion (French & Stribley, 1987), but it is not known whether daughters actually ovulated since estrogen levels were much lower than in mothers and luteinizing hormone levels were not measured. However, field studies indicate that multiple pregnancies can occur in lion tamarins when a male unrelated to the reproducing daughter is present (Baker, Dietz, & Kleiman, 1993).

In summary, although the details differ somewhat between species, some physiological reproductive suppression is seen only in females and never in males. In many species scent marks or other olfactory signals from the reproductive female maintain the suppression; exposure to stimuli from novel males can release the suppression and lead to pregnancy.

Although reproductive animals can control the fertility of female alloparents, they also display behavior indicative of reward or at least tolerance of the alloparents. Lazaro-Perea, Arruda, and Snowdon (2003) found asymmetries in grooming behavior with parents grooming alloparents significantly more than the reverse (See Figure 5, right histogram). Grooming has been shown to release endogenous opioids in the brains of those being groomed (Keverne, Martensz, & Tuite, 1989) and tactile stimulation can release oxytocin that also serves as a social reward (Carter, 1998). In most Old World primate species, subordinates groom dominant animals more than the reverse, so the fact that reproductive adult marmosets groom helpers more than the reverse is significant.

The lack of physiological suppression of male alloparents is curious in light of the clear mechanisms suppressing female fertility. Behavioral mechanisms such as aggression could be used to control mating in male alloparents, but aggression between the reproductive male and other males in the group has been rarely observed (Ginther, Ziegler, & Snowdon, 2001). In fact, when a father and son are removed from the natal group and placed with a novel female, both cotton-top tamarins (Price & McGrew, 1991) and common marmosets (Baker, Abbott, & Saltzman 1999) display extreme tolerance of each other and both males mate with the female. Even more striking is the behavior between fathers and adult sons in natal tamarin groups. We have observed sons engaging in mounting behavior with their mother on several occasions and rarely did we observe the father interfering with the copulation attempt by the son nor did we observe any aggression directed by either parent toward the son after a copulation attempt (Ginther, Ziegler, & Snowdon, 2001; Ginther, unpublished observations).

Sibling Relationships

The relationship between siblings changes with development. Older siblings play an important role in carrying infants and sharing food with infants, but as young marmosets and tamarins mature, there is potential for conflict both over carrying infants and eventually over future reproduction (Price, 1991). Although aggression between fathers and sons is quite rare as stated earlier, we have observed several serious fights in captive environments that led to injury and the need to remove an animal from its

group (Snowdon & Pickhard, 1999). Fights between brothers have been most common, with an older brother harassing and eventually attacking a younger brother. This is curious since the same older brother would have been actively involved in taking care of this brother as an infant. Fights between sisters or between mothers and daughters have been less common. Severe aggression between mothers and daughters develops when daughters begin to scent mark, an indication that reproductive suppression is not as effective. Virtually all of the serious fights have occurred when group sizes are between 6-9 animals, the typical range of group sizes found in wild populations. Similar fights have not been observed in the wild, perhaps because animals can more easily avoid one another, or an animal can migrate to a new group once tensions arise. Two other studies have reported cases of severe aggression in lion tamarins, with most of the aggression between females in contrast to cotton-top tamarins (Kleiman, 1979; Inglett, French, Simmons, & Vires, 1989). Remember that mechanisms of suppression appear to be minimally developed in lion tamarins, making direct competition between females more likely.

What happens when multiple females are pregnant at the same time? In field studies of cotton top tamarins where two females were pregnant at the same time, at least one female miscarried before birth (Savage, Giraldo, Soto, & Snowdon, 1996a). Multiple pregnancies have been observed frequently in wild groups of common marmosets (Digby, 1995; Lazaro-Perea, Castro et al., 2000). In cases where two births occurred close in time, one mother began harassing the infants of the other mother, frequently leading to the death of the infants. When multiple births were separated by at least two months, then there was much less evidence of harassment and no reported deaths. In most of the observed cases of female infanticide, the attacking female was known to be related to the female whose infants she was attacking; in several cases they were sisters. Thus, we have female marmosets killing their nieces and nephews. What can be the benefit to the infanticidal females? The best explanation is that the females are competing for the services of alloparents. Presumably if both sets of infants survived, alloparental care would be stretched between both litters. With one litter killed, all alloparental care can be directed toward the surviving infants. When females give birth asynchronously, then the same alloparents will have finished the major care of the first litter when the second litter is born. When alloparents can be time-shared, conflict between siblings is reduced.

In summary, although siblings share infant care duties with each other and appear to be highly cooperative, siblings can also become highly competitive with each other—driving each other out of family groups in captivity and killing their own relatives in the wild. Cooperative breeding, therefore, involves a delicate balance of cooperation and competition.

Infant-Caretaker Relationships

Several studies in rodents and nonhuman primates have demonstrated that variation in maternal care can influence how infants develop, both physiologically and behaviorally. Rat mothers that lick and groom their infants more produce offspring that

are more resilient to stress and will in turn groom their infants more (Caldji, Tannenbaum, Sharma, Francis, Plotsky, & Meaney, 1998). Fairbanks (1996) has documented two orthogonal dimensions in maternal behavior, an accepting-rejecting dimension intersecting with a laissez-faire-restrictive dimension. In vervet monkeys as well as in rhesus macaques (Suomi, 1987) and baboons (Altmann, 1980), variation in maternal style has an important influence on the infant's behavioral development and for female offspring, subsequent maternal style. Noteworthy is that in each of these species, mothers are typically the only caretaker of infants.

What are the consequences of having multiple caretakers on infant development? In macaques, separation of infants from their mothers can have important consequences that vary according to the degree of alloparental care available. Pigtail macaque infants, where mothers do not allow others to interact with infants, show much more distress when mothers are removed than do bonnet macaque infants where mothers allow other females to interact with their infants (Rosenblum & Kaufman, 1968).

In contrast, a study on infant common marmosets (Arruda, Yamamoto, & Bueno, 1986) found no effect of removal of either parent on infant behavior. Other family members quickly substituted for the parent that was removed. Kostan and Snowdon (2002) observed which family members spent the most time carrying and food sharing with an infant. When the infants were independent of carrying, Kostan and Snowdon presented a series of frightening stimuli and observed the response of the infant. In every case, the infant ran to the family member that had spent the most time carrying and sharing food with the infant—the father or an older brother. In no case was the mother the primary caretaker and in no case did an infant seek its mother as a secure base. Similar results are found in the biparental titi monkey. When given a choice between going to the mother or to the father, infants always prefer the father, who provides more care (Mendoza & Mason, 1986). Thus, in biparental and cooperatively breeding species, infants do not form a primary attachment to the mother or treat the mother as a secure base. Instead, infants seek out the individual that had provided the infant with the most care.

What does cooperative rearing do for maternal style effects on infant development? Washabaugh, Ziegler, and Snowdon (2002) observed caretaking behavior in three successive litters in ten tamarin families that varied in the degree of prior infant caretaking experience and in family composition. There was a wide variation in the amount of care that individual family members provided to the infants. However, when we looked at care from the perspective of what an infant received, all infants received equal quality caretaking (i.e., total time carried, transfers between carriers, rejections, food sharing) regardless of the variation in different caretakers, variation due to experience or variation due to group size. It appeared that having multiple helpers provided a buffer against the variation in care by any particular family member to assure that each infant received consistent care.

What are the consequences for infants? We looked at several measures of infant behavior including age to move independently, first independent feeding, exploration, and response to novel objects. The variation between twins within a litter was as great as the variation between litters from different families. The lack of variation between families in the amount and quality of caretaking that infants receive and the high be-

havioral variation within a pair of twins suggests that the behavioral variation is unlikely due to differences in parenting styles, but instead is likely due to inherent variation within each infant. This result contrasts with the findings from the species reviewed earlier where mothers are primary caretakers and maternal style affects infant behavioral development.

The buffering of different parenting styles and effort by multiple caretakers has important implications. Behavioral variation in infant tamarins may be more likely due to temperament or genetic variation rather than a result of parental behavior. The ability of other family members to compensate for a lack of interest in or rejection of infants by a mother, increases the quality of care an infant will receive and assures that all infants receive consistent care.

Cooperative Breeding and Human Infants

The varieties of human child rearing make difficult any comprehensive comparison of cooperative breeders with human childcare. Although there are substantial differences between humans and marmosets, here we briefly examine some interesting commonalities. Sarah Blaffer Hrdy (1999) has argued that humans are cooperative breeders due to the long period of infant and juvenile development that requires considerable parental investment for a decade or more. Such high investment makes it difficult for a single parent to successfully rear an infant without some sort of economic or social support whether it be from a spouse, partner, relatives, friends or hired day care. (Note that human infant care may be provided by unrelated alloparents such as stepparents, partners or hired caretakers.) If cooperative breeding is a characteristic of the human species, then many of the same principles of family dynamics seen in other cooperative breeders should apply to humans. We briefly review the importance of multiple parents or parental figures, the effects of the parental pair bond on children's adjustment, how the quality of parenting received influences one's own pair relationships (and subsequent parenting), sex differences in parental skills and the role of siblings as alloparents.

Divorce is a clear case where the parental pair bond is poor and where there is a loss of multiple caregivers. A recent study on infanticide in Sweden found much higher rates of infanticide of children living with a single genetic parent versus either two genetic parents or a genetic parent and a stepparent (Temrin, Buchmayer, & Enquist, 2000), suggesting the critical importance of multiple caregivers. One-parent families have reduced economic security often with psychological consequences for children (Thompson, McLanahan, & Curtin, 1992). Hetherington (1989) reported boys in divorced families and both boys and girls in remarried families showed significantly more behavioral problems than children in non-divorced families. She also reports that negative effects of divorce were least when the custodial parent had other sources of social support, including grandparents. Among non-divorced couples, closeness of the marital relationship and support by the spouse predicted parental warmth and positive involvement with children and reduced parent-child conflict. Children in high-conflict, non-divorced families had more problems in self-esteem and psychological adjustment

than children in low conflict divorced families, suggesting that parental pair bond quality is important to children (Hetherington, Bridges, & Insabella, 1998).

Many traditional hunter-gathering cultures have exhibited infant care behavior more similar to cooperative care than has been the norm in industrialized societies. The most egalitarian society noted is the Aka Pygmies (Hewlett, 1992). Aka fathers provide more direct care of infants than in any other society, and husbands and wives spend considerable time together with infant care being only one of many shared tasks. Hewlett (1992) reviewed other societies and reports a statistically significant relationship between the degree of daily interactions and shared tasks between husbands and wives and the amount of care fathers provide infants. Since time spent together is a measure we use to evaluate pair bond quality in tamarins, this is a direct parallel between species. The stronger the pair bond, the more paternal effort is seen, paralleling Hetherington's (1989) results with western cultures. Blurton-Jones (1993) compared the Hazda of Tanzania with the !Kung of Botswana and Namibia. Both cultures display cooperative care with fathers and other group members taking care of infants. Hurtado and Hill (1992) examined the hypothesis that pair bonding leads to greater reproductive success. In the Ache in Paraguay, both the death of a father or parental divorce led to a significant increase in offspring mortality. Children whose parents divorced during their first year of life were more likely to die of illness or homicide than children whose parents remained together. These results suggest that for the Ache, as for cotton-top tamarins, fathers are essential for infant survival. However, Hurtado and Hill (1992) also reported on the Hiwi, a traditional culture from Venezuela, where parents also have strong pair bonds, but the absence of a father does not affect infant survival. Hurtado and Hill (1992) suggest that strong, lasting pair bonds do not develop simply for infant survival, but may develop for other reasons such as a relative lack of suitable alternative mates. Nonetheless, the Ache data suggest that when infants are at risk, the presence of a strong pair bond between parents can affect infant survival and well being.

An emerging literature suggests that one's developmental history affects pair bonding success. Hazan and Shaver (1994) have used attachment theory as an organizational framework for studying close relationships in adults. Simpson (1990) found that couples where both partners had secure attachment styles as children had more commitment, trust, and satisfaction than couples where one or both partners had anxious or avoidant attachment styles. Collins and Read (1990) found that partners tended to match based on the similarity between the partner and one's opposite sex parent. Donnellan, Larsen-Rife and Conger (2005) found that the parent-child socialization process affected the subsequent expectations and success of romantic relationships when the children were adults. Kinnunen and Pulkkinen (2003) reported that anxiety and passivity in childhood for women and anxiety, emotional lability, and aggression in childhood for men were predictors of poor-quality adult relationships. The conclusion drawn from these studies is that parental behavior plays a major role in the next generation's quality of adult pair relationships. If biparental or cooperative infant care leads to more secure attachment, then cooperative childcare should lead to more positive adult social relationships.

Are there sex differences in how men and women parent? Field (1978) compared fathers that were primary caretakers versus fathers that were secondary caretakers dur-

ing interactions with their four-month-old infants. Field found no differences between mothers and primary caretaker fathers on measures of smiling and imitative vocalizations and gestures, whereas secondary fathers engaged in these behaviors less frequently. Lamb (1976) reported that both fathers and mothers interacted with their infants with few differences. Mothers initiated more play with daughters and fathers showed more physical and idiosyncratic play than mothers. Kotelchuck (1976) reported few differences in how infants reacted to departures and arrivals of mothers versus fathers and concluded that infants have no innate bias to prefer mothers to fathers. Furthermore, infants from families with multiple caregivers showed shorter separation protest than those with only a maternal caretaker. Lamb, Pleck, Charnov, & Levine (1987) reviewed several studies indicating fathers responded as much and as competently to newborns as did mothers. Thomson, McLanahan and Curtin (1992) found that both male and female single parents reported less restrictive rules for their children than did married parents. Stepmothers, stepfathers and cohabiting partners were less actively involved with and displayed less positive behavior toward infants than biological parents. Hall, Walker, and Acock (1995) reported that single fathers spent less time in private talks, more time in play, and more time in "masculine" household tasks than single mothers. The majority of these studies done in Western societies suggest that fathers and mothers can interact equally well with infants and older children and that children can form attachments to both parents (or both partners), if both are active as primary caretakers. It is likely that involvement of both primary infant caregivers would have a similar buffering function as seen in tamarins.

Our industrial culture has had until recently well defined economic and parental roles for males and females. These roles have changed in our post-industrial culture. Societies that allow women to contribute significant economic benefits through work outside the home allow fathers to demonstrate greater involvement in infant care. This has led to some difficulty in negotiating new parenting relationships between men and women.

Weisner (1987) reviewed societies where sibling caretaking is important and showed that sibling care of infants is widespread across many human cultures. Frequently older siblings care for infants while mothers forage (or work) and fathers are often absent. In families with extensive sibling care, there is a shared mission between parents and older siblings to provide good quality care. Mothers and fathers often model and supervise care by siblings, but sibling caregivers also develop independence and feel autonomy and competence. Childcare skills are acquired first, followed by autonomy and subsequent management of the household, paralleling how marmosets and tamarins must acquire infant care skills first before becoming independent and breeding on their own. This contrasts with the Western model where household management comes first, followed by acquisition of mate, with parenting skills developing last. Hetherington (1989) notes that children of divorced families took over more responsibility at an earlier age, and they played an important role in supervising younger siblings, with grandparents also playing an important stabilizing role. The involvement of older siblings and grandparents in infant care suggest a pattern of care reminiscent of cooperatively breeding primates.

Summary

We have described the cooperative breeding system found in marmosets and tamarins, showing how cooperative care benefits infants and we have illustrated the family dynamics involved in cooperatively breeding primates. Although a framework of cooperative breeding has not usually been applied to studies of human parenting, the data that are available suggest some interesting parallels not only for how parental care can be shared between fathers and mothers, but also how siblings can become involved in infant care. Fathers and mothers have equal capacity to care for children. Close bonds between parents and equal economic opportunities for both parents appear most conducive to shared parenting. Sibling involvement in childcare may lead to skill development that would make these children more successful parents and also more attractive as mates. A more securely attached relationship with one's own parents (or caregivers) appears to predict a stronger adult pair bond and potentially more successful infant care leading those children to become more successful parents.

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