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## *Parent-Offspring Interactions in Anthropoid Primates: An Evolutionary Perspective*

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**F**ROM an evolutionary viewpoint what is special about parent-offspring interactions? Most behavior that is performed at a reproductive or survival "cost" by one animal and that "benefits" (both terms sensu Hamilton, 1964) a recipient by increasing its chances of survival is thought to be done at some direct, usually immediate, cost to the actor. Generally such behavior will be selected against unless the cost is recouped, either through reciprocity or through inclusive fitness effects. The case of behavior directed by parents toward their offspring is an exceptional one because increases in the offspring's survival directly increase the parent's current reproductive success. Any effective parental care that is costly for the parents also, simultaneously, directly increases the parents' reproductive success. However, this increment to the parents' reproductive success is not as great as the benefit to the offspring; the increment in the parents' current reproductive success must be weighed against the cost to the parents' future reproduction.

Another feature of the benefits and costs involved in parental behavior is that any cost incurred by the parent also entails a cost for the recipient or beneficiary of the act. It does so through inclusive fitness effects, or directly through reduced parental ability to continue investment or even to survive. This self-inflicted cost places limitations on the evolution of selfishness or exploitation on the part of the offspring. However, the cost to the parent, in terms of future reproduction, will be greater than the cost to the offspring, through inclusive fitness (Trivers, 1974). Because of these asymmetries in costs and benefits to each participant, a "conflict of interest" can arise between parent and off-

spring. This conflict can be expected to shape the family interactions that evolve.

An appreciation of these features of parent-offspring interactions is due to a considerable extent to the work of Trivers (1972, 1974), which in turn is based heavily on Hamilton's (1964) pivotal papers demonstrating the importance of a consideration of inclusive fitness. Despite the widespread references to these few papers, most basic theoretical and empirical problems await analysis, particularly as they apply to vertebrates but also for seemingly simple invertebrates (Mertz et al., 1984). As we shall see, anthropoid primates are particularly appropriate subjects, and yet often frustrating ones, for a consideration of the evolution of family interactions.

### **PRIMATE LIFE HISTORIES**

Most anthropoid primates, meaning monkeys and apes, are relatively social animals. They live their whole lives in close proximity to other members of their species, many though not all of whom are close relatives—parents, offspring, full or half siblings. Primate groups represent a wide range of sizes, composition, and degrees of genetic relatedness.

Within, as well as among, primate species, variability in ecological conditions and a host of factors that lead to temporal and spatial variability in group composition lead to differences in the situations in which parents raise their offspring and in which these offspring continue to develop. I focus here, however, on aspects of infant care and development in which most anthropoids are similar to each other and in which they are quite different from almost all other mammals. Most monkeys and apes produce only a single young per gestation (Schultz, 1948; Leutenegger, 1979); they do so after an unusually long gestation period for animals of their size (Western, 1979); and the single offspring develops relative independence of its parents very slowly. This offspring then usually has a long juvenile period in which it still may be dependent on family members, but to a lesser extent than during infancy. All pre-reproductive stages occupy an unusually long part of the lifespan (Schultz, 1969; Eisenberg, 1981), and in most anthropoid species infants are totally dependent for survival on one or both parents for at least a year, much longer for the great apes.

Consequently, in primates there is no single brief season allotted to parental care, however intense. Rather, care of offspring is a continuing activity that must be integrated with all of an adult's maintenance activities over a long period. Moreover, most primates do not use nests or caches for their young, nor do they have communal hunting and sharing of food. A young infant and its parent, almost always its mother, are essentially "saddled" to each other, almost literally as well as figuratively, in that a very young infant rides on its mother wherever

she goes. These various primate characteristics lead to the expectation that primate parents and their offspring, more than parents and young of most other species, will have evolved a complex, often subtle, finely tuned set of interactions that enable them to satisfy their highly, but not completely, overlapping interests over a prolonged period. For a mother, investment in replacement offspring is very costly if the present one dies, and for an infant, its own survival is totally dependent on the survival of its mother. Although features such as potential conflict of interest may favor evolution of behavioral conflict within families (Trivers, 1974), these other factors will favor the evolution of compromise and cooperation and have as yet received less attention (J. Altmann, 1980, 1983).

Finally, primate sibship sizes are small. Siblings are usually half siblings, particularly in multi-male groups. Maternal siblings will often differ appreciably in age whereas paternal siblings are more likely to be similar in age, members of the same age cohort (J. Altmann, 1979).

Partially because primates mature so slowly and are so long-lived, it takes a long time to obtain data that enable us even to begin an evaluation of parameters that are important to evolutionary questions. Twenty-five years after the main development of primate field studies (see survey in S. Altmann, 1967), for only a few species are we even now beginning to accumulate those necessary lifetime data. One such species, *Papio cynocephalus*, includes the savannah baboons that have been the subjects of a longitudinal research project in the Amboseli National Park of southern Kenya since 1971 (e.g., Hausfater, 1975; J. Altmann et al., 1978, 1981; Post, 1982; Walters, 1981). By focusing on the results being obtained in that study, and by then considering the ways in which these animals differ from other populations and primate species, I hope to provide insights into general features of the evolution of primate family interactions.

In the sections that follow, I first highlight those characteristics of baboons that are probably very critical to shaping the parental investment and interaction patterns to be described. Then I consider selective pressures and behaviors of potential importance at three stages of parental care and family interaction: during gestation, during infancy, and during the juvenile period. My emphasis is on intra-population variability—its nature, sources, and consequences. However, I consider, as appropriate, the interactions and investment patterns that have been observed or would be predicted under conditions that differ from those pertaining to these baboons.

### **BABOON LIFE HISTORIES**

The methods used to obtain the Amboseli baboon data have been detailed elsewhere (see Hausfater, 1975, for dominance data; Altmann and Altmann, 1970, and J. Altmann et al., 1977, 1981, for demo-

graphic data; and J. Altmann, 1980, for family interaction data). Briefly, almost daily records are kept on all members of at least one social group within which all animals are individually identifiable through natural differences in appearance. Individuals are observed for changes in health, reproductive condition, physical maturation, and agonistic dominance relationships. These data, which are collected every year, have been complemented in some years by data from detailed studies of parental care and infant or juvenile development (e.g., J. Altmann, 1980; Stein, 1984; Pereira, 1984). In addition, mating records are available, but with varying degrees of completeness for different years. The animals are not trapped, handled, or otherwise overtly interacted with by the investigators.

Savannah baboon species live in semi-closed multi-male, multi-female groups in African grasslands and woodlands (e.g., for olive baboons, Washburn and DeVore, 1963; Rowell, 1964; Harding, 1977; Strum, 1982; for yellow baboons, Altmann and Altmann, 1970; Rasmussen, 1979; for chacma baboons, Stoltz and Saayman, 1970; Hamilton et al., 1976). The group that provides most of the Amboseli longitudinal data, named Alto's Group, has averaged about 45 animals over a 13-year period, but has had a membership as low as 30 or 35 and as high as the lower 60s. As in most primate species (Wrangham, 1980), males are the sex that disperses; with rare exceptions (reported in Rasmussen, 1981, for yellow baboons in Mikumi Park, Tanzania) baboon females remain in their natal group for life.

Baboons are highly dimorphic and, in Amboseli, females usually conceive their first infants at about six years of age, approximately two or three years before the males of their age cohort reproduce (J. Altmann et al., 1977, 1981). Mating within these multi-male, multi-female groups is semi-polygynous, semi-polyandrous; each male mates primarily with several females, each female with several males. Based on behavioral records during the few days of likely conception, infants can be assigned from one to three probable fathers, on the average two (J. Altmann et al., in press). Litter size is almost always one and most direct care of an infant is by its mother, although selective and directed male care (probably paternal care in most cases) is much greater for these multi-male primate groups than was originally assumed (see, e.g., Packer, 1979; J. Altmann, 1980; Stein, 1984).

Infant survivorship in Amboseli is slightly less than 70% for the first year (about 80% if miscarriages and stillbirths are excluded) and about 50% from birth through year two, which corresponds approximately to the interbirth interval. Survivorship is higher, and age of first reproduction lower, in situations of richer natural or human-provisioned food and of reduced predation risk (e.g., Strum and Western, 1982). If an infant dies, its mother quickly becomes pregnant again. Because mating and conceptions occur throughout the year, baboons, unlike most other primates, are not constrained to wait until a subsequent breeding season to recoup reproductive loss.

In Alto's Group, reproduction entails a mortality cost (J. Altmann, 1983). Adult females are at the highest risk of mortality while caring for young, moderate risk while pregnant, and lowest while in other reproductive stages, during menstrual cycles.

Finally, baboon and macaque species have highly stable adult female agonistic dominance hierarchies. During maturation, daughters assume their mothers' relative dominance position (Walters, 1980, and references therein; Hausfater et al., 1982). In contrast, male dominance is less affected (perhaps not at all in wild baboons) by mother's rank, and males change dominance throughout adulthood. For macaques, there is limited evidence from provisioned, semi-captive, semi-free-ranging animals (Meikle et al., 1984), but not yet any from wild ones, that maternal dominance rank affects sons' lifetime reproductive success. The body of evidence for a relationship between female dominance rank and fitness is basically, but not entirely, positive (Drickamer, 1974; Sade et al., 1977; Mori, 1979; Gouzoules et al., 1982; J. Altmann et al., in press). The weakness of the positive relationship may not be too surprising given the brevity of existing studies relative to the stability of female dominance ranks.

This, then, is the demographic and sociological backdrop for parental care and parental investment in savannah baboons. In the sections that follow, I consider various actions by parents that provide benefit to the current offspring (increase that offspring's chances of survival) and that simultaneously incur a reproductive cost (decrease the parents' ability to invest in future offspring). The difference between benefits and costs, rather than just benefit as sometimes appears in the empirical literature, is Trivers's "parental investment" (Trivers, 1972). The distinction is that parental investment is not synonymous with parental care. We are also concerned with behavior that offspring direct toward their parents, and the interaction patterns that emerge from the behavior of each.

## GESTATION

Gestation is truly the first stage of both parental care and investment. Pregnancy reduces, and in some aspects terminates, care in the previous offspring and it precludes immediate investment in another one. Mammalian mothers and fetuses affect each other, behaviorally and otherwise, and our data suggest that pregnancy slightly increases a female's risk of mortality. This relatively ignored preparturitional period of investment provides some rather interesting data.

Pregnancy averages 177 days in Amboseli baboons, somewhat less time in smaller monkeys and longer in the apes (Eisenberg, 1981). During this period, the fetus of most anthropoids grows to approximately 7% of its mother's body weight (Leutenegger, 1973). Pregnant females socialize less and feed more than do cycling ones. Aside from walking

enough to keep up with their group, they spend virtually all their time feeding and resting (J. Altmann, 1980; Altmann and Mututua, 1984, and unpublished data; Silk, in preparation). In Amboseli, gestation length is positively correlated with survivorship during an infant's first year. Females that are low in the dominance hierarchy tend to have slightly higher rates of spontaneous abortions, stillbirths, and short gestations (J. Altmann et al., in press). These findings raise questions about the proximal factors controlling gestation length and about the potential for female-female competition, through aggression for example, that might result in early births.

We have found that there is a sex-ratio bias by dominance rank: the highest-ranking third (ranks 1-7) of females produce three to four females to each male offspring and the lowest-ranking third produces two males to each female offspring (J. Altmann, 1980; J. Altmann et al., in press). This result has been consistent from year to year and has now been found in a second group in Amboseli as well as in several studies of captive or provisioned colony macaques (Silk et al., 1981; Simpson and Simpson, 1982), but not in all (Meikle et al., 1984). Based on a synthetic review of the literature from wild, provisioned, and captive primates, Van Schaik and Van Noordwijk (1983) conclude that social stress increases male bias in birth, but they suggest that this is not an adaptive response.

In addition to sex biases at birth, in Amboseli there is a somewhat higher survival of "right sex" offspring; that is, for high-ranking females a higher proportion of daughters (0.50) than sons (0.00) reach age six (age of first conception) and for low-ranking females, conversely, survival is higher for sons (0.33) than for daughters (0.25) (J. Altmann et al., in press). Moreover, as can be seen from these figures, daughters of high-ranking females have higher survivorship than those of low-ranking females and survivorship is higher for sons of low-ranking females than for those of high-ranking females. These differences in survivorship exaggerate the sex bias present at birth. A possible partial contribution to these survivorship differences may lie in another finding: gestation length is slightly longer for low-ranking females when they are carrying sons rather than daughters and the opposite is true for high-ranking females.

Consistent with male-biased sex ratios in low-ranking females are results of a study of captive macaques by Sackett et al. (1975) in which it was found that pregnant females received more severe aggression when they were carrying female offspring than male offspring. That finding suggests a mechanism by which low-ranking females might have shorter gestations imposed on them for female offspring, but would not contribute to an understanding of the bias against male offspring of high-ranking females. Moreover, this explanation is based entirely on the birth sex-ratio effect being one of biasing secondary sex ratios and not primary ones, whereas close examination of data for each baboon menstrual cycle allows detection of all pregnancies that lasted

at least as long as implantation (7-10 days), and few miscarriages occurred in Amboseli thereafter. Consequently, we propose that at least some sex-ratio biasing occurs by the time of conception, perhaps through timing of conception with respect to ovulation and/or through factors that affect vaginal pH (e.g., Guerrero, 1974; Harlap, 1979, and subsequent commentaries; James, 1980, for evidence in humans regarding sex ratios as a function of timing within the menstrual cycle). In sum, then, Amboseli females of a given dominance rank are producing, and probably conceiving, the sex of offspring that has the best prognosis for survival and reproduction. Both the proximate and ultimate factors resulting in sex-biased investment and in particular in biased offspring sex ratios are complex. These factors are currently the topic of much attention that should result in interesting developments in the next several years.

## INFANCY

By the time of parturition, a primate mother has already invested in her infant almost a third of the months that she will altogether; in baboons the six months of gestation is followed by at least twelve of care. The duration of infancy is roughly scaled to body size across monkey species and it is even longer than expected for size in apes than it is in monkeys (Schultz, 1969; Eisenberg, 1981).

In addition to the life history features already discussed, a complex of three physical characteristics of anthropoid mothers and infants seems to have a particularly strong influence on the care options during early development: a relatively "thin" low-lipid milk (Buss, 1971), locomotor altriciality, and a strong clinging/grasping response (Hines, 1942). This is not meant to imply that these features preceded the behavioral care systems in an evolutionary sense, but only that they are at present closely linked to, and developmentally may constrain, interaction possibilities. The low-lipid content of the mother's milk, combined with the fact that the amount of milk available at any one time in the mammary glands is small (Buss, 1971), means that the infant requires frequent nursing throughout most of the day during a considerable period of growth. The infant must therefore be kept relatively close to its mother most of the time. The infant's inability to orient and locomote independently necessitates that it be carried to obtain enough milk, and its well-developed grasping ability enables it to provide the active behavioral component to accomplish this proximity with minimal impediment to the mother's locomotion.

In primate species that travel little or those that live in small monogamous groupings in which individuals travel close together, the infant needn't be carried on the mother herself in order to have adequate access to her; it can be left nearby, often in the care of others in the relatively sedentary species. In most monogamous species the infant

rides on its father or siblings (Kleiman and Malcolm, 1981). In most other primate species, however, access necessitates or is more efficiently effected by the infant riding on its mother, to whom it clings tenaciously. In fact, a baboon infant that gets separated from its mother during the first few weeks of life will cling tightly to whoever carries it; we have witnessed one death (Shopland, in press) and one near fatal case of infants that clung to other females who had kidnapped them, and the infants thereby hindered their mothers' ability to recover them. Before the age at which an infant recognizes its mother and selectively orients to her, the mother's ability to keep contact with the infant may be critical in some species.

### **Individual Differences in Style of Maternal Care**

Although infants of high-ranking mothers and those of low-ranking mothers are probably exposed to fairly similar ecological dangers, it is the offspring of low-ranking females, and the mothers themselves, who are subjected to constant interest, harassment, and potential kidnapping. High-ranking mothers and their offspring are relatively immune to this interference. Apparently in response to this difference in social hazards, low-ranking mothers tend to be more restrictive and protective of their infants and to continue this restrictiveness until their infants are several months old (J. Altmann, 1978, 1980). These infants develop independence more slowly than their high-ranking peers, even after the restrictiveness is terminated.

The protective style of low-ranking mothers probably increases infant survival. Simultaneously, however, it may increase two other costs. Protectiveness and the resulting delay of independence probably results in delay of subsequent reproduction for the mother and, by delaying behavioral maturation, delays the ability of the youngster to survive independently if it should be orphaned. Our data remain suggestive on both these points, but Nicolson (1982) has demonstrated the former in a population of olive baboons. From the standpoint of natural selection, one would want to know whether restrictiveness is a stable characteristic of a female during her lifetime and whether it occurs disproportionately in her daughters. Because of the stability of dominance ranks, we predict that this is the case for baboons and are currently collecting the relevant longitudinal data. Other individual characters that affect offspring development and survival in primates await identification.

### **Changes in Mother-Infant Interaction Patterns During Development**

Even the youngest baboon infant can maintain the position needed to obtain transport and to reach the nipple for frequent suckling, although during the first few days its mother's assistance is occasionally

needed, especially toward the end of the day. All other behavior needed for the neonate's care is done by the mother, not the infant. The demand for care and attentiveness actually increases in the next month as the infant begins to break contact with its mother and explore nearby. The mother then repeatedly watches, follows, and retrieves her infant.

As the infant gets older, however, it obtains the contact and care it needs only if it contributes to the maintenance of contact and facilitates the mother's ability to provide other care, such as keeping track of its mother's location in case a predator attack occurs (J. Altmann, 1980; see also Hinde et al., 1964, and sequelae; Berman, 1980, for macaques). In addition, the infant increasingly must attend to the nature of its mother's ongoing activities—such as walking, feeding or resting—and time its contact or other care demands in such a way that these demands will be compatible rather than interfere with the mother's procurement of food (J. Altmann, 1980; see recent elegant experimental demonstrations of the effect of nutritional level on mother-infant relations in Rosenblum, 1982).

Thus, a major developmental feature of primate mother-infant interactions is the increasing role that the infant must play in facilitating its own care. It must become sensitive to its mother's activities and make responses that are contingent on her activities. Moreover, these contingencies change during development with alterations in the infant's size, needs, potential hazards, and so forth. Consequently, for a primate infant a premium is placed on development of social sensitivity, changing contingent responses, and coordinated, collaborative activity with a social partner. Developmentally, these interactions probably form the basis for the complex, flexible primate behavior as we know it, the most intense evolutionary pressure for which may have come as a result of severe ecological pressures on primate mothers (J. Altmann, 1980, 1983).

### **Independent Manipulation of Benefit and Cost in Maternal Care**

One of the consequences of temporal overlap between parental activities and maintenance activities such as feeding is that a given level of benefit to an infant, say that provided by a milliliter of milk, might be obtained at quite different costs to the mother, depending on her other activity at the time. If the suckling occurs when she is foraging, the suckling of a large infant probably reduces her feeding efficiency. In contrast, the suckling does not entail this extra cost if it occurs when the mother is resting. This possibility of providing the same benefit at lower cost probably is one of the factors leading to the contingent responses described above.

There is an additional way, suggested by the work of Konner and Worthman (1980) with humans, that benefits might be delivered at two

different costs. A human mother who suckles her infant, even briefly, at least once every hour will maintain high prolactin levels and experience longer post-partum amenorrhea than one who provides the same amount of suckling time and milk but distributed such that a number of long periods occur without suckling. It remains to be determined if other lactating primates, including baboons, respond in the same way to inter-nursing intervals. Of course, this example is not as simple as it at first appears because the two infants will obtain the same benefit in the short run whereas one will probably experience termination of nursing at a younger age. Nonetheless, the example serves as a striking reminder that we must distinguish costs and benefits, and be mindful of that separation and of its implications for the evolution of complex family interaction patterns.

### Paternal Care

In most primate species other than the monogamous, primarily twin-bearing ones, care is overwhelmingly by the infant's mother, partially for reasons suggested above. However, even in multi-male social systems such as those found in baboons, some care is provided by adult males and each male directs care primarily toward infants that are more likely to be his offspring. This selectivity has now been reported from several studies of anubis, chacma, and cynocephalus baboons (J. Altmann, 1978, 1980; Packer, 1979; Smuts, 1982; Busse, 1984; Stein, 1984).

Although genetic information was not available in any of the aforementioned studies, the baboons' consortship mating system and the external indicators of ovulation-timing (Gillman and Gilbert, 1946; Kriewaldt and Hendrickx, 1968) make it likely that the indicators of paternity that are available to human observers (as well as to the baboons) are fairly reliable if they are recorded in detailed, systematic records on a daily basis (J. Altmann et al., in press). It seems that persistent adult male-female bonds and consortships (e.g. Hausfater, 1975; Rasmussen, 1980; Smuts, 1982) provide much of the proximal cues for male care of those specific infants that are likely to be their own. The only series of experimental studies of anthropoid ability to identify paternal kin in the absence of experiential cues produced somewhat ambiguous results in macaques (Wu et al., 1980; Fredrickson and Sackett, 1984).

The amount of male parental care is variable at every level of organization. Variability among primate species is great even within a single genus. Within *Papio* (baboons), for example, those species with multi-male groups seem to exhibit much more direct male care than do hamadryas baboons which live primarily in single-male groups. Within *Macaca* there is considerable variability in paternal care from species to species, even among species with relatively similar social and mating systems (see Snowdon and Suomi, 1982, for a recent cross-species

review). Although there still is a relative paucity of quantitative data on primate paternal care (but see chapters in Taub, 1984), it is illuminating to consider the kinds of care that males provide infants and how this care changes during development.

In monogamous, primarily twin-bearing small anthropoids, fathers and older siblings provide virtually all non-nutritional care for infants. This care probably is critical in allowing higher rates of reproduction in these species than would otherwise be expected for primates of their size (Kleiman, 1977; Ralls, 1977). In baboons, the non-monogamous species in which male care has been best documented, the care is of several sorts, usually, but not always, complementary to maternal care rather than a substitute for it (Snowdon and Suomi, 1982), especially in the case of young infants.

One of the first roles that a baboon male plays is that of social buffer for the mother-infant dyad. In particular the male reduces the harassment of mothers that are low on the dominance hierarchy by those that are high-ranking (J. Altmann, 1980). This social buffering reduces the stress on mothers, allows their infants to explore more, and seems to facilitate the mothers' ability to feed undisturbed. Some mothers even forage away, leaving their infants with these male "babysitters" or "care-providing fathers," as the case may be. These males, unlike adult females and juveniles, rarely try to carry a young infant in this situation; rather, they sit and watch it closely, give repeated soft grunts, and follow the infant if it moves.

As the young baboon infant begins to feed on solid food, it gains a second advantage from its proximity to the male. The infant, unlike other group members, is tolerated immediately next to the male as he feeds. The infant thereby has the opportunity to learn about food sources from a second adult and also has access to scraps of food that would be costly or impossible for the infant to obtain on its own. These are usually plant food sources, but scraps of vertebrate meat are also sometimes obtained this way by those infants whose male caregivers are frequent predators.

One of the first areas in which a baboon mother rejects her infant's attempts to obtain care is in providing transport during the group's foraging and progressions. Infants often show clear signs of fatigue by mid-afternoon, particularly if the day journey has been long or the afternoon is quite hot. At such times the infant's associated adult male will often allow the infant to ride when the mother refuses to do so. At this stage, a mother will still carry her infant in the case of some external danger such as a predator. Soon, however, the growing infant's weight sufficiently slows its mother that carrying probably becomes disadvantageous to both, even though the infant cannot keep up with the group in flight. It is at these times when the male's role is particularly visible and dramatic as he dashes back and retrieves a stranded youngster.

As the older infant gradually becomes a young juvenile and its

mother begins to invest in her next offspring, another important male behavior emerges. Young juveniles begin to be the object of aggression by older animals or by those peers whose mothers are dominant to their mothers. The adult male, like the mother, will sometimes come to the aid of the youngster, primarily if the harassment escalates or persists. Because the male is dominant to all adult females and immature animals, he can provide effective support against more antagonists than can the mother.

### JUVENILE PERIOD

No sharp transition separates infancy from the juvenile period. The age at which the juvenile stage has begun is that at which a youngster is nutritionally independent, the youngster could survive its mother's death, and its mother has probably begun investment in her next offspring (Pereira and Altmann, 1985).

A surviving monkey mother, however, still provides some care, an appreciable amount in the case of the great apes (see, e.g., Pusey, 1983). In Amboseli, the young juvenile baboon usually still sleeps nestled in its mother's lap in the trees at night until the birth of the next infant. Thereafter, the juvenile sleeps against its mother's body outside her ventrum or huddles with its adult male associate or an older sibling. A juvenile sometimes continues to receive agonistic support from its likely father, if he is still present in the group. A mother also continues to provide some agonistic support for her juvenile offspring (Walters, 1980, and references therein for various macaque and baboon species; Pereira, 1984), but low-ranking mothers are less able and perhaps less willing to do so. As juveniles mature, they not only receive agonistic aid from their mothers but they in turn come to the aid of their mothers, forming agonistic coalitions with them. Even among animals of similar ranks, individual and family differences seem to occur in the amount of agonistic support, but these differences are as yet undocumented quantitatively. Family size seems to be a relevant factor, as would be expected for the female kin-based groups such as found in baboons and macaques (Silk and Boyd, 1983).

Perhaps the major area of care and of social interaction between a mother and her juvenile offspring involves social grooming. In his study of social development in baboon juveniles, Pereira (1984; Pereira and Altmann, 1985) found that a young juvenile receives over 50 times more grooming from its mother than, per capita, from other females. Moreover, a mother grooms her young juvenile son or daughter approximately nine times as much as the juvenile grooms her. Thus, the benefits of grooming are still provided for a young juvenile predominantly by its mother and grooming interactions between them are still characterized by an asymmetric, care-giving quality. This relation-

ship changes in interesting ways during maturation. By the time a juvenile is three years old, it appears that the mother expects not to be providing care, but to have a reciprocally altruistic relationship with her offspring. Male offspring, most of whom will eventually disperse from their natal group and spend their adult years in other social groups, continue to provide little grooming. In addition, mothers now refuse sons' grooming solicitations and do not initiate grooming of their sons. Consequently, few grooming interactions occur between mothers and older juvenile sons. Although the grooming interactions of older juvenile daughters are less exclusively with their mothers than was the case earlier, mothers are still their daughters' predominant adult female grooming partners. In addition, the grooming between mother and daughter is symmetric, each sharing equally the role of actor and recipient.

Thus, during the juvenile period we see a gradual shift in parent-offspring interactions from an asymmetric, parental care-giving pattern to one characterized by reciprocal altruism reinforced by kinship, a pattern that mothers and daughters will retain during adulthood in their natal groups. Sons are not likely to be future partners in reciprocal relationships. For them, the patterns of parent-offspring interactions wane. The skills and sensitivities that have been developed will have other applications for these youngsters who as adults will need to develop all their social relationships anew in another group.

### CONCLUSIONS

Primate family interactions are intense and extend over a long period. Especially for mothers and daughters and also for sisters of most species, these close relationships extend beyond the developmental stages discussed above, throughout adulthood. The complexities of these relationships have only recently been investigated quantitatively, and then for only a very few species and topics. Paternity information is less accessible than is maternity determination, and it is males that disperse in most species, including the best-studied species. Consequently, we are particularly ignorant of the life course of relationships for males, as we are for most aspects of male life histories, even for the best-studied species.

In addition, the existing data dramatically demonstrate the importance of quantitative studies that continue to delve below the surface, that are longitudinal rather than just cross-sectional, and that include investigation of variability within species and within populations as well as that between species. Serious attention to primate flexibility and within-lifetime adaptability to diverse conditions must be incorporated in investigations of this taxonomic group. Finally, we can expect recent economic and population models of the evolution of family interac-

tions to continue to enrich the study of primate behavior, but the utility of the models, and their ultimate growth, will also depend on their ability to incorporate features of the life histories of long-lived, slowly producing and developing species such as primates.

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