Triadic Interactions in Savanna-Dwelling Baboons

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Interactions between adult males and infants may have important consequences not only for males and infants, but also for mothers. Considerable attention has been paid to interactions that involve two males and an infant. Investigators have proposed three different general strategies to account for this behavior: (a) exploitation of the infant for one male's advantage, (b) protection of the infant from harassment and aggression, and (c) development of relationships with the infant's mother. We review various accounts of these interactions, detail the hypotheses used to explain the behavior, make predictions derived from the hypotheses, and evaluate available data for testing the predictions. We conclude that multiple factors are probably at work, but the development of social relations between a male and an infant's mother is a central force.

INTRODUCTION

The interactions of primate males with infants have received considerable attention (Hrdy, 1976; Mitchell, 1969, 1977; Redican, 1976; Redican and Taub, 1981; Spencer-Booth, 1970; Whitten, 1987). This scrutiny is a response to the growing interest in intrasexual selection, the evolution of parental care systems (Berenstain and Wade, 1983; Kleiman and Malcolm, 1981; Trivers, 1972), and infanticide as a possible male reproductive strate-

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gy (Hrdy, 1974, 1979; Hausfater and Hrdy, 1984). Males in monogamous species make various contributions to the care of offspring, and in several species of New World monkeys, males do most of the infant carrying. In marmosets, tamarins, titis, and owl monkeys, males carry the young and return them to the mother only for feeding (Box, 1975; Dixson and Fleming, 1981; Epple, 1975; Hoage, 1978; Ingram, 1978; Vogt *et al.*, 1978). Interactions between adult males and infants, however, are not confined to monogamous species. The interaction of males and infants outside the context of the pair bond poses some intriguing evolutionary questions because it suggests a diversity of elements ranging from care to exploitation. In the larger sense, male–infant interactions outside the context of direct parental care address an important component of the evolution of reproductive strategies.

Papio monkeys exhibit extensive interactions involving two adult males and an infant, and perhaps the best-studied members of the genus are the savanna-dwelling baboons (reviewed by Hrdy, 1976, 1979; Taub, 1984; Whitten, 1987). In the most common form of these interactions, an adult male holds or carries an infant in proximity to, or in conjunction with, another adult male. However, the precise form and context of these interactions vary from site to site and within individual sites, depending upon the actors and the circumstances. These interactions, called "triadic interactions" (after Kummer, 1967), have been described variously as "agonistic buffering" (Deag and Crook, 1971), "kidnapping" (Popp, 1978), and "infant carrying" (Busse and Hamilton, 1981).

Triadic interactions have been reported in three subspecies of savanna-dwelling baboons: (1) *Papio cynocephalus anubis* (Packer, 1980; Popp, 1978; Ranson and Ranson, 1971; Smuts, 1985; Strum, 1984, 1987), (2) *Papio cynocephalus ursinus* (Busse, 1984; Busse and Hamilton, 1981; Stoltz and Saayman, 1970), and (3) *Papio cynocephalus cynocephalus* (Altmann, 1980; Collins, 1986; Klein, 1983; Stein, 1984a). Such interactions have been studied intensively at seven African study sites [Kenya – Amboseli (Stein, 1984a), Masai Mara (Popp, 1978), and Gilgil (Smuts, 1985; Strum, 1984, 1987); Tanzania – Gombe (Packer, 1980), Ruaha (Collins, 1986), and Mikumi (Klein, 1983); and Botswana – Moremi (Busse, 1984; Busse and Hamilton, 1981)]. The considerable differences in the behaviors observed in these studies have resulted in the development of several theoretical positions on the ultimate causation of triadic interactions. The currently posited explanations hold that triadic interactions may function (a) to aid the carrier male in agonistic interactions (exploitation), (b) to protect the infant from aggression by a dominant male (protection), or (c) to improve the carrier male's chances of impregnating the infant's mother or other females by developing a special relationship with the infant (cultivation). The purpose of this paper is (a) to describe the types of variability that exist in these interactions across differ-

ent subspecies of *Papio* monkeys at different sites, (b) to detail the hypotheses that have been advanced to explain these differences, (c) to outline a number of testable predictions that arise from each of the hypotheses, (d) to summarize and evaluate the available data in an attempt to test these predictions, and (e) to consider what kinds of additional data are needed to test these predictions and/or formulate testable alternatives.

Papio cynocephalus anubis

Popp (1978) found that triadic interactions occurred in agonistic contexts between a consorting male and another adult male. Infants were unwilling participants in these encounters. The carrier of an infant typically was subordinate to his opponent and, on the basis of current social rank, was considered less likely to be the infant's father than was his opponent, given the general priority-of-access model. Infants were handled roughly and were used in potentially dangerous encounters between a consorting male and an attacker carrying the infant. The infant was used to forestall aggressive retaliation by the consorting male. The kidnapper used the infant to approach within arms' reach or to engage in physical contact with the consorting male.

Long-term studies of *P. c. anubis* at Gilgil have documented 293 cases where males carried infants in several different ways (Strum, 1984, p. 151). Typically, the interaction begins with an agonistic encounter or a displacement between two males. One of the males picks up an infant; there is considerable variability in location and relationship of the infant relative to the adult males. Strum (1984) suggested that there are two distinct types of interactions during this phase: (a) *passport*, in which the male carries the infant to another male and then either sits, threatens, or quickly moves away; and (b) *agonistic buffer*, in which the carrying male focuses on the infant and avoids the gaze of the other male. In the latter type, the carrying male may sit with the infant as the other male approaches, avoid the other male's approach while carrying the infant, or directly approach the other male while carrying the infant. Finally, the carrying male and the infant disengage. In no instance do the males groom each other or exchange the infant. Passport-like interactions were observed less frequently than interactions suggestive of agonistic buffering. Strum (1984, 1987) found that length of residence in the group is a good predictor of male–infant interactions. Long-term troop residents use infants more frequently than short-term residents or newcomers.

In a 15-month study of *P. c. anubis* near Gilgil, Kenya, Smuts (1985) described interactions between adult males ranging from exploitative to protective, with some exhibiting ambiguous properties. Smuts (1985) concluded

that, on the average, males were equally protective and exploitative and that the specific type of interaction depended upon both situational and environmental parameters. Smuts (1985, p. 187) observed that the carrying male was a possible or likely father of the infant in less than half of the 25 infant-carrying episodes for which paternity estimates were available. Similarly, Packer and Pusey (1985) also noted that the carrying male was the likely father of the infant in approximately 40% of the episodes.

Papio cynocephalus ursinus

In a study of *P. c. ursinus* conducted in the Moremi Wildlife Reserve in Botswana, Busse (1984, p. 193) noted that triadic interactions typically were initiated when a recently immigrated male approached an infant while in the vicinity of a resident male. Busse and Hamilton (1981) found that the males that carried infants were high-ranking troop members when the infants were conceived and were the probable fathers of at least 10 of the 25 infants carried. The majority of males that were the targets of adult male–infant interactions had recently immigrated into the group and could not have been the infants' fathers.

Papio cynocephalus cynocephalus

Collins (1986) described interactions between adults males and infants in Ruaha National Park, Tanzania. He found that for males, access to infants is mediated, to some extent, through relationships with the mothers and that interactions with particular infants range from protective to exploitative. Collins (1986) did not observe newcomer males carrying infants. Typically, infants were carried by subordinate males against high-ranking or recently immigrated males.

Klein (1983) observed a single troop of yellow baboons at Mikumi for approximately 2300 hr. Eleven infants were chosen for intensive observations based on the availability of mating records of their mothers. He assigned males a high or low paternity rank for given infants and found that adult males touched their probable offspring more than expected and, therefore, touched nonrelated infants less than expected (Klein, 1983, p. 69). These results suggest that the male that was a care-giver also was a likely exploiter. Klein (1983, p. 69) concluded that "given the strong relationship between caregiving and paternity... it is probable that an adult male exploits his own potential offspring and not an unrelated baboon."

Stein (1984a,b) presents a diverse and complicated set of examples of male–infant interactions that runs the gamut from exploitation of the infant (by using it as a buffer during agonistic encounters with other adult males)

to protection of the infant from harassment by other group members. He reports that males rarely used infants to gain across to an estrous female, however. Stein (1984a, p. 41) notes that "the contexts, sequences, and immediate consequences of interactions between infants and adult males are both complex and diverse. . . . Infants serve different functions in different contexts. Similarly, the effect of an infant's presence may be different for different males." For infants, the costs and benefits derived from participating in these interactions may be mediated through relatives as well as by their stage of development.

Clearly, significant differences exist in the types of interactions noted between adult male and immature animals, ranging from the protective, solicitous interactions seen in the Eburru Cliffs group of *P. c. anubis* (Smuts, 1985) to the highly exploitative, manipulative interactions of the anubis baboons in the Masai Mara (Popp, 1978). Moreover, we have described a range of interactions between these vastly different extremes both within and between particular sites. Given the diverse nature of these observations, it is of interest to consider the different hypotheses and explanations that have been advanced to account for them. A variety of hypotheses has been advanced to explain triadic interactions. Explanations center around three basic themes: exploitation, protection, and cultivation of infants.

EXPLANATIONS FOR TRIADIC INTERACTIONS

Exploitation

The exploitation hypotheses center on the common theme that infants are exploited, to some degree, for the benefit of the carrier male. These explanations suggest that males carry infants in order to gain access to critical resources, to approach other males (as "passports") (Hrdy, 1976), or to decrease the probability of aggression (as "agonistic buffers") (Stein, 1984a,b; Strum, 1984).

Protection

The infant-protection hypothesis suggests that males may be attempting to protect infants from recently immigrated males. This hypothesis argues that immigrant males might kill infants in order to bring their mothers into estrus (Busse and Hamilton, 1981; Hrdy, 1974). Males may improve their own fitness by protecting infants. A father would be expected to sustain greater costs in protecting his own offspring, but an opponent would be fighting only for a chance to mate with the mother (Packer and Pusey, 1985). Packer

and Pusey (1985, p. 180) offer an interesting evolutionary scenario for infant carrying. They argue that infant carrying initially may have been selected solely to benefit the infant and protect it from infanticide. Once this behavior was widespread, however, it became an evolutionary asymmetry whereby subordinate males carried infants in order to avoid injury and reduce aggression. Stein (1984a) also suggested the possibility that infant carrying may involve an uncorrelated asymmetry between two males with similar competitive abilities.

Cultivation

A final hypothesis suggests that males may associate with or carry infants in order to establish a close relationship with the infants' mothers, and triadic interactions may be merely a subset of a more general pattern of affiliative interactions by males with infants (Smuts, 1985). In fact, by carrying and protecting an infant, a male may be making a considerable investment in certain circumstances. The "payoff" to the male is future reproductive success with the mother of the infant he has "cultivated."

PREDICTIONS OF EACH HYPOTHESIS

Any attempt to tease apart these hypotheses and ultimately render one of them false is likely to meet with failure because, as Smuts (1985, p. 188) noted, "there is no *a priori* reason to assume that triadic interactions represent a unitary phenomenon requiring a single explanation. . . . Within a troop, male carrying of infants may range from pure protection to pure exploitation, and everything in between." Rather than attempt to disprove one or more of the competing hypotheses, we derive a number of testable predictions from the more general hypotheses and then review the available evidence to support or refute the predictions.

Several factors must be taken into account when attempting to understand these triadic behavioral interactions. For example, the context in which the interaction occurs is one important way in which the various hypotheses differ. Exploitation hypotheses predict proximity and possible aggression between the recipient male and the carrier male. The protection hypothesis, on the other hand, predicts proximity and possible aggression between the recipient male and the infant. The cultivation hypothesis could operate in the presence of an aggressive encounter or in a more general care-taking context. In general, the protection hypothesis predicts that males will be the probable fathers of the infants they carry. Exploitation hypotheses also predict some probability of a relationship between recipient and infant, but the cul-

tivation hypothesis makes no specific assumption about the relatedness of the participants.

Paternity must be identified in order to generate a set of testable hypotheses from these alternate explanations. Several measures have been used to infer paternity, ranging from social rank and inferred or tested relationships between rank and reproductive success (Busse and Hamilton, 1981; Popp, 1978) to mating or consort success during the mother's conception cycle (Smuts, 1985; Stein, 1984b), but none has relied on a precise genetic analysis to determine paternity. The available data suggest that carrier males are more closely related to the infants that they carry than are their opponents (Altmann, 1980; Busse and Hamilton, 1981; Packer, 1980; Smuts, 1985; Stein, 1984a,b). Although Popp (1978) provided evidence that opponents are more closely related to the infant than are carriers, the assumption of paternity was based on the high social rank of carrier males at the time of triadic interactions. The social rank and mating success of males at the time of conception were unknown.

The relative importance of the roles of mothers and infants in triadic interactions also helps distinguish the hypotheses. The pure exploitation hypothesis views infants as unwilling participants and mothers as helpless bystanders in competitive interactions between adult males. In the cultivation hypothesis infants (and mothers) are willing participants within the broader context of a mutualistic relationship between the infant and the carrier male. In the protection hypothesis, mothers and infants are willing participants within the context of potential infanticide by immigrant males.

Although it is difficult to specify with great precision the role of these factors using the available data, a set of predictions can be developed from the three contrasting versions of adult male–infant interactions.

Exploitation Hypothesis

Prediction 1

Triadic Interactions Should Occur Only When Carrier Males are Engaged in Agonistic Interactions with Recipient Males. Evidence: Popp (1978, p. 32) noted, "The context of kidnapping behavior in this population almost always involves a previous or ongoing agonistic encounter between the kidnapper and the opponent." However, no data on frequency of kidnappings and their contextual settings were presented.

Stein (1981) reported that during 135.2 hr of focal-adult male observations, adult males were either in connection with, in contact with, or within 5 ft of an infant for 15.91% of the total time. A male was in contact with an infant while another male was acting agonistically within 10 ft of the

male-infant pair for only 2% of the total time. Although males were in proximity to infants for a considerable proportion of the time, it seems clear that it was not in response to ongoing agonism. Nevertheless, Strum (1984, p. 154) reported that of the 233 occasions when infants were used in contexts unrelated to resource competition, the infants served as agonistic buffers in 87% ($N = 203$) of these episodes. Collins (1986) found that 26.5% of 381 interactions between adult males and infants occurred when the males were involved in agonistic interactions with other males or when there was obvious tension between males.

Prediction 2

Males that Carry Infants During Agonistic Encounters Should Receive Less Aggression and Fewer Wounds than They Receive When Not Carrying Infants. Evidence: Data on the outcomes of triadic interactions are less conclusive than data on the events preceding triadic interactions. Packer (1980, p. 513) noted that in 20 of 22 dyads (90.9%), a male received fewer threats while carrying an infant. However, Strum (1984) reported that triadic interactions seldom resulted in a shift of an interaction in favor of the infant carrier. In only about one-third of all interactions did a carrier succeed in terminating an opponent's aggression, supplanting a previous supplanter, reversing a supplant, becoming more aggressive when approaching an opponent, or inducing avoidance from an opponent. The rate of apparent success was higher within aggressive contexts than nonaggressive contexts, but it never exceeded 57% of all interactions.

These findings are difficult to evaluate, however, given the absence of data on success rates for interactions in which infants were not involved. Some studies have demonstrated advantages of infant carrying when these comparisons were made. In Gombe, male olive baboons were threatened less frequently by other males and supplanted them more often when carrying an infant (Packer, 1980) than when infants were not present. These comparisons are biased by problems of sample size, however. Carrying episodes always represent a smaller sample size than noncarrying episodes. If agonistic episodes are also infrequent, then they would be less likely to appear among carrying episodes when the data on each male or each male dyad are examined separately. Collins (1986) noted that infants appeared to inhibit certain types of aggressive behavior between males but not others. During aggressive encounters directed at males carrying infants, chases occurred more frequently. Moreover, males carrying infants were subjected to fewer threats and attacks. Collings (1986) noted, however, that these data are difficult to interpret due to a lack of baseline information on interaction rates of males with and without infants.

An alternative approach would be to pool the data for carrying events over all males. When this comparison was made for the baboons in Amboseli, it provided no evidence that infants protected ("buffered") males from aggression (Stein, 1984b). Aggression against subordinate males did not decrease when they were holding or carrying an infant. At times, the presence of an infant appeared to incite aggression in another male. In addition, every adult male aggressed against adult females carrying infants even though they avoided the same infants when they were near other males. Males with infants did appear to engage in potentially riskier interactions. Moreover, subordinate males initiated significantly more aggressive interactions and were less likely to retreat when carrying an infant than under other circumstances (Stein, 1984b).

Prediction 3

Males that are Recipients in Triadic Interactions Should Display Agonistic Behavior Toward Infants Within Other Contexts. Evidence: Males that are unlikely fathers can be extremely aggressive toward infants. Adult males at Gombe and Moremi were observed killing five infants and are believed to be responsible for the deaths of at least eight other infants (Collins *et al.*, 1984). Immigrant males were responsible for four of the five attacks. All attackers were males that had not been present in the group when the infants were conceived.

Prediction 4

Recently Immigrated Males or Other Improbable Fathers Are More Likely to Carry Infants During Triadic Interactions. Evidence: Popp (1978, p. 143) noted that kidnapping occurred against higher-ranking animals at a ratio of 17:1. Furthermore, he associated high rank with reproductive success and concluded that males that kidnap are not likely to be related to the kidnapped infants. Stein (1981, p. 103) reanalyzed Popp's (1978) findings for percentage of consort time, rate of copulation, and consortship and copulation success combined and found that the opponent exhibited greater mating success than the carrier in only slightly more than half of these measures.

Using Popp's (1978) data, Stein (1981, p. 104, 1984a, p. 63) reported that males carried the likely offspring of their opponents in only 37% (*N* = 23) of 62 bouts. In 42% (*N* − 26) of these cases, males used infants that were more likely to be their own offspring than the offspring of their opponents. Infants were carried against their probable fathers in only 3 cases, and infants were carried against impossible fathers in 19 cases. Stein (1981,

p. 106) also noted that the infant was the "best choice" (both the least likely offspring of the carrier and the most likely offspring of the opponent) in only 20 cases (32%), and the infant was the worst possible choice in 13 cases (21%).

Strum (1984, p. 154) noted that long-term resident males used infants more frequently than did short-term residents and newcomers. Moreover, short-term residents used infants more often than did newcomers but less frequently than did long-term residents. She also noted (1984, p. 162) that the opponent was a likely relative of the infant in only 4% of 107 successful cases of infant use.

Busse (1984) reported that, for 33 of 34 infant–carrier combinations in two groups of chacma baboons (*P. c. ursinus*), the carrier had been a member of the group when the infant was conceived and therefore could be considered a possible father. The carrier was not a potential father in only 1 of 112 triadic interactions.

Protection Hypothesis

Prediction 5

Triadic Interactions Should Occur When Infants Are in Close Proximity to, or Are Threatened by, Recently Immigrated Males. Evidence: Packer (1979a, p. 2) noted that both juvenile males and females were significantly ($p < .01$) more likely to exhibit ambivalence (simultaneous presenting, threatening, defecating, and vocalizing) and screaming toward newly immigrated, nonresident males than toward resident males. In response to these behaviors, resident males charged the newcomer males (Packer, 1980). Strum (1984) also showed that both long-term and short-term resident males used infants against newly immigrated males. Collins (1986) reported that 39% of 57 triadic male–infant interactions were directed against newcomer males.

Busse and Hamilton (1981) and Collins *et al.* (1984) documented three cases of infanticide in the Okavango Swamp population; all were committed by the immigrant, adult males. No males or infants were wounded during triadic interactions, however (Busse, 1984; Busse and Hamilton, 1981). On the other hand, Stein (1981) found that infants came running from a considerable distance to the site of a male–male agonistic encounter.

Prediction 6

Males Carrying Infants During Triadic Interactions Are Likely Fathers; Recipients Are Never Likely Fathers and Are Recent Immigrants. Evidence:

See the evidence under Prediction 6, particularly Busse (1984) and Busse and Hamilton (1981). Busse (1984) found that for 42 of 45 infant-recipient combinations in two groups, the recipient male was not in the group when the infant was conceived. In addition, Collins (1986) observed that 39% (N = 22) of 57 triadic exchanges were between residents (possible fathers) and newcomers (nonfathers). Klein (1983) provided data which suggested that probable fathers maintained closer proximity and engaged in significantly more affiliative behaviors with probable offspring than did nonfathers. On the other hand, Packer noted that the carrying male was a likely father in only about 40% of the observed cases of infant carrying (N = 161) where data were available on mating activity between the male and the infant's mother at the time of conception (Packer and Pusey, 1985).

Prediction 7

Infants that Are Frequently Protected Should Receive Fewer Injuries than Infants that Are Not Often Protected. Evidence: Stein (1981) found that infants were harassed much less frequently by other group members when they were near preferred males than when they were near other adult males. Furthermore, preferred males were significantly more likely than other males to punish individuals that harassed infants. However, Stein (1981, 1984a) also found no difference in the likelihood that mothers would leave their infants when preferred males were nearby than when nonpreferred males were at hand.

Cultivation Hypothesis

Prediction 8

Males Should Carry Infants Only Within Sight of Their Mothers or Other Adult Females in Order to Demonstrate Their Care-Taking, Protective Abilities, and Mothers Should Generally Be Cooperative in These Endeavors. Evidence: Smuts (1982) reported that a mother attempted to retrieve her infant from a carrying male in only 3 of 43 infant-carrying events. Moreover, Busse (1984) and Busse and Hamilton (1981) noted that a mother attempted to retrieve her infant in only 1 of 112 infant-carrying events. On the other hand, Stein (1981, 1984a) found that mothers exhibited distress in response to 43 attempts by males to engage infants in triadic interactions; the males were unsuccessful in all of these attempts. Mothers also exhibited distress in 2 of 61 infant-carrying episodes that occurred during male–male fights.

Prediction 9

Males Should Carry Infants that They Care for Within Other Contexts.
Evidence: Smuts (1982, p. 107) classified male–infant dyads into four mutually exclusive categories based on whether the male was a likely father, the putative sibling, and whether the male had a special relationship with the mother. The data (Smuts, 1982, p. 289) indicate that males having special relationships with mothers, regardless of their status as probable fathers, exhibited higher levels of affiliation with infants than did males that did not have special relationships with mothers. The existence of a special relationship between a male and a mother appears to be necessary and sufficient for the development of a male–infant affiliative relationship.

Strum (1984, p. 156) noted that "outside of the context of agonistic buffering males did not groom unaffiliated infants, and infants almost never groomed unaffiliated males." Moreover, males associated preferentially with infants that they both could and could not have sired. Relatedness did not seem to be a primary factor in influencing male choice in the baboons at Gilgil.

Packer (1980, p. 516) reported that infants which were exploited by males within agonistic contexts were also those infants cared for by males. Packer showed a significant ($p < .01$) Spearman rank–order correlation for males that (a) carried 2- to 8-month-old infants against other males and (b) groomed, supported, and spent time within 5 m of the infants.

Prediction 10

Females Should Exhibit Preferential Receptivity and/or Proceptivity Toward Males that Carry Infants. Evidence: Evidence exists that female choice may be important in nonhuman primates. Smuts (1982) noted that male baboons that have special relationships with noncycling females are more likely that nonpreferred males to mate with those females when they are cycling. Anderson (1983) suggested that adult female baboons follow particular males on the basis of prior sexual relationships or protective behavior. In female baboons, sexual receptivity (willingness to copulate) appears to decline on the presumed day of ovulation, but the frequency of male following (and, presumably, male interest) remains unchanged (Hausfater, 1975). This decline in receptivity may reflect an increase in female selectivity at a time when fertilization is most likely. Thus, females may be discriminating among males, and this differential responsiveness may have a significant effect on male copulatory success.

Smuts (1982) noted that special males were more likely than nonpreferred males to engage in affiliative interactions with infants. In addition, Smuts (1982, p. 101) observed 15 females and their special relationships

during pregnancy and lactation following their conception cycles and found that, for 6 of the females, the likely father was not a special male. However, Klein (1983) found that adult females acted more affiliatively toward males that were likely fathers than toward other males.

DISCUSSION

After reviewing the available evidence, it is apparent that some problems must be resolved in order to arrive at a general model for the evolution of triadic interactions. One problem arises from a lack of sufficient data. Although many studies have collected information relating to triadic interactions, no single study has presented data from the perspectives of all participants. Thus, it is difficult to weigh the significance of the potential benefits and costs to each participant.

It is clear from the preceding that proponents of each of the existing theoretical positions have assembled a different set of facts with which to support their individual points of view. These data differ not only in the habitat type and demographic composition of the study groups, but also in the behaviors which have been recorded during triadic interactions. Moreover, subspecific differences have not been considered. In addition, the behaviors of all participants in triadic interactions have not been examined systematically. Although adult males were the only focus of observation in most studies, adult males and infants were observed in one study (Stein, 1981, 1984a,b), while females were the primary focus in another study (Smuts, 1985). Few investigations have attempted to qualify maternal behavior during triadic interactions.

Another problem is the lack of information regarding paternity. Knowledge concerning the relatedness of participants and the reproductive success of participant males is critical when distinguishing these hypotheses or other alternatives. This information could be obtained by collecting serological data and conducting paternity-exclusion tests.

A third problem arises from the variability in triadic interactions observed both across and within studies. There are several possible explanations for this variability. First, observer bias may have influenced the interpretation of triadic interactions. Second, there may be more than one type of triadic interactions occurring (Collins, 1986; Packer, 1980; Smuts, 1985; Strum, 1984); in this case, lumping all interactions into one category would confuse interpretation. To test this possibility, behavioral sequences must be quantified, but only a few studies have attempted to do so (Packer, 1980; Smuts, 1985; Strum, 1984). Finally, if there is more than one type of triadic interaction, then the frequency of occurrence of triadic types may vary among

populations and subspecies of *Papio* in response to variations in genome, demography, and/or ecological setting.

Given these caveats, it is nevertheless possible to derive some general conclusions from the existing data. Evidence suggests that triadic interactions are not primarily exploitative in nature. Male–infant interactions do not occur solely within agonistic contexts. In addition, the evidence for reduction of aggression to the carrier male is equivocal. Moreover, nonrelated males are more often the recipients than the initiators of triadic interactions. Similarly, although the interaction of infants and immigrant males suggests that protection may play a role in some triadic episodes, not all episodes provide clear evidence of male protection. However, the most common denominator of triadic interactions is a close affiliative relationship of the carrier male, whether genetically related or not, with the infant and its mother. This common thread suggests that the cultivation and/or maintenance of special relations with females may be central to triadic interactions.

As noted above, an attempt to discredit all but one of the existing alternative hypotheses for triadic interactions would be a fruitless enterprise. The thousands of observation hours devoted to studying free-ranging baboons have demonstrated not only the complexity of these animals' behaviors, but also their ability to make refined, sophisticated, context-specific behavioral decisions. Clearly, adult male baboons engage in a refined set of strategizing behaviors with respect to interactions with mothers and infants, and these interactions range across the entire behavioral spectrum. An understanding of triadic interactions will depend upon our ability to chart this complexity with equally sophisticated and wide-ranging analyses.

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REFERENCES

Altmann, J. (1980). *Baboon Mothers and Infants*, Harvard University Press, Cambridge.
Anderson, C. M. (1983). Levels of social organization and male-female bonding in the genus *Papio. Am. J. phys. Anthrop.* 60: 15-22.

Berenstain, L., and Wade, T. D. (1983). Intrasexual selection and male mating strategies in baboons and macaques. *Int. J. Primatol.* 4: 201-235.

Box, H. O. (1975). A social developmental study of young monkeys (*Callithrix jacchus*) within a captive family group. *Primates* 16: 419-435.

Busse, C. D. (1984). Triadic interactions among male and infant chacma baboons. In Taub, D. M. (ed.), *Primate Paternalism,* Van Nostrand Reinhold, New York, pp. 186-212.

Busse, C. D., and Hamilton, W. J., III (1981). Infant carrying by male chacma baboons. *Science* 212: 1282-1283.

Collins, D. A. (1986). Interactions between adult male and infant yellow baboons (*Papio anubis cynocephalus*) in Tanzania. *Anim. Behav.* 34: 430-443.

Collins, D. A., Busse, C. D., and Goodall, J. (1984). Infanticide in two populations of savanna baboons. In Hausfater, G., and Hrdy, S. B. (eds.), *Infanticide: Comparative and Evolutionary Perspectives,* Aldine, New York, pp. 193-205.

Deag, J. M., and Crook, J. H. (1971). Social behaviour and "agonistic buffering" in the wild Barbary macaque *Macaca sylvana L. Folia primatol.* 15: 183-200.

Dixson, A. F., and Fleming, D. (1981). Parental behavior and infant development in owl monkeys (*Aotus trivirgatus grisiemembra*). *J. Zool.* (London) 194: 25-39.

Epple, G. (1975). The behavior of marmoset monkeys (Callithricidae). In Rosenblum, L. A. (ed.), *Primate Behavior: Developments in Field and Laboratory Research, Vol. 4,* Academic Press, New York, pp. 195-239.

Hausfater, G. (1975). Dominance and reproduction in baboons (*Papio cynocephalus*). *Contrib. Primatol.* 7: 1-150.

Hausfater, G., and Hrdy, S. B. (eds.). (1984). *Infanticide: Comparative and Evolutionary Perspectives,* Aldine, New York.

Hoage, R. J. (1978). Parental care in *Leontopithecus rosalia rosalia.* In Kleiman, D. (ed.), *The Biology and Conservation of the Callitrichidae,* Smithsonian Institution Press, Washington, D.C., pp. 293-306.

Hrdy, S. B. (1974). Male-male competition and infanticide among langurs (*Presbytis entellus*) of Abu, Rajastan. *Folia primatol.* 22: 19-58.

Hrdy, S. B. (1976). Care and exploitation of non-human primate infants by conspecifics other than the mother. In Rosenblatt, J. S., Hinde, R. A., Shaw, E., and Beer, C. (eds.), *Advances in the Study of Behavior, Vol. 6,* Academic Press, New York, pp. 101-158.

Hrdy, S. B. (1979). Infanticide among animals: A review, classification and examination of the reproductive strategies of females. *Ethol. Sociobiol.* 1: 13-40.

Ingram, J. C. (1978). Parent-infant interaction in the common marmoset (*Callithrix jacchus*). In Kleiman, D. (ed.), *The Biology and Conservation of the Callithrichidae,* Smithsonian Institution Press, Washington, D.C., pp. 281-292.

Kleiman, D. G., and Malcolm, J. R. (1981). The evolution of male parental investment in mammals. In Gubernick, D. J., Gubernick, P. H., and Klopfer, P. H. (eds.), *Parental Care in Mammals,* Plenum, New York, pp. 347-387.

Klein, H. (1983). *Parental Care and Kin Selection in Yellow Baboons,* Papio cynocephalus, Ph.D. dissertation, University of Washington, Seattle.

Kummer, H. (1967). Tripartite relations in hamadryas baboons. In Altmann, S. A. (ed.), *Social Communication Among Primates,* University of Chicago Press, Chicago, pp. 63-71.

Mitchell, G. D. (1969). Paternalistic behavior in primates. *Psychol. Bull.* 71: 399-417.

Mitchell, G. D. (1977). Parental behavior in primates. In Money, J., and Musaph, H. (eds.), *Handbook of Sexology,* Elsevier, Amsterdam, pp. 749-759.

Packer, C. (1979). Inter-troop transfer and inbreeding avoidance in *Papio anubis. Anim. Behav.* 27: 1-36.

Packer, C. (1980). Male care and exploitation of infants in *Papio anubis. Anim. Behav.* 28: 521-527.

Packer, C., and Pusey, A. (1985). Asymmetric contests in social mammals: Respect, manipulation and age-specific aspects. In Greenwood, P. J., Harvey, P. H., and Slatkin, M. (eds.), *Evolution: Essays in the Honour of John Maynard Smith,* Cambridge University Press, Cambridge, pp. 173-186.

Popp, J. L. (1978). *Male Baboons and Evolutionary Principles,* Ph.D. dissertation, Harvard University, Cambridge.

Ransom, T. W., and Ransom, B. S. (1971). Adult male-infant relations among baboons (*Papio anubis*). *Folia primatol.* 16: 179-195.

Redican, W. K. (1976). Adult male-infant interactions in nonhuman primates. In Lamb, M. E. (ed.), *The Role of the Father in Child Development*, John Wiley and Sons, New York, pp. 345-385.

Redican, W. K., and Taub, D. M. (1981). Adult male-infant interactions in nonhuman primates. In Lamb, M. E. (ed.), *The Role of the Father in Child Development*, 2nd ed., John Wiley and Sons, New York, pp. 203-258.

Smuts, B. B. (1985). *Sex and Friendship in Baboons*, Aldine, New York.

Spencer-Booth, Y. (1970). The relationship between mammalian young and conspecifics other than mother and peers: A review. In Lehrman, D. S., Hinde, R. A., and Shaw, E. (eds.), *Advances in the Study of Behavior, Vol. 3*, Academic Press, New York, pp. 119-194.

Stein, D. M. (1981). *The Nature and Function of Social Interactions Between Infant and Adult Male Yellow Baboons* (Papio cynocephalus). Ph.D. dissertation, University of Chicago, Chicago.

Stein, D. M. (1984a). *The Sociobiology of Infant and Adult Male Baboons*, Ablex, Norwood, N.J.

Stein, D. M. (1984b). Ontogeny of infant-adult male relationships during the first year of life for yellow baboons (*Papio cynocephalus*). In Taub, D. M. (ed.), *Primate Paternalism*, Van Nostrand Reinhold, New York, pp. 213-243.

Stoltz, L. P., and Saayman, G. S. (1970). Ecology and behaviour of baboons in the northern Transvaal. *Ann. Transvaal Museum* 26: 99-159.

Strum, S. C. (1984). Why males use infants. In Taub, D. M. (ed.) *Primate Paternalism*, Van Nostrand Reinhold, New York, pp. 146-185.

Strum, S. C. (1987). *Almost Human; A Journey into the World of Baboons*, Random House, New York.

Taub, D. M. (ed.) (1984). *Primate Paternalism*, Van Nostrand Reinhold, New York.

Trivers, R. L. (1972). Paternal investment and sexual selection. In Campbell, B. G. (ed.), *Sexual Selection and the Descent of Man*, Aldine, Chicago, pp. 136-179.

Vogt, J. L., Carlson, H., and Menzel, E. (1978). Social behavior of a marmoset (*Saguinus fuscicollis*) group, I: Parental care and infant development. *Primates* 19: 715-726.

Whitten, P. L. (1987). Infants and adult males. In Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W., and Struhsaker, T. T. (eds.), *Primate Societies*, University of Chicago Press, Chicago, pp. 343-357.