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MALE/INFANT INTERACTIONS IN THE CHIMPANZEE

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DIANA L. DAVIS

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ADULT MALE/INFANT INTERACTIONS IN THE CHIMPANZEE

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MALE/INFANT INTERACTIONS IN THE CHIMPANZEE

Abstract. Adult male/infant interactions were observed in captive chimpanzees, housed at the Chimpanzee Sign Language Laboratory in Norman, Oklahoma. The focal points of the study were maternal restrictiveness and its relationship to the quality and quantity of adult male/infant interactions. Video tape analysis was utilized and data were recorded over a four month period. In the initial episodes, maternal restrictiveness was found to be an important variable in the degree to which the male and infant interacted. This restrictiveness decreased with time and an intense social bond between the male and infant was formed.

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CHAPTER I

INTRODUCTION

Purpose, Rationale, and Significance of the Study

Paternal behavior, as an area of study, has until recently, received minimal attention. This is true for both human and nonhuman primates. Perhaps, the most significant reason for this paucity in research is the past and current emphasis placed upon the maternal figure as the principle care-giver, the important variables involved in the mother/child bond, and the subsequent effects of these variables on the offspring's development. However, the role of the adult male as a care-giver is currently receiving more and more attention, and it is likely that such research will attain comparable scientific significance to that of similar investigations of maternal behavior.

The purpose of the present study is to examine adult male/infant interactions in the chimpanzee (Pan troglodytes). As in the human literature, a great deal of attention has been given to the mother/infant bond in the chimpanzee, and very little attention has been given to the role of the adult male chimpanzee and its significance to the development of the infant. In fact, heretofore, it has never been the focal point of investigations in either feral or captive conditions.

The role of the adult male in ontogeny will be discussed from a comparative (cross-species) and evolutionary perspective. Although these two perspectives involve different levels of analysis [e.g. individual development (ontogeny) vs. history of the species (phylogeny)], they are

not mutually exclusive. That is, the purpose of cross-species comparisons is to identify similarities and differences, and a major assumption of these comparisons is that they aid in the understanding of evolutionary trends in behavior. This in essence is the basis for many primatological studies.

Chimpanzees and humans are frequently utilized in cross-species comparisons, and the rationale for this comparison in the present study is as follows:

1. Since chimpanzees are considered one of our closest living relatives (King and Wilson, 1975), knowledge concerning paternal roles of these animals should provide pertinent information as to the evolution of paternal behavior in the human species. Such questions can be addressed as: At what point in human evolution did the adult male become an important and stable member of the familial unit; what were the environmental contingencies that brought about the transition from a predominantly female/offspring familial unit to one that also included the adult male; and what selective advantages did the adult male accrue by forming social bonds with younger members of his social group?
2. The only valid generalizations are between species that are genetically similar (Eibel Eibesfeldt, 1975). By thoroughly investigating the adult male chimpanzee and his relationship to young members of the group, it will be possible to determine the feasibility of utilizing these animals as a model for paternal behavior in the human species. That is, to what

degree are patterns similar or different between species and across cultures? And to what degree can these patterns be attributed to similar environmental or genetic influences?

3. This type of research also has implications for the species preservation of the chimpanzee which is especially important when the chimpanzee's endangered existence is considered. There has been a dramatic reduction in importation of chimpanzees. Thus, proper rearing of these animals in captivity is crucial for successful breeding to occur. Primatologists must now rely upon currently existing primate centers within their respective countries for subjects (National Institute of Health, 1978). Thus, an important question to ask, is to what extent the presence or absence of an adult male will have on the normal social development of the immature chimpanzee in captivity. Should contact be minimal, maximal, or nonexistent? If in captivity, maximal contact is permitted (e.g. the male has free access to females and their dependent offspring), then infant survival may become an issue. For example, in feral conditions, males have been observed to engage in inter-group infanticide and cannibalism (Bygott, 1972; Suzuki, 1977; and Goodall, 1977), and to use the infants as display objects, flailing them in the air and throwing them against the ground. Perhaps, it is for these reasons that captive studies on male/infant interactions have not been conducted. Even if the male in captivity does not intentionally kill the infant, there may be a high risk of the infant suffering injuries during an adult male display.

In summary, the significance of this comparison focuses upon evolutionary implications, generalizability, and the precarious condition of the chimpanzee's existence, both in feral and captive environments.

Paternal Behavior: A Sociobiological Perspective

A growing interest has developed concerning paternal behavior in nonhuman primates as evidenced in general reviews by Raphael (1969), Mitchell (1969 & 1977), Mitchell and Brandt (1972), Spencer-Booth (1970), Redican (1976), and Blaffer-Hrdy (1976). As Redican (1976) noted, there are various ways in which the information can be organized. His approach was to present the information according to patterns in which primate groups are socially organized such as in one male/one female units, one male/multifemale units, and multimale/multifemales units. In contrast, Mitchell (1969) and Spencer-Booth (1970) chose to organize the information according to individual species. A third approach has been to organize by categorizing the types, degrees, and quality of the interactions between adult males and immature members (Mitchell & Brandt, 1972; and Raphael, 1969).

Regardless of the manner in which the information is organized, it is important to first determine exactly what is meant by paternal behavior in nonhuman primates. Defining paternal behavior in these animals is problematic since 'paternal' often implies that a male and immature members are genetically related; specifically, that the male contributed 1/2 of the immature member's genes. Given that many of the primates are promiscouous, it is rarely apparent which male sired

which infant. As Redican (1976) noted, both the terms 'father' and 'paternal' are unsuitable because of their genealogical connotations. For this reason, he chose to use the terms 'male care' or 'male parental care' as defined by Deag and Crook (1971) which refer to such behaviors as grooming, carriage, holding, and protection. These terms address specified behaviors of the adult male directed towards an infant in the context of care-giving, irrespective of genealogical relationship.

While such terms may be operationally descriptive, they are not explanatory in nature. That is, at the ontogenetic level of analysis, it is indeed possible and highly desirable to describe adult male/infant interactions, but ontogenetic description does not in itself provide an explanation at the phylogenetic level for these behaviors. Why would an adult male of a species, where paternity is unknown, have evolved care-giving capacity? What gains/advantages, if any, does he receive from this energy expenditure? Given uncertain paternity, what selective evolutionary advantage is there in such investments?

Answers to these questions are necessarily speculative, but recent attempts (e.g. Trivers, 1972) have been made to provide an explanation in terms of a cost-benefit analysis, where the term 'investment' plays a key role. The term 'parental investment', being closely affiliated with a sociobiological perspective, has received extensive attention, and it is to this term that many primatologists address themselves. 'Parental investment' as defined by Trivers (1972) includes "any investment by the parent in an individual offspring that increases the offspring's chance of surviving

at the cost of the parent's ability to invest in other offspring" (p. 139). Parental investment is both biological (production of gametes) and behavioral (nurturing of offspring). From this perspective, an individual is expected to invest in those members of its group with whom it shares common genes. That is, the greater the genealogical relationship, the greater is the expectation (prediction) of parental investment. This in essence, would guarantee that the individual's genes will be expressed in the subsequent generation when the offspring becomes reproductively active. This approach emphasizes the individual, the individual's genes, and the degree to which genes are shared. It therefore, offers an explanation of the evolutionary selection of kinship ties and bonds, and hence, the familial unit.

From this perspective, all related individuals need not produce offspring for the genealogical heritage to be passed on. For example, a sub-adult brother of a dominant male may not be himself reproductively active, but he may typically aid in his brother's defense of a territory which includes females of reproductive age and offspring. He therefore contributes to the survival of his brother's offspring. Although he is not the genetic father of the offspring, he nevertheless is thought to make a parental investment biologically (since he and his brother share common genes) and behaviorally (since he forms a coalition with his brother). Once the sub-adult male reaches adulthood, he may then become as sexually active as his brother, copulating with the same females. Both brothers as well as other related males are free to copulate with the same females, and neither they themselves nor their genes will be in competetion because of the shared genetic component.

Thus, even in the face of promiscuity, males can be guaranteed that shared genes will be passed on in subsequent generations. This is the gain or evolutionary advantage that an adult male receives by enhancing the survival of an infant.

The concept of shared genes between adult males therefore offers an explanation for adult male care-giving behavior (or investment) in the context of uncertain paternity. Any behavioral investment on the part of the adult male which enhances an infant's survival will not only be advantageous from an evolutionary perspective for that adult male, but also for those adult males with whom it shares a common genetic component. Likewise, it can be argued that this advantage exists for investment in all offspring produced by the adult male's mother (or even his sister) since all members of the matrifocal unit carry her genes. In summary, an adult male benefits genetically from his investment in immature group members as long as the contingency of a genealogical relationship is met.

In terms of the chimpanzee, it is believed that these genealogical relationships do exist within a group, and for this reason, some degree of care-giving behavior should be exhibited by the adult male. In subsequent sections in this paper, what is known about these behaviors in feral and captive chimpanzees will be examined and discussed.

Human Paternal Behavior

Since chimpanzees are believed to be one of our closest living relatives, it is important to provide a general overview of what is known about the human father, before addressing in detail

the adult male chimpanzee. Lamb (1976) has provided a detailed overview on the role of the human father and the following is a brief discussion of the salient points in his paper. In general, Lamb views the role of the father as extremely important in normal development and disagrees with the concept of monotropy (Ainsworth, 1962; and Bowlby, 1969). Monotropy, according to Lamb, operates under the assumption that the mother/infant relationship is unique and is much more important than any other relationship involving the infant.

He points out that a monotropic perspective developed from studies which emphasized the importance of time engaged in interacting. Obviously, with time as the focal variable, the importance of the father would seem insignificant to that of the mother. Lamb, as does the present author, stresses quality of interactions, noting that time spent together is not a good predictor of the quality of either the father/infant relationship or mother/infant relationship.

Another important point is that the human literature is fraught with methodological problems. For example, Lamb noted that many of the earlier studies examined the role of the father through interviews or reports by the mothers. This in essence provides nothing more than the mother's biases. In addition, many of the results are contradictory and at the very least, ambiguous. What is needed is some degree of commonality in methodology. Furthermore, very little causality can be inferred, since many of the studies report correlational statistics. Lamb stressed the need for more longitudinal studies and utilization of cross-lag correlational techniques (Cook & Campbell, 1975; and Kenny, 1975) from which causality can be inferred.

Some of the topics which have been investigated are infant attachment and preference, differences in parental roles during infancy, sex role development, moral development, and intellectual development. Research indicates that infants tend to have a maternal preference. However, Lamb has cautioned that this preference occurs specifically in stressful conditions (e.g. a novel environment such as the research laboratory), and in stressfree situations, this preference does not occur. In terms of parental roles during infancy, most studies indicate that care-taking is the focal characteristic of the mother/infant relationship, while for the father/infant relationship, it is play (Lamb, 1976a; Lamb, 1976b; and Lynn & Cross, 1974). Interestingly, Lamb noted that while it is realized that the female continues in this capacity, little is known about the changes which may occur in the father's role during the course of development.

The area of sex role development is fraught with contradiction. However, one of the most consistent findings is that warmth, nurturance, and extensive participation in childrearing are characteristics of fathers who have masculine sons and feminine daughters (Biller, 1976). This is regardless of the father's assessed masculinity or punitiveness. Research on moral development is also problematic due to its paucity and methodological problems. Nevertheless, there is indication that fathers do play a role which has a greater effect on males than females (Grief, 1976). Some important variables of moral development appear to be the children's perception of the father and the attitudes and behaviors of the father. For the father's role in intellectual development, there also appears to be a sex difference. Radin (1976)

noted that paternal nurturance was very closely affiliated with cognitive competence in boys, but not in girls. For girls this compentency seems to be associated with some degree of autonomy and distance from the father, although her intellectual development appears to be stimulated by the father's interest in her academic performance. Also, with an authoritiarian father, academic performance suffers for both males and females.

In conclusion, there is a tremendous need for future research on paternal behavior and on the role the father plays in development. As Lamb pointed out, before we can determine what the effects are, it is necessary to first determine unambiguously what are the roles. Sophisticated methodological techniques need to be utilized as well as some degree of commonality in methodology between studies. This would reduce the high incidence of contradictory results which in turn would provide a more lucid picture of the father's role.

Interactions between Adult Male and Infant Chimpanzees Under Feral Conditions

Chimpanzees typically form a multimale/multifemale group with offspring. This larger group consists of smaller temporary subgroups, where membership frequently changes. The membership of the main group therefore, is somewhat unstable (van Lawick-Goodall, 1968). This instability is related to the fact that migration occurs between social communities, with permanent migration believed to be exclusively associated with sub-adult females and sometimes females with their dependent offspring (Teleki, Hunt, and Pfifferling, 1976). Older males then, are not known to permanently change groups, which suggests that

at least some of these males are related (e.g. half-brothers) and form a kinship group which co-operatively patrolls and defends the group's home range (Pusey, 1979; and Nishida, 1979). Thus, it appears that the adult males never permanently leave their natal community and may typically maintain a close association with their mother. The matrifocal unit, irrespective of age of offspring, is therefore a strong focal point within the chimpanzee community. In fact, it is through this close association with the mother that adult males have the greatest opportunity to interact with an infant. Implicit in this association, is a familiarity index. That is, the more familiar a female is with an adult male (e.g., her older son), the more likely she is to be less restrictive with her infant.

The chimpanzee lives in African forest areas and is omnivorous with fruit and meat being important constituents of their diet. Thus, chimpanzees must forage in an environment where highly valued food items are scattered, and vary with seasonality. This dietary requirement affects the group's dispersion which in turn affects the opportunity for adult male/infant interactions. For example, a female with dependent offspring is frequently found alone for long hours (Goodall, 1977). As noted above, chimpanzees have an omnivorous diet, focusing on foods of highly nutritive value such as fruit, meat, and termites. While the former two food items may involve group feeding, the latter typically involves solitary feeding and requires individual skill. It is an activity generally associated with the matrifocal unit. Females with dependent offspring do not move about in the community to the extent that adult males do (van Lawick-Goodall, 1968; and

Wrangham, 1979), and therefore, the patrolling males have a greater opportunity for locating widely dispersed, rich food sources. In fact, when this activity, known as a 'carnival' (Reynolds and Reynolds, 1965) occurs, the males emit loud vocalizations and drumming which attract the other members of the group including the matrifocal units. Thus, an important role of the male is to locate food items that the female and offspring would not otherwise discover. During these group feeding encounters, the adult males and immatures would necessarily have the opportunity to interact. Males also locate food through their cooperative hunting endeavors, which they share with other group members. Thus, while the female and her dependent offspring may forage for food in the absence of the adult male, as in the case of termite fishing, they also forage in his presence during group feedings. This in turn, increases adult male/immature exposure and the opportunity for interaction.

This patrolling behavior on the part of the males not only locates rich food items, but it also serves to locate possible danger. However, it is not generally thought that the matrifocal unit is particularly dependent upon these adult males for protection. The adult female chimpanzee, due to her large size and her arboreal propensity, does not require the constant presence of the adult male as a defense mechanism against predation. As such, it is the adult female's responsibility to provide direct protection against predation for dependent offspring.

As in the case of all the pongids, females appear to be most restrictive with their infants during the period after birth, when

the infant lacks coordinated motor skills and is particularly vulnerable to danger. During the first several months of an infant's life, the female chimpanzee inhibits almost all of its contact with other group members (van Lawick-Goodall, 1968). However, in those cases where adult males are in proximity to the infant, there is interest taken in the infant on the part of the male. For example, during the infant's first six months of life, van Lawick-Goodall (1968) has noted that adult males may reach out to the infant, touching it on its head or face.

During the second half of the first year, when continuous mother/infant contact has broken, these males have greater opportunity to interact with infants. During this period, irrespective of which individual approaches, the adult male may greet the infant by reaching out to touch or pat the infant, usually on the back, under its chin, or on the white tail tuft (a distinguishing mark of older infants). Adult males also exhibit a degree of tolerance when the infant interferes with his activities. For example, even if the adult male appears to be ignoring an approaching infant, the infants will frequently jump onto their laps. Infants, who climb around the male's body during grooming bouts or during copulation, are gently pushed away by the male, as they are when they reach out for food that the male is eating.

Comfort and protection are also directed toward the infant. When adult males aggress toward females, the infants are sometimes accidentally involved. In such cases, an infant, sitting near its mother, may be left alone screaming while its mother attempts to flee

from the aggressing male. When this occurs, nearby adult males have been known to pick up the infant, embrace, it, and offer comfort until it is reunited with its mother. In one case, the contact lasted for ten minutes in which the male carried the infant ventrally, followed its ascent into a tree, and threatened or chased off others as they approached. van Lawick-Goodall (1968) and Nissen (1931) have also noted that males are protective of infants when observers approach too closely. In another incident, a still uncoordinated infant, in an attempt to climb, was assisted by a nearby adult male, who had been watching the infant.

It is during the latter part of the second year that adult males appear to become less tolerant of the infant's activities. While during the first half of the second year, adult males exhibit tolerance as the infants climb around the male's body, this tolerance wanes toward the end of the latter half, as indicated by the fact that males push the infants away more roughly when the latter interfere with feeding or copulation. It is during this time that an infant appears to learn when to approach or avoid an adult male. In one case, for example, an infant failed to recognize signs of potential excitement displayed by a male (e.g. rocking and pilo-erection), and upon the infant's approach, he was attacked by the male, being dragged and flung into the air as the charging display began. Subsequently, during the same day, the infant was observed to exhibit the first signs of avoidance when the same male approached. Although the infant at times continued to ignore signals of an ensuing charging display, by the end of the second year, it clearly had learned the significance of these

signals. Perhaps, it is not coincidental that the infant's aggressive displays increase during the second year of life. Another type of behavior that adult males sometimes direct toward infants of this age is mounting in which thrusting movements are made against the infant's back in the context of play or sometimes during greeting. Likewise, infantile sexual patterns such as mounting and thrusting are observed during this period.

While play interactions between the males and infants during the second year increase, they begin to wane during the third year. During the earlier part of the third year, infants are still approached and embraced by mature males, and are allowed to climb into their laps; by the end of this year, the interactions consist mainly of grooming, greeting, aggressive-submissive enocunters, and sometimes play. Although males still tolerate and protect infants during the third year, they direct threatenting gestures toward them more frequently. Coincidentally, as early as the third year, but more typically during the fourth year, infants begin to emit a submissive behavior, bobbing, which is directed at the adult male. After the fourth year, the weaning process begins and even though the social bond between the mother and the offspring continues to be strong, the juvenile chimpanzee is less under her protection and therefore is left with its own devices for coping with the environment and interacting with other group members. Nevertheless, these juveniles or adolescents may seek out their mother's protection when threatened by an adult male by running to her side. If the female is high-ranking, she may threaten or chase the aggressor; or if she is low-ranking, she may approach the male and emit an appeasement

gesture.

It therefore seems that even though the adult male chimpanzee is capable of positively interacting with younger chimpanzees, there is considerable danger in being near an adult male who is socially excited. Adult males as well as adult females have been known to engage in infanticide and cannibalism (Suzuki, 1971; Bygott, 1972; and Goodall, 1977). Rather than implying intentional infanticide on the part of the adult males, Goodall suggested that these cases are better explained in terms of inter-group aggression directed at the infant's mother, rather than at the infant itself. In fact, in one case, she reported that an infant, still alive but severely wounded, was carried and groomed by several males after it had been seized from its mother, who had escaped, although badly wounded herself. One of these males had actually participated in the attack. Also, it is important to note that intra-group infanticide involves attack by adult females and that adult males are known to defend new mothers from these attacks. Goodall has postulated that females, immediately after parturition, travel with the males in order to avoid attacks by other females within the group.

Taking the foraging strategies and predatory defense mechanisms into consideration, the female chimpanzee has considerable responsibilities as a mother. In terms of food procurement, she with her dependent offspring, must employ individual skill in extracting highly valued food items such as termites from the environment. In addition, during group feedings, it is her responsibility to oversee and regulate the activity of her dependent offspring with other group members. Thus,

given that she must provide protection against inter-group and intra-group aggression, it is not surprising that during the early months of the infant's life, she is restrictive. Nevertheless, an immature chimpanzee does have early contact with other group members, and it is suggested that this opportunity for early contact, especially with adult males, is a function of the foraging strategies employed and that the degree to which these interactions occur is a function of the female's familiarity with her older mature offspring. An adult female with a small infant is familiar with her older adult son and as a result, exercises some control over his interactions with the infant. Thus, while she may be permissive at times in allowing contact between her older son and the infant, she is relatively assured that she will have little difficulty in inhibiting the interactions or retrieving the infant when appropriate.

As noted previously, females with infants typically spend a great deal of time separated from the other group members and that continuous female/infant contact is not broken until the infant is 4-6 months old (van Lawick-Goodall, 1968). As a result, an adult male chimpanzee does not typically have direct access to an infant. Thus, early direct interactions between adult males and infants are restricted to those in which the infant is in contact with the female; direct contact, in the early days, may simply involve touching, tickling, or grooming the infant while on its mother's body. In contrast, after continuous mother/infant contact is broken, the male may have the opportunity to be in possession of the infant. It is therefore important to consider the degree to which a female restricts adult male/infant interactions

by restricting his and/or the infant's behavior or by simply avoiding the male. This topic will be specifically addressed in a subsequent section of the paper.

Interactions between Adult Male and Infant Chimpanzees in Captivity

As noted earlier, the role of the adult male chimpanzee in infant development has received minimal attention. Although it has never been the focal point of an investigation, adult male/infant interactions have been examined as part of a study involving the social behavior of captive chimpanzees (King, Stevens, and Mellen, 1980). In general, it was found that the social behavior of a captive group of chimpanzees, comprised of one adult male and three mother/infant pairs, was similar to that of feral chimpanzees. It is important to note that unlike other captive conditions, an adult male was housed with the mother/infant pairs, and that the group had lived together for many years.

Of particular interest to the present paper is the behavior of the adult male in the above study and his interactions with the other group members. Over half of the adult male/female interactions occurred with one particular female, who had a male infant. This male infant interacted as frequently with the adult male as he did with the infant females. Over half of the male infant/adult male interactions were initiated by the mature male, who interacted with the infant male over eight times as frequently as with the infant females combined. King, et.al. suggested that one possible explanation for the adult male's preference for the infant male was his preference

for the infant's mother as a prosocial partner. That is, their familiarity may have contributed to the quality and quantity of adult male/infant interactions. Another contributing factor may have involved the propensity for males to form strong social bonds with each other and as van Lawick-Goodall (1968) noted, in feral conditions the adult males show a preference for infant males.

In terms of play, the male infant's mother was the only other adult with whom the adult male interacted, again indicating a preference. The adult male's play activities with the infants were similar to those observed in feral adult males. He frequently initiated and his actions were of a gentle nature. In terms of food sharing, it was found that the infant male was the only member of the group to regularly beg from the adult male, who often shared his food with the infant. In one incident, the mature male actually held the infant up and spit milk into his mouth several times. This preference for the infant male was also demonstrated when he allowed the infant to take food from his pile, and even from his hands or mouth. Further demonstration of this preference involved his defense of the infant male. If the infant was threatened by an adult female, the male would aggress toward her, return to the infant, pick him up, carry him to a pile of food, and place fruit in the infant's mouth.

As in feral conditions, the adult male exhibited tolerance toward all infants when they interfered during copulation. The infant male typically would stomp on his mother's back and hit the adult male in the face. The infant females would stand on either side of the adult male, hitting him or pulling on his arms.

In summary, it appears that the social behavior of this captive group is quite similar to that of feral groups. This includes the social interactions between the adult male and infants. It was concluded that the social environment imposed by the particular captive situation appears to play a more significant role in the maintenance of normal behavior than does the actual physical restrictions of the enclosure. For the purpose of the present study, it is most significant that an adult male was present and that the adult females were familiar with him. It is likely that the normal behavior of the group was, in part, a function of his presence and that the freedom with which he interacted with the infants was, in part, a function of the above familiarity. Furthermore, it is not unreasonable to assume that his presence played a role in the normal social development of the infants, including both male and females.

The Assessment and Significance of Interactions

While the above discussion addresses the importance of interactions involving direct contact, it should also be recognized that other types of interactions take place and may be as equally important. Specifically, it is suggested that visual attentiveness between the male and infant is necessarily an important variable that merits investigation and as a result, direct contact should not be considered the sole indicator of the interactants' awareness of each other and interest in each other. For example, it is not unreasonable to assume that some aspects of an infant's social development are

acquired through observation and imitation of an adult male, precluding a necessity for frequent direct contact. This may be particularly true for male infants, who at some later date will attempt to integrate into the all male group. It is also suggested that in conjunction with visual attentiveness, other non-contact behaviors directed by the male and infant toward each other and which may occur prior to, during, or after a glance or stare should also be considered. These would include for example, reaching toward, displaying at, and avoidance of each other. By including visual attentiveness and other non-contact behaviors along with contact behaviors as functional parts of the adult male/infant relationship, the adult male begins to emerge as a much more significant figure in an infant's development and hence its integration into the group's social structure. While it is readily admitted that the documentation of non-contact behaviors are problematic (e.g. which individual in a group is the actual recipient of such behavior), it is suggested that they nevertheless should be considered in the assessment of the male's role.

In those situations in which obvious (e.g. contact interactions) male/immature interactions are extremely rare, as in the case of the orang-utan, it is possible that less obvious interactions are occurring where touching or approaching may not be involved. Important subtle social signals may be exchanged and go unnoticed to the observer. It is also important to consider if the mere presence of an adult male has an effect on an immature individual. As Lindburg (1971) has suggested, even in the absence of an interaction, the adult male rhesus may be the cynosure of the infants' attention, where for example, a group of

infants may sit close to an adult male without interacting with him. Does the male's presence and interaction with other group members contribute to the development of social skills through imitation and observational learning?

One of the underlying contentions of this paper is that absence or rarity of any overt behavior on the part of the adult male, directed at an immature, is not necessarily indicative of negligible male input in the immature's development. This of course, is subject to controversy. For example, Horr (1977) has noted that in the orang-utan, the male lives a solitary existence and has minimal contact with immatures, and therefore, his influence on offspring development was suggested to be minimal and certainly questionable. However, the seemingly absence of adult male/immature interactions should not necessarily be taken as evidence for negligible input. It is questionable to assume that quantity is in any way indicative of quality concerning parental behavior; minimal contact, irrespective of its observable intensity, may necessarily have tremendous social significance. It is argued then that absence or rarity of contact interactions does not necessarily imply negligible or minimal input. It is also argued that aggressive encounters, which in some cases are thought to predominate, do not necessarily reflect that an adult male lacks the capacity for care-giving behavior and that these aggressive encounters, may themselves, facilitate the normal integration of an immature into the group. This may be particularly true in the adolescent male chimpanzee. In his persistent attempts to integrate into the adult male group, he is often the recipient of aggression and comfort by the

adult males. Nishida (1979) has referred to this phenomenon as 'ambivalent psychology'.

The above discussion has focused upon male/infant interactions of chimpanzees in feral and captive conditions. Although not systematically doucmented, some degree of care-giving behavior is exhibited by the adult male. Thus, from a sociobiological perspective, the adult male does make an investment, and it is very likely that his investment occurs under the contingency of a genealogical relationship. Behavioral investment may be direct, involving contact and non-contact interactions; or it may be indirect, where the mere presence of the male allows for imitation and observational learning on the part of the infants. Whether direct or indirect, this investment enhances the survival of the infant. From the infant's perspective, the adult male provides enrichment in its social milieu and is an important focal point for the infant's integration into the social group. And although this integration occurs predominantly under the auspices of the mother, it nevertheless is subject to the influence of the adult male. The male may have less opportunity to come into direct contact with immatures than does the female, but this does not necessarily dictate that his influence and role in social development is any less significant. To be redundant, quantity is not indicative of quality or significance.

Female Restrictiveness in Nonhuman Primates

Given that the chimpanzee mother is restrictive, referring to the degree to which she allows her offspring to interact with other

group members, she can be viewed as a monitor of adult male/infant interactions. Maternal restrictiveness has been examined in other nonhuman primates. Redican (1976) has noted that maternal restrictiveness is somewhat negatively correlated with high incidences of adult male/infant interactions in some nonhuman primates. For example, viewed along a continuum, rhesus and pigtail macaques are thought to be very restrictive mothers in that there is minimal contact between infants and other adult members of the group, while the bonnet and barbary macaque females exemplify the opposite end of the continuum (i.e., the infants are relatively free to interact with any member of the group). For the species in which the females are relatively restrictive, there will be little opportunity for the adult males to interact with infants. In contrast, for those species in which the female exhibits relatively minimal restrictiveness, the adult males will have greater opportunity for interaction. Kaufman (1963) has demonstrated the polarity in types of maternal care between the bonnet and pigtail macaques and its effect on infants when their mothers are removed from the group. Although the pigtail infant does seek contact comfort from other females when the mother is absent, it receives little regard and may even be harassed. As a result, the infant subsequently exhibits a depressive reaction. In contrast, the bonnet infant receives the attention it seeks and therefore, does not experience depression. In one case, a bonnet infant was even 'adopted' by an adult male.

In the species where female restrictiveness is extreme, male/infant interaction is expected to be minimal or nonexistent. For the

rhesus, this is particularly evident in free-ranging groups, where adult male infant interactions are rare, and those that do occur, may even be aggressive (Lindburg, 1971; Southwick, Beg, and Siddiqi, 1965). As Kaufmann (1966) noted, there are few interactions; the males never approaching an infant. If an infant was seen to approach an adult male, he usually would withdraw or direct aggressive behaviors toward the infant such as threats or slaps. In contrast, the barbary macaque exhibits a high degree of interaction with infants. For example, in a free-ranging group of barbary macaques, Deag and Crook (1971) found that adult males held, groomed, carried, and protected infants. Similar male/infant interactions have also been noted in captive barbary macaques, where a dominant male and infant formed a strong social bond from the infant's first day of life (Lahiri and Southwick, 1966).

If female restrictiveness is an important variable in determining the degree of adult male/infant interactions, then it would follow that in the absence of the mother, adult male/infant interactions would be expected to increase. Using the two extremes, the pigtail and rhesus macaques, there is some evidence, especially in the rhesus, for this prediction. Kaufman and Rosenblum (1969) did not observe any contact interactions between adult males and infants when the pigtail mothers were removed from the group, but they did observe that the adult male threatened animals aggressing toward the infant and positioned himself between the infant and the aggressor. Although this is rather inconclusive evidence, there is significant evidence that the adult male rhesus, given the opportunity, will exhibit care-giving behavior toward the infant. This is true, when adult male/infant dyads

are formed (Redican and Mitchell, 1973a & 1973b; Mitchell, Redican, and Gomber, 1974; Gomber and Mitchell, 1974; and Redican, 1975). In general, it was concluded that the adult male rhesus can adequately raise an infant when paired alone with one in a cage. Of particular interest, is that when separated after six months of continuous contact, both members of the dyad showed extreme agitated distress, resulting in self-inflicted wounds on the part of one adult male (Mitchell, Redican, and Gomber, 1974). Reunion of this dyad was similar to that of mother/infant dyads. The pair immediately embraced and clung to each other. It therefore, appears that in the absence of a restrictive mother, the opportunity for interaction occurs, allowing a strong social bond to form between an adult male and infant rhesus.

Other evidence indicates that the adult male rhesus in captivity will exhibit care-giving behavior toward an infant if the opportunity arises. Females, who were subjected to bilateral lobectomies of the temporal neocortex, exhibited a reduction in maternal care and as a result, the domiant male of the group assumed the role of care-giver (Bucher, 1970). Two similar incidences have occurred in a free-ranging group of rhesus (Taylor, Teas, Richie, and Southwick, 1978). Although adult male/infant interactions were rare, two adoptions occurred in which a dominant male in two subsequent years was seen in possession of young infants, whose mothers were assumed to be dead. Both infants died soon after the adoption, probably due to starvation; the male made no attempt to feed the infants. However, his behavior was described generally to be like that of an inexperienced mother. That is, he was

extremely restrictive, tended to isolate himself from the group, and engaged in less aggressive interactions with other members.

From the above studies, it appears that even though an adult male rhesus is reputed to be merely tolerant or even aggressive toward infants, to the extent of engaging in infanticide (Carpenter, in Collias & Southwick, 1952; Mitchell and Brandt, 1972), there is strong evidence that in the absence of a restrictive female, he will emit strong affinitive and care-giving behaviors toward an infant.

There is some evidence for this phenomenom in the apes. Both the siamang and gibbon mothers are less restrictive mothers. That is, the adult male gibbon or siamang has the opportunity to interact with offspring. For example, adult male feral gibbons have been observed to inspect and groom neonates while in captivity a small juvenile was carried by an adult male throughout the day (Carpenter, 1940). Also, with increasing independence, an immature interacts more frequently with the adult male (Berkson, 1966). Chivers (1971 &1972) found that after 12 to 16 months of age and up until the third year, when independence occurs, siamang infants are carried by the adult male, who also grooms and sleeps with juveniles. In captivity, an adult male, while feeding, even allowed a juvenile to take a preferred food item out of his hand (Fox, 1974). This same male was also found to be, in general, the most frequent recipient of grooming by the immature siamangs within the group (Fox, 1974).

Like the chimpanzee, female gorillas are also initially very restrictive. However, Fossey (cited in Redican, 1976) reported a case where a silver-back adult male, when given the opportunity, exhibited

care-giving behavior through adoption and rearing of a three year old infant female whose mother had died. This infant had attemtped to construct nests adjacent to that of the male's. After several nights, the male took the infant into his nest, and thereafter, a close bond between the two emerged. The infant constantly travelled behind him, although he never carried her, and he remained in constant contact with the infant during the group's resting period. As in the case of the rhesus adoption noted earlier, this male behaved like an inexperienced mother; he groomed the infant more frequently than would an experienced gorilla mother, and his protection of the infant was to such an extent that he did not allow other group members to play with it.

In a study on captive gorillas, the concept of maternal restrictiveness in relationship to male/infant interactions was specifically addressed (Tilford and Nadler, 1978). It was found that the strength of the affiliation bond between the adult male and females was a better predictor of adult male/infant interactions than was infant assessibility (proximal to the male and distal to its mother). As a result, maternal protectiveness, which affects infant accessibility, was concluded not to be an important determinant in the frequency of adult male/infant interactions; the male interacted or attempted to interact with the infants, irrespective of maternal restrictiveness.

From the above discussion, it is obvious that the concept of maternal restrictiveness should be included in an investigation male/infant interactions in the chimpanzee. The purpose of the present study is to examine adult male-infant interactions in captive chimpanzees, where

the mother, infant, and male will be periodically grouped in the same cage. In doing so, it will be possible to determine the degree to which female restrictiveness affects the quantity of male/infant interactions and the extent to which this restrictiveness will change over time. Also, this study is designed to identify the degree to which a male is interested in an infant (i.e., interacts or attempts to interact with the infant) and vice-versa. Thus, three main areas will be focused upon: 1) the female's restrictive behavior directed toward both the male and the infant, 2) the male's interest in the infant, and 3) the infant's interest in the male. All three foci are postulated to affect the quality and quantity of adult male/infant interactions and are expected to change over time. This change over time is directly related to the fact that as the infant matures, it begins to explore aspects of its environment other than its mother. Although females initially restrict this exploratory behavior, eventually, they become more permissive but, nevertheless, maintain a close watch over the infant's activities. This exploratory behavior is coupled with increased social interactions, and in this study, the only other individual that the infant can interact with is the adult male.

CHAPTER II

RESULTS

Method

Subjects.

Initially, the study was planned to involve three subjects: the biological mother (Washoe), the biological father (Ally), and the infant, and to begin immediately after parturition. However, due to complications with the natal pair, the male was housed in an adjacent cage rather than in the same cage with the mother and infant. Unfortunately, the infant died two months later, and the original study was terminated.

Fifteen days after the infant's death, a 10 1/2 month old male infant (Loulis) was introduced to Washoe for the purpose of adoption. The infant, therefore had been with its biological mother during its first 10 1/2 months and was then housed with the above female. The adult male, from the onset of Loulis' arrival, was housed in the adjacent cage and was allowed access to Washoe and Loulis' cage only during the data collection process. This housing arrangement did not preclude male/infant interactions through the cage.

The cages were centered in a large room and each cage was 8 1/2' X 7 1/2' X 7 1/2'. Adjacent cages were divided by a sliding door which was secured and locked, except during the actual study. The cage material consisted of expanded metal; the subjects therefore, had visual access to each other, but actual physical contact was

limited to touching or poking with the fingers, when the sliding door was closed.

Loulis was received on loan from Yerkes Regional Primate Center, where he had been housed with his mother and two other mother/infant pairs. During that time he had neither visual or physical access to an adult male chimpanzee. His first exposure to a male occurred upon his arrival in Norman, Oklahoma.

At the beginning of the study, the adult male was 10 years old, and the adult female, approximately 14. Both subjects were home-reared, the male for four years and the female for 5 1/2 years. During that time, both subjects had extensive exposure to the American Sign Language of the Deaf (Gardner & Gardner, 1971 &1975; Fouts, 1976; and Fouts, Chown, Kimball, & Couch, 1976). This exposure continued after their arrival in Norman, Oklahoma.

Both Ally and Washoe have been housed previously with various social groups, either together or separately. They have also been housed alone as a pair. As a result, they have had extensive social interactions with other chimpanzees and with each other. The female at the time of the study was still clearly dominant to Ally, although there was some indication during the course of the study that the dominance relationship was under transition.

Both adults had previous exposure to infants; they had been housed adjacent to a mother/infant group. Washoe, in addition, had had direct access to infants; her first infant died several hours after birth, and her second infant died two months after birth. While the second infant was alive, Ally on several occassions, had direct

access to the mother/infant pair, but this access was limited and carefully monitored by experimenters.

Data Collection.

Data collection for the triadic interactions began approximately 6 months after Loulis' arrival in Norman and continued for the following 4 months. Loulis, at the beginning of the study, was 1;4 years, and at the end, 1;8 years. In total, there were 9 episodes in which the male was allowed to enter Washoe and Loulis' cage. Each of these episodes were filmed and subsequently analyzed for the following variables:

1. Maintenance of proximity between adults (which adult withdrew and which adult approached the other).
2. Adult male/female interactions. This would include grooming, playing, touching, holding hands, for example.
3. Adult male/infant interactions. This would include playing, grooming, holding, etc. Initiations and terminations were recorded and defined as follows:

   Initiations. Any groos behavior emitted by the male or infant which clearly could be observed as being directed at a recipient. Such behaviors included, for example, approach, move toward, lean toward, reach toward, touch, etc. (see Appendix A). It should be pointed out that any of the above initiations could progress into the above interactions if not immediately terminated.

the chimpanzee, as subjects of investigations, may provide a clearer understanding of the role of the adult human male as a father or care-

Terminations. Any gross behavior emitted by the male, female, and/or the infant which clearly could be observed as being directed at a recipient and which resulted in a cessation of an interaction. Four separate categories were listed and based upon which subject acted as terminator:

Female. In this case, the female was the sole participant in the termination which could be directed at the male and/or the infant.

Infant. The infant was the sole participant in the termination which could be directed at the male and/or utilization of the female as a buffer (e.g. move toward and sit behind the female).

Female and Infant. In these terminations both infant and female participated. Any combination of the two immediately preceding categories could be involved (e.g. the female blocks the male with her arm, the infant moves away from the male and toward the female).

Male. In this case, the male was the sole participant in the termination. Typically, such terminations involved moving away or withdrawing.

In addition to the above terminations, which clearly had a recipient, terminations also occurred when the initiator terminated its own actions. For example, the infant would move toward the male and immediately move away, or the male would reach toward the infant and immediately retract his hand.

In some situations, a gross behavior was repeated consecutively

(e.g. touching, patting, etc). If in some manner during the course of these repeated behaviors, an attempt was made to terminate, the interaction was considered completed. The continuation of the behavior was then considered an initiation of a new interaction. If the intermediate attempt to terminate did not occur, then the whole series of repeated behaviors was considered to be part of one interaction. Thus, for clarity, an interaction was demarcated as an initiation and any termination or attempt to terminate.

4. Success or failure of male/infant initiations. Success for male initiations was defined as achieving actual contact with the infant. A touch or pat, for example, was considered a successful initiation. In contrast, simply reaching toward without subsequent contact was considered unsuccessful, regardless of who terminated it. Success for infant initiations was defined as any behavior directed toward the male, which was not terminated by either adult. Actual contact with the adult male was not necessary, as in the case for adult male initiations. This differentiation between male and infant success was established due to the fact that the infant's initiations in the earlier episodes primarily involved the gaining of proximity, such as moving or leaning toward the male, without necessarily attempting contact. In contrast, the adult male's initiations, throughout the study, usually involved an attempt to achieve contact. Thus, one was considered

an infant strategy, and the other was considered an adult strategy.

Analysis.

The data were recorded as frequencies for each episode and reported as proportions (percentages) and plotted over time. The following variables were examined:

1. Maintenance of adult male/female proximity. This variable was examined in order to determine which adult was principally responsible for maintaining their spatial relationship. This was particularly important since the infant in the earlier eipsodes was in constant proximity to the female. The following categories were reported:
   Male approached and male withdrew
   Male approached and female withdrew
   Female approached and female withdrew
   Female approached and male withdrew
2. Proportion of adult withdrawals preceded by adult male/infant interactions. This variable was examined to determine to what extent the female used withdrawal as a strategy for making the infant inaccessible to the male. Note that the infant withdrew with the female. It also provided a means for determining the extent to which the male's withdrawals from the female were related to prior terminations of interactions with the infant. The categories for this variable were:
   Male withdrawals preceded by male/infant interactions

Male withdrawals not preceded my male/infant interactions

Female withdrawals not preceded by male/infant interactions

Female withdrawals preceded by male/infant interactions

3. For male withdrawals preceded by male/infant interactions, which subject acted as terminator. This variable was examined to determine if any one terminator was more effective in causing the male to withdraw from the vicinity of the female (and the infant). For example, was the male more likely to withdraw when the infant terminated the interaction, or when the female terminated the interaction. The categories for this variable were:

   Termination by female only

   Termination by infant only

   Termination by female and infant

   Termination by male only

4. Porportions of successful or unsuccessful adult male initiations of male/infant interactions relative to prior adult male/female interactions. This variable was examined to determine whether or not the male, in an attempt to reduce female restrictiveness, used the strategy of first interacting with the female before attempting to interact with the infant, and if the attempt resulted in contact (successful) or not (failure). The categories for this variable were:

   No prior male/female interaction and male initiation was successful

   Prior male/female interaction and male initiation was successful

   No prior male/female interaction and male initiation was unsuccessful

Prior male/female interaction and male initiation was unsuccessful

5. Proportion of adult male and infant initiations. This variable was examined to determine if either the male or infant was more frequently the initiator of their interactions.
6. Terminator of male/infant interactions initiated by the male. This variable was examined to determine which subject most frequently terminated the adult male initiations. The categories were:

   Termination by female only

   Termination by infant only

   Termination by female and infant

   Termination by male only
7. Terminator of male/infant interactions initiated by the infant. This variable was examined to determine which subject most frequently terminated the infant initiations. The categories were:

   Termination by female only

   Termination by infant only

   Termination by female and infant

   Termination by male only

As noted above, the data were reported as percentages and plotted over time. Inter-observer reliability measures on the occurrences of behaviors were obtained by randomly selecting ten second intervals from each video tape and utilizing Pearson's r correlation coefficient.

CHAPTER III

RESULTS

Quantitative

Inter-observer reliability was found to be r=.94. Each variable noted above has been listed below and will be discussed separately. It should be pointed out that emphasis will be placed upon a comparison between the earlier and later stages of the study. The reason for such emphasis was the tendency for reversal in certain variables.

Maintenance of adult male-female proximity. Figure 1 and Table 1 indicate that overall the male was principally responsible for the maintenance of proximity. For example, in all but three of the episodes the male both approached and withdrew from the female over 60%

Insert Figure 1 and Table 1 About Here

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of the time. And for two of the three exceptions noted above, the largest percentage occurred when the male approached and the female withdrew. In contrast, for example, the female rarely both approached and withdrew from the male. This category was 0% in all but one episode where it was only 17%. Given that the infant was usually in contact with the female (or at least sitting beside her) until the latter episodes, the male in order to gain access to the infant, had to approach the female. Given that the infant typically followed the female's movement until the

latter episodes, the female's failure to approach the male could be taken as restrictive behavior on her part. That is, she did not typically make the infant accessible to the male, but it was the male who actively attempted to overcome the restrictiveness by approaching her.

Proportion of adult withdrawals from the triad preceded by adult male-infant interactions. Of the female's withdrawals (Figure 2 and Table 2), there does not appear to be much difference between those that

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Insert Figure 2 and Table 2 About Here

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involved a prior adult male-infant interaction and those that did not. Thus, the female did not typically utilize withdrawal as a strategy for inhibiting or terminating interactions between the male and the infant. In constrast, it appears that a high incidence of the male's withdrawals were associated with prior male-infant interactions, particularly in the earlier and latter episodes of the study. It therefore appears that upon termination of a male-infant interaction, the male typically increased the distance not only between himself and the infant but also between himself and the female. This strategy may serve to reduce the probability of an aggressive encounter, or in the later episodes, the boredom of becoming a babysitter.

For male withdrawals preceded by male-infant interactions, which subject acted as terminator. Figure 3 and Table 3 indicate that the male rarely terminated interactions with the infant priot to his own withdrawals from the female and infant; in only one episode was this

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Insert Figure 3 and Table 3 About Here

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percentage above zero (23.8%). The terminations therefore involved the Female and/or the infant. Of particular interest is a comparison of the female as sole terminator and infant as sole terminator. A dramatic reversal occurs from the onset of the study to its completion. In the initial stages, the female was principle terminator of these interactions with the infant having minimal input. However, as the study progressed her participation in the terminations decreased dramatically. For example, in the last four episodes, the female acted as sole terminator at or near 0% of the time. In these episodes, the infant became the principle terminator of male-infant interactions which were followed by male withdrawals. In summary, when the male withdrew, he rarely terminated interactions with the infant, while the female in the earlier episodes was responsible for most terminations. The infant in the latter episodes was responsible for most terminations. It appears then that the male's withdrawals were a function of specific terminators (e.g. the female or the infant) which in turn was a function of time. The infant's effectiveness as terminator in the end was clearly as effective as the female's terminations at the beginning of the study in bringing about male withdrawals.

Proportion of successful or unsuccessful adult male initiations of male-infant interactions relative to prior adult male-female interactions. From Figure 4 and Table 4, it appears that for both the initial and latter episodes of the study, there was a higher frequency of successful initiations than unsuccessful. Throughout the study, the category which typically had the lowest frequency was unsuccessful

Insert Figure 4 and Table 4 About Here

male initiations following male-female interactions (US/YES). In comparison, there was typically more successful male initiations following male-female interactions (S/YES). Likewise, more unsuccessful initiations occurred when there was no prior male-female interactions (US/NO). Of particular interest is the reversal in the S/YES and S/NO categories over time. In both categories the male initiations were successful (S). In the first episode successful initiations (S) followed male-female interactions (YES) 36% of the time and 28% of the time there was no prior interaction (NO). In contrast, in the last episode, 70% of the male initiations were successful without prior male-female interaction (S/NO) whereas, only 5% of the time successful male initiations followed male-female interactions (S/YES). Furthermore, this latter category gradually decreased with time. It appears then that while the male to some degree may have utilized the strategy of first interacting with the female, he did so with less frequency as the study progressed and by the end of the study his success in achieving contact with the infant was not contingent upon prior interaction with the female.

Proportions of adult male and infant initiations. From Figure 5 and Table 5 it can be seen that the adult male initiated most of the interactions throughout the study until the last two episodes. In the next

Insert Figure 5 and Table 5 About Here

to last episode, the infant initiated 44% of the interactions and the adult male, 56%. In the last episode the male interactions and the last episode the male initiations dropped to 33% and the infant's increased to 67%. This reversal in initiations is significant since it indicates that with time the infant became more assertive while in the presence of the male. That is, the infant switched from being a passive recipient of the male's attention to an active solicitor of the male's attention. The male's initiations in contrast, decreased drastically possibly indicating a waning of interest on his part and boredom with his role of babysitter.

Terminator of male-infant interactions initiated by the male. Figure 6 and Table 6 reveal another reversal. In the first episode the female terminated 80% of the male-infant interactions, whereas the infant terminated only 5%. In contrast, in the last episode, the infant

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Insert Figure 6 and Table 6 About Here

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terminated 63% of the interactions, and the female, 15%. Thus, in terms of male initiations, the female with time became less restrictive, putting the infant in more of a position of having greater control in the management of the interactions. In addition, Figure 6 indicates that the male rarely terminated the interactions that he initiated.

Terminator of male-infant interactions initiated by the infant. Figure 7 and Table 7 also reveal reversals in terminators. In the first episode, both the infant and female acted as sole terminator an equal amount of time (43%) and in the second episode the female only category

Insert Figure 7 and Table 7 About Here

was at 100% and the infant only category at 0%. For the last three episodes, this pattern was reversed: 0%, 1%, and 1% for the female and 100%, 90%, and 63% for the infant. This further substantiates that the female with time was becoming less restrictive. It should also be pointed out that the male never terminated interactions initiated by the infant until the last two episodes at 8% and 31% respectively. This sudden increase may indicate again a waning interest in the infant on the part of the male. Also, if compared to the female only category as terminator another reversal appears.

The above results provide quantitative data on adult male/infant interactions with emphasis placed upon change over time. In summary, they demonstrate that the adult male exhibited great interest in the infant. The infant initially was hesitant, but with time began to seek social contact with the male. The female initially was restrictive of both the infant and the male, but with time she began to be much more permissive. In addition, the male, being principle monitor of spatial relationship between himself and the female, did not always use the strategy of first interacting with the female as a mechanism for gaining access to the infant. The female did not utilize the strategy of increasing the spatial distance as a means for decreasing the infant's accessibility to the male. Thus, negotiations between the adults necessarily involved close proximity and contact. The following is a description of thegeneral interactions involved in the

the triad. It provides qualitative information which with the above quantitative data demonstrates the development of a strong social bond between the male and the infant while in the presence of the infant's surrogate mother.

Results (Qualitative)

Female-infant Relationship. It should be pointed out that at the commencement of the study a strong social bond had formed between the female and infant. They had been housed together for approximately 7 months with the male in the adjacent cage. The social bond was similar if not identical to that of a typical mother-infant pair. They slept together, played, the female was protective, and she groomed the infant, for example. The infant sought reassurance when frightened, initially maintained constant contact, and followed her movements closely. Thus, when the male was introduced into their cage, it was not surprising that the infant sought protection from the female and that she in turn was very protective.

Adult male-female relationship. As noted earlier, the female was dominant to the male but there was some indication that this relationship was in transition during the course of the study. The male had put on considerable weight (musculature) since the last time they had been housed together (approximately 7 months). He also appeared to be less intimated by aggressive behavior on the part of the female. For example, during the study two fights occurred. When younger,

under the same circumstances, the male would submit, scream, and withdraw from the female. During the above fights, the male actually aggressed (retaliated) failed to submit, and much less readily withdrew. Both fights were believed to be a result of the male's unusual persistence in attempting to gain access to the infant.

The fights however should not be taken as indicating a poor relationship. The adults over a course of 6-7 years had spent considerable time together and as a result, formed a strong social bond. In fact, it was believed that the male was the father of the female's last infant. During the course of this study, the adults frequently played together and groomed each other. The male courted the female, but no actual copulations were observed. As noted earlier, the male was principally responsible in the maintenance of adult proximity.

Triadic interactions. In the initial stages of the study the female was very restrictive. When the male would approach, she would typically orient away from him, toward the infant, and frequently pull the infant to her. The infant upon the male's approach would typically move toward the female assuming a ventral-ventral position. If the male first interacted with the female before attempting to interact with the infant, he would typically groom her or initiate play. Play usually began in the form of hand grappling with the female's hand behind her back. If adult play did occur, it was usually quite vigorous and lasted for extended periods of time. Playing and grooming also occurred if the male first attempted to interact with the infant and was inhibited by the female. It is suggested that this was a male

strategy for reducing female restrictiveness. In these situations both adults acted as initiator of their interactions. Thus, it appears that adult male-female initiations were often used as a distraction device. Such behavior may have also served to mollify any ensuing aggression or excitement. There is also reason to believe that the male's propensity to withdraw after his initiation attempts with the infant were terminated may have served in this capacity.

The infant, during these interactions, directed considerable attention toward the male. Initially this would simply involve peering around the female's body while maintaining contact with her. Eventually he would break contact with the female and actually move toward the male. If the male then directed attention to the infant, the latter would typically retreat. As the study progressed, the infant actually attempted to participate in the adult play sessions. These attempts actually became more and more assertive to the extent that the infant would play kick or reach toward the male actually touching him at times. Thus, the adult male-female interactions also served to provide the infant with a situation where proximity or contact with the male was less aversive. In fact, it was during a vigorous adult play session that the infant made first contact with the male. The infant very cautiously reached toward the male with bent wrist and placed his wrist in the male's mouth. It should also be pointed out that the infant was often ignored during vigorous play which resulted in the infant pouting, whining, and once having a tantrum. This is not surprising since much of an infant chimpanzee's activity involves play.

As the study progressed the female became less restrictive to the extent of withdrawing from the infant and male. In one episode she actually entered the adjacent cage and closed the door behind her. She nevertheless payed close attention to the male and infant's activity. When she did interfere with the interactions, she would typically block the male's reach with her arm or hand or gently push his hand away. She would even hold his hand if he was too persistent. Often she would use her body as means of interference. For example, she would orient away from the male (perhaps presenting for grooming) and lean over or toward the infant, pulling the infant closer to her. Often her actions were so subtle that they could only be detected with slow motion analysis. In the last two episodes, her interference was minimal and her interest in their activity was rare. A large portion of these last two episodes primarily involved interactions between the male and infant. It is suggested that her waning interest was a function of her confidence in the social bond that had formed between the male and infant. They had obviously become play partners and her protectiveness was minimally needed.

Adult male-infant interactions. The interactions at the beginning of the study can be characterized as one of approach-avoidance. The infant exhibited anxiety and fear at the male's solicitations and generally utilized the females as a site of refuge. In the beginning, the male's contact with the infant would simply involve a quick touch, since neither the infant nor the female permitted easy access. With time the male began to pat the infant or attempt to groom it while

on or by the female. Eventually, the infant began to increase its distance from the female and this often occurred while the adults were interacting. In fact, it is under these circumstances that the infant began to initiate interactions with the male. Initially these initiations simply involved moving toward the male and staring but eventually contact was involved as noted earlier. Thus, it appeared that the infant was attempting to make himself accessible to the male.

As the study progressed, the male and infant made contact for extended periods of time although these interactions took place alongside the female. Initially, the female monitored these interactions very closely, but with time, she began to give them less attention. These interactions occurred under the context of play which became more vigorous with time.

As infant initiations began to increase, the male-infant interactions were no longer under the female's close supervision. This is due to the fact that the infant would withdraw from the female and approach the male. The initial initiations usually served no other purpose than to make the infant accessible to the male. With time however, the infant's initiations actually involved contact such as play slapping or play kicking or even assuming a ventral-ventral embrace on the male.

As noted above, male-infant interactions typically involved play and with time the play became more vigorous. If at some point during play, the infant became frightened, the male would stop the play and place the infant at his ventrum and hold and pat it. In

one situation when the infant screamed, the male actually turned to the female and signed SORRY three times. It should be pointed out that the male never exhibited any signs of aggression toward the infant. Also, whenever the male attempted to groom the infant, the infant would withdraw. The infant was never observed attempting to groom the male.

The latter two episodes are of particular interest since it was here that dramatic changes began to appear. As noted earlier, most of the interactions were dyadic, involving the male and infant; the female showed little interest in the male or infant. The infant was particularly solicitous of the male to the extent that in the last episode it appeared that the male had become weary of these solicitations. Not only did the male fail to respond in some situations, but he also began to withdraw from the infant. When this occurred, the infant would follow holding onto the male and attempt to sit in a ventral-ventral position on the male when the male sat down. If the male discouraged this position, the infant would sit beside or behind the male with his arms around him, and very frequently with his head resting on the male's body. The male was even observed to push the infant away when the latter attempted to gain contact. Thus, it appeared that the approach-avoidance condition noted earlier was reversed with the male now avoiding the solicitations of the infant. In essence, it was discovered that once the male had total access to the infant and was able to interact freely, a point was reached in these interactions where he lost interest. It should be pointed out

that the infant never gave up in his attempts to prolong these interactions. For example, in the last episode, the male entered the adjacent cage and closed the door blocking the infant's entrance. The infant attempted to pull the door open and upon failure stomped his feet on the door and toward the male.

CHAPTER IV

DISCUSSION

Ontogenetic Implications

From the above results it can be concluded that a strong social bond can form between an adult male and infant chimpanzee in the presence of an initially restrictive mother. The male's interactions with the infant were similar to those between the female and infant which suggests that an adult male chimpanzee if given the opportunity will exhibit care-giving behaviors towards a familiar infant.

While many of the activities observed in this study have also been observed in feral conditions, the male nevertheless does not act as principle care-giver. What must be addressed then is the role the adult male does play in the enhancement of the infant's survival and its development. Certainly, the infant who can utilize both adult male and adult female will be at a greater advantage than the infant who utilizes only the mother.

What role does the adult male play? This topic will be approached from two perspectives: indirect and direct roles with the latter given emphasis in this paper. Indirect roles are behaviors performed by males which do not necessarily involve interactions with the infant, but nevertheless enhance the infant's survival. Such behaviors include patrolling of the group's territory which serves to locate strangers,

predators, and rich food sources. Food procurement and protection are also roles exhibited by the human male.

Direct roles encompass behaviors which involve some form of interaction with the infant or which require attention on the part of the infant. These behaviors may or may not involve contact with the infant but at the very least, the male is necessarily visible to the infant. The general demeanor and social behavior of the male is the focal point here. It is most important that an infant chimpanzee as it develops learns the significance of the adult male as a part of the group. The infant learns through its own interactions with other group members and observation of interactions involving the mature male, that the adult male is dominant and therefore, exercises tremendous control over the group. It is important that an infant learn the appropriate social signals for submission and when these signals are appropriate. This may be even more important for the infant male chimpanzee since at some point in the future he will begin to integrate into the adult male group. The mature male chimpanzee therefore, as a salient and focal member of the group, provides a social stimulus to infants who as a result learn their own status as well as the status of other group members relative to the adult male. Particularly for the infant males, he is someone to emulate. It is suggested then that another role of the male in development concerns the ontogeny of social skills. Witnout this input, it is doubtful that normal integration into the group would occur; an individual as it matures must learn through contact and observation the importance and dominance of the adult male.

It is suggested that in this learning process, quality of interaction or observation may be more significant than quantity. For example, one encounter with a displaying male should be sufficient experience for an infant to learn to recognize the potential danger involved. It could also be argued that if quantity were more important than quality for the learning of social skills, the chance of surviving could indeed be reduced given the strength and dominance of the males.

In summary, the infant's social development and the role in which the adult male plays can be illustrated by Figure 8. The outer circle represents the chimpanzee's social environment in which the adult males

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Insert Figure 8 About Here

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are typically dominant. The middle circle represents the infant's mother which the infant uses as a base in the exploration of its social milieu. The inner circle represents the infant. At any early age, the infant principally interacts with its mother and she therefore, provides the core of its social environment. She nevertheless, is a part of the larger environment and as a result comes into contact with other group members. She can be viewed at this stage as a vehicle upon which the infant first learns about the larger social environment. When contact with the mother begins to break, the female will serve as a base and refuge in the infant's exploration of the outer social milieu. This exploration will occur until at some point in the infant's development, it will integrate successfully into the outer circle.

Phylogenetic Implications

If indeed strong social bonds can and do form between mature male and infant chimpanzees, then there must be a selective advantage in terms of evolutionary significance. That is, what advantage does the male receive in expending energy which enhances an infant's survival, particularly where a genealogical relationship, paternity confidence, (Alexander, 1974) is unknown? Parental investment theory (Trivers, 1972) predicts the greater the paternity confidence the higher the probability for paternal investment. Clearly in the chimpanzee where partnity confidence is low there is no indication of what could be considered actual paternal behavior exhibited by one male towards one specific immature individual. Thus, the male does not typically remain with one particular female and aid her in the rearing of a particular infant.

The adult male does however exhibit care-giving behaviors toward infants and his role in their survival is significant. What evolutionary advantage does the male receive by exhibiting these behaviors? One explanation may involve the concept of shared genes. Since adult males do not typically migrate from their groups, then a significant number of them are biologically related, and hence, share common genes. From a sociobiological perspective, any behavior that an adult male exhibits which enhances an infant's survival, regardless of paternity confidence, will simultaneously enhance the probability that those genes will be passed on in future generations. Thus, a male need not sire an infant to gain genetically as long as there is a genealogical relationship with the actual father of the infant. This explanation can also be applied to the male's interactions with any offspring that his mother may produce.

Another explanation which also entails a sociobiological perspective has been offered by McGrew (personal communication, 1979). Male chimpanzees have been reported to single out a female in estrous and remain with her, isolated from the group, until her tumescence subsides (McGinnis, 1979 & Tutin, 1975). During that time it is believed that he is the only male who copulates with her and in this case, paternity confidence is at 100%. However, in order to engage the female in this activity, he not only needs the necessary social skills to persuade the female to accompany him, but he also needs skills for interacting with her still dependent offspring. Should he intimidate either the female or her offspring, their resistance (e.g. screams) would attract all nearby males. Promiscuous mating would then occur and should he be a participant, his paternity confidence would drop considerably. Thus, it is to his advantage to have in his repertoire of social skills, those behaviors which will be attractive and least intimidating to the infant as well as its mother. It is interesting to note that the parous female most frequently engages in the safaris then does the adolescent female, who typically engages in promiscuous mating, (Tutin, 1975) and that the first several years during sexual development, the adolescent female is not yet fertile.

It logically follows then that males who are most successful in their interactions with immature members will gain genetically. In turn, these unaversive behaviors will be selected for. It is suggested that this may indeed be the mechanism through which paternal behavior evolved. This suggestion raises the question of whether or not the chimpanzee, as our closest evolutionary relative, can be used as a

model for the evolution of human paternal behavior. More specifically, does the chimpanzee represent some previous stage in human evolution where the familial bond began to include the adult male? Lancaster (in press) has suggested that food sharing is an importnat variable to consider in the phylogeny of familial ties. When either or both adults share food with immature members, strong social bonds are expected. Thus, at some point in human evolution when the adult male began to share the food he procured with not only a female, but also with her dependent offspring, he began to be an integral and necessary part of the familial unit. Adult male chimpanzees do engage in this activity most notably after a kill; females and their dependent offspring are provided with meat which they would otherwise not be able to obtain. In addition, Tutin (1975) found that the adult male who is most likely to form a successful consortship (i.e. persuade a female to engage in a safari) was especially generous with a specific female during meat-sharing activities. This suggests the incipience of strong pair bonding between adult male and adult female. Further evidence provided by Tutin for the inclination toward pair bonding in these animals is that during group situations, the consort male spent more time grooming the consort female than any other individual. If Lancaster's suggestion is correct, and considering the results of the present study and the social nature of the chimpanzee in general, then the answer to the above question is probably yes. Further more, it is suggested that as a model for human paternal behavior (male care-giving behavior), the chimpanzee, as subjects of investigations, may provide a clearer understanding of the role of the adult human male as a father or care-

giver. For example, if in the course of an infant chimpanzee's development, it is isolated from any contact with an adult male, what social defects may emerge. Is there a critical period where this isolation may take its greatest toll? Mitchell and Brandt (1972) have suggested that the absence of an adult male may be more detrimental to a young male nonhuman primate than to the young female. Likewise, what social defects will emerge when an infant chimpanzee is reared solely by an adult male? Studies which address these questions may necessarily have important implications for the development of fatherless and motherless infants in the human species.

Implications for Captivity

The chimpanzee is now an endangered species. Given its intelligence and its significance to the scientific community, it is most important that these animals receive the most humane treatment that captivity will allow. The results of this study clearly indicate an affinity between the adult male and infant. It is very likely that an infant chimpanzee reared without the benefit of contact with adult males may be deficient in some social skills. This in turn may enhance the problems associated with captivity (e.g. failure for any one individual to normally integrate into a group coupled with inability to escape from a fight). For these reasons, it is suggested that when possible captive chimpanzees should be housed under free-ranging conditions. This would provide the infants with exposure to both adults while also allowing the familial unit (female and offspring) enough space for avoidance of the adult males when their displaying and charging commences. Under these circumstances an

infant chimpanzee will have the opportunity to develop under conditions similar to a feral milieu which in turn may affect later sexual development and the breeding success of the particular institution involved.

As in the King et. al. (1980) study, which compared the social behavior of a captive group of chimpanzees to that of feral chimpanzees, it is suggested that the social environment imposed by captivity should be carefully considered. In their study an adult male was housed with mother/infant pairs. Given that adult females engage in infanticide and that new mothers have been observed to closely associate with adult males in order to avoid female aggressors (Goodall, 1977) it is likely that the presence of an adult male in captivity will reduce the probability of infant deaths due to intra-female aggression. In summary, there is presently enough data on captive chimpanzees which indicate that the adult male chimpanzee plays an important role in the maintenance of normal group behavior and normal social development of immature group members.

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APPENDIX A

The following is a list of behaviors recorded in this study. Descriptions will only be provided for those behaviors which need clarification.

Approach vs. Move Toward. A decrease in distance between subjects was considered an 'approach' when the subjects were out of arm's reach. If within arm's reach, it was considered a 'move toward'.

Withdraw vs. Move Away. An increase in distance between subjects was considered a 'withdrawal' if the movement extended beyond arm's reach. If within arm's reach, it was considered a 'move away'.

Lean Toward and Lean Away. These behaviors were recorded only if in arm's reach.

Grooming.

Play. This behavior included tickling, play slap, laughing, play face, and foot & hand grappling, for example.

Blocking. This behavior was recorded for the female and involved blocking with her foot, arm, head, hand, leg, and trunk. Also orienting away was considered as blocking with the body.

Patting and Touching.

Reach Toward.

Hugging (Embrace).

Follow. This was considered an initiation after an immediately preceding withdrawal (termination).

Pull On and Pull To. This occurred when either the male or female pulled on the infant.

Swinging and Dangling. This behavior was recorded as an infant's initiation when it was directed at the male.

Fighting.

Figure 1. Maintenance of Adult Male/Female Proximity

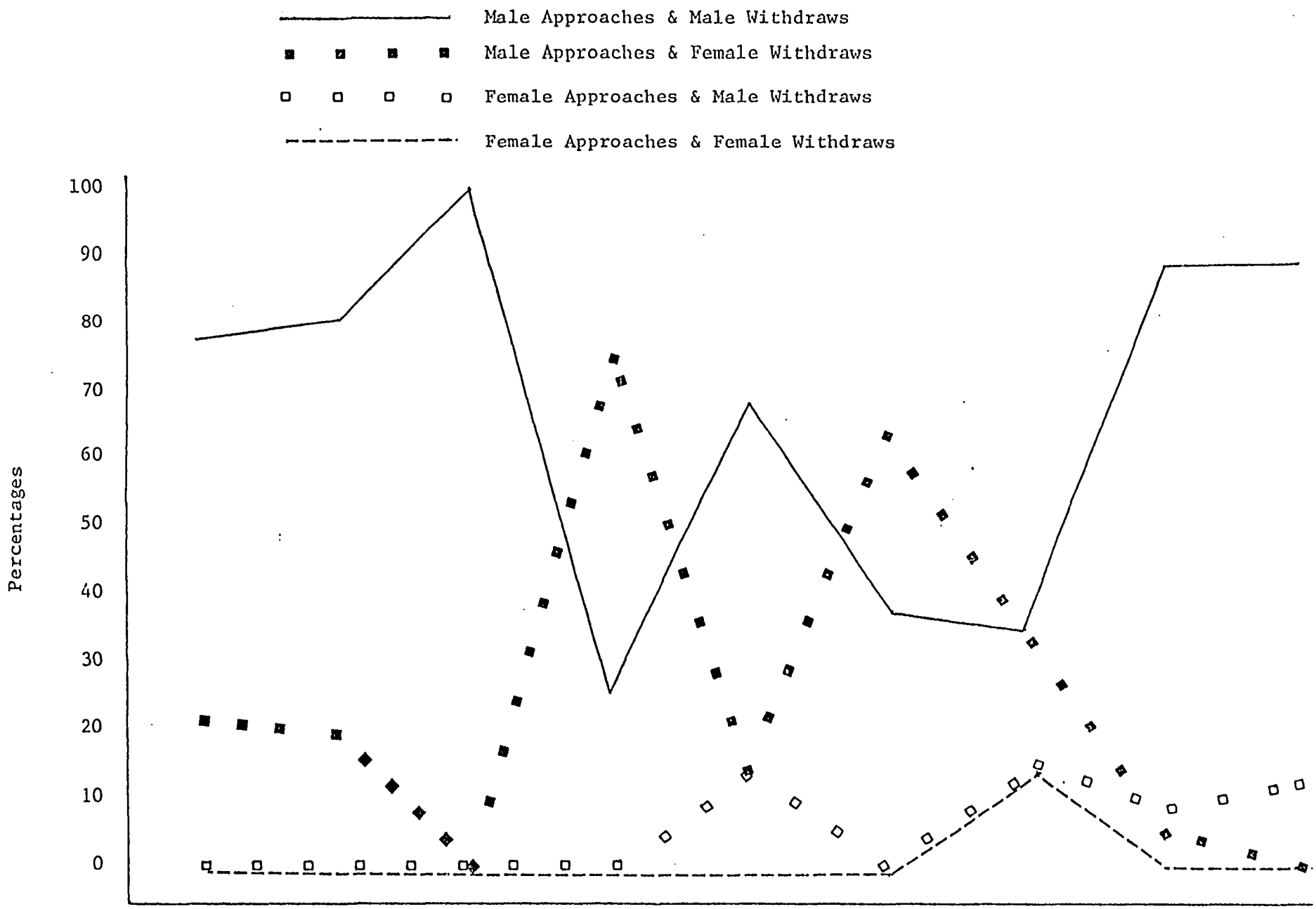

Table 1

Maintenance of Adult Male/Female Proximity

Episodes

	1	2	3	4	5	6	7	8	9
Male Approaches/ Male Withdraws	77.8	80	100	25	69.2	37.5	33.3	87	87.5
Male Approaches/ Female Withdraws	22.2	20	0	75	15.4	62.5	33.3	4.3	0
Female Approaches Female Withdraws	0	0	0	0	0	0	16.7	0	0
Female Approaches Male Withdraws	0	0	0	0	15.4	0	16.7	8.7	12.5

Percentages

Figure 2. Proportion of Adult Withdrawals from the Triad Preceded by Male/Infant Interactions

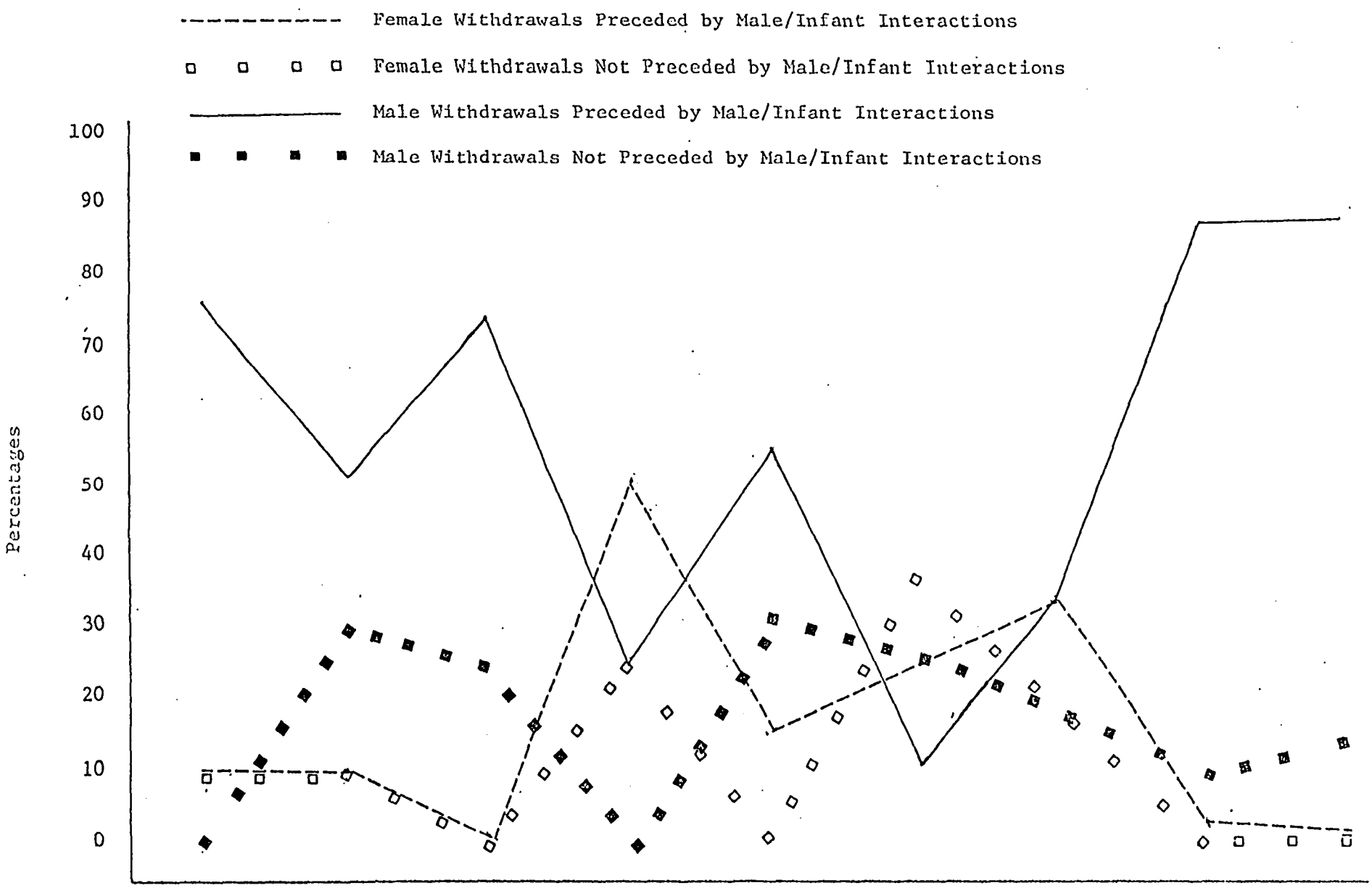

Table 2

Proportion of Adult Withdrawals from the Triad Preceded by Male/Infant Interactions

Episodes

	1	2	3	4	5	6	7	8	9
Male Withdrawals preceded by male/ infant interactions	77.8	50	75	25	53.8	12.5	33	87	87.5
Male withdrawals not preceded by male/infant interactions	0	30	25	0	30.8	25	16.7	8.7	12.5
Female withdrawals preceded by male/ infant interactions	11.1	10	0	50	15.4	25	33	4.3	0
Female withdrawals not preceded by male/infant interactions	11.1	10	0	25	0	37.5	16.7	0	0

Percentages

Figure 3. For Male Withdrawals Preceded by Male/Infant Interactions, Which Subject Acted as Terminator

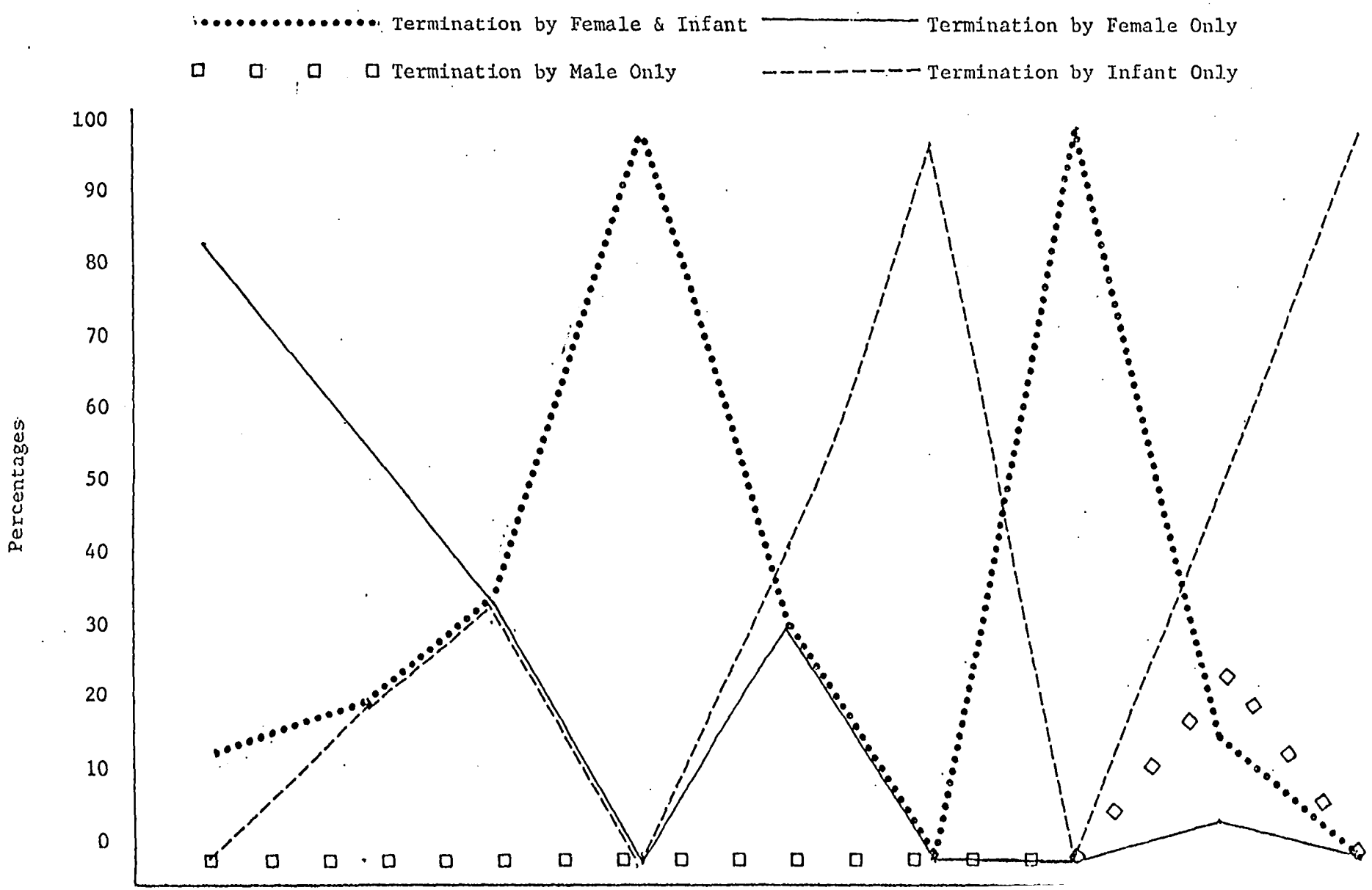

Table 3

For Male Withdrawals Preceded by Male/Infant Interactions, Which Subject Acted as Terminator

Episodes

	1	2	3	4	5	6	7	8	9
Termination by female only	85.7	60	33.3	0	28.6	0	0	4.8	0
Termination by infant only	0	20	33.3	0	42.9	100	0	57.1	100
Termination by female & infant	14.3	20	33.3	100	28.5	0	100	14.3	0
Termination by male only	0	0	0	0	0	0	0	23.8	0

Percentages

Figure 4. Proportions of Successful (S) and Unsuccessful (US) Adult Male Initiations of Male/Infant Interactions Relative to Prior Adult Male/Female Interactions (Yes-prior male/female interactions & No-no prior male/female interactions).

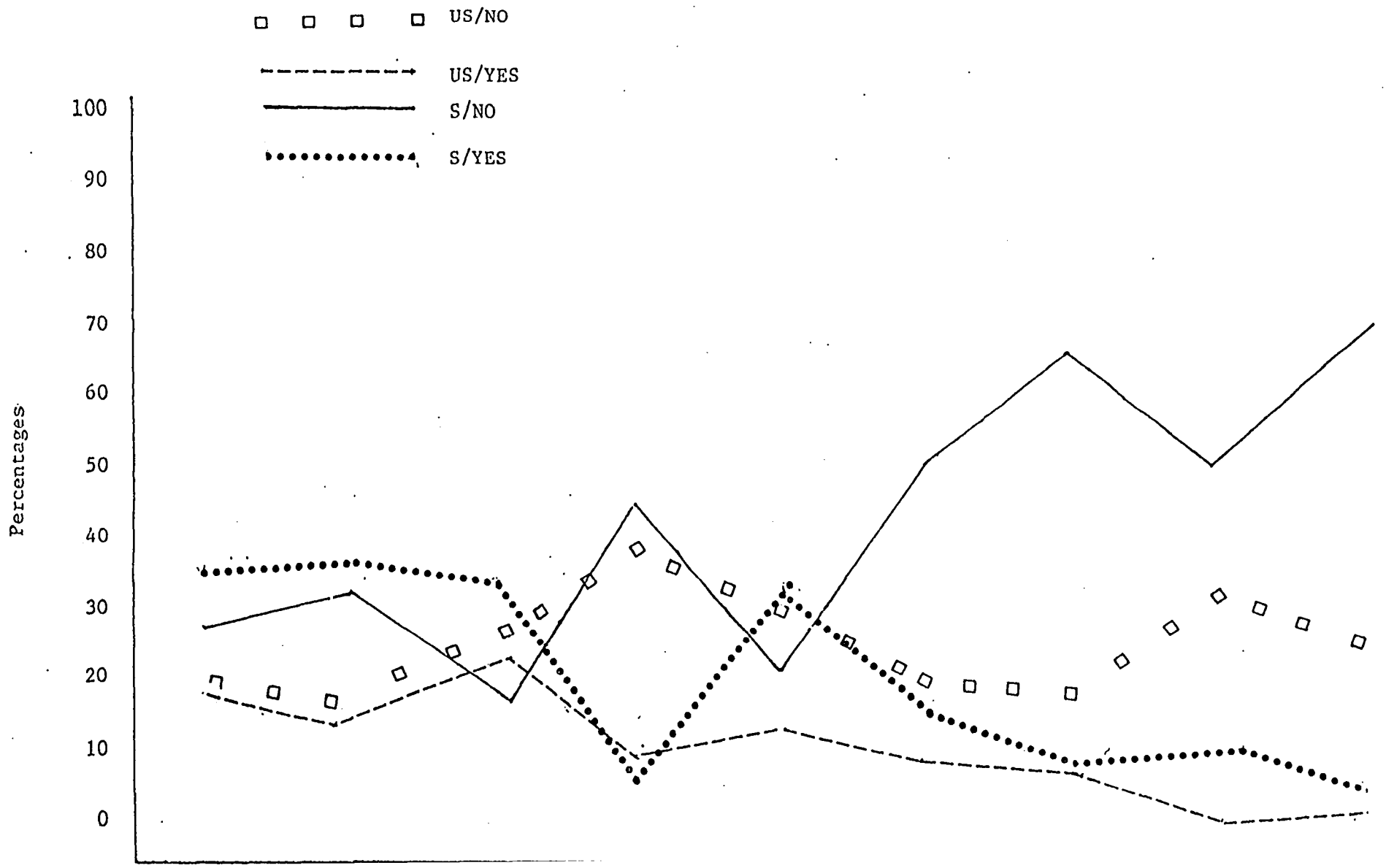

Table 4

Proportions of Successful (S) and Unsuccessful (US) Adult Male Initiations of Male/Infant Interactions Relative to Prior Adult Male/Female Interactions (Yes-prior male/female interactions & No-no prior male/female interactions

		Episodes								
		1	2	3	4	5	6	7	8	9
S/Yes	Percentages	36	37.5	32.7	5.3	32.5	17.2	9.3	11.1	5.5
US/Yes		16	12.5	23.6	9.2	13.5	8.6	7.4	.7	.9
S/No		28	33.3	16.4	47.4	21.6	55.2	66.7	56.3	70
US/No		20	16.1	27.3	38.1	32.4	19.	16.6	31.9	23.6

Figure 5. Proportion of Adult Male and Infant Initiations

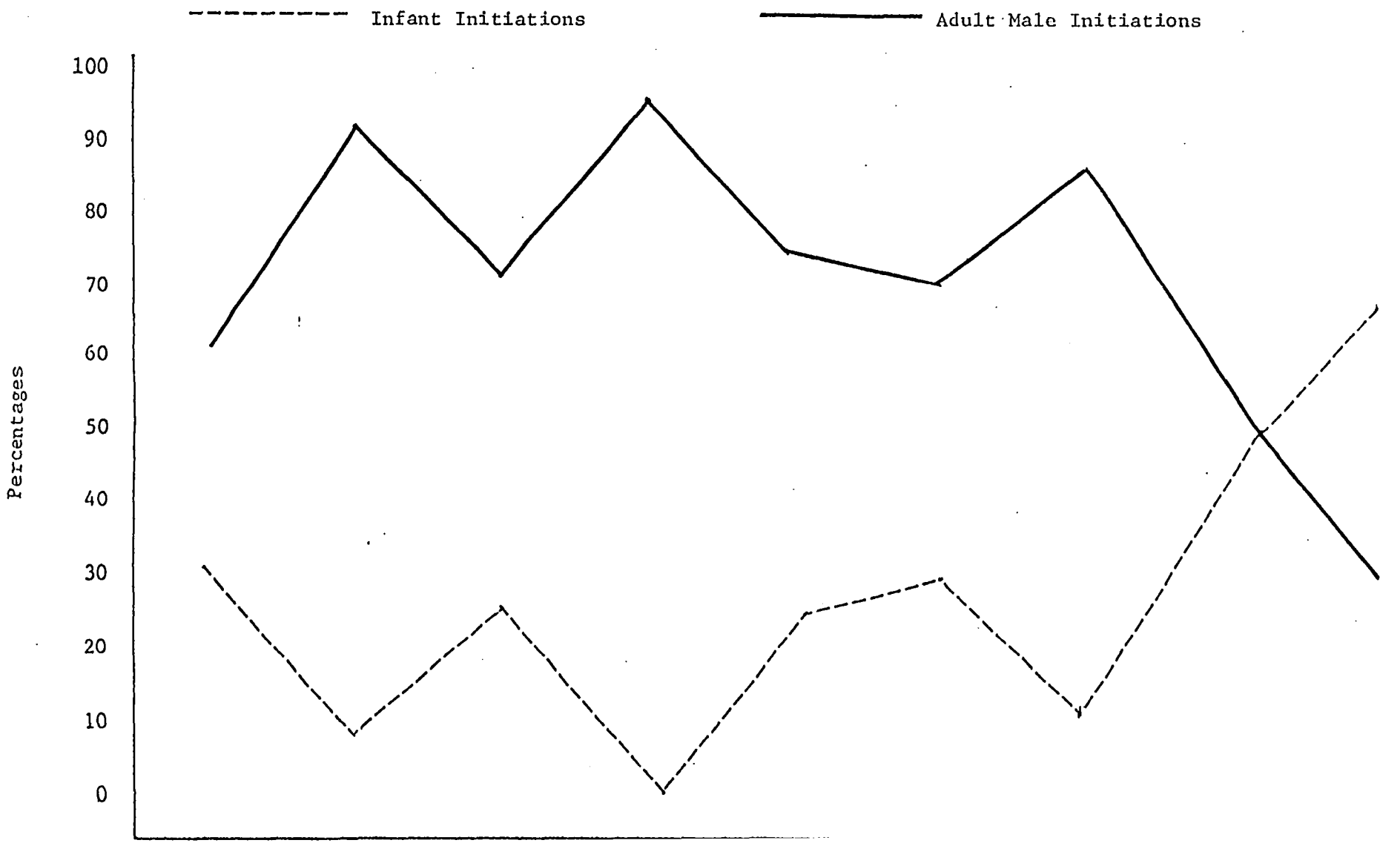

Table 5

Proportions of Adult Male and Infant Initiations

Episodes

rercentages	1	2	3	4	5	6	7	8	9
Male initiations	69.6	92	74	96.2	75.7	71.2	86	55.6	33.1
Infant initiations	30.4	8	26	3.8	24.3	28.8	14	44.4	66.9

Figure 6. Terminator of Male/Infant Interactions Initiated by the Adult Male

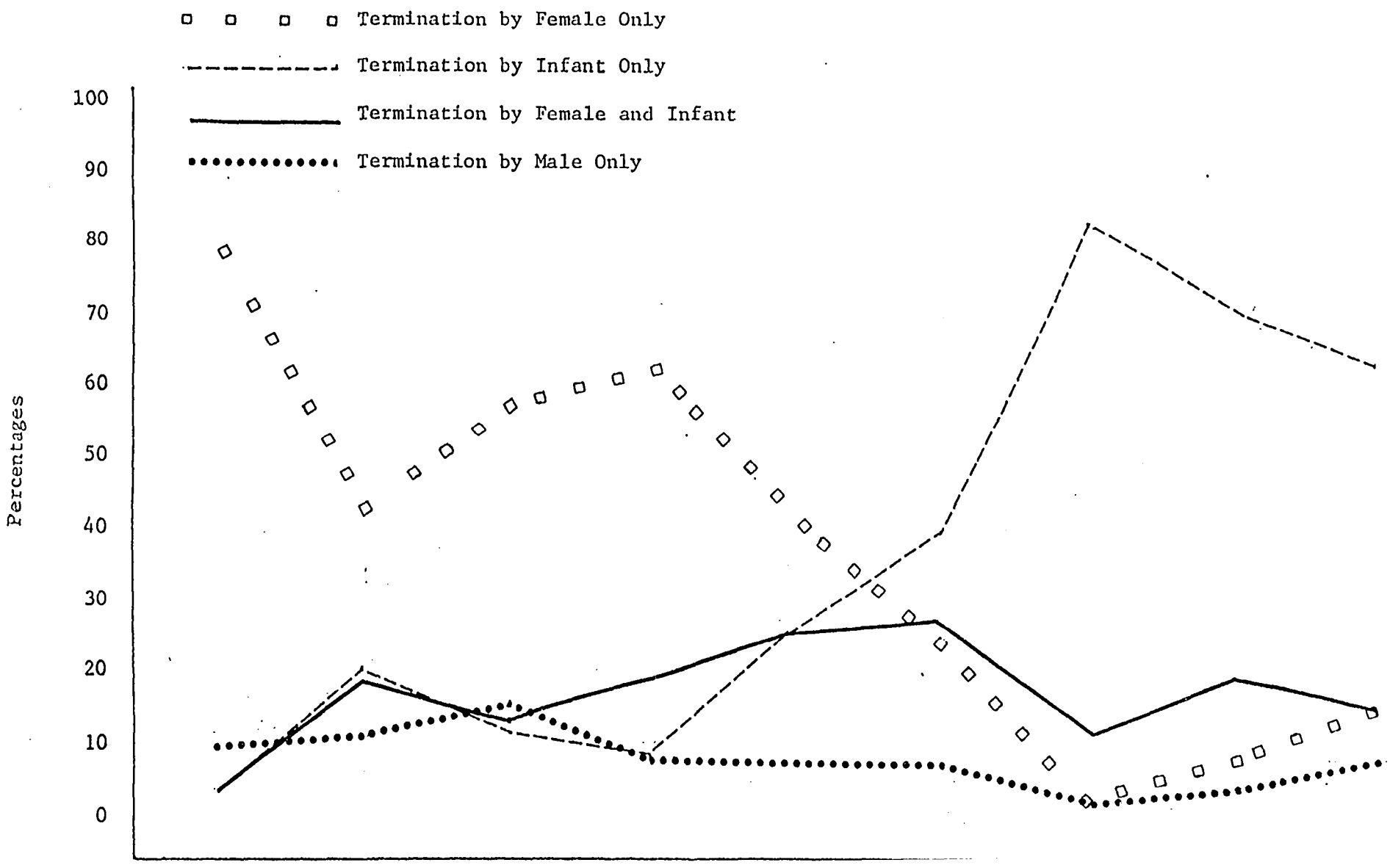

Table 6

Terminator of Male/Infant Interactions Initiated by the Adult Male

Percentages

	Episodes								
	1	2	3	4	5	6	7	8	9
Termination by female only	80	44	58.9	63.2	41.1	25	2.1	8.2	14.8
Termination by infant only	5	24	12.5	9.2	25	39.6	83.3	69.1	63
Termination by female & infant	5	20	14.3	21	26.8	27.1	12.5	19.1	14.8
Termination by male only	10	12	14.3	6.5	7.1	6.3	2.1	3.6	7.4

Figure 7. Terminator of Male/Infant Interactions Initiated by the Infant.

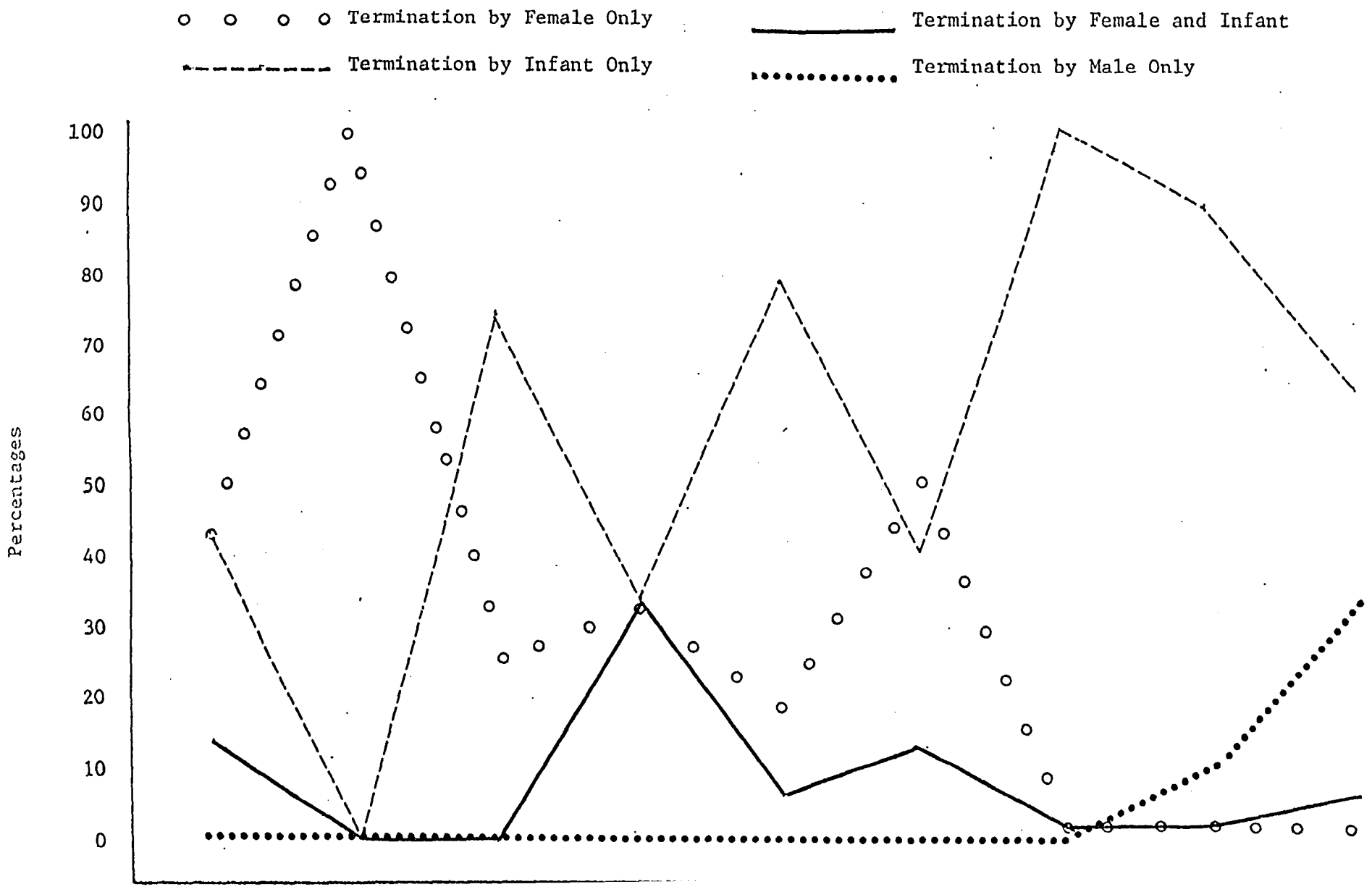

Table 7

Terminator of Male/Infant Interactions Initiated by the Infant

	Episodes								
	1	2	3	4	5	6	7	8	9
Terminations by female only	42.9	100	25	33.3	16.7	50	0	1.1	.9
Terminations by infant only	42.9	0	75	33.3	77.7	38.9	100	89.7	63.1
Terminations by female & infant	14.2	0	0	33.3	5.6	11.1	0	1.1	5.4
Terminations by male only	0	0	0	0	0	0	0	8.1	30.6

Figure 8. Representation of the Infant Chimpanzee's Social Environment. Inner Circle-infant, middle circle-mother, and outer circle-general social environment, including adult males.