Triadic Interactions in Captive Barbary Macaques (*Macaca sylvanus*, Linnaeus, 1758): "Agonistic Buffering"?

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This study presents data on the expression of male-immature triadic interactions, previously termed agonistic buffering, in a captive *Macaca sylvanus* group. Agonistic buffering has been hypothesized as inhibiting or modifying the expression of aggression. This was tested by examining (1) the dominance ranks of the animals involved in the triadic interactions, (2) the events preceding and following the triadic interactions, and (3) the presence of an infant in nonagonistic encounters between juvenile, subadult, and adult males. The results obtained do not support the hypothesis of agonistic buffering as the single explanation for triadic interactions, but emphasize the contextual variability in the expression of these triadic interactions.

INTRODUCTION

Agonistic buffering was first described by Deag and Crook [1971] in free-ranging Barbary macaques (*Macaca sylvanus*) as "those interactions in which a young monkey is 'used' by a male in social interactions with other individuals, usually males" [Deag & Crook, 1971]. Deag notes further that these behavior patterns ". . . involve interactions between the male, the baby (characteristically playing a passive role), and one or more other males. The presence of the baby appears essential; it seems that the interaction cannot take place without it" [1980]. In another study of free-ranging Barbary macaques [Taub, 1978; 1980], triadic interactions between males and infants were observed to involve "one male carrying an infant to another (or a male without an infant approaching one who had an infant), after which both males sat together for a few seconds displaying a series of exaggerated and steriotyped behaviors to each other and to the infant" [Taub, 1980]. This paper describes a system of triadic interactions [Kummer, 1967; Kummer et al, 1974] in a captive *M. sylvanus* group and relates it to the phenomenon previously referred to as agonistic buffering [Deag, 1980; Deag & Crook, 1971].

Implicit in the concept of agonistic buffering is the assumption that infants are used to regulate social relationships between dominant and subordinate males. In this context, such interactions have been reported in several other primate species (eg, *M. fuscata* [Itani, 1959], *M. arctoides* [Gouzoules, 1975], *M. fascicularis* [de Waal et al, 1976], *Papio hamadryas* [Kummer, 1967], *P. anubis* [Packer, 1980; Ransom & Ransom, 1971; Stoltz, 1972], and *P. cynocephalus* [Stein, 1981]). Most researchers believe that the interactions function to benefit the older individual more than the infant in terms of enhanced social status [Deag, 1980; Deag & Crook, 1971; Nash, 1973; Russell & Russell, 1971], enhanced reproductive success [Taub, 1975], or through mediation of aggression [Gouzoules, 1975; Kummer, 1967; Nash & Ransom, 1971; Packer, 1980; Ransom & Ransom, 1971; Rowell, 1967; Stein, 1981; Stoltz & Saayman, 1970]. Alternative hypotheses have been suggested, such as increased infant protection [Busse & Hamilton, 1981; Deag & Crook, 1971; Hamilton & Busse, 1980] and enhanced infant social experience [Burton, 1972; Hrdy, 1976]. The belief that the use of infants inhibits or curtails aggressive behavior has received the most attention, but as Redican [1976] noted, further investigation is required to delineate precisely the functions of these social interactions.

The purpose of this paper, therefore, is to test the agonistic buffering hypothesis by examining three specific predictions (following [Taub, 1980]): (1) if agonistic buffering is used to inhibit aggressive interactions between dominant and subordinate animals, then one would expect a negative correlation between individual dominance rank and frequency of initiating agonistic buffering episodes; (2) if agonistic buffering indeed buffers agonism, then one would expect aggression to precede and certainly not to follow the episodes; and (3) if infant carriage enhances social relations between males, then one would expect more nonagonistic encounters between males when infants are in proximity than when they are not in proximity.

METHODS

Subjects

A captive group of 11 Barbary macaques (*Macaca sylvanus*) served as subjects. The group initially contained one adult male, three adult females, two subadult males, one juvenile male, one juvenile female, two infant males, and one infant female (age/sex classification follows Burton [1972]). During the study, changes occurred in the group through the death of an adult female and the emigration of the two subadult males from the island on which they were housed. Although records are incomplete, it is suspected that all group members were captive born; some had previous contact with wild-born animals.

Study Site

The study was conducted from November, 1975, through March, 1976, at Lion Country Safari Park near Stockbridge, Georgia. The group was housed on a 0.1-hectare island in sight of three other islands which housed nonhuman primates. Monkey chow was fed in the morning, while fruit with chow was fed in the afternoon. No data were collected during feeding.

Observation Techniques

Data were collected from the shore, approximately 30 m from the island. Although visibility was not completely unobstructed, animals rarely went out of sight (less than 1% of the time) because of the configuration of the island.

Forty-two hours of direct quantified observations consisting of over 10,000 interactions were made using the focal animal observational technique [Altmann, 1974].

Observations were made using a tape recorder, a 30-sec interval timer, and 7-mm × 35-mm wide-angle binoculars. Individuals were observed for 5-min intervals in a random order without replacement for a given series of observations. A series of observations consisted of 5-min test sessions for all group members. Additional qualitative, hand-written notes (*ad libitum*) were added whenever possible. These qualitative observations were not used in the calculation of the rate of agonistic buffering or in the examination of behaviors preceding or following agonistic buffering bouts, but were used to examine the participants involved.

Analysis

Data were keypunched and stored on a Univac 90/80 computer system. SPSS [Nie et al, 1975] programs were used for all data manipulation and analysis. Dominance relations in the group were determined by observation of agonistic encounters following the technique described by Bernstein [1968].

Terminology

For purposes of this study, the traditional definition of agonistic buffering [Deag & Crook, 1971] was not utilized, but a modification of Kummer's [1967] definition of tripartite relations was employed, as follows: three animals, one of which is an infant, all interact simultaneously with each other in three essentially different behavior patterns, with the infant typically playing a passive part in these interactions [Deag, 1980; Merz, 1978]. The participants in the triadic encounter were defined as: (1) the subject, the recipient of the interaction; (2) the initiator, the animal with the infant; and (3) the target, the infant being manipulated. Several researchers [Hinde & Proctor, 1977; Seyfarth, 1976] have noted that a female carrying an infant may receive differential treatment than a female without an infant. Triadic interactions involving a mother as initiator and her offspring as target were excluded from analysis, however, since it would be difficult to differentiate those interactions in which the mother used her infant primarily to her own advantage in a social situation from general maternal behavior. No mother was ever observed to present her infant to another animal.

RESULTS

A commonly seen example of a triadic interaction in this group involved a male, the initiator, who invited an infant to ride dorsally, approached the subject with the infant in a dorsal position, and hesitated as if presenting the infant to the subject. The initiator would then move within 1 m of the subject while the subject reached out its arms to hold the initiator. At this point, all three individuals lipsmacked synchronously. The infant would dismount and any of a variety of interactions would ensue. Variations in the initiation of these encounters were noted: (1) occasionally, two animals would run to an infant simultaneously; (2) the subject might approach the initiator (animal with the infant); or (3) the initiator might approach the subject and come into proximity just as the infant climbed onto the initiator.

Thirty-five instances of triadic interactions were observed, 18 interactions were observed during the formal testing sessions (out of a total of 10,000 interactions), while 17 interactions were added from qualitative notes sampled *ad libitum* [Altmann, 1974]. From the time-sampled data, an average rate of 0.43 interaction per hour was calculated, or one triadic interaction every 2.35 hr.

The distribution by age class of participation in triadic interactions is given in Figure 1. Typically, the subject of the episode was the adult male, but the interactions were never initiated by adults (cf [Deag, 1980]). Subadult and juvenile animals participated almost equally as initiators, while the target of the interaction was always an infant.
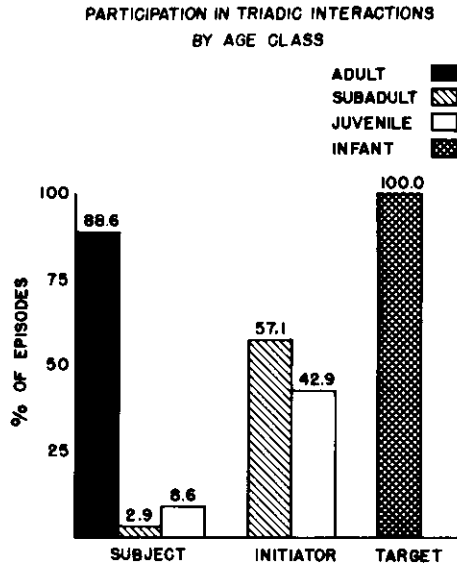
PARTICIPATION IN TRIADIC INTERACTIONS
BY AGE CLASS

ADULT ■
SUBADULT ▨
JUVENILE ☐
INFANT ▓

Fig. 1. Participation in triadic interactions by age.

PARTICIPATION IN TRIADIC INTERACTIONS
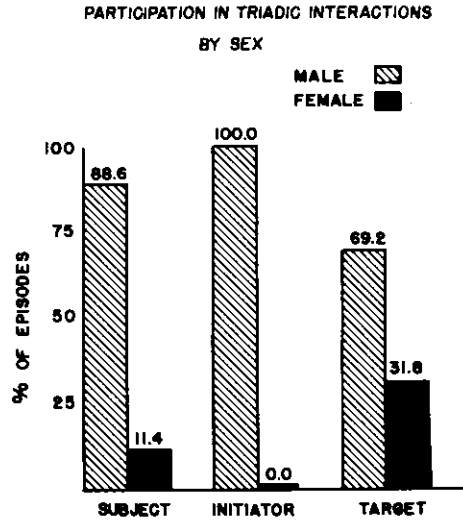
BY SEX

MALE ▨
FEMALE ■

Fig. 2. Participation in triadic interactions by sex.

No clear pattern emerged from the data with respect to the sex of the interactants (Fig. 2). In 88.6% of the total encounters, the subject was a male (77.1% involved the adult male), while the subject in 11% of the encounters was an adult female. In all cases, the initiator was either a subadult or juvenile male. This is of some interest, since there were one juvenile and three adult females present in the group that could have potentially participated. In 82.9% of the encounters, the target infant could be positively identified.

TABLE I. Summary of Interactions Preceding and Following Triadic Interactions Between the Subject and the Initiator

	Agonism	Affiliation	Other social	No interaction	Total
Preceding	2[a]	0	3	10	15[b]
Following	3	5	7	3	18

[a]Only one of these instances involved the subject aggressing against the initiator.
[b]In three of the episodes, interactions preceding the triadic interaction were not observed.

In 69.2% of these instances, the target infants were males, but this is not significantly different from chance, since there were two males and one female in the group.

Do these triadic interactions occur in response to agonistic situations, as Deag and Crook [1971] suggest? If high-ranking animals in the group frequently initiated triadic interactions to lower-ranking animals, then it would follow that this type of behavior was not functioning to reduce the probability of aggression. Conversely, the agonistic buffering hypothesis is supported if low-ranking animals initiated to high-ranking animals. In 77% of the encounters, the alpha animal was the subject, whereas in 11% of the encounters, the initiator was of a rank higher than the subject.

Analysis of the interactions which preceded and followed the triadic interactions observed during focal animal observations is presented in Table I. Examination of the interactions preceding a triadic interaction reveals that only one episode of agonism between subject and initiator preceded a triadic interaction, whereas affiliation followed a triadic interaction five times. In three instances, the triadic interaction actually resulted in agonism between initiator and subject. On the other hand, whereas 28% of the interactions following a triadic interaction resulted in affiliation, a total of 83.3% of the interactions did not result in agonistic interactions.

Nonagonistic interactions between juvenile, subadult, and adult males were observed both with and without an infant present. No significant difference (t = 0.87, df = 10, p > 0.05) was found in the frequency juvenile, subadult, and adult males interacted nonagonistically with and without an infant present.

DISCUSSION
Testing Specific Hypotheses

Inhibition of aggression. Our data do not clearly substantiate the hypothesis that male-immature triadic interactions inhibit aggressive interactions between initiator and subject. The analysis of behaviors preceding the triadic interactions revealed that agonism preceded on only two occasions, with only one of these in the direction predicted by the hypothesis; specifically, the subject of the triadic interaction aggressed against the subsequent initiator of the triadic interaction. These results strongly suggest that although male-immature triadic interactions may occur in response to agonistic encounters on occasion, the antecedent behaviors are much more variable than some have suggested. It should be noted, however, that in over three-fourths of the triadic episodes, the subject animal was the alpha male, and in the one case where the triadic interaction was preceded by aggression, the encounter was dramatic and aggressive interactions ceased when the initiator with the infant contacted the subject. These few observations are certainly concordant with the agonistic hypothesis as proposed by Deag and Crook [1971]. Nevertheless, the bulk of the episodes preceding triadic encounters were characterized by no overt interaction between the participants. In general, these results parallel the work of Taub [1978, 1980], who demonstrated that agonistic interactions rarely preceded male-young triadic interactions.

Outcome of triadic interactions. Subordinate animals use infants to stabilize or regulate relationships with those more dominant and, consequently, reduced levels of agonistic behavior [Deag, 1980; Deag & Crook, 1971]. It seems unlikely, however, that such a single phenomenon could be the cause of what seems to be a species-typical pattern – low rate of aggression. From the observed bouts, it is not possible to discern if these interactions regulate any type of social interaction, since affiliation rarely followed a triadic episode, and even aggression occasionally followed. Although from Table I it might be inferred that even though these triadic interactions often did not result in affiliation, in most cases they did not exacerbate aggressive behavior. When interpreted this way, the agonistic buffering hypothesis may be supported. However, in only 2 of the 15 encounters (where the contextual nature of the preceding events was recorded) did aggression precede the encounter, which fails to support the interpretation that initiator males were acting in response to ongoing agonism. It could be argued, however, that males were anticipating what they perceived to be a potentially aggressive interaction, and were acting accordingly.

Enhancement of male-male relations. Contrary to Taub [1978,1980], who believed agonistic buffering did not bring males together, Deag [1980], Deag and Crook [1971] and Gouzoules [1975] observed few friendly male-male approaches without an infant present. We found no significant difference in the amount of time males interacted nonagonistically with or without an infant in proximity. On several occasions, the initiator was already in proximity to the subject before the episode began. Only 5 of the 18 interactions (22.2%) following triadic interactions involved affiliative behavior between the participants. Similarly, agonistic buffering in Gilmore's [1977] baboon group resulted mostly in avoidance and ignoring, with no affiliative behavior following the interaction. These findings do not support Deag and Crook's [1971] contention that agonistic buffering promotes friendly contacts between males and, therefore, may help produce a more peaceful social life for the group than in those macaque species where there is little social interaction between males (eg, *M. mulatta*). Agonistic buffering may not produce a more peaceful life, but, on the other hand, a more peaceful life may be allowed because of it.

Classification of Interactions

The male-young interactional system in Barbary macaques has been extensively reviewed [Deag, 1980; Deag & Crook, 1971; Redican, 1976; Taub, 1978; 1980] and is recognized as an extremely complex set of interactions. Observations reported in this paper lead to the conclusion that hasty generalizations concerning the function of these interactions are unwarranted, and "the use of the term agonistic buffering should be dropped as a functional descriptor of triadic male-infant interactions in this species" [Taub, 1980]. It is suggested that agonistic buffering be used as a referent only for those interactions in which an infant is retrieved in response to overt aggressive behavior or while displaying submissive behavior. This clarification of type (b) interactions [Deag & Crook, 1971] will help in explicating the nature of these triadic interactions in Barbary macaques.

Male-immature triadic interactions in most species usually involve adult and subadult animals [Burton, 1972; de Waal et al, 1976; Gilmore, 1977; Itani, 1959; Kummer, 1967; Packer, 1980; Ransom & Ransom, 1971; Rowell, 1967; Stoltz & Saayman, 1970; Whiten & Rumsey, 1973]. However, in this study, juveniles were observed both as subjects and initiators. Deag [1980], Deag and Crook [1971], and Taub [1978, 1980] also observed juvenile participation in *M. sylvanus* triadic interactions, which suggests that juvenile participation in triadic interactions may be species specific.

Adult female *M. sylvanus* were involved in triadic interactions, but their participation was relatively infrequent and somewhat variable. Adult females were observed as the

subject in 4 of the 35 triadic episodes, but were never observed to receive or hold the initiator, nor did the initiator present the infant to them. Adult females never initiated the interactions. Similarly, Kummer [1967] and Stoltz and Saayman [1970] observed that females under threat never picked up an infant. Perhaps the relative lack of female participation in triadic interactions is related to the differential effects of male care on the development of behavior in male and female infants (see [Deag, 1980]).

Species Differences

Taub [1978] stressed that agonistic buffering in Barbary macaques is a different phenomenon from that seen in other species of macaques and baboons. Barbary macaque infants are handled carefully and these interactions do not necessarily occur in agonistic contexts [Taub, 1978, 1980]. Also, it does not appear that species other than *M. sylvanus* have developed a system of infant presentation. The buffering role of the infants may be more likely among baboons and macaques other than *M. sylvanus*; there are numerous references to baboon males interacting with infants during overt aggressive encounters [Bernstein, 1975; Busse & Hamilton, 1981; Gilmore, 1977; Kummer, 1967; Packer, 1980; Popp & DeVore, 1979; Rowell, 1967; Stein, 1981; Stoltz & Saayman, 1970], while Deag and Crook [1971] noticed only a few such interactions in Barbary macaques. However, these interactions in different species seem somewhat related structurally and, perhaps, functionally. It is possible that they evolved from the male-care system and are expressed differently according to the type of social organization or the kinds of interactions infants receive during maturation.

CONCLUSIONS

1. This study has documented the existence of a complex set of triadic interactions between males and young in a captive Barbary macaque (*Macaca sylvanus*) group.
2. Based on an analysis of the patterns of interactions that preceded or followed these triadic interactions, the hypothesis that they serve to mediate or buffer agonism was not supported.
3. Contrary to Deag [1980], no significant differences were found in the frequency males interacted with or without an infant present.
4. The uncritical application of the term agonistic buffering to a broad class of triadic encounters in Barbary macaques is questioned.
5. Male-young triadic interactions in Barbary macaques are a different phenomenon from that reported for other Cercopithecoidea.

ACKNOWLEDGMENTS

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