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POST-CONFLICT BEHAVIOR IN JAPANESE MACAQUES AT THE INDIANAPOLIS ZOO: AGE OF OPPONENTS INFLUENCES RECONCILIATION

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ABSTRACT: In many primate species, opponents may affiliate soon after an agonistic encounter. This study examined how the individual characteristics of opponents affected post-conflict interactions in a captive group of Japanese macaques (*Macaca fuscata*). Reconciliation and selective attraction of opponents was shown to occur following agonistic encounters. The factor most strongly influencing post-conflict interactions was age. Juveniles were significantly more likely than adults to initiate reconciliation. Sex, kinship, and dominance status were not associated with contact initiation. Because juveniles were the most likely victims of aggression, juvenile reconciliatory contact initiative may reduce the threat of further aggression.

KEYWORDS: Age, aggression, conflict, Japanese macaque, primate, reconciliation, social behavior.

INTRODUCTION

In many primate species, opponents may attempt to reaffiliate soon after the agonistic encounter (de Waal, 1989). De Waal and van Roosmalen (1979) interpreted such behavior as reconciliation. De Waal and Yoshihara (1983) developed a controlled method to quantify this behavior. Whereas their null hypothesis predicts random interaction of opponents following a conflict, two alternative hypotheses predict either post-conflict avoidance (dispersal) or attraction (reconciliation). Chimpanzees (de Waal and van Roosmalen, 1979), bonobos (de Waal, 1987), patas monkeys (York and Rowell, 1988), golden monkeys (Ren, *et al.*, 1991), redfronted lemurs (Kappeler, 1993), and several macaque species (de Waal and Yoshihara, 1983; Judge, 1983; Thierry, 1984: Cords, 1988; de Waal and Ren, 1988; Aureli, *et al.*, 1989) are known to exhibit reconciliatory behavior.

Either the aggressor or the victim may initiate post-conflict affiliation. In rhesus macaques, post-conflict affiliation is most often initiated by the aggressor (de Waal and Luttrell, 1989), whereas among pigtail macaques, the victim initiates this behavior (Judge, 1991). Questions regarding contact initiation, however, must also be addressed from a multi-component perspective, because different factors may interact to produce unique behavior. For example, age and

sex might influence which opponent makes initial contact. Aureli, *et al.* (1989) found that within a troop of long-tailed macaques, the victim most often sought reconciliation, whereas Cords (1988) found that in an isolated group of immature male long-tailed macaques, the aggressor did so. Kinship might also influence reconciliation, but several studies have shown either no differential reconciliation among kin (Aureli and van Schaik, 1991a; Aureli, *et al.,* 1994) or kin-oriented reconciliation that was a consequence of the elevated affiliative behavior generally found among kin (Cheney and Seyfarth, 1989).

Because combinations of attributes vary among group members, one might expect individuals to express different reconciliatory behavior depending on factors such as sex, age, relatedness, dominance rank, or reproductive condition, especially if difference in these factors influence the value of a relationship between a pair of individuals (see Cords and Thurnheer (1993) for a discussion of social value and reconciliation). This study was designed to quantify reconciliation in a captive group of Japanese macaques (*Macaca fuscata*), taking into account characteristics such as the sex, age, kinship, and dominance status of the opponents. While other studies have examined reconciliation in this species (Friedlen and Chaffin, 1991; Aureli, *et al.,* 1993), none have reported on whether such factors influence post-conflict interactions between opponents.

MATERIALS AND METHODS

The Study Group. A captive group of 15 Japanese macaques was observed from June to August 1992 at the Indianapolis Zoo. The group, established at least two years prior to the study, consisted of one adult male (AM; > 5 years), six adult females (AF; > 5 years), two juvenile males (JM; 1-4 years), four juvenile females (JF; 1-4 years), and two infants (I; < 1 year). Kin relationships (hyphenated) and descending matrilineal dominance rank were as follows: AM1; AF1-JF1-JM1; AF2-JF2-JF3; AF3-JF4-I1; AF4; AF5-JM2-I2; and AF6. No adults were related. During the day, the group inhabited an outdoor enclosure with adequate room to run and climb (167 m^2). Behavioral observations were made only on days that were at least partly sunny from 10:00 until the animals were fed at 16:00.

Data Collection. Observational procedures were similar to those used by de Waal and Yoshihara (1983; but see Kappeler and van Schaik (1992) for a discussion of methodological concerns). Immediately following a spontaneous agonistic encounter, one of the opponents was selected at random and observed for a 10-minute focal period (post-conflict observation). Agonistic conflict was defined as an interaction that included lunging or chasing, accompanied by eyeflashing or certain vocalizations (i.e., screaming directed toward the opponent). On the next observation day, the same individual was watched for 10 minutes, beginning at the same time that the agonistic encounter had ended on the previous day (matched control observation). The matched control observation was postponed until the next day if the focal animal participated in an agonistic conflict immediately prior to or during the first minute of the focal period.

Data were recorded on a hand-held computer and included the following: identity of the opponents, minute block in which contact with the other individuals occurred, identity of contact partners, identity of contact initiators , and specific behavioral patterns (chase, vocalize, eye-flash, hit, bite, sit-near, touch, groom, mount, move-away).

Opponent pairs were classified as either attracted, dispersed, or neutral, according to the definitions of de Waal and Yoshihara (1983). Attracted pairs were those in which non-agonistic contact (touching or sitting within arm's reach for more than 10 seconds) occurred only during post-conflict observation or earlier in the post-conflict than in the matched control observations. These pairs were designated as reconciliatory. Dispersed pairs showed the opposite configuration (i.e., contact in the matched control observations only or earlier in the matched control than in the post-conflict observations). Neutral pairs made no contact at all or made contact in the same minute block in both the post-conflict and matched control observations.

For the purposes of this study, the behavior of the infants was not recorded. Also, because this study was primarily concerned with interactions between individuals, solitary behaviors such as self-grooming or foraging were not recorded.

Data, unless otherwise indicated, were analyzed using two-tailed nonparametric procedures (Siegel and Castellan, 1988) to avoid making the stringent assumptions generally associated with parametric statistics. To avoid the statistical error associated with the pooling of data across individuals, χ^2 procedures were not used. Therefore, unless otherwise indicated, sample size was 13 with $\alpha = 0.05$.

RESULTS

One hundred two post-conflict and corresponding matched control observations were conducted. Because conflicts were sometimes triadic or polyadic, a total of 131 matched opponent pairs was observed. In the analyses of opponent characteristics, frequencies of attraction or dispersal for a given individual were treated as proportions of the total number of conflicts in which that individual was paired.

Overall Occurrence of Reconciliatory Behavior. Post-conflict interactions between opponents generally involved an individual approaching to sit in contact or within arm's reach of a former opponent. While this behavior sometimes resulted in renewed aggression (such instances were dropped from the analysis), most often the two opponents remained seated together for at least 10 seconds. On many occasions, this contact immediately led to a grooming bout. Reconciliation between juveniles, particularly the young males, often involved play behavior.

The null hypothesis predicted equal frequencies of attraction and dispersal. The results of the present study, however, revealed that individuals were significantly more likely to show attraction than dispersal (Figure 1; Wilcoxon Signed Rank Test: T+ = 77, T- = -14, and $P = 0.0303$). When the frequencies of

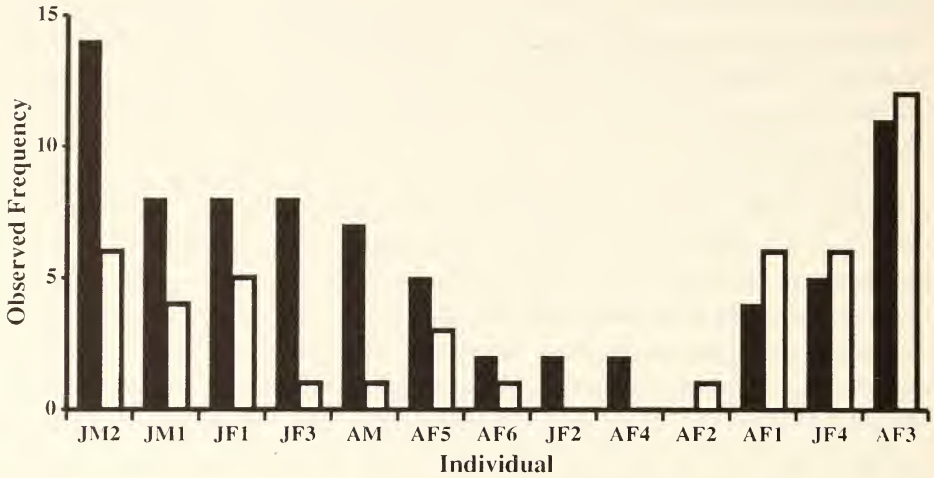

Figure 1. The number of times each individual appeared in attracted (shaded bar) or dispersed (clear bar) pairs (A = adult; J = juvenile; M = male; F = female; Wilcoxon Signed Rank Test, $P = 0.0303$).

attraction and dispersal are expressed as proportions of the total interactions per individual, the difference was reduced to a strong trend (Wilcoxon Signed Rank Test: T+ = 73, T- = -18, $P = 0.06$).

De Waal and Yoshihara (1983) stressed the importance of distinguishing between actual reconciliation and a general increase in contact following an agonistic encounter. Their concern was addressed by comparing the proportion of non-agonistic contacts between opponents and between the focal animal and all other individuals in both post-conflict and matched control observations. Focal animals made significantly more contacts with opponents relative to all other individuals during post-conflict rather than during matched control observations (Figure 2; Wilcoxon Signed Rank Test, 2 zero scores: T+ = 56, T- = -10, $P = 0.0454$). These Japanese macaques, therefore, exhibited selective post-conflict attraction for opponents.

Aggressors and victims displayed no difference in contact initiative (active approach and solicitation) following a conflict (Wilcoxon Signed Rank Test, 6 zero scores: T+ = 19.5, T- = -8.5, $P = 0.3980$). Contact initiative was attributed to the opponent who first approached and sat at least within arm's length of the other for more than 10 seconds.

Opponent Characteristics. Among individuals, differences in attraction with respect to opponent sex approached significance (male:male vs. male:female vs. female:female; Kruskal-Wallis, $P = 0.065$). In opposite sex pairs, the trend was for males, more than females, to be the contact initiator (Wilcoxon-Mann-Whitney Test, one-tailed, $P = 0.0917$). In general, however, sex was not a significant factor influencing reconciliation. Males and females did not differ in frequencies of attracted and dispersed interactions (Wilcoxon-Mann-Whitney

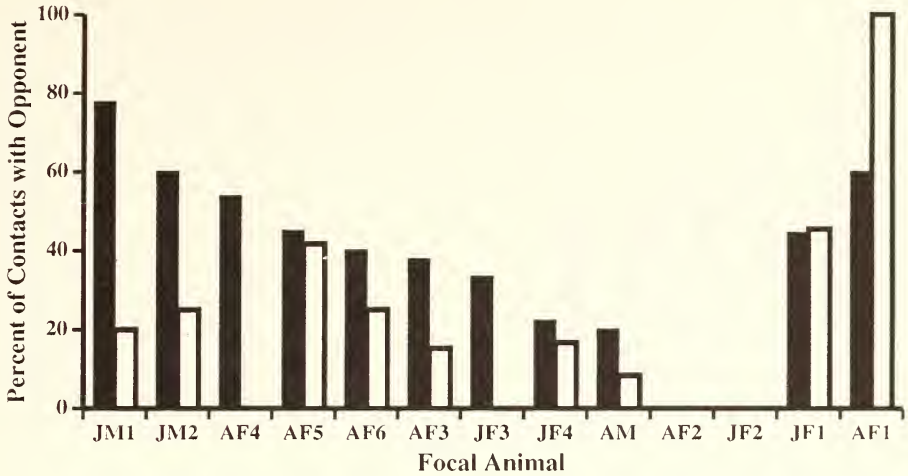

Figure 2. The proportion of a focal animal's total contacts that involved the opponent during post-conflict (shaded bar) and matched control (clear bar) observations (A = adult; J = juvenile; M = male; F = female; Wilcoxon Signed Rank Test, $P = 0.0454$).

Test, $P = 0.2049$) nor were members of either sex more likely, in general, to be contact initiators (Wilcoxon-Mann-Whitney Test, $P = 0.2719$).

Dominance status and the kinship of opponents also had no detectable effect on which individual initiated post-conflict interactions. Whether an individual was more or less dominant than its opponent did not influence contact initiation (Wilcoxon Signed Rank Test, 5 zero scores: T+ = 21, T- = -15, $P = 0.7263$). Likewise, relatedness of opponent did not influence whether an individual initiated reconciliation (Wilcoxon Signed Rank Test, N = 10, 3 zero scores: T+ = 9, T- = -19, $P = 0.4469$). Individuals with no kin were excluded from the analysis. Note that no matrilines contained more than one adult female, simplifying the application of kinship and dominance data.

Of the factors analyzed, the age of the opponents appeared to have the strongest influence on reconciliation. Regardless of age, aggressors were more likely to attack juveniles than to attack adults (Wilcoxon Signed Rank Test, 2 zero scores: T+ = 59, T- = -7, $P = 0.0234$). Juveniles were significantly more likely than adults to be contact initiators (Figure 3; Wilcoxon-Mann-Whitney Test, $P = 0.0321$). There were also significant reconciliatory differences among individuals with respect to the age of the opponent (adult:adult vs. adult:juvenile vs. juvenile: juvenile; Kruskal-Wallis, $P = 0.0344$) with juvenile:juvenile pairs more likely to be attracted than adult:adult pairs (Multiple Comparisons, $P < 0.05$).

DISCUSSION

Although zoo personnel have attempted to simulate natural conditions for this group of macaques, restricted space, small group size, and human presence necessitate caution when relating the findings of this study to wild populations.

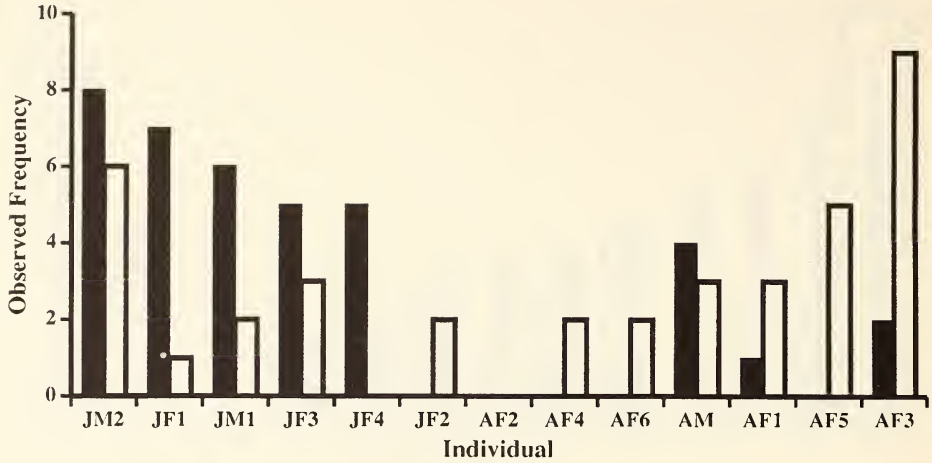

Figure 3. The number of times each individual was an active contact initiator following a conflict (shaded bar) and a passive contact (clear bar) recipient (A = adult; J = juvenile; M = male; F = female; Wilcoxon-Mann-Whitney Test, $P = 0.0321$).

Nevertheless, some general tendencies are apparent regarding the social behavior of Japanese macaques in captivity.

Selective attraction, as defined by de Waal and Yoshihara (1983), involves both an absolute and relative increase in post-conflict affiliation between opponents. This occurred in the captive Japanese macaque troops studied by Friedlen and Chaffin (1991) and Aureli, *et al.* (1993) as well as in the Indianapolis group discussed here. The Japanese macaque is part of a growing list of primate species in which such reconciliatory behavior occurs. Contact between opponents following a conflict is thought to function not only in the repair of social relationships (de Waal and van Roosmalen, 1979) but also in the maintenance of group cohesion (de Waal, 1986) and in the reduction of acute stress in victims of aggression (Aureli, *et al.*, 1989; Aureli and van Schaik, 1991b). The prevalence of reconciliation among primate groups has prompted de Waal (1986, 1987) to call for its inclusion as a fundamental concept in the study of social dominance.

Although sex, dominance status, and kinship of opponents did not influence reconciliation, the age of opponents played an important role in post-conflict interactions. Juveniles were the individuals most likely to initiate contact following an aggressive encounter. Adults almost never actively reconciled conflicts involving juveniles. Perhaps juveniles benefit from affiliative post-conflict interactions more than adults. In this study, aggression between individuals of differing age classes was directed almost entirely toward juveniles. Therefore, juveniles should be more likely to initiate reconciliation if such behavior diminishes the threat of aggression from an adult. Other studies support this hypothesis: long-tailed macaques exhibit a decreased frequency of displacement behavior following allogrooming (Schino, *et al.*, 1988) and the threat of future aggression

appeared to diminish among pigtail macaques following reconciliation (Judge, 1983). However, other studies have offered only weak support for this trend (Aureli, *et al.*, 1989).

The occurrence of defensive coalitions could partly explain the age bias in reconciliation behavior. Kurland (1977) found that adult Japanese macaques often came to the defense of juveniles that were victims of aggression, thereby halting further aggression. Although this type of coalition was most common among related females, other individuals, particularly the dominant male, often defended non-relatives. This observation suggests that juveniles should actively solicit reconciliation with adults, as such action could secure valuable allies in future conflicts.

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