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RESEARCH ARTICLE

Successive Aggression: Another Pattern of Polyadic Aggressive Interactions in a Captive Group of Japanese Macaques

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Several patterns of polyadic aggressive interactions have been previously reported. Here, we describe another pattern of polyadic interactions in a captive group of Japanese macaques (*Macaca fuscata fuscata*) that we designate as ''successive aggression''. We defined successive aggression as aggression by the original actor toward a second recipient within a very short time interval after the initial aggression toward the first recipient. We compared the patterns and characteristics of successive aggression to those of redirection. Among 2,698 recorded aggressive interactions, 80 involved successive aggressions and 75 were classified as redirections. Females, especially adult females, performed and received more successive aggression, whereas males, especially adult males, performed and received more redirection. Successive aggression often occurred when the first recipient exhibited counter-aggression. Successive aggression was then directed toward an individual related to the first recipient, such as the mother, offspring or sibling. The targets of redirection were not relatives of the first aggressor in most cases, but were clearly subordinate individuals. The dominance relationships among the aggressor, the first recipient and the second recipients were usually non-linear for successive aggression, but were linear for most cases of redirection. These results suggest that monkeys can anticipate possible opponents who may intervene in ongoing aggressive interactions and suppress them, even though they are not yet hostile toward these individuals. Successive aggression may function to establish and maintain dominance relationships among matrilineal groups through repeated confirmations. Am. J. Primatol. 70:349–355, 2008.

Key words: successive aggression; redirection; polyadic interaction; Japanese macaque

INTRODUCTION

Most primate species live in well-organized social groups that entail many potential benefits for its members. However, social living also entails a number of costs, because group-living animals inevitably compete with each other for resources such as food, water and mates [Mason & Mendoza, 1993; Walters & Seyfarth, 1987]. In a social group, aggressive interactions between two individuals can be influenced by the many monkeys that surround the original dyad [Chapais et al., 1991, 1995; Cheney & Seyfarth, 1986; Das, 2000; Walters & Seyfarth, 1987; Watts et al., 2000]. A third individual, such as the mother or a sibling, may support its relatives [Berman, 1980; Chapais, 1991; Chapais et al., 1991, 1995, 1997; Chapais & Gauthier, 2004; de Waal et al., 1976; Eaton, 1984; Kaplan, 1977; Kurland, 1977; Pereira, 1989; Walters, 1980; Watanabe, 1979]. Such aggressive intervention by a third individual in an ongoing dyadic interaction typically leads to a polyadic interaction.

Additionally, patterns of polyadic aggressive interactions other than direct intervention have been described. Monkeys sometimes direct their aggression toward a third party while they are still dealing with the opponent from the first aggressive interaction. For instance, monkeys may be able to pass the aggression received from an aggressor on to a third individual. In this case, the recipient may frequently turn back to the aggressor while repeatedly looking at and threatening other individuals, which may make the original direction of the aggressive act ambiguous and uncertain. This behavior has been designated as redirection [Aureli et al.,

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1992; Castles & Whiten, 1998; de Waal et al., 1976; Scucchi et al., 1988; Watts, 1995]. Redirection may also function to divert the attention of the original aggressor toward a new target and involve him or her in a joint action [de Waal & van Hooff, 1981; Itani et al., 1963]. Some researchers have described redirection as a post-conflict interaction that functions to reduce anxiety [Aureli et al., 1993; Aureli & van Schaik, 1991; Castles & Whiten, 1998; Cheney & Seyfarth, 1989; Watts, 1995] or to retaliate against the aggressor's kin [Aureli et al., 1992].

In other cases, the aggressor may be observed to quickly change its target to a second individual. The second target is often closely related to the first recipient and this second act of aggression is apparently related to the first interaction. In this study, we designate such an interaction pattern as ''successive aggression''. Successive aggression is characterized by sequential expansion of the interaction by the aggressor toward a second individual within a very short time interval. Although such interactions have usually been regarded and analyzed as two independent dyads (or events), we regard them as related interactions that are influenced by the presence of other individuals nearby.

Successive aggression has received less attention than redirection and no detailed analyses have been carried out to date, with the exception of brief descriptions by Eaton [1984] and Zaragoza and Colmenares [2002]. We observed this interaction pattern in a captive group of Japanese macaques (*Macaca fuscata fuscata*). The aims of our study were to describe the successive aggression pattern in comparison with that of redirection in Japanese macaques, to clarify the roles of these behaviors in their social lives and to deduce the possible functions of these behaviors. We hope that our findings will be useful for better understanding of the complexity of the social interaction patterns in macaque societies.

METHODS

The study was carried out in a captive group of Japanese macaques in the Primate Research Institute, Kyoto University that were introduced from Takahama, Fukui Prefecture, Japan, in 1970 and 1971. The monkeys were maintained in a 960-m^2 open-air enclosure surrounded by a 5 m high concrete wall topped with an electric fence. Several huts, some climbing apparatus, a pool and a shade tree were available inside the enclosure. They were fed with monkey chow every morning, and sweet potatoes two or three times a week. Wheat, peanuts and several kinds of fruit and vegetables were given occasionally. Water was available at all times throughout the day. The monkeys were maintained with minimal interference, except for the periodic removal of specified individuals permanently. The study group was composed of 43 individuals, comprising nine juvenile males (1–4.5 years of age), nine juvenile females (1–3.5 years of age), one sub-adult male (5 years of age), three sub-adult females (3.5–5 years of age), six adult males (>6 years of age) and 15 adult females (>5 years of age) in 2006. Ten infants were born during the study period, but were not included in the analysis. All group members were born in the enclosure and 11 matrilineal groups consisting of two to eight individuals were known among them.

Data were collected during 300 hr of observation from January to October 2006. Observations were carried out between 07:00 and 17:00 h. Aggressive interactions between group members were recorded according to the ''all occurrence'' sampling method [Altmann, 1974]. We recorded aggressive interactions among all group members chronologically (except for infants aged <1 year); that is, those that started an aggressive interaction, the target individual and its progress. We noted the identities of all individuals involved, the contents of those interactions and the consecutive changes. Aggressive behavior included open-mouth threats, lunging, chasing, slapping, grabbing, wrestling and biting. Submissive behavior included fleeing, grimacing, fear screaming, avoidance and retreat. Whenever the recipient of aggression responded with aggressive behavior instead of immediate submission, we classified this behavior as ''counter-aggression'' [Cooper & Bernstein, 2002]. In particular, we took note of successive aggression and redirection patterns. When the aggressor continued his/her aggression toward a second recipient immediately after attacking the first recipient, this was defined as successive aggression. In contrast, if a third individual comes to direct aggression toward an individual already engaged or immediately following a separate dyadic aggressive interaction, it was defined as aggressive intervention by that individual.

In contrast, redirection followed the criteria of Cheney and Seyfarth [1989], Gore [1994], and Scucchi et al. [1988], in which the recipient (victim) of an aggressive interaction attacked a third individual (second recipient) immediately after receiving aggression from the first aggressor. Each redirection and successive aggression pattern was divided into two dyadic components (i.e., first and second dyads). Only when the first and second dyads which occurred consecutively and when the time interval between these two dyads was less than 1 min, they were considered to be successive aggression or redirection. In successive aggression, the first dyad included the aggressor and the first recipient and the second dyad involved the aggressor and a second recipient. In redirection, the first dyad included the aggressor and the recipient, whereas the second dyad involved the recipient turned into an aggressor and a newly targeted recipient. These aggressive interactions usually occurred spontaneously and it was difficult

to clarify the original context for both successive aggression and redirection, although the conflicts often occurred during feeding.

It is possible that monkeys may attack an additional individual standing near the original recipient without choosing a specific target. To avoid bias resulting from such accidental situations, we only regarded the second recipient as the target of successive aggression when the aggressor directed its second round of aggression toward an individual who was in the opposite direction from the first victim, that is, at a position with an angle of $>90^\circ$ between two imaginary lines from the aggressor to the victim and from the aggressor to the target.

The dominance rank order among group members was deduced on the basis of asymmetric patterns from 1,728 episodes of submissions and avoidances. The clear rank order was detectable from dyadic interactions among them by each age/sex classes (adult males, adult females and juveniles) throughout the study period though some rank changes occurred. A matrilineal rank was assigned to each individual based on the highest individual rank of the adult female of each matrilineal group [Aureli et al., 1992].

Statistical analyses were carried out using *Z*-test for two proportions, *G*-test for goodness-of-fit, the χ^2 test of independence with continuity correction, and the χ^2 goodness-of-fit test [Sokal & Rohlf, 1995]. We used the *G*-test for goodness-of-fit to compare the frequency of behaviors between each age–sex classes. The expected value was calculated from the number of possible dyadic combinations between relevant age–sex classes divided by the total number of possible combinations for all group members. As the expected values between some age/sex classes were very small, we included sub-adult males in the adult male class, sub-adult females in the adult female class and juvenile males and females in a juvenile class.

We used the *Z*-test for two proportions to examine the difference between males and females in performing successive aggression and redirection. We also used the *Z*-test to compare the proportion of aggression directed to relatives (individuals belonging to the same matrilineal group) and non-relatives of recipient individuals. In the case of redirection, we compared the proportion of redirected aggression toward the initial aggressors relative or non-relatives. As the number of available relatives is different for each individual, we calculated the expected values from the total number of relatives and non-relatives that could be involved in each bout of successive aggression and redirection, respectively.

The research complied with protocols approved by The Committee of Research and Animal Welfare, Primate Research Institute, Kyoto University [2002], which meet the legal requirements of the Japanese Government. Observers had obtained a Certificate of Husbandry and Experiments on Primates (No. GN-0025) before carrying out the observations, as well as an observation permit (No. 06-1436).

RESULTS

We recorded a total of 2,698 aggressive interactions, including 80 successive aggressions and 75 redirections (Table I). In addition, we observed an additional 37 possible cases of successive aggression directed toward second recipients at $<90^\circ$ to the axis of

TABLE I. Frequency of Successive Aggression and Redirection Observed Among Group Members

	Successive aggression	Redirection	*Z*-test for two proportions
Performer			
Male (16)	28	41	
Female (27)	52	34	$Z = 2.510$, $P = 0.012$
Juvenile male (9)	21	18	
Juvenile female (9)	19	16	$Z = 0.038$, $P > 0.05$
Sub-adult male (1)	1	2	
Sub-adult female (3)	2	10	$Z = 0.569$, $P > 0.05$
Adult male (6)	6	21	
Adult female (15)	31	8	$Z = 5.567$, $P < 0.001$
Second recipient			
Male (16)	19	44	
Female (27)	61	31	$Z = 4.758$, $P < 0.001$
Juvenile male (9)	15	16	
Juvenile female (9)	9	16	$Z = 0.943$, $P > 0.05$
Sub-adult male (1)	3	8	
Sub-adult female (3)	2	5	$Z = 0.060$, $P > 0.05$
Adult male (6)	1	20	
Adult female (15)	50	10	$Z = 11.746$, $P < 0.001$
Total (43)	80	75	

The number of individuals belonging to each age/sex class is indicated in parentheses.

the first interaction. Of the 369 aggressive interventions observed, 46 were performed by individuals related to the first recipients that were nearby when the initial aggressive bout occurred (loser-supports). It was difficult, however, to discriminate their roles precisely in some cases because the interactions progressed very quickly over short distances. Therefore, we excluded these 37 examples from our analysis according to the definition of the behavior.

Males and females showed different trends in performing or receiving successive aggression or redirection; females performed and received successive aggression more often while males performed and received redirection more often (Table I). The difference was more conspicuous between adult males and adult females. These trends were not found in juveniles. The difference between males and females was not discernible in sub-adults although the number of examples observed was low. Thus, this trend may only appear when the animals become adults.

Successive aggression and redirections varied significantly between age–sex classes (G-test of goodness-of-fit; successive aggression: $G = 28.547$, $df = 8$, $P < 0.001$, redirection: $G = 91.947$, $df = 8$, $P < 0.001$). Successive aggression occurred most often between adult females (Fig. 1). Adult females were involved in a total of 75% (60/80) of all successive aggressions. In contrast, redirection occurred mainly between adult males. Adult males were involved in a total of 32% (24/75) of redirections while adult females rarely displayed redirection.

Successive aggression occurred significantly more often when counter-aggression was observed in the first dyad. Counter-aggression by the victim was observed in 25% (20/80) of first dyads, compared with only 13% (44/337) of dyadic aggressive interactions that involved the same aggressor and victim pairs (χ^2 test of independence: $\chi^2 = 6.209$, $df = 1$, $P = 0.013$). Counter-aggression was seen in 14% of all dyadic aggressive interactions ($n = 2{,}367$), which was also significantly different from that of successive aggression ($\chi^2 = 6.424$, $df = 1$, $P = 0.011$). In contrast, counter-aggression was rare in the first dyad of a redirection, and was 9.3% (7/75) with no significant differences noted between that of dyadic aggressive interactions 7.2% (23/320) ($\chi^2 = 0.152$, $df = 1$, $P = 0.697$).

Successive aggression was directed more often toward a relative of the victim (Z-test: $Z = 24.231$, $P < 0.001$; Fig. 2). Among the 80 successive aggressions observed, 66 (84%) were directed toward a mother–offspring pair (43 cases of offspring first and then mother, and 23 cases of mother first and then offspring), three toward a sibling pair, two toward an aunt–niece pair and one toward a grandmother–grandson pair. Among the remaining eight successive aggressions performed toward a non-relative, four involved a 3-year-old female and the mother that adopted her after removal of her original mother. In contrast, redirection was not directed significantly more often toward a relative of the aggressor (Z-test: $Z = 1.184$, $P = 0.236$, Fig. 2). We found that males, especially adult males, did not attack aggressors' relatives but attacked lower-ranked individuals. Out of 75 cases of redirection only six cases were directed toward the related individuals of first aggressors, in which five cases were performed by females and one case performed by a juvenile male. In successive aggression, most of the targets (81%) belonged to lower-ranked (sixth to 11th) matrilineal groups that involved 42% of group

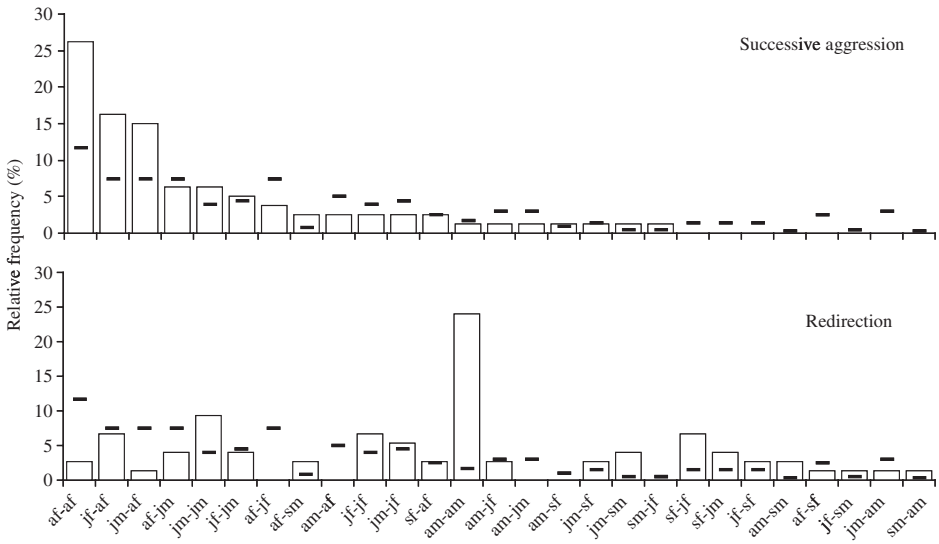

Fig. 1. Relative frequencies of successive aggressions and redirections in the combinations of performers and the second recipients. The combination of performer (left) and second recipient (right) is indicated at the bottom of the figure. af, adult female; sf, sub-adult female; jf, juvenile female; am, adult male; sm, sub-adult male; jm, juvenile male. Dashes indicate expected frequency for each combination. Some possible combinations with no interaction observed are not shown.

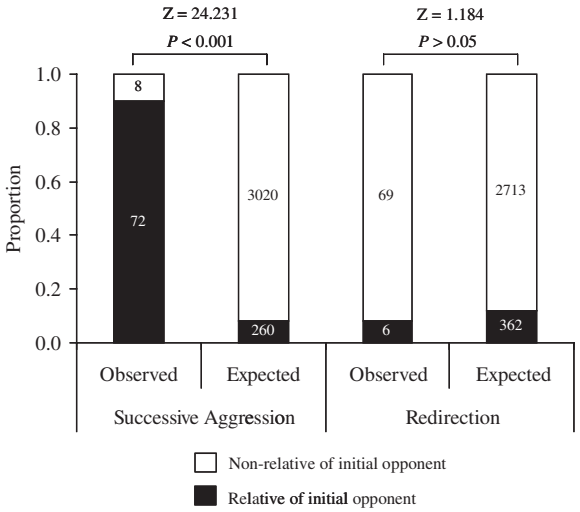

Fig. 2. The proportions of initial opponent's relative as the second recipient in successive aggressions and redirections.

members (Z-test = 4.590, $P < 0.001$). In redirection, most of the targets were adult males.

Analyses of these two types of interactions revealed that the dominance relationships among aggressor, first and second recipient were non-linear for successive aggression, but were linear for redirection. The aggressors in successive aggression consecutively directed their aggression from a lower-ranked recipient toward a higher-ranked second recipient (compared with the original recipient). For example, 19 of 21 (90%) successive aggressions that involved only adult female recipients were of this type (χ^2 goodness-fit-test: $\chi^2 = 13.762$, df = 1, $P < 0.001$). Many successive aggressions were directed toward offspring as the first recipient and then the mother as the second recipient. In redirection, the aggressors attacked a low-ranked victim and the victim then passed the aggression on to an even lower-ranked target. Overall, in all 26 and 14 cases of redirection that involved only adult males or adult females as the aggressor, the victims and targets were of these types.

DISCUSSION

Although polyadic aggressive interactions in macaques have been studied by many authors [for reviews, see Aureli et al., 1992, 1993; de Waal & Yoshihara, 1983; Gore, 1994; Scucchi et al., 1988], the successive aggression pattern has not been described in detail and has received less attention. Successive aggression can be considered to be a polyadic interaction pattern, as the first and second dyads occur in close association: (1) they occur as sequential interactions within a very short time interval; and (2) the participants, especially the recipients, are mainly closely related individuals. The aggressor attacks a second individual related to the first recipient, which may indicate that the aggressor understands the relationship between the two recipients and anticipates possible attacks by the related individual. Aggressors were often observed to search for specific target individuals. Specifically, they stood up on their hind legs to look for the target and then rushed toward a specific target. This pattern may not be a simple ''escalation'' [Eaton, 1984] and may have different functions.

There is a possibility that the second dyad in successive aggression could occur as a response to threatening signals given by the second recipient. We should admit that the subtle changes in facial expression and/or posture of surrounding individuals could not be fully recognized. The initiators of the second dyads, however, always attacked the second recipient spontaneously and without discontinuation from the initial act of aggression. When behavior cues from the third individual before attacking the first aggressor were obvious (e.g., rushing or lunging to attack), the data were recorded as an aggressive intervention. When, however, this individual's behavior or role was ambiguous (i.e., when the successive aggression targeted a second recipient in close proximity and within 90° of the axis of the first recipient), these interactions were excluded. Therefore, the influence of subtle behavioral changes in surrounding individuals should be negligible.

Females performed and received more successive aggression than males, whereas males performed and received more redirection than females. This could be due to differences in social life within the group. Females usually live in the central part of the group [Itani et al., 1963; Rasmussen & Farrington, 1994] and are always surrounded by other group members. Accordingly, females need to pay more attention to the behavior of other individuals, and when they have a conflict with another group member, they need to act in anticipation of the upcoming behavior of surrounding individuals at any time. Monkeys may understand accurately the relationships among group members [Byrne, 1995; Cheney & Seyfarth, 1986, 1989, 1999; Seyfarth & Cheney, 2000; Silk, 1999] and therefore immediately attack a nearby individual related to the victim, even if they did not receive any aggression from them. This may make them more secure from unexpected attacks by surrounding individuals, especially closely related monkeys such as the mother or offspring, who are most likely to carry out such behavior.

Most adult/adolescent males live in peripheral parts of the group and are therefore rarely supported by other group members [Watanabe, 1979]. Regarding attacks by males on other individuals in peripheral parts of the group, the sparse distribution of the monkeys may allow them to easily detect other individuals and their behavior. In such situations, redirection can be carried out quite easily. Therefore,

the functions of these behaviors may be different. In other words, successive aggression is an act by the aggressor that anticipates possible subsequent attacks on them by the victim's relatives to suppress such acts before relatives can intervene in the ongoing dyad. In contrast, redirection may mediate the original aggression toward the victim by involving another target and dispersing the focus of the original aggression [de Waal & van Hooff, 1981; Scucchi et al., 1988].

Scucchi et al. [1988] reported that adult monkeys were rarely involved in redirection. However, the criteria for their age–sex classes differed from those in our study, in that adults only included animals above 9 years of age for males and above 7 years of age for females. Even taking this into consideration, many adult monkeys performed and received redirections as well as successive aggressions in this study. One possible reason could be that redirections were mainly performed by males and the study group of Scucchi et al. [1988] only included two adult males. Some individual differences and/or different conditions of the study groups may also contribute to the discrepancy.

It is interesting that successive aggression occurred more often when counter-aggression by the first recipient was observed. When the victim of aggression is hostile toward its aggressor, a third individual may intervene in the dyad more often [Watanabe, unpublished data]. The performers of successive aggressions seem to be able to predict precisely who may interfere and the possible outcomes of ongoing social interactions in the group. In the case of redirection, counter-aggression was rare in the first dyad. Part of the reason for this could be that redirection was performed by males, especially adult and adolescent males. The dominance order among adult males is very clear [Koyama, 1967] and no more supports for losers by group members could be predicted [Watanabe, 1979]. Males may confirm and maintain their dominance relationships through redirection patterns.

Successive aggression may function to establish and maintain dominance relationships among matrilineal groups through repeated confirmations. Monkeys in the group should be aware of the relationship between other members in relation to their own status. They might be able to recognize matrilineal kin groups and behave appropriately as if he/she recognizes such relationships [Seyfarth & Cheney, 2000]. The many different patterns of polyadic interactions among Japanese macaques are likely related to the monkey's ability to predict forthcoming social interactions.

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