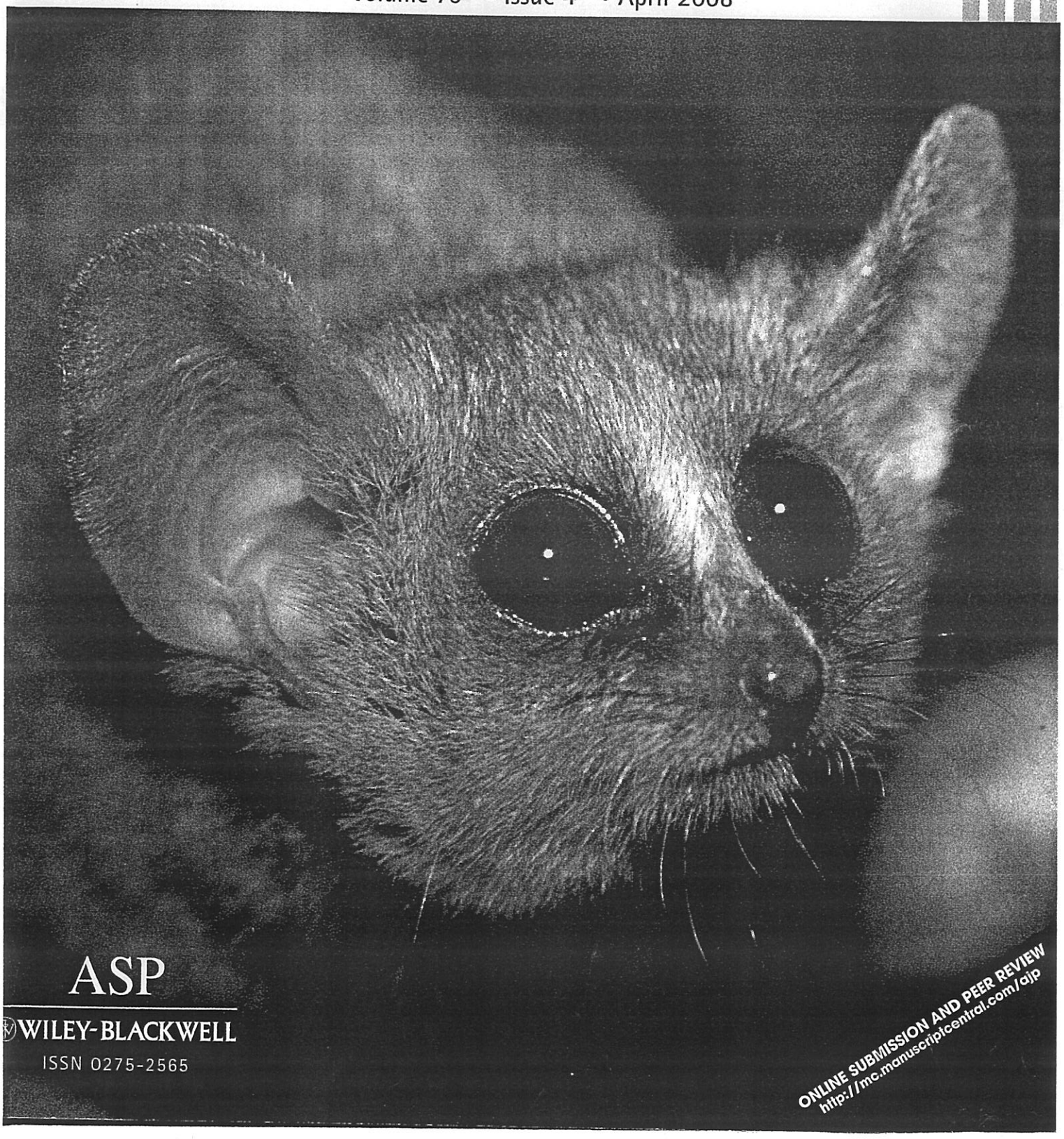
Official Journal of The American Society of Primatologists

AMERICAN JOURNAL OF PRIMATOLOGY

Volume 70 • Issue 4 • April 2008



ASP
WILEY-BLACKWELL
ISSN 0275-2565

1-7

American Journal of Primatology 70:349–355 (2008)

RESEARCH ARTICLE

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

RIZALDI[1,2*] AND KUNIO WATANABE[1]
[1]*Primate Research Institute, Kyoto University, Inuyama, Japan*
[2]*Department of Biology, Andalas University, Padang, Indonesia*

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.,

*Correspondence to: Rizaldi, Primate Research Institute, Kyoto University, Kanrin, Inuyama, Aichi 484-8506, Japan.
E-mail: rizaldi@pri.kyoto-u.ac.jp

Received 17 February 2007; revised 20 August 2007; revision accepted 27 September 2007

DOI 10.1002/ajp.20492
Published online 23 October 2007 in Wiley InterScience (www.interscience.wiley.com).

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 $>90°$ 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 $<90°$ 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.

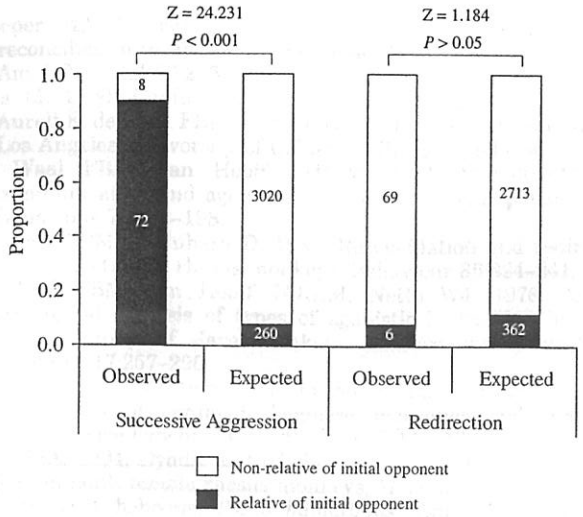


Fig. 2. The proportions of initial opponent's relative as the second recipient in successive aggressions and redirections.

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,

Cooper MA, Bernstein IS. 2002. Counter aggression and reconciliation in Assamese Macaques (*Macaca assamensis*). Am J Primatol 56:215–230.

Das M. 2000. Conflict management via third parties. In: Aureli F, de Waal FBM, editors. Natural conflict resolution. Los Angeles: University of California Press. p 263–280.

de Waal FBM, van Hooff JARAM. 1981. Side-directed communication and agonistic interactions in chimpanzees. Bahaviour 77:164–198.

de Waal FBM, Yoshihara D. 1983. Reconciliation and redirected affection in rhesus monkeys. Behaviour 85:224–241.

de Waal FBM, van Hooff JARAM, Netto WJ. 1976. An ethological analysis of types of agonistic interaction in a captive group of Java monkeys (*Macaca fascicularis*). Primates 17:257–290.

Eaton GG. 1984. Aggression in adult male primates: a comparison of confined Japanese macaques and free-ranging olive baboons. Int J Primatol 5:145–160.

Gore MA. 1994. Dyadic and triadic aggression and assertiveness in adult female rhesus monkeys, *Macaca mulatta*, and hamadryas baboons, *Papio hamadryas*. Anim Behav 48: 385–392.

Itani J, Tokuda K, Furuya Y, Kano K, Shin Y. 1963. The social construction of natural troops of Japanese monkeys in Takasakiyama. Primates 4:1–42.

Kaplan J. 1977. Pattern of fight interference in free-ranging rhesus monkeys. Am J Phys Anthropol 47:279–288.

Koyama N. 1967. On dominance rank and kinship of a wild Japanese monkey troop in Arashiyama. Primates 8:189–216.

Kurland JA. 1977. Kin selection in the Japanese monkey. In: Szalay FS, editor. Contribution to primatology. New York: Karger. p 1–145.

Mason WA, Mendoza SP. 1993. Primate social conflict: an overview of sources, forms, and consequences. In: Mason WA, Mendoza SP, editors. Primate social conflict. Albany: State University of New York Press. p 1–11.

Pereira ME. 1989. Agonistic interactions of juvenile savanna baboons. II. Agonistic support and rank acquisition. Ethology 80:152–171.

Primate Research Institute, Kyoto University. 2002. Guide for the care and use of laboratory primates, 2nd edition (in Japanese). Inuyama: PRI. 60p.

Rasmussen DR, Farrington M. 1994. Relationships between position in the central-peripheral structure, age, and the dominance index in the Tanaxpillo colony of stumptail macaques (*Macaca arctoides*). Primates 35: 393–408.

Scucchi S, Cordischi C, Aureli F, Cozzolino R. 1988. The use of redirection in a captive group of Japanese monkeys. Primates 29:229–236.

Seyfarth RM, Cheney DL. 2000. Social awareness in monkeys. Am Zool 40:902–909.

Silk JB. 1999. Male bonnet macaques use information about third-party rank relationships to recruit allies. Anim Behav 58:45–51.

Sokal RR, Rohlf FJ. 1995. Biometry, 3rd edition. New York: W.H. Freeman and Company. 850p.

Walters J. 1980. Interventions and the development of dominance relationships in female baboons. Folia Primatol 34:61–89.

Walters JR, Seyfarth RM. 1987. Conflict and cooperation. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT, editors. Primate societies. Chicago: University of Chicago Press. p 306–317.

Watanabe K. 1979. Alliance formation in a free-ranging troop of Japanese macaques. Primates 20:459–474.

Watts DP. 1995. Pos-conflict social events in wild mountain gorillas. II. Redirection, side direction, and consolation. Ethology 100:158–174.

Watts DP, Colmenares F, Arnold K. 2000. Redirection, consolation and male policing: how targets of aggression interact with bystanders. In: Aureli F, de Waal FBM, editors. Natural conflict resolution. Los Angeles: University of California Press. p 281–301.

Zaragoza F, Colmenares F. 2002. Redirection of the aggression by the victim and the aggressor in Hamadryas Baboons (*Papio hamadryas hamadryas*). [Abstract]. Folia Primatol 73:295.

AMERICAN JOURNAL OF PRIMATOLOGY

Volume 70, Number 4 **April 2008**

Volume 70, Issue 4 was mailed the week of March 17, 2008.

Cover photo: Gray mouse lemur (*Microcebus murinus*), Kirindy Forest, Western Madagascar.
Courtesy of: Manfred Eberle, www.phocus.org

WILEY-BLACKWELL
A WILEY-LISS, INC., PUBLICATION