Intergroup Encounters in Wild Moor Macaques (*Macaca maurus*)

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ABSTRACT. We studied intergroup encounters among moor macaques at the Karaenta Nature Reserve, South Sulawesi, Indonesia. Group B has been observed on the basis of individual identification since 1988. We analyzed 85 encounters between members of Group B and members of neighboring groups from September 1990 to November 1998. The average frequency of intergroup encounters was 0.035/hour. Neither the presence of females in estrus nor rainfall had an effect on encounter frequency. Behaviors of moor macaques during intergroup encounters differed from those of Japanese macaques. In moor macaques, no intergroup interactions with body contact were observed during encounters, and females never directed aggression toward members of different groups. The present study did not confirm the prediction of the model of VAN SCHAIK (1989). Extension of the existing models is required to explain the difference in female dominance styles among macaques by socioecological factors.

Key Words: Intergroup encounter; Between-group competition; Moor macaques; *Macaca maurus*.

INTRODUCTION

Encounters between groups of gregarious primates are essentially agonistic, though considerable variations are found (CHENEY, 1987). Many authors have studied behavior during intergroup encounters as an expression of different types of competition (VAN SCHAIK et al., 1992; PERRY, 1996; SAITO et al., 1998). Behavior of group members during encounters varies according to the gender of the members involved in the encounter (CHENEY, 1987). Females are considered to compete mainly for food resource and males mainly for mates (WRANGHAM, 1980; DAVIES, 1991). The degree of competition, both within groups and between groups, depends on the abundance and distribution patterns of the resource (WRANGHAM, 1980; VAN SCHAIK, 1989; ISBELL, 1991).

Between-group competition plays an important role in recent socioecological models (WRANGHAM, 1980; VAN SCHAIK, 1989; STERCK et al., 1997). The model of VAN SCHAIK (1989) explained how social relationships among females are influenced by ecological factors. Recently, an extended model was proposed by STERCK et al. (1997). On the basis of the strength of within-group contest competition (WGC) and between-group contest competition (BGC), four types of social categories were determined for female primates: DE (Dispersal-Egalitarian), RE (Resident-Egalitarian), RN (Resident-Nepotistic), and RNT (Resident-Nepotistic-Tolerant) (STERCK et al., 1997).

Macaques in general were considered to be representatives of the RN type by STERCK et al. (1997). However, macaques living on Sulawesi Island were categorized as being of the RNT type. This difference corresponds to the difference in dominance styles among macaques (DE WAAL & LUTTRELL, 1989; THIERRY et al., 1994). Variations in social characteristics among macaque species have been studied intensively under captive conditions. Some macaque species such as Japanese and rhesus macaques show a strict or despotic dominance style, which is characterized by highly asymmetrical dominance relations and a strong nepotistic tendency. By contrast, stumptail macaques and Sulawesi species exhibit a more relaxed or egalitarian dominance style. The socioecological models tried to explain such social differences as being caused by ecological factors.

The RN type is characterized by strong WGC for food. RN type is expected among those primates living in cohesive groups whose food is distributed in clear-cut patches that are usually too small to accommodate all group members (VAN SCHAIK, 1989). When WGC is strong, females should form long-term agonistic alliances with relatives and stable, linear and nepotistic hierarchies are expected. Primates of the RNT type are expected to occur in environments where the resources are (at least seasonally) distributed in rare but large patches and the predation risk is low (VAN SCHAIK, 1989). This condition may be satisfied on oceanic islands (including Sulawesi), where carnivores and large raptors are absent. The high population density expected in predator-poor environment leads to strong BGC for food. High-ranking females need cooperation from lower-ranking females because they suffer a loss if low-ranking females tend to leave their group or are reluctant to participate in intergroup encounters. Therefore, high-ranking females should not enforce dominance too strongly, and these dominance relationships normally become more tolerant.

Theoretically, a key to distinguishing between RN and RNT types is in the strength of BGC. However, there is little evidence that BGC is stronger in macaques of the RNT type than those of the RN type. For example, some researchers expect that female aggression during intergroup encounters is more frequent and intense when BGC is stronger (e.g. ISBELL, 1991; CHENEY, 1992). However, few studies have provided quantitative data on female aggression during encounters (CHENEY, 1987), although female aggression has been reported in many macaque species, including Japanese macaques (KAWANAKA, 1973), rhesus macaques (SOUTHWICK et al., 1965), long-tailed macaques (WHEATLEY et al., 1996), Tibetan macaques (ZHAO, 1997), pig-tailed macaques (OI, 1990), lion-tailed macaques (KUMAR & KURUP, 1985), and barbary macaques (MEHLMAN & PARKHILL, 1988). Recently, comparative studies of Japanese macaques in two different habitats provided quantitative data on intergroup encounters (SAITO et al., 1998; SUGIURA et al., 2000). Quantitative data from the RNT type macaques are necessary for cross-species comparisons between the RN type macaques and the RNT type macaques.

Moor macaques, which live on the southwestern peninsula of Sulawesi Island, are considered to be egalitarian (MATSUMURA, 1998), RNT type macaques (STERCK et al., 1997). MATSUMURA (1998, 1999) argued that the BGC hypothesis (VAN SCHAIK, 1989) does not appear to fit moor macaques because he did not observe aggressive behavior of females during 16 intergroup encounters during four months of observation in 1990 – 1991. In this paper, we analyzed long-term data about intergroup encounters in moor macaques (85 encounters from September 1990 to November 1998). We examined factors influencing the encounter frequency and intergroup behaviors. Then, we compared the results with recent reports about wild Japanese macaques in two different habitats (SAITO et al., 1998; SUGIURA et al., 2000). Finally, we examined the validity of the existing socioecological models.

MATERIALS AND METHODS

SUBJECTS

Group B of moor macaques (*Macaca maurus*) in the Karaenta Nature Reserve, South Sulawesi, Indonesia, has been observed since 1988 on the basis of individual identification. For a detailed description of the study site, see WATANABE and MATSUMURA (1996). We analyzed encounters between Group B and neighboring groups for nine years between 1990 and 1998. The total observation time was 2235.5 hr (709 days). Group B consisted of 22 individuals (3 adult males and 9 adult females) at the beginning of the study and 40 individuals (7 adult males and 14 adult females) at the end of the study.

DEFINITION

The definitions of intergroup encounter and behavior during encounters followed that of studies on Japanese macaques (SAITO et al., 1998; SUGIURA et al., 2000). An intergroup encounter was defined as occurring when two groups approached one another and members of the study group were regarded as having recognized the other group.

We recorded the presence or absence of the following seven types of behavior (SAITO et al., 1998) during the encounter:

Rush: when the study group swiftly shifted toward another group until they confronted

Flee: the study group "fled" when it swiftly retreated from the opponent group

Tension: tension was recorded if we observed an increase in vocalization, vigilance, or scratching behaviors in the study group

Line-up: when we observed that two group members lined up and confronted to the other group, either screaming or threatening

Contact: when the intergroup encounter involved inter-individual interaction between different group members, such as agonistic interaction (in the present study, we restricted this to agonistic interaction with body contact), grooming, and social play, we recorded that "contact" occurred between groups

Aggression: inter-individual agonistic interaction between different group members, e.g. threat and submission, charge, hit, etc.

Displace: displacement of a group from its original direction by another group. (In the present study, *displace* was regard to occur only when the original direction of group movement changed clearly.)

METHODS OF ANALYSES

Based on the studies of Japanese macaques, we considered the following three factors as possibly influencing encounters. The first factor is the *presence of females in estrus*. As a clear mating season is not recognized in moor macaques, the number of estrous females was counted daily. The second one is *rainfall seasonality*. The amount of rainfall would influence the abundance and distribution patterns of food resources, in particular, fruits (MITANI, 1999). If the average rainfall in a given month is more than 200 mm, the month is considered as part of the rainy season. The dry season is from May to October, and the rainy season is from November to April. The third factor is the *group size*. The group size increased from 22 to 40 during the study period, which we divided into two periods: the former period (1990 – 1994) and the latter period (1994 – 1998). The average group size was 24.8 in the former period and 35.4 in the latter period. Although the size differed significantly between the two periods (Mann-Whitney *U*-test, $U=0$, $p<0.05$), the annual population growth rate and annual number of births did not differ significantly (Mann-Whitney *U*-test, $U=8$ and 7.5, n.s.) (OKAMOTO et al., 2000).

To analyze the effect of the three factors, we divided the data of each year into four units according to the presence/absence of estrous females and rainy/dry season. Then, we calculated the frequency for each unit (number of encounters observed during each unit/observation time of each unit). The frequency of encounters may be biased when the observation time was too short. When we calculated the overall frequency by pooling data for each year, the mean interval between encounters was 28.8 hr. Using this value as a criterion, we excluded the data units where observation time was less than 28.8 hr from the analyses. We tested the effect of the three factors on the frequency of encounters using ANOVA.

We analyzed the occurrence of intergroup behaviors during 84 encounters (1 encounter was excluded from the analysis because of an incomplete observation). We used Mantel-Haenszel statistics for the analyses of the effect of three factors on the frequency of seven types of behavior. These statistics are used to assess average partial association in three-way contingency tables. The relationship between two of the variables can be tested while controlling for the effects of a set of covariables.

We conducted statistical tests with SPSS version 9.0J software (1999).

RESULTS

The average frequency of intergroup encounters was 0.035/hour. This means that Group B encountered another group every 28.8 hr on the average. Table 1 shows the results of the ANOVA. According to our analysis, the presence of estrous females did not influence the frequency of encounters, and encounter frequency during the dry season did not differ significantly from that during the rainy season. The frequency of encounters was significantly higher when the group size was small than when the group size was large.

Table 2 shows the proportions of encounters in which the seven types of behavior were

Table 1. The effect of three factors on the frequency of intergroup encounters.

	df	*F*-value
Factors		
Ⅰ. Presence of estrous females	1	4.24
Ⅱ. Rainfall seasonality	1	1.48
Ⅲ. Group size	1	7.95*
Interactions		
Ⅰ×Ⅱ	1	1.40
Ⅱ×Ⅲ	1	0.26
Ⅰ×Ⅲ	1	3.19
Ⅰ×Ⅱ×Ⅲ	1	0.29

*$p<0.05$.

Table 2. Proportion of encounters in which seven types of intergroup behaviors were observed.

	Intergroup behaviors						
	Rush	Flee	Tension	Line-up	Contact	Aggression	Displace
Proportion	0.27	0.27	0.52	0.04	0.00	0.27	0.17

Table 3. The effect of three factors on the frequency of intergroup encounters.

Variable		Dependent variable Rush	Flee	Tension	Line-up	Contact	Aggression	Displace
Estrous females		0.00	0.92	0.00	0.00	–	0.09	2.25
	Absent	*0.32*	*0.16*	*0.47*	*0.00*	*0.00*	*0.26*	*0.00*
	Present	*0.26*	*0.31*	*0.54*	*0.05*	*0.00*	*0.28*	*0.22*
Rainfall		0.04	0.28	0.19	0.02	–	0.11	0.01
	Dry	*0.24*	*0.32*	*0.57*	*0.05*	*0.00*	*0.24*	*0.19*
	Rainy	*0.30*	*0.23*	*0.49*	*0.02*	*0.00*	*0.30*	*0.15*
Group size		0.17	0.02	0.11	0.17	–	2.40	0.00
	Small	*0.29*	*0.28*	*0.54*	*0.03*	*0.00*	*0.32*	*0.15*
	Large	*0.21*	*0.26*	*0.47*	*0.05*	*0.00*	*0.11*	*0.21*

For each variable, Mantel-Haenszel statistics are shown in the top box. The frequency of each bahavior averaged for each category is shown in italics below the Mantel-Haenszel statistic.

observed. The most common behavior was *tension. Contact* was never observed. *Line-up* was rarely observed. The presence of estrous females, rainfall seasonality, and the group size did not have significant effects on the frequency of these behaviors (Table 3).

The proportion of encounters in which a female or a male of Group B directed aggression toward members of different groups was calculated. Male aggression was observed more frequently than was female aggression (Male: 0.12, Female: 0.00, Wilcoxon signed rank test, N=9, Z=−0.2060, p<0.05).

DISCUSSION

We discuss the present findings in relation to the recent reports about the two natural populations of Japanese macaques. The average frequency of intergroup encounters of our study group was 0.035 /hour. This value was similar to that of Japanese macaques in Yakushima (0.039) and higher than that in Kinkazan (0.012) (Sugiura et al., 2000).

Although the frequency of encounters was similar between Japanese macaques of Yakushima and moor macaques of Karaenta, we observed differences in intergroup behavior. In Yakushima, reproductive seasonality influenced behaviors during encounters. The frequency of *line-up, contact,* and *aggression* was significantly higher in mating season than in non-mating season (Saito et al., 1998). By contrast, the presence of estrous females did not have a significant effect on the occurrence of intergroup behaviors at Karaenta. A striking contrast existed in the frequency of *contact,* which occurred during more than 50% of encounters in Yakushima (Saito et al., 1998). In Karaenta, we have never observed agonistic interactions with body contact, grooming, play, or mating between different groups. It was also noteworthy that females never directed aggression toward members of different groups at Karaenta. From the viewpoint of resource defense, females have been expected to behave aggressively during intergroup encounters (Wrangham, 1980; van Schaik et al., 1992). Female aggression during intergroup encounters has been reported commonly in primates characterized by female philopatry (Cheney, 1987; Isbell, 1991). The lack of female aggression during intergroup encounters in moor macaques at Karaenta is conspicuous.

It has been assumed that female aggression during intergroup encounters is more frequent and intense when BGC is stronger (Isbell, 1991; Cheney, 1992). The present result, however, strongly suggested that the degree of female aggression during intergroup encounters might not be simply correlated to the degree of BGC. Variations in intergroup behavior might be determined by the costs and benefits of their active participation in intergroup encounters. Group members would weigh the advantage of participation, for example, defense of food resource, acquisition and/or defense of mating partners, with a potential risk of injury during encounters. Thus, female intergroup behavior is expected to differ according to various factors such as their dominance rank or reproductive strategies. Although our data are insufficient to analyze behavior of each individual in detail, studies of intergroup encounters as expressions of individual decision-making appear to be promising.

The present study did not confirm the prediction of the model of VAN SCHAIK (1989) that female moor macaques would participate actively in intergroup encounters. According to the above view of female intergroup behavior, the present result may not contradict the viewpoint that the evolution of the difference in dominance styles among macaques can be explained by socioecological factors. It is possible to assume that female moor macaques appeared to compete with females of neighboring groups in more indirect way than that the VAN SCHAIK's (1989) model originally expected. When the group size was large, encounters occurred less frequently. This might result from avoidance by neighboring groups before encounters. As the group size became larger, the home range expanded (OKAMOTO et al., unpubl. data). These suggested that the group size had an effect on the outcome of encounters. We need to extend the existing models to explain the difference in female dominance styles among macaques by socioecological factors.

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