Variation in intergroup encounters among two provisioned free-ranging populations of Japanese macaques *Macaca fuscata*

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Abstract  Typically, Japanese macaques are thought to avoid encountering other groups wherever possible. Intergroup relations between macaques on Shodoshima Island, however, appear exceptional. We show that neighboring groups of Shodoshima monkeys spent 32.8% of their active time in proximity to (<100 m) and even foraged simultaneously at the same provisioning site with another group. The average duration and rate of intergroup encounters at Shodoshima (59.8 min, 0.33 times/hour, n=269) were approximately ten times longer and 16.5 times more frequent than those at Jigokudani (6.1 min, 0.02 times/hour, n=14). Since both populations have similar provisioning and ecological conditions, such variation cannot be explained by the socioecology model alone. Compared with other populations of Japanese macaques, intergroup relations of Shodoshima monkeys are also characterized by more frequent neutral encounters, less frequent agonistic encounters, more frequent unsuccessful displacement, a lower intensity of aggression, and more frequent counter-aggression between groups. These characteristics suggest that intergroup relationships on Shodoshima Island are more tolerant than those in other Japanese macaque populations. This study reveals considerable differences in intergroup encounters within local populations of Japanese macaques living in similar environments, and emphasizes the role of social factors in such intra-specific variation [Current Zoology 58 (4): 517–524, 2012].

Keywords  Intergroup encounter, *Macaca fuscata*, Intra-specific variation, Tolerance

Relationships between groups of primates can range from peaceful to highly antagonistic, and are typically thought to depend on the distribution of resources in a given environment (Wrangham, 1980; Van Schaik 1989; Sterk et al. 1997). Intergroup relations are important factors in numerous theoretical models of primate socioecology, but empirical data on intergroup relations are still limited (e.g. Vessey, 1968; Sugiura et al., 2000; Sicotte and Macintosh, 2004; Boesch et al., 2008). The lack of data is due, in part, to the short duration of intergroup encounters, the low rate of intergroup encounters and the difficulty in reliably observing group-level interactions under conditions of poor visibility in wild populations (Cooper et al., 2004).

The Japanese macaque is one of the most studied non-human primate species. Encounters between groups of Japanese macaques have been studied since 1960s’ (Kawai, 1964). In this species, individuals generally tend to avoid encountering conspecifics of neighboring groups under natural conditions (Kawanaka, 1973). Saito et al. (1998) and Sugiura et al. (2000) have recently reported substantial differences in the intergroup relationships across populations; intergroup encounters are more likely to be agonistic and result in displacement among macaques on Yakushima Island than those on Kinkazan Island. Yakushima is characterized by evergreen forests with more clumped but higher quality food resources than the deciduous forests of Kinkazan, leading Sugiura et al. (2000) to suggest that variation in intergroup relations in this species are primarily associated with food resource defensibility. Among provisioned populations of Japanese macaques, intergroup relations are generally agonistic, and intergroup encounters are rarely observed (Kawanaka, 1973). Aggressive defense of food resources by provisioned monkeys likely reflects the higher value of these resources compared to those available under natural conditions (Yamagiwa and Hill 1998). As a result, provisioning sites for Japanese macaques are generally monopolized by a dominant group, while other neighboring groups avoid provisioning sites occupied by such dominant group (Kawanaka, 1973; Izawa, 1982; Mizu-
Intergroup relationships among the macaques of Shodoshima Island however provide an exception to this rule. In this population, neighboring groups often share the provisioning site and even forage simultaneously (Zhang and Watanabe 2007). Such intergroup tolerance is common in several provisioned and wild groups in the island (Yamada, 1971; Kawamura et al., 1974), but has not been reported in any other populations of Japanese macaques. Shodoshima is located in western Japan, with ecological conditions and monkey population densities and group compositions similar to those of many other habitats of Japanese macaques (Yamagiwa and Hill, 1998). Provisioning history and amount of provisioning food per individual at the Choshikei Monkey Park at Shodoshima do not vary from those of other monkey parks in Japan. Therefore, it is difficult to explain the intergroup tolerance in this population simply as a difference in food resource defense. However, Yamada (1971) and Koyama et al. (1981) reported behavioral differences between Japanese macaques on Shodoshima and those of other populations, including co-feeding in small areas and close inter-individual distances. The behavioral patterns within groups suggest Shodoshima macaques may have more tolerant social relationships among individuals than Japanese macaques elsewhere (Kawamura et al., 1974; Koyama et al., 1981; Zhang and Watanabe, 2007). This difference may relate to the inter-group tolerance and co-feeding at provisioning sites, as any group-level behavior indeed is a complex summation of various individual behaviors (Mehlman and Parkhill, 1988; Cooper et al., 2004). Still, since previous studies have not directly examined intergroup encounters on Shodoshima, the mechanisms underlying their apparent tolerance remain unclear.

We conducted a comparative study of intergroup encounters between the Japanese macaque populations on Shodoshima Island and at Jigokudani in the Shiga Heights, north-central Japan. In this study, we examined whether the rates and durations of intergroup encounters differed between populations. If, as described previously, groups on Shodoshima do not avoid other groups, we expect that their rate and/or duration of intergroup encounters should be higher than at Jigokudani. We also examined variation between populations in the nature of intergroup encounters (whether neutral, approach-retreat or agonistic), the outcome of agonistic encounters (displacement or not), and the intensity of aggression observed (whole-group aggression, partial-group aggression, threats, chases, physical attacks or counter-aggression). According to the female resource defense model (Wrangham, 1980), groups of females tend to form alliances in order to compete against neighboring groups over access to food resources that have patchy distributions and agonistic defense is expected if the benefits of defending a food resource outweigh the costs. This is more likely to be the case when resources are clumped (as provisioned food inherently is) and limiting, then we expect that intergroup encounters at provisioning sites should be agonistic rather than peaceful at both study sites. Where pre-established dominance relations exist between groups, subordinate groups benefit by avoiding potentially costly fights by yielding access to dominant groups. This study will help delineate causal factors behind intra-specific variation in Japanese macaque intergroup relationships, and the relationships between groups of primates in general.

1 Materials and Methods

1.1 Study subjects

We observed SA and SB groups at the Choshikei Monkey Park of Shodoshima Island (34°30’ N, 134°19’E) during non-mating seasons from July 4 to September 14, 2004, and from July 19 to September 11, 2005 (105 observation days: 814 hrs). Shodoshima Island covers 153.5 km², and is located in the Inland Sea of Japan. Seven groups with a total of about 1,700 Japanese macaques live on the island (Watanabe, 2004). Provisioning began at Choshikei Monkey Park in 1956 (ca. 90 individuals in the group), where after the provisioned group increased rapidly in number (ca. 440 individuals in 1967, Mrs. Sakai, senior staff of the monkey park, pers. comm.). The group split into two groups in the 1960s (Yamada, 1971); SA and SB. The fission history was similar as many other provisioned groups of Japanese macaques, but the difference is that the two groups consistently visited the Monkey Park and could feed together at the provisioning site (Zhang P, personal observation). During our study, SA and SB consisted of ca. 452 and 345 individuals, respectively (Table 1). The food was simultaneously spread as wide as possible over an area of 700 m² for each group. Sweet potatoes, wheat grains and vegetables were provided three times a day at 10:00, 14:00, and 16:00. The total amount of food is 0.11 kg/individual/day for the SA group and 0.15 kg/individual/day for the SB group. During provisioning, staff at the monkey park usually spread food at two separate locations within the provisioning site, separated by ca. 30 m. Monkeys of different groups
Table 1  Composition of the study groups

<table>
<thead>
<tr>
<th></th>
<th>Adult male</th>
<th>Adult female</th>
<th>Subadult male</th>
<th>Juvenile</th>
<th>Infant</th>
<th>Unidentified</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>SA group</td>
<td>10</td>
<td>148±9</td>
<td>21±2</td>
<td>164±8</td>
<td>18±7</td>
<td>452±20</td>
<td></td>
</tr>
<tr>
<td>SB group</td>
<td>8</td>
<td>120±7</td>
<td>14±2</td>
<td>113±10</td>
<td>90±9</td>
<td>345±16</td>
<td></td>
</tr>
<tr>
<td>Shiga A1 group</td>
<td>17±1</td>
<td>62±2</td>
<td>12±1</td>
<td>40±3</td>
<td>71±2</td>
<td>177±6</td>
<td></td>
</tr>
<tr>
<td>Shiga A2 group</td>
<td>6</td>
<td>18±1</td>
<td>2</td>
<td>6±1</td>
<td>4±1</td>
<td>41±1</td>
<td></td>
</tr>
</tbody>
</table>

Compositions of SA and SB Groups were surveyed 10 times during provisioning period in 2004. Composition of Shiga A1 group was surveyed 10 times during provisioning period in 2006. Composition of Shiga A2 group was surveyed 3 times during intergroup encounters. The value ± SDs indicate miscounts in some surveys.

could see each other during feeding, but would neither approach nor retreat from each other. Occasionally, staffs distributed provisions at the same location, at which point the two groups could feed together. Still, the macaques did maintain a clear border line between groups at the feeding site. In addition to the provisioning by park staffs, tourists can feed monkeys small amounts of peanuts and soybeans. Monkeys in both groups commonly foraged nature food. In the evening, both groups left the park and slept in different locations between 1 and 4 km away in the mountains.

We observed Shiga A1 and Shiga A2 groups at the Jigokudani Monkey Park of Shiga Heights (36°43′N, 138°27′E) from January 18 to March 10, and from July 8 to September 10, 2006 (100 observation days: 730 hrs). Provisioning began in the Jigokudani Valley in 1963, and like at Shodoshima, the provisioned group increased rapidly in size before splitting into two groups in 1979 (Wada and Matsuzawa 1986); Shiga A1 and Shiga A2. Only Shiga A1 continued to visit the park every day. It consisted of ca. 178 individuals during the study (Table 1). The monkeys are provided 0.11 kg/individual/day of wheat grains and a small amount of soy beans three times per day, at 09:00, 12:00 and 15:00. Forty kilograms of sliced apples were also provided each day at 17:00 during the study period. The amount of provisioning food per individual is not smaller than that at Shodoshima. The food was spread as wide as possible over an area of 1,000 m², like at Shodoshima, but the two groups have never been observed to eat simultaneously at the provisioning site in the past 40 years (Mr. E. Tokida, the manager of the monkey park, pers. comm.).

We classified our study subjects as adult males (estimated to be ≥ seven years old), adult females (estimated to be ≥ six years old), subadult males (estimated to be from four to less than seven years old), juveniles (estimated to be from one to less than six years old), and infants (estimated to be less than one year old, Zhang and Watanabe, 2007). To distinguish the border lines between study groups, especially those during neutral encounters, we identified those members of SB and Shiga A1 groups that were often observed at provisioning sites. Individual identification for Shiga A1 was aided by Mr. E Tokida. Members of SB group were distinguished by dye marking using nontoxic commercial hair dye (Redken deco color, Redken Laboratories Inc., Savage et al., 1993). We sprayed the dye on the backs of all individuals of SB from a distance of ca. 50 cm while they were feeding at the provisioning site. The dye faded on some individuals during the study period, and was reapplied for a second time.

1.2 Data collection and analysis

We followed the dominant group (SB group in Shodoshima or Shiga A1 in Jigokudani) from 08:00 h until 17:00 h during study periods and recorded inter-group encounters ad-libitum (Altmann, 1974). As the focal groups spend most of their time in the Monkey Parks, inter-group encounters were mostly recorded in open area in the parks or at periphery of the park. An inter-group encounter occurred when the distance between groups was less than 100 m, and individuals of the study group had recognized the presence of the other group (Saito et al., 1998). An encounter terminated when two groups separated for greater than 100 m and more than 20 minutes. During encounters, we recorded the time of onset and end, type of encounter (neutral, approach-
retreat, and agonistic; see definitions below), outcome of agonistic encounters (displacement and unsuccessful displacement), intensity of aggression and counter-aggression (Table II). We measured the intensity of agonistic interactions between groups by two criteria: the proportion of group members participating in the interactions (whole-group aggression and partial-group aggression), and the nature of intergroup aggression (threats, chases, physical attacks).

Table 2  Type, outcome and intensity of intergroup encounters

<table>
<thead>
<tr>
<th>Encounter types</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neutral encounters</td>
<td>Those in which the effects of the encounter on the behavior and movement of each group were neutral or unclear, characterized by tolerance of proximity and the absence of intergroup displacement.</td>
</tr>
<tr>
<td>Approach-retreat encounters:</td>
<td>Those in which one group retreated following the approach of another group (in the absence of overt aggression). These interactions began much like neutral encounters, but ended in an approach-retreat sequence between groups.</td>
</tr>
<tr>
<td>Agonistic encounters</td>
<td>Those in which aggressive interactions occurred between two or more individuals of different groups, resulting in displacement or unsuccessful displacement between groups.</td>
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Results of agonistic encounters

| Displacement | One group moved out of sight for more than 20 minutes on encountering another group that was not observed to alert its position or direction of movement. |
| Unsuccessful displacement | Neither group retreated beyond 100 m, or returned within 20 minutes of a temporary retreat |

Intensity of aggressions

| Whole-group aggression | Entire groups or more than roughly one third of the members of both groups participated (e.g. showing aggression, moving forward, showing submission, retreat) and these interactions often culminated in a forced movement (displacement) of one of the groups. |
| Partial-group aggression | Aggressive interactions took place between parts of groups (less than roughly one third of group members) rather than between entire groups. |
| Threat                  | Aggression without physical contact, including staring, open mouth, head bobbing, laid back ears, ‘cough-grunt’ vocalization. |
| Chasing                 | Aggressive pursuit and rapid submissive flight, often coincident with screams. |
| Physical attacks        | Contact aggression between groups, e.g. pushing, slapping, biting, etc. |
| Counter-aggression       | Aggression in response to any intensity of aggression during intergroup encounters. |

To test variation in intergroup relations between the two study populations, we calculated the rate per observation hour and duration of intergroup encounters. The rate was obtained by dividing the number of encounters observed by the overall duration in which we followed the focal group. Then we compared the proportion of neutral encounters, approach-retreat encounters, and agonistic encounters at the two sites. As agonistic encounters were common in both populations, we tested for variation in agonistic intensity between groups across sites using two criteria: the number of individuals actively participating in encounters (whole-group encounters versus partial-group encounters), and the intensity of encounters (threats, chases or physical attacks). In some cases, several aggressive interactions were observed between a single dyad. In such cases, only the highest-intensity aggressive behavior was analyzed. We also compared the results of displacement and unsuccessful displacement during agonistic intergroup encounters between the two populations. We used a Mann-Whitney U test for intergroup comparisons. All statistical tests in this study are two-tailed and nonparametric. We set the level of statistical significance at α=0.05.

2 Results

2.1 Variation in the rate and duration of intergroup encounters

We observed 269 encounters in 814 observation hours between SB and SA groups at Shodoshima. The rate of encounters was 0.33 times/hour and the two groups encountered up to five times a day in the park. Encounters lasted for a mean±SD of 59.4±47.8 min, ranging from 15–240 min. SB group spent 267.2 hours (32.8%) of the total observation hours engaged in encounters. In contrast, we observed only 14 encounters between Shiga A1 and Shiga A2 at Jigokudani over 730 observation hours. The rate of intergroup encounters was 0.02 times/hour in the different seasons (January-March and July-September in 2006) and the two groups never encountered each other more than once in the same day. Encounters lasted for a mean of 6.1±6 min, ranging from 1-25 min. The two groups spent 1.4 hours (0.2%) of the total observation hours engaged in encounters. Intergroup encounters in Shodoshima occurred 16.5 times more frequently and lasted ten times longer than those in Jigokudani. As a result, the proportion of
time spent in proximity to the other group in Shodo-
shima is significantly longer than that in Jigokudani
\( (n_1=105, n_2=100, \ z=-12.9, \ P<0.001) \).

2.2 Variation in intergroup encounter types

At Shodoshima, neutral, approach-retreat and agonistic
encounters accounted for 96 (36%), 48 (18%) and
125 (46%) of the 269 intergroup encounters observed,
respectively. By contrast, approach-retreat encounters
and agonistic encounters accounted for 8 (57%) and 6
(43%), respectively, of the 14 intergroup encounters
recorded at Jigokudani (\( df=2, \chi^2=15.4, \ P<0.001 \)).
Neutral encounters were not observed in the Jigokudani
population. Compared with Jigokudani, the Shodoshima
population showed a higher proportion of neutral en-
counters and a lower proportion of approach-retreat
encounters. The proportion of agonistic encounters,
however, was similar between the two populations.

Despite that the proportions of agonistic encounters
did not differ across study sites, there was variation in
the outcomes of such encounters (Fig. 1). SB group
successfully displaced SA group in 45 (36%) of the 125
agonistic encounters observed at Shodoshima, thereby
forcing SA from the park grounds. The former group
appeared dominant over the later, nevertheless, SB
group failed to displace SA group during 78 encounters
(62.4%), and was also displaced by SA during 2 other
encounters (1.6%). At Jigokudani, by contrast, Shiga A1
was dominant over and invariably displaced Shiga A2
during all agonistic encounters (\( df=2, \chi^2=9.86, \ P<0.01 \)).
The Shodoshima population showed a lower proportion
of agonistic encounters resulting in displacement than
the Jigokudani population, and thus agonistic encoun-
ters between groups at Shodoshima often resulted in
unsuccessful displacement.

2.3 Variation in aggression intensity during en-
counters

Shodoshima monkeys showed a higher proportion of
partial-group aggression (58 or 46.4% of the 125 ago-
nistic encounters) and a lower proportion of whole-
group aggression (67 or 53.6%) than Jigokudani mon-
keys (partial-group aggression: 1 or 16.7% of the 6 ago-
nistic encounters; whole-group aggression: 5 or 83.3%;
Fig. 2). In Shodoshima, threats were most commonly
observed during encounters with partial-group aggres-
sion (47 cases or 81%), followed by chases (11 cases or
19%). A similar tendency was observed during whole-
group aggression, as threats and chases accounted for 46
(68.7%) and 17 (25.4%) cases, respectively. Physical
attacks between groups were rare, occurring in only 4
(5.9%) cases during whole-group aggression and not
observed during encounters with partial-group aggres-
sion. At Jigokudani, by contrast, chases were the most
commonly observed type of aggression during agonistic
intergroup encounters (one case during partial-group
aggression and 4 cases during whole-group aggression),
Fig. 3 Counter-aggression during inter-group encounter in Shodoshima

The photo was taken during an encounter between SB group (below) and SA (up) group at the provisioning site of the Choshikei Monkey Park on March 9, 2005. Monkeys of the dominant SB group threaten and physical attacked those in the subordinate SA group, but they failed to displace the latter. The subordinate group responded counter-aggression or re-approach to the feeding site shortly after being excluded. As a result, the two groups foraged together for ca. 50 min at the provisioning site, while the individuals maintained a clear border line between groups.

followed by threats (one case during whole-group aggression). Physical attacks between groups were not observed at Jigokudani. Finally, counter-aggression was frequently observed between Shodoshima groups, occurring in 33 (56.9%) of the 58 encounters with partial-group aggression and 19 (28.4%) of the 67 with whole-group aggression. However, counter-aggression was not observed during intergroup encounters at Jigokudani.

3 Discussion

Our study illustrates that the characters of intergroup encounters differs between the two provisioned, free-ranging populations of Japanese macaques examined here. The average duration and rate of intergroup encounters at Shodoshima were approximately ten times longer and 16.5 times more frequent than those at Jigokudani, leading to the two groups spending over one third of their active time in proximity. This variation was unlikely to have been caused by provisioning alone, since the provisioning history and amount of provisioning food per individual do not vary between study populations. Even there are differences of provisioning methods at some locations, Kawanaka (1973) reported that intergroup encounters at provisioned sites normally occur at very low rates among Japanese macaques, and when they do occur, encounters are generally agonistic and commonly terminate within minutes. Our results from Jigokudani are consistent with this tendency. In extreme cases, intergroup encounters were observed to occur less than once per month at Taishakukyo Valley (Mizuhara, 1986), Takagoyama Mountain (Kawamura et al., 1974) and Hakusan Mountain (Izawa, 1982). Among wild populations, intergroup encounters have been shown to occur at considerably low rates: 0.012 times/hour on Kinkazan and 0.039 times/hour on Yaku-shima Island (Sugiura et al., 2000). Groups of macaques in these areas tend to avoid each other. Thus, it might be a unique characteristic of the Japanese macaques on Shodoshima that mutually competing groups that we observed often share the same feeding sites on a regular basis.

Neutral encounters accounted for more than one-third of the intergroup encounters observed at Shodoshima. For a subordinate group, neutral encounter might convey several benefits related to the expansion of its home range and resource base, with negligible risks (the group can always retreat if and when the dominant group becomes hostile; Cheney, 1987). It might equally benefit the members of a dominant group, by preventing the occurrence of energetically expensive and potentially hazardous displays of aggression. Moreover, neutral encounter may serve several other functions, such as the evaluation of neighbors and assessment of mating or dispersal options, the probing of a group’s resistance to a possible takeover, and the conveyance of information about an individual’s status or quality (Sicotte and Macintosh, 2004). However, an important question arises as to why neutral encounters were common at Shodoshima but rarely observed at Jigokudani or other provisioned populations of Japanese macaques. Intraspecific variation in intergroup relations among Japanese macaques is usually considered to be associated with the explanation based on food resource defense (e.g. Saito et al., 1998; Sugiura et al., 2000). This explanation, however, might not be applicable to the variation in our study populations. Since the food resource is high value and more clumped under provisioned conditions than under natural conditions, it is expected that groups at the feeding sites should defend such food resources aggressively (Wrangham, 1980; Zhang, 2008). Nevertheless, the high frequency of neutral encounters and long duration of proximity between mutually competitive groups appear to contradict the predictions of the food resource defense theory. Moreover, the intergroup tolerance behavior is common in several provisioned and wild groups in Shodoshima (Yamada, 1971; Kawamura et al., 1974). It is also difficult to explain from other ecological factors, such as forest type, group density, moving speed and range
overlap, because these ecological conditions in Shodoshima do not appear to differ from many other sites in Japan (Yamagiwa and Hill, 1998; Watanabe, 2004). For example, despite monkeys at Shodoshima and Takasakiyama share similar living conditions and temperate-warm forest type (Koyama et al., 1981; Sugiyama and Ohsawa, 1988), their intergroup relationships differ considerably. Based on these observations, we suppose the characters of intergroup relations in Shodoshima populations might not be determined by ecological factor alone.

Neutral encounters near food resources require a high degree of tolerance between two groups. At Shodoshima, two-thirds of agonistic intergroup encounters between study groups resulted in unsuccessful displacement. That even the dominant group frequently fail to displace and occasionally is displaced by the subordinate group may reflect tolerance, by the dominant group on the one hand, and resistance, by the subordinate group on the other. The latter often responded with counter-aggression or re-approaches to the feeding sites shortly after being excluded. At Jigokudani, since the group size of Shiga A1 is 4.3 times larger than that of Shiga A2, the unbalanced competitive power might influence the result of intergroup encounters. Nevertheless, the factor of group size alone could not explain the inter-group tolerance. The study groups at Shodoshima have very large group size and skewed adult sex ratio, which are not exceptional but were noticed in many other provisioned groups of Japanese macaques (Yamagiwa and Hill 1998). In some populations, such as those at Takasakiyama and Shodoshima, smaller groups were observed to consistently displace larger groups at the feeding site (Sugiyama and Ohsawa, 1988). The inter-group relations at Takasakiyama, Jigokudani and many other locations however differ from those in Shodoshima, and are consistent with the tendency of antagonistic relations between mutually competitive groups (Kawanaka, 1973). The lack of tolerance may explain the rarity of neutral encounters between groups in most populations of Japanese macaques.

Previous comparative studies on interactions within groups revealed Shodoshima monkeys display a number of differences in their behavioral patterns compared to Japanese macaques at other locations, and tend to have the highest degree of gregariousness among group members within the species (Yamada, 1971; Koyama et al., 1981). Specifically, macaques on Shodoshima show apparently higher frequency of counter-aggression than a captive group (Chaffin et al., 1995); they also show more frequent affinitive interactions, shorter inter-individual distances, less frequent exclusion from resources, more frequent but less intense aggression, and more frequent counter-aggression than those at Takasakiyama (Zhang and Watanabe, 2007). Their behavioral measures resemble those of tolerant societies such as the stump-tailed macaque (M. arctoides, O’Keeffe et al., 1983) and the Assamese macaque (M. assamensis, Cooper and Bernstein, 2002) to some extent. Various studies suggested the apparent tolerance among individuals in Shodoshima populations may not be caused by inter-group encounter, e.g. tolerant behavior traits among individuals have been reported since 1960’s, which is earlier than the original fission of SA and SB groups in 1970’s (Kawai, 1964; Yamada, 1966; Koyama et al., 1981), but may relate to other factors, such as social factors (e.g. behavior tradition Kawai, 1964; Zhang and Watanabe, 2007), genetic and developmental factors (e.g. individual temperament, Yamada, 1971) or tolerant personality types (Inoue-Muroyama et al., 2010). It is interesting that the total time engaged in intergroup encounters on Shodoshima was also higher than that found in the despotic rhesus macaques (M. mulatta) of Cayo Santiago (8.5%, Hausfater, 1972), but similar to that of tolerant macaque species, e.g. 34% in Tibetan macaques (M. thibetana, Zhao 1997) and 45.5% in Barbary macaques (M. sylvanus, Mehlman and Parkhill, 1988). The prolonged intergroup encounters at Shodoshima also resemble those of Barbary macaques, which were shown in one study to last for 110 minutes on average (Mehlman and Parkhill 1988). The specific inter-group encounters may relate with tolerant behavior traits in the study populations.

Finally, this study indicates that intergroup relationships may be apparently different among Japanese macaques, as they can be in some other primate species (Cheney, 1987). For example, Barbary macaques are expected to have strong intergroup competition according to the socioecology model (Wrangham, 1980), but encounters between groups of these animals in some wild populations are more peaceful than in other despotic species (Mehlman and Parjhill 1988). Considerable intra-specific variation in intergroup encounters has been reported for many other primate species (Papio cynocephalus, Cheney, 1987; C. guereza, Sicotte and Macintosh, 2004; M. mulatta, Vessey, 1968; Cercopithecus aethiops, Cheney, 1981). While range size, population density, and food distribution may certainly affect the rate and type of intergroup encounters observed (e.g. Sugiura et al., 2000), they do not do so in all species or...
populations (Cheney, 1987; Okamoto and Matsumura, 2002). The role of social factors should also be considered in future studies of the relationships between groups of primates.

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