Social Interactions Between Rhesus Macaques (Macaca mulatta) and Assamese Macaques (M. assamensis) in Nepal: Why Do Male Rhesus Macaques Follow Social Groups of Assamese Macaques?

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INTRODUCTION

A wide range of taxa including fish, birds, and mammals form mixed species groups (MSGs) to increase feeding efficiency, reduce predation risk, and increase social or reproductive advantages (Stensland et al., 2003). MSGs typically involve multiple individuals of two or more species, but a single animal has sometimes been observed to join another species group (Baraff & Asmutis-Silvia, 1998). Various primate species form MSGs (Chapman & Chapman, 2000; Heymann & Buchanan-Smith, 2000; Waser, 1986), yet there is little information on MSGs in macaques. For example, Japanese macaques (Macaca fuscata) formed a MSG with sika deer (Cervus nippon) (Tsuji et al., 2007). Rhesus (M. mulatta) and long-tailed macaques (M. fascicularis) formed a MSG, in which hybridization occurred (Jadejaroen et al., 2015; Malaiivijitmon & Hamada, 2008). Besides released macaques (e.g., Kawamoto et al., 2007; Malaiivijitmon & Hamada, 2008), however, reports of macaques forming MSGs with another species-group in Macaca are rare, even when habitats are shared.

This study is the first to report that male rhesus macaques in a fascicularis species-group joined a social group of Assamese macaques (M. assamensis), which belong to a sinica species-group. We report social interactions within the MSG and intergroup encounters between rhesus and Assamese macaques at Shivapuri Nagarjun National Park (SNNP) in central Nepal.

MATERIALS AND METHODS

Study site and animals

We directly observed rhesus and Assamese macaques in SNNP, Kathmandu District, Nepal (27°44’N, 85°17’E, Fig. 1). Both macaque species form multi-male multi-female social groups with female philopatry, male dispersal, and linear dominance relationships. Both species are seasonal breeders, and rhesus and Assamese macaque females give birth from April to July and from March to July, respectively (Ogawa, unpublished data). Compared with the rhesus macaque, however, the Assamese macaque is more arboreal, frequently staying in the higher canopy and on cliffs, has a larger body, is less kin biased, and has a more relaxed dominance style (Balasubramaniam et al., 2018; Koirala et al., 2017; Zhou et al., 2014).

We observed free-ranging focal groups of rhesus and Assamese macaques (Fig. 1). The Rhesus Balaju (RB) group was provisioned with offered food and food left by visitors to Balaju Garden and a temple within the garden, adjacent to the southern border of SNNP (Upadhayay et al., 2018). The Assamese Army (AA) group was provisioned with leftovers and garbage at the kitchen area of an army camp in SNNP (Koirala et al., 2017). The Rhesus Army (RA) group was also provisioned at the army camp. We identified all adult males and females in these provisioned groups based on their physical characteristics. The demographics of the study groups are shown in Table 1. We also found solitary males and small all-male groups of rhesus macaques, whereas no
solitary Assamese macaques or hybrids between rhesus and Assamese macaques were found during the study periods in SNNP and Balaju Garden. Possible predators, such as common leopards (*Panthera pardus*), inhabit SNNP (Koirala et al., 2017; Shrestha & Thapa, 2016).

**Behavioral observations**

From July 2014 to April 2015 (Period 1), we (HO and SK) observed social interactions between the AA and RA groups by *ad libitum* sampling. We observed monkeys in the AA group during the same period by focal animal sampling.

From April 2017 to March 2018 (Period 2), we (SK and PKP) observed one of the two rhesus macaque males with the AA group for 10 hours each during the birthing and mating seasons by focal animal sampling. During Period 2, we recorded social interactions between the AA and RB groups by *ad libitum* sampling, while SK, SKh, and PU observed monkeys in the AA and RB groups by focal animal sampling. PKP and SKh observed two free-ranging non-provisioned groups, the Assamese Simpani (AS) and Rhesus Nagi (RN) groups, by scan sampling. HO observed a male rhesus macaque following the free-ranging non-provisioned Assamese Raniban (AR) group in March 2018, and PKP observed an adult male Assamese macaque in the AS group in April 2018 by focal animal sampling.

**RESULTS**

Rhesus and Assamese macaques used the same provisioning site

During Period 1, rhesus macaques in the RA group and Assamese macaques in the AA group used the same provisioning site at the army camp (Fig. 2). These groups generally avoided each other, and they maintained a distance
of several meters when both groups were at the provisioning site. Monkeys in one group sometimes showed aggressive behaviors to those of the other group, but this aggression was rarely accompanied by physical contact. One of the interactions was the disturbance of Assamese macaque copulation by a male rhesus macaque on 11th December 2014.

On 27th December 2014, wild Assamese macaques in an adjacent group also approached the provisioning site at a point 100 m west of the site and had an agonistic encounter with the AA group.

Agonistic encounters between the rhesus and Assamese macaque groups

During Period 2, we recorded encounters between the RB group of rhesus macaques and the AA group of Assamese macaques. On 1st August 2017, the RB group went to the army camp. Males and females in both the RB and AA groups showed severe aggressive behaviors with physical contact toward monkeys in the other group. After 90 minutes, the RB group finally escaped the AA group and left the army camp. On 10th March 2017 and in January 2018, we recorded other agonistic encounters between the RB and AA groups when the AA group entered Balaju Garden.

Male rhesus macaques remained at the provisioning site with a social group of Assamese macaques

During Period 2, one adult rhesus macaque male approached the provisioning site at the army camp in the presence of AA group Assamese macaques. The male remained with the Assamese macaques and returned to the forest with them every day. Another adult rhesus macaque male also sometimes stayed at the army camp with the AA group. These males appeared to be approximately 7–12 years old. Neither was a resident male in a multi-male multi-female group of rhesus macaques during Period 1 or 2. A total of 20 hours of focal animal sampling on the first male showed that he was involved in 11 aggressive interactions with male and female adult Assamese macaques, but he also groomed and was groomed by other adult male Assamese macaques 5 and 4 times, respectively. During the time with non-focal animal sampling on 12th January 2018, he was mounted by the highest-ranking adult male in the AA group. Of the 10 hours of sampling during the mating season, 5-minute interval scans showed that the distance between the male and the closest monkey was 9.7 m (SD: 5.3 m; range: 1–20 m). Of the 139 closest monkeys, 71 (51.1%) were adult males. The male was close to adult males in the AA group more frequently than to monkeys in other age classes (Chi-square test, df = 1, $\chi^2 = 118.3$, $p < 0.05$). Though the two rhesus males frequently looked at female Assamese macaques in the AA group, we recorded no affiliative interaction or copulation between the males and female Assamese macaques.

Male rhesus macaques followed a social group of non-provisioned Assamese macaques

During Period 2, two other adult male rhesus macaques sometimes followed the AS group (wild Assamese macaques) from morning until evening, sometimes leaving the group during other periods. Both males appeared to be approximately 7–12 years old. Neither was a resident male in a multi-male multi-female group of rhesus macaques during Period 1 or 2.

At 12:30 on 21st March 2018, we found one of the two males with another wild group, AR. This male always followed the AR group until they stopped ranging at 17:00. During this period, he supported an adult male Assamese macaque against a juvenile male Assamese macaque in the AR group. Five-minute interval scans showed that the distance to the closest monkey was 15.2 m (SD: 8.6 m, range: 1–50 m), and that he spent 11.6% (5/43) of this time on the ground, whereas an adult male Assamese macaque in the AS group did not descend (0/122) (Fisher’s probability test, $p < 0.05$). The male rhesus macaque was not found with either the AR or AS group the following morning.

DISCUSSION

Agonistic relationships between Assamese and rhesus macaques

Our observations showed that social relationships between groups of rhesus and Assamese macaques were agonistic, similar to intergroup relationships among Assamese macaques.
Reasons for male rhesus macaques to follow an Assamese macaque social group

Despite the agonistic relationships observed between rhesus and Assamese macaques, they formed MSGs. At Ramdi Village, Pyuthan District, Nepal (27°54'N, 83°38'E), an adult male rhesus macaque was observed to remain with Assamese macaques in March 2016 (Ogawa and Paudel, unpublished data). At Tukreswari Temple, Assam State, India (26°03'N, 90°38'E), an adult male rhesus macaque was observed resting near and looking at Assamese macaques in February 2009 (Ogawa, unpublished data). Therefore, our observations of male rhesus macaques remaining with a group of Assamese macaques are not unusual.

Male rhesus macaques were unlikely to mistake Assamese macaques for their own species. Experimental tests have shown that rhesus macaques can distinguish rhesus and Japanese macaques in photographs (Yoshikubo, 1985), indicating that macaques can recognize their own species and other sympatric macaques, a mechanism that may prevent hybridization.

Three adaptive benefits of forming MSGs have been proposed: increased feeding efficiency, reduced predation risk, and increased social or reproductive advantages (Stensland et al., 2003). Although several Assamese macaques have been observed to be tolerant toward, and sometimes have affiliative interactions with male rhesus macaques, they kept their distance and did not follow the male rhesus macaques. Thus, male rhesus macaques likely received greater benefit from the MSG than did the Assamese macaques. Each possible benefit for the males is examined below.

First, it was not clear whether the two males following wild Assamese macaques increased or decreased their feeding efficiency. Although the agonistic relationship indicates competition between the two species, the competition may not be intense because they have differences in diet and habitat use (Zhou et al., 2014). A low-level feeding competition might make it possible for the male rhesus macaques to forage with Assamese macaques. However, the two males that remained with provisioned Assamese macaques could not have increased their feeding efficiency, because they would have had greater access to leftovers and garbage if they had visited the provisioning site alone.

Second, the males may have reduced their predation risk through association with MSGs. Fecal analyses revealed that rhesus macaques are prey of common leopards in SNNP (Shrestha & Thapa, 2016). Solitary males must be at a higher risk of predation than individuals in a large group. The RB group contained only four central males, and there were many solitary male rhesus macaques in the study area. Such solitary males that could not immigrate into multi-male multi-female social groups of their own species might reduce predation risk by joining a group of Assamese macaques. Such a strategy would be more effective against predation than remaining solitary or forming a small male group. By contrast, Assamese macaques might reduce their predation risk when they are followed by male rhesus macaques. The male rhesus macaques were more likely to be between Assamese macaques and terrestrial carnivores because rhesus macaques are more terrestrial than Assamese macaques (Koirala et al., 2017; Zhou et al., 2014). This may be one of the reasons why Assamese macaques tolerate male rhesus macaques’ following behavior.

Finally, the male rhesus macaques might be attracted to female Assamese macaques. Indeed, infants of both rhesus and Japanese macaques preferred photographs of rhesus macaques (Fujita, 1990), whereas adult rhesus macaques preferred their own species (Yoshikubo, 1985). This finding suggests that males of one macaque species are attracted to females of another macaque species. However, we observed neither copulation nor hybrids of rhesus and Assamese macaques. The males followed Assamese macaques during the mating season and the birthing season, suggesting that male rhesus macaques did not increase their reproductive success by forming MSGs. However, the male rhesus macaques received the social benefit of grooming from male Assamese macaques. Conversely, we never recorded affiliative interactions between resident male rhesus macaques in multi-male multi-female social groups and male Assamese macaques. The tolerant social relationships with a relaxed dominance style of Assamese macaques may allow males of other species to join their social group, whereas the despotic social relationships in rhesus macaques may not.

As a tentative conclusion, the male rhesus macaques observed in this study may have followed Assamese macaque social groups to reduce predation risk and increase social advantages.

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We report observations of male rhesus macaques (Macaca mulatta) following multi-male multi-female groups of Assamese macaques (M. assamensis), forming mixed species groups (MSGs), as well as intergroup encounters between rhesus and Assamese macaques at Shivapuri Nagarjun National Park (SNNP), Kathmandu District, Nepal. We observed both macaque species from July 2014 to April 2015 (Period 1) and from April 2017 to March 2018 (Period 2). In addition to wild groups, we observed the provisioned Rhesus Army (RA) and Assamese Army (AA) groups at the army camp in SNNP and the Rhesus Balaju (RB) group at Balaju Garden, adjacent to SNNP. During Period 1, macaques in the RA and AA groups entered the same provisioning site, sometimes showed aggressive behaviors between groups. During Period 2, macaques in the RB and AA groups had encounters at the army camp and Balaju Garden, showing severe aggressive behaviors between groups. Thus, intergroup relationships among these macaque species were agonistic. Nevertheless, two adult male rhesus macaques entered the provisioning site with the AA group of Assamese macaques, remained there, and then returned to the forest with the AA group during Period 2. Two other adult male rhesus macaques followed Assamese macaques in the wild Assamese Simpani (AS) group from morning until evening during Period 2. These males exhibited both aggressive and affiliative interactions with male Assamese macaques. Although these males appeared to have been attracted to female Assamese macaques, we observed neither copulation nor hybrids between rhesus and Assamese macaques during our study. Since common leopards (Panthera pardus) inhabit SNNP, male rhesus macaques that could not immigrate into multi-male multi-female social groups of their own species might reduce predation risk and increase social advantages by joining groups of Assamese macaques, which would be a more effective strategy than remaining solitary or forming a small male group.
Male *Macaca mulatta* following *M. assamensis*

**Key words:** mixed species group, *Macaca mulatta, Macaca assamensis*, following behavior, predation risk, intergroup encounter, tolerant social relationship

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