Postconflict behavior among female Sichuan snub-nosed monkeys *Rhinopithecus roxellana* within one-male units in the Qinling Mountains, China

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**Abstract** For group-living primates, the information on postconflict management is crucial for understanding primate competition and cooperation. However, such information is poorly known for snub-nosed monkeys, especially for wild populations. In this study, from September 2007 to June 2008, we investigated postconflict behavior among adult females Sichuan snub-nosed monkeys *Rhinopithecus roxellana* within one-male units in a wild, provisioned group in the Qinling Mountains of China by means of the time-rule method and the PC-MC method. We obtained a total of 81 PC-MC pairs and each individual was involved in only 0.004 aggressive behavior per observation hour. The first affiliative behavior was more likely to occur within the first minute after a conflict. The postconflict affiliative behaviors most often seen were contact-sit, embrace and grooming. The affiliative contacts between adult females occur due to selective attraction, i.e. reconciliation. The pattern of postconflict affiliation demonstrates that the *R. roxellana* belongs to a tolerant species [Current Zoology 56 (2): 222–226, 2010].

**Key words** Sichuan snub-nosed monkey, *Rhinopithecus roxellana*, Female, Postconflict behavior, Reconciliation

Animals have developed behavioral mechanisms to manage conflict in order to reduce the costs of aggressive competition for resources and gain the benefits of group living (de Waal, 2000; Aureli et al., 2002). Such conflict management via post-conflict friendly interactions can take place between former opponents (i.e. reconciliation) as well as between opponents and bystanders (i.e. consolation) (Cords, 1993; Aureli and de Waal, 2000; Silk, 2002). Reconciliation is assumed to be a mechanism to repair a relationship (de Waal, 1989; Aureli and Schaaffner, 2006) and reduce stress in the victim (Aureli et al., 1989; Aureli and van Schaik, 1991) while the function of consolation is likely to alleviate stress in victims, protect against further attacks, and prevent spread of aggression (Das, 2000; Watts et al., 2000). Nowadays postconflict management is found in a variety of primates (Aureli and de Waal, 2000; Arnold and Aureli, 2007). Within Old World monkeys, much of what we know about postconflict behavior comes from studies on cercopithecines (e.g. *Macaca fascicularis*: Aureli and van Schaik, 1991) while less is reported in colobines (e.g. *Rhinopithecus bieti*: Grütter, 2004; Arnold and Aureli, 2007).

As one folivorous colobine endemic to China, the Sichuan snub-nosed monkey *Rhinopithecus roxellana* is strictly seasonal-breeding species. Its basic social and reproductive unit is the one-male unit (OMU), which consists of a single resident male, a number of adult females, sub-adult females, juveniles and infants. Many OMUs form a band (Li and Zhao, 2007). To date, only one postconflict study has been reported in two captive breeding groups of *R. roxellana*, which revealed high proportion of the average conciliatory tendency (Ren et al., 1991). In this study, we aim to explore postconflict behavior among females *R. roxellana* within one-male units in a wild, provisioned group that located at Zhouzhi National Nature Reserve in the Qinling Mountains, China.

Based on life history characteristics of *R. roxellana*, we made the following predictions on postconflict behavior among females within OMUs in this species. Firstly, it is generally believed that folivorous primate species experience little intra-group food competition (van Schaik, 1989). Thus we predict that the occurrence...
frequency of conflicts among females should be relatively low in *R. roxellana*. Secondly, the care of infants by unit females other than their mothers is a prominent feature in wild *R. roxellana* (Xi et al., 2008) as common in many other colobine species (Maestripieri, 1994). Females Sichuan snub-nosed monkeys could obtain some benefits (e.g. receiving more grooming for hygiene, saving energy) from allowing others to care for their infants with the one-male unit (Xi et al., 2008).

For females *R. roxellana*, keeping good relationship with other females is propitious to maintain their basic survival and energy requirements. Thus we predict that females should show high degree of postconflict affiliation within OMUs in *R. roxellana*. Thirdly, for seasonal-breeding primate species, the mating season is a period in which increasing female-female competition for mating partners influence female social relationships (Majolo and Koyama, 2006). Thus, we predict that the conciliatory tendency between females in the mating season should be much lower than that in the non-mating season in this polygynous species.

1 Materials and Methods

1.1 Study site and species

This study was carried out in the Zhouzhi National Nature Reserve, on the northern slope of the Qinling Mountains, Shaanxi Province, China (for ecological details of habitat: Li and Zhao, 2007; Zhao, 2009). Two troops of this species, the East Ridge troop and the West Ridge troop, are present in the study area (Zhao et al., 2008). We studied a wild, provisioned band of *R. roxellana*, which is part of the west ridge troop. At the start of our observation, there were 10 one-male units totaling 100 individuals in the focal band. All individuals in the focal band were identified via their prominent physical features. Based on their estimated age and physical characteristics (Zhao, 2009), we classified the age classes of *R. roxellana* in the focal band as infants (0–1 year old), juveniles (estimated at 1–3 years old), subadults (females: estimated at 3–4 years old) and adults (females: estimated at more than 5 years old; males: estimated at more than 7 years old). Only adult females, totaling 38 individuals, were considered as focal subjects in this study.

1.2 Food Provisioning

We established one provisioning site for the focal band at Sanchakou (1646 m above sea level) in Gongnigou valley (33° 48′68"N, 108° 16′18"E) since October 2001. The monkeys were located by the field assistants in the morning and herded towards the provisioning site at approximately 9:00 h every day when research was being conducted (Zhao et al., 2008). Apples, radishes, and corns were provided at the provisioning site three times per day. The quantity of provisioned food was approximately 200 g per monkey per day, which is a minor proportion of their daily food consumption (Qi, 1989; Li and Zhao, 2007). After provisioning, the monkeys would leave the provisioning site and move to adjacent trees and surrounding area. Their nightly roosts tend to locate within a radius of approximately 3 km of the provisioning site. We observed monkeys with a distance of 5–50 m.

1.3 Data collection

From September 2007 to June 2008, we collected conflict data via behaviour sampling (Martin and Bateson, 2007) and recorded data on postconflict behavior among females using the postconflict-matched-control (PC-MC) method (de Waal and Yoshihara, 1983). We collected data outside the provisioning context. In other words, we began data collection after monkeys ate up provisioned food per observation day. The total observation time was 528 h. Postconflict sessions began ≤30 seconds following the conflict between two adult females, and then we collected data on victim or the aggressor for 10 minutes. When more than two females were involved in the conflict, only the two first antagonists were taken into account. For each aggressive interaction, we recorded the identity of the individuals involved and the time elapsed from the end of the conflict to the first affiliative interaction. We scored postconflict behavior when individuals performed six types of behaviors (contact sit, crouch, embrace, groom, hold-hand, hold-lumbar). Definitions of these behaviors followed Ren et al. (1991). On the next possible day we made the matched-control observation on the same subject. We postponed the session for ≥10 min if the focal individual was involved in an agonistic interaction within 3 min before a planned MC (Aureli et al., 1993).

Based on the method mentioned by Majolo and Koyama (2006), the session started only when the context was similar to that of the PC and the other females involved in the previous conflict were visible.
1.4 Data analysis

Data on postconflict behavior among females were analyzed using two methods, the time-rule method (Aureli et al., 1989) and the PC-MC method (de Waal and Yoshihara, 1983). First, we determined the time (in minutes) of the first affiliative interaction between the opponents after a PC. For the time-rule method (Aureli et al., 1989), we applied the Kolmogorov-Smirnov test to analyze the distribution of the interactions over time in the PCs and MCs. For the PC-MC method (de Waal and Yoshihara, 1983), on one hand we applied the Wilcoxon matched-pairs signed-rank test to compare the occurrence of affiliative interactions between former opponents between PCs and MCs at the individual level in order to determine the occurrence of reconciliation. On the other hand, in order to determine the occurrence of consolation, we applied the Wilcoxon matched-pairs signed-rank test to compare the occurrence of affiliative interactions between the focal animal and the group member other than the former opponent between PCs and MCs at the individual level.

For the PC-MC method, we compared the timings of the first friendly interactions involving the victim during the PC and MC (de Waal and Yoshihara, 1983). If an affiliative interaction between former opponents occurred only in the PC, or earlier in the PC than in the MC, the pair was “attracted”. If the interaction occurred earlier in the MC than in the PC (or only in the MC), the pair was classified as “dispersed”. If the affiliative interaction took place earlier or only in the MC, the pair is dispersed. If there was no affiliative interaction occurred in the PC and the MC or when the interaction occurred at the same time in both observations, the pair was considered to be “neutral”. Based on the assignation mentioned above, we calculated the corrected conciliatory tendency (CCT) per individual or per dyad measure (Veenema et al., 1994):

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CCT = \frac{\text{number of attracted pairs} - \text{number of dispersed pairs}}{\text{total PC-MC pairs}}
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In this study, we applied the SPSS 10.0 to do all the analysis, which were bilateral with a level of significance of \( P < 0.05 \). Data are expressed as mean ± SE.

2 Results

We obtained a total of 81 PC-MC pairs (the mean number of PC-MC pairs per female, 2.13 ± 0.27), including 40 in the mating season and the remaining 41 in the non-mating season. The overall conflict frequency was low and each individual was involved in only 0.004 aggressive behavior per observation hour. The overall conciliatory tendency is 58.02%; the conciliatory tendency in the mating season is significantly lower than that in the non-mating season (Wilcoxon signed ranks test, \( n = 40, t = 26, P = 0.001 \)). Among these PC-MC pairs, 85.19% of conflicts had clear winners, whereas the winners could not be decided for 14.81% of the conflicts. 88.89% of the conflicts involved >2 individuals, while the remaining 11.11% were dyadic conflicts. The behaviors’ most often shown as first affiliation after a conflict were contact sit (\( n = 21 \)), embrace (\( n = 17 \)) and grooming (\( n = 14 \)). The distribution over time of first affiliative contacts between former opponents is significantly different between PCs and MCs (Kolmogorov-Smirnov test: \( D = 0.387, P < 0.001 \)) (Fig. 1).

Similarly, at the individual level, the percentage of attracted pairs was significantly higher than that of dispersed pairs (attracted pairs: 0.83 ± 0.05; dispersed pairs: 0.09 ± 0.04; Wilcoxon signed ranks test: \( n = 38, t = 0, P < 0.001 \)), indicating that affiliative contacts between adult females did not occur by chance but instead were due to selective attraction, i.e. reconciliation.

![Fig. 1 Number of PCs and MCs with an affiliative contact between former opponents in each minute (1–10 minutes)](image)

The distribution over time of first affiliative contacts between the focal animal and group members other than the former opponent is significantly different between PCs and MCs (Kolmogorov-Smirnov test: \( D = 0.499, P < 0.001 \)) (Fig. 2). However, the percentage of attracted pairs was similar with that of dispersed pairs (attracted pairs: 0.51 ± 0.04; dispersed pairs: 0.39 ± 0.04; Wilcoxon signed ranks test: \( n = 49, t = 4, P = 0.118 \)), indicating no occurrence of consolation at the individual level in *R. roxellana*. 
Discussion

This study confirmed the occurrence of reconciliation among female Sichuan snub-nosed monkeys in wild conditions, as previously found in captive settings (Ren et al., 1991). Our findings validated our predictions. Firstly, the occurrence frequency of conflicts among females *R. roxellana* is low. Secondly, friendly interactions between former opponents were more likely to occur following a conflict that during the matched-control period and the overall CCT (58.02%) is higher than that of cercopithecine species (Arnold and Aureli, 2007) and similar to CCT values for other *Rhinopithecus* species (e.g. *Rhinopithecus bieti*: 54.5%, Grüter, 2004). Lastly, as we predicted, the CCT between females in the mating season is significantly lower than that in the non-mating season in this polygynous species.

In the primate order, some species employ “explicit reconciliation” via conspicuous behavior patterns that are rarely used in other social contexts while other species display “implicit reconciliation” by means of regularly observed behavior (Arnold and Aureli, 2007). In *R. roxellana*, there are six types of reconciliatory behavior involving both “explicit” behavior (embrace, hold-lumbar) and “implicit” behavior (contact sit, grooming) following conflicts among females, which is consistent with the findings of a study of a captive population (Ren et al., 1991).

Sommer et al. (2002) suggests that captivity may increase the likelihood of postconflict affiliation from their study on wild hanuman langurs *Semnopithecus entellus*. For the *R. roxellana*, the phenomenon that the overall CCT in the wild conditions (58.02%) is higher than that in the captive settings (43.4%) (Ren et al., 1991) does not support such notion that primates’ postconflict affiliation is an artifact of captivity (Aureli et al., 2002; Colmenares, 2006).

Since the first report on postconflict affiliation between recipient of aggression and the third party (i.e. consolation) by de Waal and van Roosmalen (1979), a large number of relevant studies have been carried out across the primate order. It is showed that consolation has only been demonstrated convincingly in great apes to date (Arnold and Aureli, 2007). Our study shows no evidence on the occurrence of consolation at the individual level in *R. roxellana* based on the PC-MC method, which accords with other Old World monkey species (e.g. *Macaca fuscata*: Aureli et al., 1993; *Papio hamadryas hamadryas*: Romero et al., 2009). Such lack of consolation in *R. roxellana* could be due to one possible explanation that monkeys lack the appropriate degree of empathy to perceive and respond to distress in others (de Waal and Aureli, 1996; Preston and de Waal, 2002).

There are some evidences that, in seasonal breeding primates, the mating season disturbs female social relationships and accelerates female’s competition over food and mating partners (D’Amato et al., 1982; Mehlman and Chapais, 1988; Majolo and Koyama, 2006). For *R. roxellana*, a strictly seasonal-breeding species, our results support the prediction that the CCT between females in the mating season is significantly lower than that in the non-mating season. To some extent, it shows the effect of seasonal mating on female reconciliation, which is consistent with results from other primates studies (e.g. *Macaca fuscata*: Majolo and Koyama, 2006).

On the whole, the postconflict behavior among females within one-male units that observed in wild conditions demonstrates that the *R. roxellana* is a tolerant species because of its low aggression frequency, high reconciliation rates and explicit reconciliatory behavior. However, it should be considered that provisioning in this study may increase intra-group female feeding competition so as to influence the frequency and intensity of conflicts. Accordingly, it is required in the future research to compare this population with a nearly non-provisioned population so as to evaluate the provisioning effects. Furthermore, the effect of kinship and dominance on postconflict interactions should be investigated, so as to further explore the overall pattern of postconflict behavior among females in this species.
Aknowledgements We are grateful to the staff of Zhouzhi National Nature Reserve for their permission to conduct this research. The Natural Science Foundation of China (No. 30970444, No. 30770375, No. 30630016) and the Cosmo Oil Eco Card Fund of Japan (2005-2010) support this study. We appreciate Dr. Weihong Ji for improving English expression on the earlier manuscript.

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