

Male juvenile golden snub-nosed monkeys acting as the mounTEE to receive grooming in their same-sex mounts

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Abstract

Same-sex mounts provide male juvenile golden snub-nosed monkeys (*Rhinopithecus roxellana*) with opportunities to practice heterosexual copulatory skills and are often followed by grooming (post-mounting grooming, PMG). We hypothesized that juveniles acted as the mounTEE and provided mounting opportunities to receive grooming from their peer mounTER. Here, we observed same-sex mounts among male juveniles ($N = 5$) in a captive group of *R. roxellana* in Shanghai Wild Animal Park, China, from November 2014 to June 2015. Among 1,044 mounts recorded, 45.40% were accompanied by PMG initiated by the mounTER and only 3.74% were followed by PMG initiated by the mounTEE. MounTEEs were more likely to receive PMG when they performed a mounting solicitation than when they did not, or when they were mounted for a longer time (even if they did not solicit). Over a long timeframe (1 month), mounTEEs tended to choose partners who groomed them more often than others after mounting, regardless of how long the grooming lasted. However, whether the mounTER groomed the mounTEE did not predict the mounting direction in their subsequent mount. Our results suggest that, in the context of same-sex mounts, juveniles provide mounting opportunities to receive grooming from peers on a long-term, rather than on a short-term basis. This study provides the first evidence that juveniles' same-sex mounting strategy may be associated with the grooming market in nonhuman primates, which necessitates further investigation with large free-ranging groups due to the limited sample size of individuals and the captive setting of the current study.

Key words: biological markets, cooperation, needing-to-learn hypothesis, partner choice, post-mounting groom, same-sex mount.

In many gregarious animal species, group members act cooperatively to gain fitness benefits (Boesch and Boesch 1989; Cheney 2011). Cooperative behavior may occur when it immediately benefits both the cooperator and the recipient (Stevens and Hauser 2004). In other cases (i.e., reciprocity), however, cooperative behavior may involve an initial cost to one of the participants (West et al. 2007; Cheney 2011). Nonhuman primates exhibit a large variety of cooperative behaviors and social trade is one mechanism that explains why 2 individuals would cooperate even when there is a temporary expense to one of them (Boesch and Boesch 1989; Gumert 2007).

Same-sex mounting behavior has been documented in a large number of primate species, especially in Cercopithecinae and great apes (Vasey 1995, 2007). Similar to heterosexual mounts, same-sex mounts typically involve solicitations, genital contact, and sometimes genital manipulation (Vasey 1995; Vasey and Sommer 2006; Bailey and Zuk 2009). According to the needing-to-learn hypothesis, same-sex mounts may provide youngsters with opportunities to practice copulatory skills and train for adult sexual roles (Chevalier-Skolnikoff 1976) (e.g., rhesus macaque, *Macaca mulatta*, Goy and Wallen 1979; Japanese macaque, *M. fuscata*, Gunst et al. 2013). Some affiliative behaviors, for example, grooming,

kissing, huddling, or playfighting, may also follow same-sex mounting behaviors (Vasey 1995; Dixson 2010). One of these post-mounting behaviors, grooming, has been widely explored and, besides its social functions, can also serve a utilitarian function in parasite removal (Dunbar 1991). Indeed, this benefit of grooming has been suggested to be traded as payment for heterosexual matings in long-tailed macaques (*M. fascicularis*) (Gumert 2007).

The aim of this study was to examine the relationship between same-sex mounting and post-mounting grooming (PMG) in male juvenile golden snub-nosed monkeys (*Rhinopithecus roxellana*). This species lives in multilevel societies with one-male multi-female unit (OMU) and all-male unit (AMU) as the basic social units (Qi et al. 2014). Several independent OMUs compose a breeding band, while bachelor males live together in several AMUs and form an all-male band (Qi et al. 2014). In the breeding band, male juveniles disperse from their natal OMUs before sexual maturity when they are expelled by their resident male (usually around 3–4 years of age) (Yao et al. 2011). Same-sex mounting behaviors between male *R. roxellana* have been analyzed in both captive (Huang et al. 2017) and free-ranging all-male groups (Lv et al. 2007; Fang et al. 2018). The pattern of same-sex mounts in male *R. roxellana* is typically hindquarter presentation and

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ventrodorsal mounting, commonly accompanied by pelvic thrusting and penile erections (by either of the participants), although intromissions and ejaculations occur occasionally (Fang et al. 2018). In a free-ranging all-male band, juveniles mounted each other in affiliative contexts (e.g., during play) and nearly half of (47.62%) mounting cases were accompanied by allogrooming (Lv et al. 2007). Generally, it was the mounter who initiated and groomed the mountee after the mounting interaction (Fang G., pers. commun.; Fang et al. 2018). Besides single mounts, series mounts (2 or more in succession) are also common among juveniles and can be reciprocated or nonreciprocated (Huang et al. 2023). At the end of a mount, the mounting participants may engage in PMG but huddling is also observed (Huang et al. 2017).

We previously provided evidence that same-sex mounting behaviors provide male juvenile captive *R. roxellana* opportunities to practice copulatory skills, supporting the needing-to-learn hypothesis (Huang et al. 2023). Given that, juvenile mounters benefit from same-sex mounts by learning copulatory skills at the expense of mountees because the latter provide valuable learning opportunities without gaining an obvious benefit. We also found evidence that, compared with the mounting dyads of other age groups, the mounter is more likely to initiate PMG in juveniles' mounting interactions (Huang et al. 2023), indicating that the same-sex mounting strategy adopted by male juveniles may be associated with the grooming exchange strategy in this species.

To more fully understand the relationship between same-sex mounting behavior and PMG, here we examine the behavioral pattern and the partner choice of PMG among juveniles in a captive group of *R. roxellana* at the Shanghai Wild Animal Park, China. In accordance with biological market theory, we hypothesize that male juveniles act as the mountee to receive grooming from the peer mounter (Table 1). We predict that: 1) The mountee is more likely to receive PMG when he solicits before the mount than when he does not. In light of the needing-to-learn hypothesis, juvenile mounters learn copulatory skills through mounting interactions (Huang et al. 2023). We thus predict that: 2) when a mountee allows the mounter to mount longer, he is more likely to receive PMG. After the mounting ends, we also predict that: 3) The mounter is more likely to initiate PMG than the mountee. At the dyadic level, we examine the partner choice of the mountee on a long-term and a short-term basis, respectively. We predict that: 4a) The more frequently the mountee receives PMG from a partner, the more often he chooses him as his mounter; and 4b) Whether the mounter grooms the mountee predicts the mounting direction of their subsequent mount.

That is, if juvenile A mounts juvenile B without grooming B, the likelihood of B mounting A is larger than that of A mounting B in their subsequent mount. Although A mounts B and then grooms B, the likelihood of B mounting A equals that of A mounting B in their subsequent mount. Finally, we test the mounting partner choice of the mountee at the individual level and predict that: 5) At the individual level, a juvenile mountee prefers males who groom him longer than others as his frequent mounting partner.

Materials and Methods

Study site and study group

We studied 2 units in a captive social group of golden snub-nosed monkeys in Shanghai Wild Animal Park, Shanghai, China (31°3'13" N, 121°42'51" E). Fifteen subjects formed an OMU (N = 7) and an AMU (N = 7–8). Each individual was recognizable by the pelage color, body size, and other physical characteristics. All of them were well habituated to the presence of the observer. We conducted the observations in the exhibition area, which was an open grassy land (approximately 900 m²) bordered by a semicircle rockery. There were 2 pavilions and a few dwarf artificial stones in this area, providing excellent visibility for observations. The details of the captive setting and care conditions have been presented by Huang et al. (2017).

We distinguished individual age classes based on Zhang et al. (2006) in which males aged 1–4 years old are juveniles. Before April 2015, there were 14 individuals in the exhibition area. An adult male (i.e., 971, see Supplementary Table S1) was released and joined the AMU on April 9th. In addition, although they were in the same enclosure, the OMU and the AMU in our study group always had their respective within-unit dominance hierarchy. The juveniles of the OMU frequently interacted with the AMU individuals, but other than this, there were no other affiliative interactions and only occasional aggression between adults and/or subadults of the 2 units. We thus tested our hypothesis on the 4 AMU juveniles and the one juvenile male from the OMU (N = 5). Supplementary Table S1 gives detailed information on each individual and the composition of 2 units in the study group.

Behavioral observation

Data were collected from November 2014 to June 2015 and a total of 108 days (786.5 contact-hours) of observation were completed. The behavioral data collected were composed of 3 parts. First, we used the all-occurrence recording method to document same-sex mounts and contextual information

Table 1. Summary of the predictions examined to test our hypothesis, that is, male juveniles act as the mountee to receive grooming (PMG) from the peer mounter, in the AMU juveniles and the male juvenile of the one-male unit of golden snub-nosed monkeys (*R. roxellana*) at Shanghai Wild Animal Park, Shanghai, China.

Predictions		Result
1)	The mountee is more likely to receive PMG when he solicits before the mount than when he does not;	Supported
2)	In light of the needing-to-learn hypothesis, when a mountee allows the mounter to mount longer, he is more likely to receive PMG;	Supported
3)	The mounter is more likely to initiate PMG than the mountee;	Supported
4a)	The more frequently the mountee receives PMG from a partner, the more often he chooses him as his mounter;	Supported
4b)	Whether the mounter grooms the mountee predicts the mounting direction of their subsequent mount;	Partially supported
5)	A juvenile mountee prefers males who groom him longer than others as his frequent mounting partner.	Not supported

(Martin and Bateson 2012), including whether the would-be mountee performed hindquarter presentation (i.e., mounting solicitation) or not, the participants, mounting duration, any post-mounting behaviors (i.e., huddling and/or grooming) and the duration. The duration of behaviors was identified by a stopwatch (seconds). Second, to assess dominance ranks, we recorded the whole foraging process using a SONY DCR-SX60E DV when the monkeys were provisioned. When we processed the videos after an observational day, we noted and counted displacement behaviors among juveniles using the all-occurrence recording method. Third, to evaluate dyadic proximity-based association levels among juveniles, we also scanned each juvenile at a 25-min interval during the daytime and recorded the activity, behavioral partner/s, and the neighbor/s within 1 m from January to June 2015 (Zhang et al. 2012).

In male golden snub-nosed monkeys, same-sex mounting behaviors of juveniles occurred in 3 social contexts, that is, peace, play, and tense. In the peaceful context, the atmosphere of the whole group was calm. The playful social context was determined when 2 or more juveniles were involved in play movements, such as chasing, grabbing, or mock fighting. A tense social context occurred when an AMU individual approached or glared at a juvenile, and in most cases, the latter then screamed and presented their hindquarters. Juveniles also sometimes screamed, crouched, and solicited mounting when extreme aggression occurred or when an adult was displaying, which was considered a tense context as well. A would-be mountee may or may not show this pre-mounting solicitation. When there was no solicitation, the mouter directly approached the mountee and placed its hand on the mountee's waist to start the mount. A mounting event was deemed terminated after the mouter dismounted from the mountee and no more mounting occurred, which could be immediately followed by huddling and/or grooming (if any). If the participants first huddled for a while at the end of a mount and then started grooming, we still regarded the grooming event as PMG. PMG cases could be unidirectional or bidirectional and initiated by either of the mounting participants.

The introduction of the new adult male (i.e., 971) in April 2015 led to changes in the social relationships among the AMU members (Huang et al. 2018). Therefore, we evaluated the dominance relationship and dyadic proximity-based association levels among juveniles before and after the demographic change. A total of 1,242 displacements among juveniles were recorded during our study period with 858 occurring before the demographic change and 384 noted after. We obtained juvenile social rankings for each time period represented by normalized David's score (NDS) using the *DS* function of the "EloRating" package in R 4.1.2 (Neumann and Kulik 2020; R Core Team 2021). In addition, we calculated frequencies of co-occurrence between 2 juveniles as their proximity-based association levels before (January to March 2015) and after the demographic change (April–June 2015). As there was no distinct rank reversal from November 2014 to March 2015 (see Figure 1 in Huang et al. 2017), we considered the dyadic association levels during this period to be equivalent to those from January to March 2015.

Statistical analysis

To test Predictions 1 and 2, we built a generalized linear mixed model (GLMM) with binomial errors and logit link for all

same-sex mounting cases and examined whether the performance of a mounting solicitation and the mounting duration predicted the likelihood of the mouter initiating PMG. The response variable was whether or not the mouter initiated PMG. Whether the mountee had performed a solicitation and the mouter's mounting duration were set as the explanatory variables. The social context in which the mount occurred and the dyadic association level were control variables. These control variables were included in the models to rule out their potential effects on the relationship between explanatory variables and the response variable (Becker 2005). When assessing whether the mouter was more likely to initiate PMG than the mountee (Prediction 3), we ran another GLMM with binomial errors and a logit link for the same-sex mounting cases with a following PMG without fixed effects included. The mounting dyad ID, the mouter ID, and the mountee ID were set as random factors in these 2 models.

During our 8-month study period, we defined each month as a time frame and examined potential long-term contingency through testing the partner choice of a juvenile mountee. We established a GLMM with Poisson distribution and log link to test Prediction 4a, that is, there was a positive across-dyad correlation between the monthly probability of a mountee receiving PMG and his preference for this mouter. For each dyad, we used a monthly count of a mountee being mounted to quantify the intensity of the mountee's partner preference, which was entered as the response in the model. The frequency of the mountee receiving PMG in each month, that is, the number of times the mountee was groomed divided by the total number of times the mountee was mounted by this mouter, was included as the explanatory variable. Dyadic association level and the rank difference (i.e., the NDS difference between the mouter and the mountee) were included as control variables. Random factors included in this GLMM were the mounting dyad ID, the mouter ID, the mountee ID, and the sampling month.

We tested for short-term contingency by examining the immediate effect of the occurrence of PMG between 2 participants on the mounting direction of their subsequent mount in a sampling day (Prediction 4b). For 2 specific juveniles, we screened their mounting interactions to see if they performed at least twice within a sampling day and if so, included these data. When building the GLMM with binomial errors and logit link, whether the mount was a single mount or one of the series mounts, whether the mouter had groomed the mountee, and the interaction of the 2 variables were set as predictors. Whether the mountee mounted the mouter in their subsequent mount was set as the response. The dyadic association level and the absolute rank difference between the participants were entered as control variables and the random factors were the mounting dyad ID, the mouter ID, and the mountee ID.

At the individual level, we predicted that a mountee preferred to choose as his mounting partner those who invested in longer grooming duration than other potential partners (Prediction 5). We applied the monthly frequency of a juvenile being mounted to quantify the extent to which this juvenile preferred this peer as his mouter. This frequency was calculated by the number of mounts where the juvenile was mounted by this peer divided by the total number of mounts the juvenile received from all peers in a month. We built the last GLMM with a beta distribution to account for this proportional response variable. The explanatory variable was the

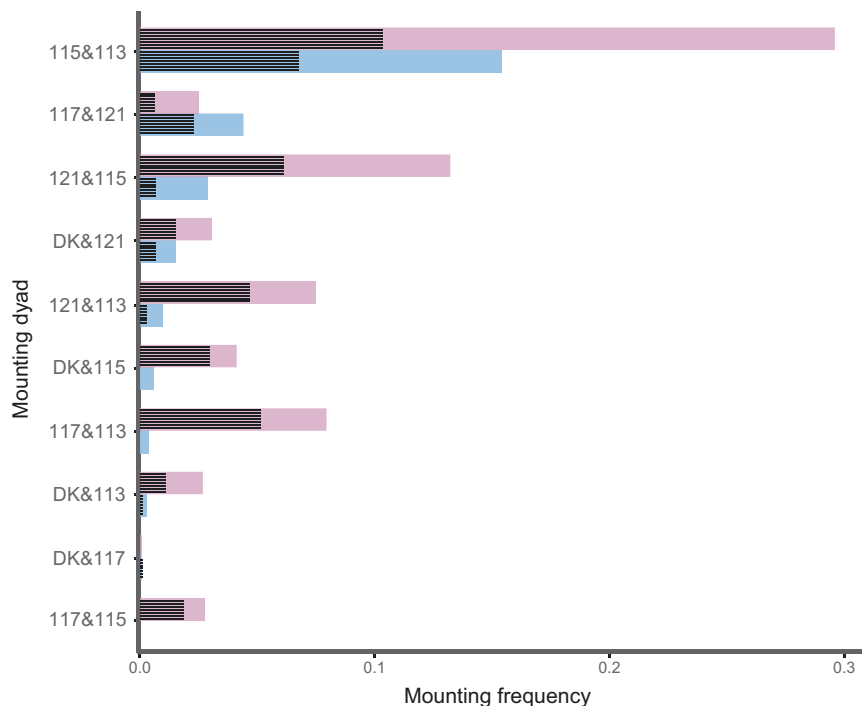


Figure 1. During our study period, the distribution of mounting frequency across all mounting dyads from the 4 juveniles of the all-male unit and the juvenile of the one-male unit of golden snub-nosed monkeys (*R. roxellana*) at Shanghai Wild Animal Park, Shanghai, China. For a specific dyad ‘A&B’ indicated on the y axis, the upper bar represents the mounting frequency where A mounts B and the lower bar represents the mounting frequency where B mounts A. The shaded part in each bar shows the frequency of mounts which is accompanied by PMG initiated by the mounter.

difference in the amount of grooming (in seconds) invested by this mounter and the mountee. In the PMG cases where the mountee groomed the mounter, the mounter’s investment in grooming was negative. Again, the dyadic association level and the rank difference were set as the control variables. The random factors in this model were the mounting dyad ID, the mountee ID, and the sampling month.

Data processing was carried out in the statistical environment R 4.1.2 (R Core Team 2021). We used the “lmerTest” package to analyze GLMMs with a binomial/Poisson distribution and ‘glmmTMB’ package for the beta-distributed model (Brooks et al. 2017; Kuznetsova et al. 2017). Residual diagnostics were performed with the ‘DHARMA’ package which assesses model fit using a simulation-based approach. All models were checked for dispersion and outliers by carrying out the tests with the *testResiduals* function (Hartig 2022). It turned out that all models were not over-dispersed ($P > 0.272$). No outliers were detected ($P > 0.204$) except for the model for testing Prediction 5 ($P = 0.009$) (Supplementary Figures S1 and S2). We did not remove the outliers or alter the model structure as we believe the outliers represent the existing variation and should not be removed from our dataset. A likelihood ratio test was subsequently performed for each model to compare the difference between the model and the respective control model (only control variables included) with the ANOVA function. In addition, the difference in the mounting duration between the 2 groups was detected with a Student’s *t*-test. The binomial test was used to check whether the frequency distribution of the variable corresponded to an expected distribution. The graphics were constructed using “ggplot2” and “reshape2” packages (Wickham 2007, 2016). All tests were 2-tailed and the significance level was 0.05.

Results

During the study period, a total of 1,044 same-sex mounts were recorded from the 5 juveniles, of which 706 were single mounts and 338 occurred within 160 bouts of series mounts. The mounting frequencies of different juveniles’ pairs varied a lot, with a notable bias observed in a pair (individuals 115 and 113) (Figure 1). Nearly half of the mounting cases were accompanied by PMG initiated by the mounter (45.40%, 474/1,044) (Figure 1). Only 39 mounting cases (3.74%) were followed by PMG initiated by the mountee and no PMG occurred in the others (50.86%, 531/1044).

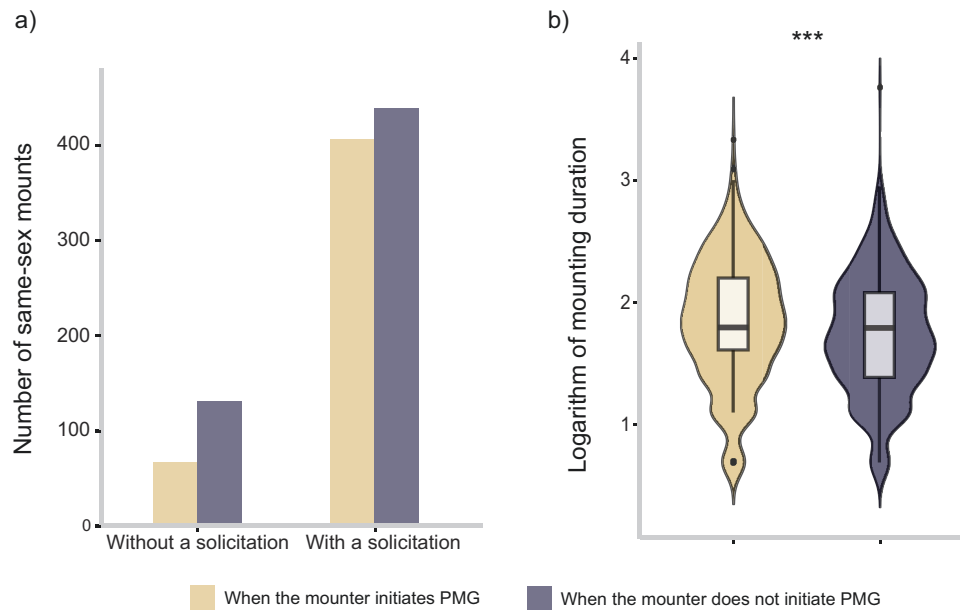
Predictions 1 and 2

We assumed that the mountee was more likely to receive PMG when he solicited before the mount than when he did not (Prediction 1), or when he allowed the mounter to mount longer (Prediction 2). In support of both predictions, the results of the model including all same-sex mounting cases revealed that the mounter was more likely to initiate PMG when the mountee had solicited than when he had not (Estimate \pm SE = 0.55 ± 0.19 , $Z = 2.90$, $P = 0.004$) (Table 2) (Figure 2a). The longer a mount was, the more likely the mountee received PMG (Estimate \pm SE = 0.08 ± 0.02 , $Z = 3.76$, $P < 0.001$), too. Specifically, the mounting duration was 7.16 ± 3.68 s ($M \pm SD$, $N = 474$) when the mountee received PMG and it was significantly but slightly shorter ($M \pm SD = 6.39 \pm 3.48$ s, $N = 570$) in other mounting cases (*t*-test: $t = -3.43$, $P < 0.001$) (Figure 2b). Besides, the mountee was more likely to receive PMG when the mount occurred in non-tense than tense social contexts (playful vs. tense, estimate \pm SE = 0.84 ± 0.18 , $Z = 4.81$, $P < 0.001$; peaceful

Table 2. The response variable and statistics of the respective explanatory variable for each GLMM (control variables not included) testing the predictions in this study.

Predictions	The response variable	The explanatory variable	Estimate	SE	Z	P
1)	Whether the mountee receives PMG	Whether the would-be mountee solicits	0.55	0.19	2.90	0.004**
2)	The mounter or the mountee initiates PMG	The mounter's mounting duration	0.08	0.02	3.76	<0.001***
3)		(Intercept)	2.56	0.50	5.12	<0.001***
4a)	The count of the mounts the mountee receives	The frequency of PMG the mountee receives	0.60	0.18	3.35	<0.001***
4b)	Whether the mountee mounts back next time	Series mount or not × The mountee received PMG or not	-1.52	0.46	-3.31	<0.001***
5)	The frequency of the mountee being mounted	The difference in the participants' grooming investment	0.00	0.00	0.92	0.358

Note: Multiplication sign (×) represents the interaction between 2 variables.

**Figure 2.** For the 4 juveniles of the all-male unit and the juvenile of the one-male unit of golden snub-nosed monkeys (*R. roxellana*) at Shanghai Wild Animal Park, Shanghai, China, (A) the number of same-sex mounts in relation to whether or not the mountee performed a mounting solicitation; (B) the comparison of logarithms of same-sex mounting durations between the cases where the mounter initiates PMG or not. Student's *t*-test is indicated by ****P* < 0.001.

vs. tense, estimate \pm SE = 0.57 ± 0.22 , $Z = 2.60$, $P = 0.009$), whereas the dyadic association level exerted little to no effect (Estimate \pm SE = -1.05 ± 1.04 , $Z = -1.00$, $P = 0.315$). This model significantly differed from the respective control model (ANOVA: $\chi^2 = 25.72$, $P < 0.001$).

Prediction 3

Among the 513 same-sex mounts with PMG, the mounter was more likely to initiate PMG than the mountee (Estimate \pm SE = 2.56 ± 0.50 , $Z = 5.12$, $P < 0.001$). Prediction 3 was thus strongly supported.

Predictions 4a–b

Based on Prediction 4a, the more frequently a mountee receives PMG from a partner, the more often he chooses

him as his mounter. In favor of this prediction, the results indicated that, for a specific mounting dyad in a sampling month, the frequency of the mountee receiving PMG significantly predicted the total count of their mounting interactions (estimate \pm SE = 0.60 ± 0.18 , $Z = 3.35$, $P < 0.001$) (Table 2, Figure 3). One of the control variables, the dyadic association level, also explained the variation in how frequently their mounting interactions occurred (estimate \pm SE = 2.44 ± 0.88 , $Z = 2.77$, $P = 0.006$), whereas the rank difference did not (estimate \pm SE = -0.11 ± 0.10 , $Z = -1.04$, $P = 0.296$). This model showed a significant difference from its control model ($\chi^2 = 11.17$, $P < 0.001$).

After removing the same-sex mounts of a specific dyad that occurred only once in a sampling day, there were 804 mounting interactions included in the analysis testing Prediction 4b, that is, whether the mounter grooming the

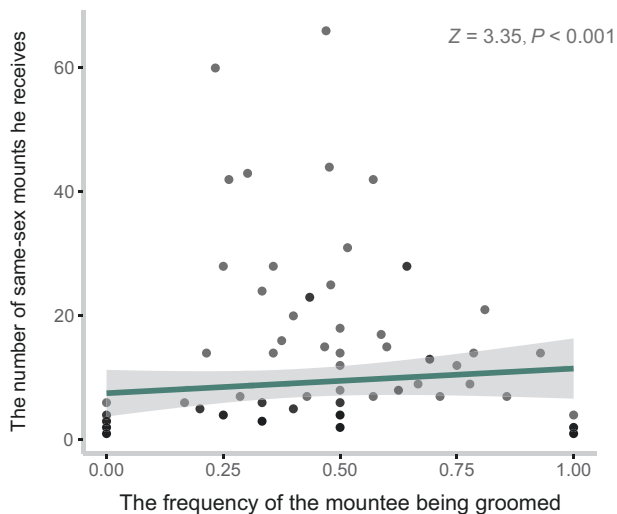


Figure 3. For a specific mounting dyad among the 5 juvenile golden snub-nosed monkeys (*Rhinopithecus roxellana*) at Shanghai Wild Animal Park, Shanghai, China, the frequency of the mountee receiving PMG significantly predicts the number of same-sex mounts he receives in a sampling month ($Z = 3.35$, $P < 0.001$). Each data point is semi-transparent. The transparency value of the data points is accumulated when they are overlapped, making them appear darker. The line is fitted on the raw data with a linear model and the shaded areas represent 95% confidence intervals.

mountee predicts the mounting direction of their subsequent mount. Model statistics revealed that the interaction between whether the mounter had groomed the mountee and whether the mount was a single mount or one of the series mounts significantly predicted the mounting direction of their next mount (estimate \pm SE = -1.52 ± 0.46 , $Z = -3.31$, $P < 0.001$) (Table 2). We thus divided the dataset by whether the mount was single or not and ran 2 separate models. The results showed that when 2 juveniles performed a single mount, whether the mounter groomed the mountee did not predict the direction of their subsequent mount (estimate \pm SE = -0.44 ± 0.31 , $Z = -1.44$, $P = 0.151$). Nevertheless, this was not the case when the mount was one of the series mounts (Estimate \pm SE = -1.76 ± 0.37 , $Z = -4.74$, $P < 0.001$). Specifically, if the mounter had not groomed the mountee, the mountee was more likely to mount back in their subsequent mount (binomial test: $P < 0.001$). Although the mounter had groomed the mountee, there was no difference in the mounting direction of their subsequent mount (Binomial test: $P = 0.349$). In these models, neither the association level nor the absolute rank difference of a dyad predicted the response variables (data not shown). Therefore, Prediction 4b was only supported when the juveniles engaged in series mounts but not when they performed single mounts.

Prediction 5

At the individual level, we predicted that a juvenile mountee preferred males who groomed him longer than others as his frequent mounting partner. However, among the 513 PMG cases (79.92% unidirectional and 20.08% bidirectional), there was no evidence revealing that the difference in the participants' grooming investments correlated with how frequently a mountee was mounted by a partner (estimate \pm SE = 0.00 ± 0.00 , $Z = 0.92$, $P = 0.358$) (Table 2). This

model did not significantly differ from its control model, either ($\chi^2 = 0.85$, $P = 0.356$).

Discussion

As an affiliative behavior, grooming can also directly benefit the recipients in ectoparasite removal (Hutchins and Barash 1976; Henzi and Barrett 1999). Our results supported the hypothesis that juvenile male *R. roxellana* acted as the mountee to receive grooming from their peer mounters in same-sex mounting interactions (Table 1). Specifically, the mountee was more likely to receive PMG when he had performed a pre-mounting solicitation than when he had not. The longer he allowed the mounter to mount, the more likely he received PMG. At the end of a mount, the mounter, rather than the mountee, was more likely to initiate PMG. We also found evidence of both short-term and long-term contingencies in the grooming–mounting interchanges of the juveniles, although the short-term contingency effect was only detected when they performed series mounts but not in their single mounts. In particular, a juvenile mountee preferred a partner who groomed him more often than others after a mount. Overall, our data indicate that, in the context of same-sex mounts, the interchange of being mounted for grooming and the partner choice of the mountee are subject to a “market effect” in our study species.

In *R. roxellana*, all-male groups provide juveniles with a transitional social environment for the development of survival and social skills required in their future life (Yao et al. 2011; Su 2014). Practicing mating behaviors can be important for young males in AMUs because in the free-ranging groups, extra-unit copulations (i.e., females in OMUs mating with neighboring resident males or AMU individuals) are quite common (Qi et al. 2020; Xiang et al. 2022). Therefore, if they are skilled in the physical behaviors of mounting and pelvic thrusting before sexual maturity, they will be prepared to engage in these opportunities when they present themselves. In wild bands, there is evidence that young adults in AMUs can sire infants through extra-unit copulations before they form an OMU of their own (Qi et al. 2020). It is thus expected that juveniles acquire adult-like mounting skills in the all-male band and that their mounting behavioral patterns gradually develop during the period while they are reaching maturation. Our previous work on the same study group provided evidence supporting this argument (Huang et al. 2023), indicating that same-sex mounting opportunities represent a valuable resource for juveniles to practice mating skills. The current study further demonstrates that mounters who devote grooming to their mountees, enhance their mounting partnerships and increase their probability of being allowed to access and mount the partner in their future social interactions.

The partner-choice model posits that the likelihood of providing a service depends more on the overall history of previous interactions between partners, rather than their most recent interactions (Noë 2006b; Schino and Aureli 2009, 2010). Compared with long-term contingency, short-term contingency should thus be less common and can only be expected in partners who rarely interact (Schino and Aureli 2009, 2010). For example, in female Japanese macaques, receiving grooming from a partner did not increase the short-term probability of supporting them when the latter was involved in overt aggression, and being supported by the partner during aggression did not increase the short-term

probability of grooming them, either. However, there was a strong positive across-dyad correlation between the 2 behaviors over the whole year of observation (Schino et al. 2007). Our analyses add more supportive evidence to this argument. Of the 2 mechanisms that potentially underlie the exchange of grooming and mounting opportunities, partner choice of this trading-based strategy in male juvenile *R. roxellana* is more of a long-term rather than a short-term contingency. Specifically, the short-term contingency observed among juveniles in this study is likely due to the immediately reciprocal characteristic specific to their series mounts (Fang et al. 2018; Huang et al. 2023), but fulfills the criteria of reciprocal exchange in within-day and dyadic short-term analyses (de Waal 1997; Gilby et al. 2010). However, our sampled juveniles performed single same-sex mounts in most cases (67.62%, 706/1,044), which could not be explained by the short-term contingency effect. The results of the long-term contingency effect were based on the monthly aggregate data across the study period (Schino and Aureli 2010, 2017), indicating that juveniles were offering mounting opportunities to receive grooming on a longer-term basis.

The biological market theory posits that individuals compare how much different partners have to offer to make their decision on who to cooperate with (Noë and Hammerstein 1994, 1995). The attractiveness of an individual as a partner is largely dependent on the relative value of the services that they can provide or trade (Fruteau et al. 2009; Schino and Aureli 2009, 2017). For instance, during grooming/infant-handling interchanges, female olive baboons (*Papio anubis*) groomed mothers longer when they were with the infant than when they were not in an attempt to gain access to the infant. This pattern was independent of the maternal kinship between the female and the mother (Frank and Silk 2009). However, in our study, no evidence was detected in favor of Prediction 5 that the more grooming the mounter invested in the mounTEE, the more preferred this partner was by the mounTEE juvenile. One potential reason may be the differences that exist in our between-individual comparison relative to the between-group comparison of the baboon study (i.e., females without an infant vs. females with an infant). The other reason may be the specific feature of the commodity (i.e., mounting opportunity) in this grooming market. In the markets where females groom mothers for access to their infants, the commodities traded are competitive and can only be offered by mothers. In contrast, a mounting opportunity for juveniles in the AMU is less scarce, as it can be offered and is required by any of the juveniles. That is to say, a juvenile who has provided mounting opportunities for his partners also needs these partners as his potential mounTEEs in their future social interactions. The relatively high availability of mounting opportunities may result in males lack of concern about whether or not they will receive more grooming from their preferred partners than that from others.

Our results illustrate that juvenile male *R. roxellana* act as the mounTEE in same-sex mounts to receive grooming from the mounter on a long-term basis. The formation of this cooperative relationship during same-sex mounting episodes may benefit from the long-term and relatively stable existence of the all-male band in the multilevel society of *R. roxellana* (Qi et al. 2014; Su 2014). In this polygynous species, after joining the all-male band, the male juveniles may stay until reaching adulthood and leave when they become sexually mature if they can successfully form breeding units and join

the breeding band (Yao et al. 2011). The deposited resident males who have been rejected from the breeding units and those who temporarily have no reproductive opportunities also join the all-male band, seeking and waiting for further mating chances (Zhang et al. 2008; Qi et al. 2020; Xiang et al. 2022). In addition, the all-male band maintains close spatial association and coordinates their movement patterns with the breeding band (Qi et al. 2014). However, adult and subadult females rarely join the all-male band and affiliate with bachelor males. This maintains the stability and integrity of the all-male band to some extent as once observed by the resident male, the all-male band will be attacked and chased away (Xiang et al. 2022). We suggest that these species-specific characteristics may provide conditions for the development of the mounting–grooming interchange behavioral trait among juveniles in the all-male band, which further contributes to the evolutionary benefits of same-sex mounting behaviors. Detailed studies on same-sex mounts are needed in other primate species that have all-male groups or form a multilevel society to confirm if these conditions favor mounting–grooming interchange.

To the best of our knowledge, the relationship between same-sex mounts and the presence of PMG has been rarely reported in nonhuman primates (but see Sommer et al. 2006; Faraut et al. 2015). The cooperative relationship we report among juvenile males during their same-sex mounting interactions has not been reported before in the literature. There are limitations to our study in which we had a small sample size of individuals and in the closed captive setting. Our focal monkeys may have different time budgets relative to wild individuals. They may have been able to spend more time socializing and less time feeding and thus were unconstrained in exhibiting behaviors that may be relatively infrequent in wild (cf. Fang et al. 2018). The variations in mounting frequencies exhibited by different pairs of juveniles in our study group also underscore the necessity of considering the non-negligible individual differences in performing same-sex mounting behavior. In addition, the statistical power of our analysis is constrained by the small sample size, which may affect the robustness of our results and limit their generalizability to other *R. roxellana* populations or primate species. There is also a possibility that the behavioral patterns of same-sex mounting and the following grooming interactions in *R. roxellana* are not clearly captured by our small study group as subgroups formed in the wild/large all-male band could not be adequately represented. We encourage a measured perspective on the results and emphasize the need for future research in large wild/free-ranging groups to validate and extend our observations.

Despite these limitations, the analyses presented in our study are therefore an illustration of the possible cooperative interchange that can develop between same-sex mounts and the occurrence of PMG, which has not been previously detected. Beyond that, more analyses on the relationship between same-sex mounts and PMG, using long-term data to monitor the dynamics of individual partner choice, may further help to shed light on their biological significance in future studies.

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Conflict of Interest Statement

The authors declare that they have no conflicts of interest.

Authors' Contributions

P.H. and J.A.T. conceived the study. E.Z. and M.C. acquired funding and managed the project. P.H. conducted fieldwork, analyzed the results, and drafted the manuscript. P.H. and J.A.T. discussed the results and revised the manuscript with specific contributions by E.Z. and M.C. All authors critically contributed to drafts and gave final approval for publication.

Ethical Statement

Our behavioral observations are performed at a distance with limited disturbance to the monkeys. All research methods comply with protocols approved by the Ethics Committee of the School of Life Sciences, East China Normal University.

Data Availability

The data on which this study is based are available on Figshare at <https://doi.org/10.6084/m9.figshare.23633625>

Supplementary Material

Supplementary material can be found at <https://doi.org/10.1093/cz/zoae020>.

References

- Bailey NW, Zuk M, 2009. Same-sex sexual behavior and evolution. *Trends Ecol Evol* 24:439–446.
- Becker TE, 2005. Potential problems in the statistical control of variables in organizational research: a qualitative analysis with recommendations. *Organ Res Methods* 8:274–289.
- Boesch C, Boesch H, 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Am J Phys Anthropol* 78:547–573.
- Brooks ME, Kristensen K, Van Benthem KJ, Magnusson A, Berg CW et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400.
- Cheney DL, 2011. Extent and limits of cooperation in animals. *Proc Natl Acad Sci USA* 108:10902–10909.
- Chevalier-Skolnikoff S, 1976. Homosexual behavior in a laboratory group of stump-tail monkeys (*Macaca arctoides*): forms, contexts, and possible social functions. *Arch Sex Behav* 5:511–527.
- de Waal FBM, 1997. The chimpanzee's service economy: food for grooming. *Evol Hum Behav* 18:375–386.
- Dixson AF, 2010. Homosexual behaviour in primates. In: Poiani A. editors. *Animal Homosexuality: A Biosocial Perspective*. Cambridge: Cambridge University Press, 381–400.
- Dunbar RIM, 1991. Functional significance of social grooming in primates. *Folia Primatol (Basel)* 57:121–131.
- Fang G, Dixon AF, Qi X, Li B, 2018. Male-male mounting behaviour in free-ranging golden snub-nosed monkeys (*Rhinopithecus roxellana*). *Folia Primatol* 89:150–156.
- Faraut L, Northwood A, Majolo B, 2015. The functions of non-reproductive mounts among male Barbary macaques (*Macaca sylvanus*). *Am J Primatol* 77:1149–1157.
- Frank R, Silk J, 2009. Grooming exchange between mothers and non-mothers: the price of natal attraction in wild baboons (*Papio anubis*). *Behaviour* 146:889–906.
- Fruteau C, Voelkl B, van Damme E, Noë R, 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc Natl Acad Sci USA* 106:12007–12012.
- Gilby IC, Thompson ME, Ruane JD, Wrangham R, 2010. No evidence of short-term exchange of meat for sex among chimpanzees. *J Hum Evol* 59:44–53.
- Goy RW, Wallen K, 1979. Experiential variables influencing play, foot-clasp mounting and adult sexual competence in male rhesus monkeys. *Psychoneuroendocrinology* 4:1–12.
- Gumert MD, 2007. Payment for sex in a macaque mating market. *Anim Behav* 74:1655–1667.
- Gunst N, Leca JB, Vasey PL, 2013. Development of sexual and socio-sexual behaviours in free-ranging juvenile male Japanese macaques, *Macaca fuscata*. *Behaviour* 150:1225–1254.
- Hartig F, 2022. DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models. R package version 0.4.6. Available from: <https://CRAN.R-project.org/package=DHARMa>
- Henzi SP, Barrett L, 1999. The value of grooming to female primates. *Primates* 40:47–59.
- Huang P, Fang G, Teichroeb JA, Zhang E, Chen M, 2023. Examining postmounting grooming in male golden snub-nosed monkeys to investigate the functions of same-sex mounts. *Am J Primatol* 85:e23550.
- Huang P, He X, Zhang E, Chen M, 2017. Do same-sex mounts function as dominance assertion in male golden snub-nosed monkeys (*Rhinopithecus roxellana*)? *Am J Primatol* 79:e22636.
- Huang P, Zhang E, Chen M, 2018. The influence of a demographic change on social relationships among male golden snub-nosed monkeys (*Rhinopithecus roxellana*). *Primates* 59:413–421.
- Hutchins M, Barash DP, 1976. Grooming in primates: implications for its utilitarian function. *Primates* 17:145–150.
- Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. lmerTest package: tests in linear mixed effects models. *J Stat Softw* 82:1–26.
- Lv J, Zhao D, Li B, 2007. Homosexual mounting within one all-male juvenile unit in wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Acta Theriol Sin* 27:14–17.
- Martin P, Bateson P, 2012. *Measuring Behaviour: an Introductory Guide*, 2nd edn. Cambridge: Cambridge University Press.
- Neumann C, Kulik L, 2020. EloRating: animal dominance hierarchies by Elo-rating. R package version 0.46.11. Available from: <https://CRAN.R-project.org/package=EloRating>
- Noë R, 2006b. Cooperation experiments: coordination through communication versus acting apart together. *Anim Behav* 71:1–18.
- Noë R, Hammerstein P, 1994. Biological markets: supply and demand determine the effect of partner choice in cooperation, mutualism and mating. *Behav Ecol Sociobiol* 35:1–11.
- Noë R, Hammerstein P, 1995. Biological markets. *Trends Ecol Evol* 10:336–339.
- Qi X, Garber PA, Ji W, Huang Z, Huang K et al., 2014. Satellite telemetry and social modeling offer new insights into the origin of primate multilevel societies. *Nat Commun* 5:5296.

- Qi X, Grueter CC, Fang G, Huang P, Zhang J et al., 2020. Multilevel societies facilitate infanticide avoidance through increased extra-pair matings. *Anim Behav* 161:127–137.
- R Core Team, 2021. *R: a Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Available from: www.r-project.org
- Schino G, Aureli F, 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. *Adv Study Behav* 39:45–69.
- Schino G, Aureli F, 2010. Primate reciprocity and its cognitive requirements. *Evolut Anthropol* 19:130–135.
- Schino G, Aureli F, 2017. Reciprocity in group-living animals: partner control *versus* partner choice. *Biol Rev Camb Philos Soc* 92:665–672.
- Schino G, di Sorrentino EP, Tiddi B, 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame reciprocation. *J Comp Psychol* 121:181–188.
- Sommer V, Schauer PM, Kyriazis D, 2006. A wild mixture of motivations: same-sex mounting in Indian langur monkeys. In: Sommer V, Vasey PL editors. *Homosexual Behaviour in Animals: an Evolutionary Perspective*. Cambridge: Cambridge University Press, 238–272.
- Stevens JR, Hauser MD, 2004. Why be nice? Psychological constraints on the evolution of cooperation. *Trends Cogn Sci* 8:60–65.
- Su Y, 2014. *A Field Study of the Society of Rhinopithecus Roxellana*. Beijing: Beijing University Press.
- Vasey PL, 1995. Homosexual behavior in primates: a review of evidence and theory. *Int J Primatol* 16:173–204.
- Vasey PL, 2007. Function and phylogeny: the evolution of same-sex sexual behavior in primates. *J Psychol Hum Sex* 18:215–244.
- Vasey PL, Sommer V, 2006. Homosexual behaviour in animals. Topics, hypotheses and research trajectories. In: Sommer V, Vasey PL editors. *Homosexual Behaviour in Animals: an Evolutionary Perspective*. Cambridge: Cambridge University Press, 3–42.
- West SA, Griffin AS, Gardner A, 2007. Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J Evol Biol* 20:415–432.
- Wickham H, 2007. Reshaping data with the reshape package. *J Stat Softw* 21:1–20.
- Wickham H, 2016. *Ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag; NY.
- Xiang Z, Yu Y, Yao H, Hu Q, Yang W et al., 2022. Female countertactics to male feticide and infanticide in a multilevel primate society. *Behav Ecol* 33:679–687.
- Yao H, Liu X, Stanford C, Yang J, Huang T et al., 2011. Male dispersal in a provisioned multilevel group of *Rhinopithecus roxellana* in Shennongjia Nature Reserve, China. *Am J Primatol* 73:1280–1288.
- Zhang P, Li B, Qi X, MacIntosh AJJ, Watanabe K, 2012. A proximity-based social network of a group of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). *Int J Primatol* 33:1081–1095.
- Zhang P, Watanabe K, Li B, Qi X, 2008. Dominance relationships among one-male units in a provisioned free-ranging band of the Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, China. *Am J Primatol* 70:634–641.
- Zhang P, Watanabe K, Li B, Tan CL, 2006. Social organization of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Central China. *Primates* 47:374–382.