

Dominance rank of adult females and mating competition in Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, China

HE HaiXia^{1†}, ZHAO HaiTao^{1,2†}, QI XiaoGuang¹, WANG XiaoWei², GUO SongTao¹,
JI WeiHong^{2,3}, WANG ChengLiang², WEI Wei¹ & LI BaoGuo^{1,2*}

¹ College of Life Sciences, Northwest University, Xi'an 710069, China;

² Institute of Zoology, Shaanxi Academy of Sciences, Xi'an 710032, China;

³ Institute of Natural Resources, Massey University, Albany, Auckland 1311, New Zealand

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Dominance hierarchy reflects resource competition in male primates as well as females. In this study, we collected data on the social rank and mating competition of female Sichuan snub-nosed monkeys from September 2009 to June 2010 in the Qinling Mountains, Shaanxi, China. Displacement was used to determine social hierarchy of the studied wild females. A total of 1223 displacement bouts between adult females and 316 mating behaviors within one-male units (OMUs) were recorded. Competitive displacement among females was very low (0.22 displacements per observation hour). The dominant ranks of females in target OMUs were determined by displacement, from one OMU to another: JB unit: YL > DBC > YCM > XBC > BD; JZT unit: XHW > JG > DT; PK unit: QQ > TM > HF; LP unit: SK > TH > WM. Higher-ranking females performed significantly more sexual behavior than lower-ranking females in this rare monkey. High-ranking females were more likely to win mating contests within those OMUs. Based on these studies, we assessed the social relationships among adult females and clarified possible explanations for the strategies of female mating competition in the OMUs. Furthermore, the notion that reproductive success may also be related to female dominance hierarchies in this polygynous species should be considered in future research.

Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), female dominance rank, displacement behavior, mating competition, reproduction

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Dominance status plays a fundamental role in social interactions of individuals in group-living primates [1,2]. Dominance rank is defined as the ability of one individual to consistently evoke submissive behavior in all individuals within the same unit. Such social relationships are useful to describe social organizations [3] and to estimate an individual's priority access to resources [4]. Currently, dominance rank is regarded as a self-regulatory mechanism to reduce competition, and to sustain social affinity and organization stability because all individuals know their own social status

in the given social network [5].

Competition among males, which is usually intense in most nonhuman primates because of their physical features and social roles, was widely concerned. Social dominance rank in males is easily detected and conspicuous, but that of females may be obscure and weak because females are generally more tolerant and responsive with one another than are males [6]. Walters and Seyfarth [6] considered the dominance rank in females to be weak, especially in tolerant primate species. Reproductive skew theories state that dominance rank influences adult females' resource acquisition [7]. Wherein, mating opportunity is an important predictor for measuring female benefits, which is ultimately

[†]These authors contributed equally to this work.

*Corresponding author (email: baoguo.li@nwu.edu.cn)

influenced by female dominance rank. Dominance rank can be reflected as frequencies and intensities of social activities, including food competition and mating opportunities among different females [7]. In addition, dominant individuals influence the mating opportunities of subordinates, and have higher reproductive fitness in species that form hierarchical family groups [7], indicating that dominant individuals may spend more time mating with their own breeding males than do subordinates [8–11]. In spite of this, the highest-ranking individuals do not monopolize all desired resources and mating opportunities still exist for subordinates in the majority of primate species [8–11].

The pattern of female dominance hierarchy varies in primate species with different social structure. For example, in despotic species high-ranking females always monopolize desired resources and dominance rank among females is obvious, whereas female rank is much weaker in leaf-monkeys which are tolerant species and not despotic. Following the evolution of social systems, female dominance hierarchy is more complex than male dominance hierarchy in relation to function and mechanism. Multi-level societies, where social relationships among individuals are organized into two or more levels within the community, are the most complex and complete social structure, wherein one-male units (OMU) are the basic social and reproductive unit [12]. This multi-level society has only been observed in gelada and hamadryas baboons and snub-nosed monkeys [12]. According to research on aggressive behavior in matrilineal society gelada baboons, female dominance ranks exist, with the highest-ranking female gaining more mating opportunities than the lowest-ranking female [13] because females do not migrate among OMUs and often form female-bonds within OMUs. Conversely, female ranks do not exist and mating opportunities are more equally distributed among adult females within hamadryas OMUs because females migrate among OMUs and maintain a particular, intimate relationship with the leader male [12–14]. To date, however, no such research has been conducted on Sichuan snub-nosed monkeys [12].

Sichuan snub-nosed monkeys exhibit a multi-level social stratum that varies over time, although female migration between OMUs occurs less often in Sichuan snub-nosed monkeys than in hamadryas. A troop includes all-male units (AMUs) and several OMUs, which consist of one breeding male, multiple females, and their offspring. Conflicts among different individuals within OMUs do occur, including aggressive and submissive behavior [15]. Aggressive behaviors of adult females include biting, fighting, chasing, threatening, and displacing when experiencing scramble competition [16]. Displacement occurs when a high-ranking individual approaches and a low-ranking individual moves away. In Sichuan snub-nosed monkeys, dominance rank in males is determined by aggression and aggressive behaviors. For females, however, this method might not be particularly effective [16]. Because females are generally regarded as

less aggressive and more tolerant, in this study we hypothesized that female social rank could be determined by displacement rather than aggression, this displacement has been successfully applied in many other primate species [17–19].

Based on the social structure and relationship characteristics of the Sichuan snub-nosed monkeys, we made the following preliminary predictions regarding female dominance rank and female mating competition within the OMUs. Firstly, females will have few interactions in the female-migration group, thus further reducing the frequency of female displacement [12]. We predicted that the frequency of displacement among females would be relatively low in Sichuan snub-nosed monkeys. Secondly, displacement behavior between females under natural conditions exists and is useful to delineate the female dominance hierarchies [20,21]. Thus we predicted that dominance hierarchies among females could be determined using only displacement behavior in free-ranging Sichuan snub-nosed monkeys. Thirdly, the dominance ranks among females within OMUs are propitious to maintain group cohesion and energy requirements. Furthermore, it was presumed that high-ranking individuals possess greater reproductive potential and that high-ranking females should be more attractive as mating partners than other females within the OMU, affecting the mating strategies of others [22–24]. Thus we predicted that high-ranking females gained more mating benefits than low-ranking females within the OMUs of this polygynous species.

In this study, we aimed (1) to examine the presence of dominance ranks among adult females by displacement; (2) to examine the power of female dominance rank in mating competition; and (3) to discuss possible strategies of female mating competition in OMUs in Sichuan snub-nosed monkeys.

1 Materials and methods

1.1 Study area and animals

This study was conducted near Yuhuangmiao village (108°14′–108°14′E, 33°45′–33°50′N) in Zhouzhi National Nature Reserve on the northern slopes of the Qinling Mountains in Shaanxi Province, China [25]. The altitude of the study site is 1400–2890 m above sea level. The vegetation varies with altitude from coniferous forests above 2600 m to mixed coniferous broadleaf forests above 2200 m and deciduous broadleaf forests at low elevations [25]. Two groups of Sichuan snub-nosed monkeys, the West Ridge Group and the East Ridge Group, inhabit this area and they are separated by the Nancha River [25].

We studied the behavior of adult females in four OMUs of the West Ridge Group. The group consisted of fourteen adult females, four adult males, and seven infants (Table 1). Based on physical characteristics such as facial features and

Table 1 Basic information of four target units^{a)}

Resident-male	LP	JB	PK	JZT
Adult female	WM, SK, TH	YL, YZM, BD, DBC, XBC	HF, TM, QQ	JG, XHW, DT
Sub-adult	XH, XB, XD, XF, XM, XW, GG	NY, X ₁ Y ₁ , XK, XY, GY, GXC	GF, GS, J3.5 years, J2.0 years	J3.5 years, J3.5 years, J3.5 years
Juvenile	Y ₁ M ₁ , YH, YW, ♂	YD, YDC, YM	YQ, YT	
Infant		H ₁ Y ₁ , HYM, HDC, HY	H ₁ F ₁	HG, HD
Total	14	19	11	9

a) The unit is named after its resident male.

body size, all the individuals were identified.

1.2 Food provisioning

Provisioning was conducted in a 15 m × 30 m area at Sanchakou (1646 m above sea level) in Gongnigou valley within the home range of the West Ridge group. Every morning for 113 d, the monkeys were located and herded to the provisioning site. We began our observations at about 10:00 am. Provisioned food consisted of corn, radishes, and apples. Food was provided three times a day at 10:00 am, 12:00 am, and 2:00 pm. On average, 200 g of food were provided per monkey per day, which is a minor proportion of their daily food consumption [26,27]. The distances between the monkeys and the observers were shortened between 0.5 and 50 m and we could recognize the identities of focal females easily when they were feeding. Following provisioning, the monkeys would freely leave the provisioning site [28,29].

1.3 Data collection

The troop was observed for six hours per day from September 2009 to June 2010. Focal observations with continuous recording were conducted to avoid oversight of relevant behaviors. Displacement is defined as one individual leaving at the approach of another individual within 1 m, including supplanting and avoidance [30]. All adult females within each target unit were focal animals for one day from 10:00 am to 4:00 pm and the observation times were equal among focal units. The data on displacement and mating behavior were recorded. Female dominance hierarchies were constructed based on displacement behaviors [31].

1.4 Data analysis

Displacement data of adult females within OMUs were calculated as the ratio of displacement = number of displacement by actor/total of (displacement by actor and by partner) within OMUs, and were entered into matrices with “winners” plotted along columns and “losers” plotted along rows to determine dominance ranks [32].

In addition, the nonparametric Spearman Rank Correlation test was used to test for correlation between female ranks and mating frequencies.

2 Results

2.1 Adult female rank

During the 113-d study period, no females dispersed among different OMUs. A total of 1415 displacement bouts were recorded, with 1223 displacements occurring between adult females within OMUs. The additional 192 displacements occurred among different OMUs and were excluded in the data analysis. Of 1223 displacements, 416 occurred in the JB unit, 210 occurred in the JZT unit, 345 occurred in the PK unit, and 252 occurred in the LP unit.

Displacement behavior among female Sichuan snub-nosed monkeys occurred at a rate of 0.22 interactions per hour per unit. Rank orders among females were determined from one OMU to another (Table 2): JB unit: YL > DBC > YCM > XBC > BD; JZT unit: XHW > JG > DT; PK unit: QQ > TM > HF; LP unit: SK > TH > WM. Furthermore, the highest-ranking individuals did not attack only the lowest-ranking females. For example, displacement between YL and BD ($n = 28$) was not higher than that between YL and XBC ($n = 56$) in Table 2.

2.2 Female rank and mating competition

During the study period, 316 mating events were observed, with 104 recorded in the JB unit (0.15 interactions per hour), 72 in the JZT unit (0.11 interactions per hour), 65 in the PK unit (0.10 interactions per hour), and 75 in the LP unit (0.11 interactions per hour) (Table 2). There was a positive correlation between frequencies of mating (the 14 females in target units during the study period) and female ranks (with different ranks ranging from the highest rank, 1, to lowest rank, 5) ($-1 < r_s = -0.879 < 0$; $P_{JB, JZT, LP, PK} < 0.05$), indicating higher-ranking females mated more than lower-ranking females ($P < 0.05$) (Table 3, Figure 1).

3 Discussion

Dominance rank among adult females of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) was positively correlated with mating competition as is often observed in other leaf monkey species [33]. The frequency of displacement behavior among adult females within the OMUs was low, indicating that *R. roxellana* females exhibited affiliative

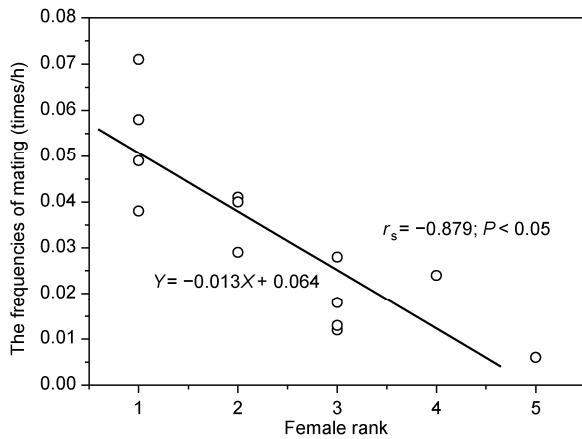
Table 2 Dominance of displacement among adult females and the frequencies of mating in four target OMUs during the study period^{a)}

Actor/Receiver	YL	DBC	YCM	XBC	BD	Total _{JB}	SK	TH	WM	Total _{LP}	XHW	JG	DT	Total _{zr}	QQ	TM	HF	Total _{pk}
YL	1	1.000 [▲] (56)	0.929 (52)	1.000 (56)	1.000 (28)	192	7	6	5	8	3	3	4	-	-	2	2	
DBC	0	1	1.000 (44)	1.000 (48)	1.000 (16)	108	6	1	1	3	3	3	-	-	-	-	2	
YCM	0.061 (4)	0	1	0.938 (45)	1.000 (36)	85	1	1	-	1	3	3	-	-	-	3	-	
XBC	0	0	0.062 (3)	1	0.857 (24)	27	-	-	2	1	2	2	2	-	-	-	1	
BD	0	0	0	0.143 (4)	1	4	-	-	-	-	-	-	-	-	-	-	-	
Total _{JB}	4	56	99	153	104	416												
SK	-	-	-	3	4		1	0.949 (111)	0.944 (68)	179	1	-	3	-	-	4	4	
TH	-	-	-	1	3		0.051 (6)	1	1.000 (63)	69	-	2	4	-	1	3	4	
WM	-	-	-	-	-		0.056 (4)	0	1	4	-	-	1	-	-	-	-	
Total _{LP}							10	111	131	252								
XHW	1	-	-	3	7		2	-	3	1	0.969 (93)	1.000 (30)	1.000 (30)	123	5	7	5	
JG	-	-	-	-	3		-	-	5	0.031 (3)	1	0.940 (79)	0.940 (79)	82	1	1	6	
DT	-	-	-	-	-		-	-	2	0	0.060 (5)	1	1	5	-	5	1	
Total _{zr}										3	98	109	109	210				
QQ	-	-	-	-	5		-	-	1	-	4	-	-	1	1	1.000 (135)	0.963 (130)	265
TM	-	-	1	-	3		1	-	3	-	-	-	1	0	0	0.853 (64)	0.853 (64)	64
HF	-	-	-	1	-		-	-	4	-	-	-	3	0.037 (5)	0.037 (5)	0.147 (11)	0.147 (11)	16
Total _{pk}														5	146	194	194	345
Frequency of mating	0.071	0.041	0.012	0.024	0.006		0.058	0.040	0.013	0.049	0.040	0.018	0.018	0.038	0.029	0.028	0.028	
Total _{JB}	4	56	99	153	104	416												

a) There are a total of 1415 displacement behaviors, 1223 occurred between adult females within the four target OMUs, lying in the area labeled by broken lines as shown, and the remaining 192 occurred among OMUs which was not useful to determine the female ranks within the OMUs in this study; ▲, The ratio of displacement = number of displacement behavior by actor/total of (displacement by actor and by partner) within OMUs; ●, Figures in parentheses indicate the number of displacement between individuals within OMUs; -, No displacement behavior was recorded between individuals among OMUs.

Table 3 *P* and correlation coefficient (r_s) values between female rank and mating behavior in target units

	JB unit	JZT unit	PK unit	LP unit
Correlation coefficient (r_s)	-0.900	-1.000	-1.000	-1.000
Value of <i>P</i>	0.037	0.000	0.000	0.000

**Figure 1** Positive correlation between the frequency of mating and female rank (ranks ranged from highest rank, 1, to lowest rank, 5): the high-ranking females had higher mating frequencies than the low-ranking females within OMUs.

behavior. However, high-ranking females still mated more often than low-ranking females in this polygynous species.

Like other leaf monkey species [29], the *R. roxellana* adult females in our study group rarely fought physically, stopping at threatening (e.g. displacement) and vocal warnings [34,35]. Compared with interaction rates of the Thomas langurs (*Presbytis thomasi*; 1.20 interactions per unit per observation hour [33]) and black-and-white colobus monkeys (*Colobus polykomos*; 0.70 interactions per unit per observation hour [36]), the aggressive rate of the Sichuan snub-nosed monkey was rather low. Previous research has determined that dominance hierarchy is “indulgent” for dominant individuals and “relaxed” for subordinate individuals in captive Sichuan snub-nosed monkeys [37]. A low rate of agonistic interactions may coincide with weak or indiscernible dominance hierarchies [38,39], but female dominance hierarchy in *R. roxellana* did exist. Similar observations have been made in other primate species, e.g. chimpanzees in Gombe [40] and in Mahale [41,42].

Although dominance rank was not confirmed as the determinant factor of social relationships in our study, it certainly plays an important role in the social lives of female Sichuan snub-nosed monkeys. The difference in female rank likely represented differences in the quality of the social relationships. The mating data were, to some extent, more easily influenced by the presence of female rank. However, female ranks may be affected by more than two factors, which could not necessarily be exclusive. Firstly, it is possible that these female ranks were influenced by kin-

ship, whereby a dominance hierarchy matrix was observed where some younger females possessed a higher rank. For example, DBC in JB unit was the offspring of YL and was younger than XBC, but had a higher rank than the latter. Secondly, the dominance rankings may be related to the age of female. It is generally believed that older females have more experience than younger females, with the former having priority to dominant resources. Unfortunately, due to a lack of systematic data on these focal females, we were unable to address these kinship-related and age-related issues. Additionally, because female rank is a complex phenomenon with many relative factors remaining unclear, further long-term studies are required to elucidate the various characteristics of female rank.

The presence of female ranks is beneficial perhaps for group stability and can predict mating benefit in polygynous primates [43]. High-ranking females are generally more attractive, leading to the greater frequency of social interactions and mating opportunities between adult females and breeding males [43]. High-ranking *R. roxellana* females exhibited greater mating frequencies than did the low-ranking females, which suggests high-ranking females were more attractive to the breeding male. Although reproductive skew theory was initially defined for insects and birds [7,11], the concept of dominance based on aggression in mammalian social structures [20,21,44] has been highlighted in many primate species recently [45]. In this study, the relational result on social behavior in the Sichuan snub-nosed monkey group was consistent with that observed in gelada baboons [13] and the predictions of the reproductive skew theory. According to the dominance relationship of females, it can be deduced that dominant females might gain more mating opportunities than subordinates. More importantly is the fact that high-ranking females may affect the mating strategies of lower-ranking females within OMUs.

Because female Sichuan snub-nosed monkeys within OMUs were relatively non-aggressive and displayed friendly contact with each other, they could share advantageous resources (i.e. mating opportunity) with other individuals under natural conditions. Such results are similar with our previous findings that antagonistic levels among adult females within OMUs are low and that the Sichuan monkey is a tolerant species [16]. This may explain why subordinates disperse into other OMUs for mating opportunities when competitive suppression of advantageous resources is intense. Unlike other colobine monkeys, free-ranging Sichuan snub-nosed monkey females mate with males throughout the year (even during the birthing season) and the birthing time of new offspring shows diversity under our observation in wild. Accordingly, we preliminarily concluded that the frequency of mating was a possible indicator of reproductive success, and reproductive success was likely related to female rank. However, because reproductive success is limited by many factors [46], further studies

on this species are required to clarify the relationship among female rank, mating, and reproductive success.

In conclusion, our results support our hypotheses. Firstly, among the study group of Sichuan snub-nosed monkeys, female dominance rank was observed to be weak. Secondly, the positive correlation between female rank and mating competition might reflect male mating preference. Thirdly, higher-ranking females were more likely to be a recipient in a mating relationship than lower-ranking females were, influencing the mating strategies of the latter within the OMUs.

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