

Article

Dispersal patterns in Yunnan snub-nosed monkeys

Wancai XIA^{a,b}, Fan WANG^{a,b}, Dali WANG^{a,b}, Xiaoqin ZENG^{a,b}, Chan YANG^{a,b}, Ali KRZTON^c, Baoping REN ^{d,e,*}, and Dayong LI^{a,b,*}

^aKey Laboratory of Southwest China Wildlife Resources Conservation (Ministry of Education), China West Normal University, Nanchong City, Sichuan 637009, China, ^bInstitute of Rare Animals and Plants, China West Normal University, Nanchong City, Sichuan 637009, China, ^cAuburn University Libraries, Auburn University, Auburn, AL 36849, USA, ^dKey Laboratory for Ecology of Tropical Islands (Ministry of Education), Hainan Normal University, Haikou, Hainan 571158, China, and ^eKey Laboratory of Tropical Animal and Plant Ecology of Hainan Province, Hainan Normal University, Haikou, Hainan 571158, China

*Address correspondence to Dayong Li and Baoping Ren. E-mail: 980119lsc@163.com and renbp@163.com

Handling editor: Zhi-Yun JIA (贾志云)

Received on 23 April 2021; accepted on 6 August 2021

Abstract

Sex-biased dispersal is common in group-living animals. Due to differences in local demographic and environmental factors, sex-biased dispersal presents many irregular patterns. In this study, a habituated, individually identified Yunnan snub-nosed monkey *Rhinopithecus bieti* group was observed over 9 years; 192 dispersal events, including 97 male dispersal events (25 natal dispersal and 72 secondary dispersal) and 95 female dispersal events (34 natal dispersal and 61 secondary dispersal) were observed. Males and females showed different dispersal paths, dispersal ages, and dispersal patterns. Females had 2 dispersal paths, whereas males had 4 paths. In terms of age of dispersal, the male age of natal dispersal was younger than for females. Males prefer single dispersal, whereas females prefer parallel dispersal. Our study indicates that the dispersal pattern of *R. bieti* should be classified as a bisexual dispersal pattern. The differences in dispersal path, average age at dispersal, and dispersal path pattern indicate that Yunnan snub-nosed monkeys may still retain a loose matrilineal social system.

Key words: bisexual dispersal, dispersal, parallel dispersal, *Rhinopithecus bieti*.

Dispersal, defined as the movement of individuals or populations between their natal sites and breeding or subsistence sites, is ubiquitous among group-living mammals and birds (Greenwood 1980). Dispersal can be further categorized as natal dispersal—movement by which an individual leaves its birthplace to engage in mating or reproduction somewhere else (Wey et al. 2015), and secondary/breeding dispersal—movement that occurs between reproductive events for the same individual (Ronce 2007). Dispersal plays an important role in maintaining the long-term survival of small and isolated populations (Chang et al. 2013); thus, an understanding of dispersal patterns is critical for developing effective conservation

management strategies designed to maintain or increase genetic variability in endangered species (Broquet and Petit 2009).

The significance of dispersal is widely debated, with current hypotheses focusing primarily on inbreeding avoidance and on competition (Bowler and Benton 2005; Ronce 2007). Dispersal lowers the risk of inbreeding and the cost of inbreeding depression (known as the inbreeding avoidance hypothesis; Bengtsson 1978; Packer 1979; Dobson 1982; Waser and Keane 1986; Pusey 1987; Clutton-Brock 1989; Perrin and Mazalov 2000; Clutton-Brock and Lukas 2011). In particular, natal dispersal before sexual maturity supports the inbreeding avoidance hypothesis (Moore and Ali 1984; Clutton-Brock 1989).

In most animals, the asymmetry in parental investment is greater, with females bearing most of the costs of reproduction. When inbreeding loads exceed their tolerance threshold, females should prefer immigrant males and reject male relatives, promoting the dispersal of related males (Lehmann and Perrin 2003). Regarding secondary dispersal, the competition hypothesis emphasizes individual dispersal when competition for resources is greater at the current location than elsewhere (Greenwood 1980; Johnson and Gaines 1996; McNutt 1996). In polygynous species where resident males effectively monopolize mating access to females, the sex bias within 1-male units (OMUs) leads to fierce male–male mating competition, resulting in male dispersal and female philopatry (Perrin and Mazalov 2000; Zhao et al. 2011). In addition, male dispersal is often linked to eviction by resident males, such as in *Presbytis senex senex* (Rudran 1973), *Presbytis entellus* (Bogges 1980), and *Trachypithecus leucocephalus* (Zhao et al. 2011).

Similar to other mammals, sex-biased dispersal patterns are common in primates (Jack and Fedigan 2004a, 2004b). Initial studies suggested that the mating system was the fundamental determinant of which sex was more likely to disperse (Greenwood 1980; Dobson 1982; Prugnolle and de Meeus 2002; Nagy et al. 2007). For many polygynous primates, male-biased dispersal and female philopatry is a common pattern (Greenwood 1980; Clutton-Brock 1989; Clutton-Brock and Lukas 2011; Wang et al. 2017). However, there is growing evidence that dispersal patterns are not entirely determined by the mating system (Boinski 2005; Chang et al. 2013). Many polygynous primate species have predominantly female-biased dispersal, such as *Brachyteles arachnoides* (Strier 1994),

Trachypithecus phayrei (Borries et al. 2004), *Theropithecus gelada* (Snyder-Mackler et al. 2014), *Colobus vellerosus* (Teichroeb and Sicotte 2009), and *Ptilocolobus badius* (Fashing 2011; Table 1). Others have bisexual dispersal, such as *Alouatta palliata* and *Alouatta pigra* (Di Fiore et al. 2010) and *Procolobus verus* (Fashing 2011; Table 1). The pattern of sex-biased dispersal is determined by the degree of kinship between different sexes within the core social group. Among species with multilevel societies, females are philopatric in geladas, with core units formed around closely related females (Snyder-Mackler et al. 2014). In contrast, males are philopatric in hamadryas baboons, with male–male bonds linking family units together into higher-order groupings (Städle et al. 2015).

Dispersal is often accompanied by substantial benefits, but can also be costly, with risks to the individual involved (Marty et al. 2017a, 2017b). Some birds (Riehl 2013), carnivores (Packer et al. 1991), and primates (Schoof et al. 2009) disperse together with familiar individuals (parallel dispersal) for mutual defense, reducing the costs of dispersal (van Hooff 2000). Parallel dispersal enables dispersing individuals to maintain long-term relationships with known others (Wikberg et al. 2014) and form alliances more easily (Jack and Fedigan 2004a, 2004b; Koenig et al. 2011; Ridley 2012). Though most of the benefits of alliances accrue to dominant individuals (Ridley 2012), less dominant individuals also gain from cooperating with dominant kin (Riehl 2013; Bourke 2014; Díaz-Muñoz et al. 2014).

Yunnan snub-nosed monkeys *Rhinopithecus bieti* are an endangered species of Asian colobine endemic to China, inhabiting high altitude mountain forests on the Tibetan Plateau within a narrow

Table 1 Dispersal in polygynous primates

Family	Species name	Predominant dispersing sex			References
		Male	Female	Both	
Atelidae	<i>A. palliata</i>	—	—	+	Di Fiore et al. 2010.
	<i>A. pigra</i>	—	—	+	Di Fiore et al. 2010.
	<i>Alouatta seniculus</i>	+	—	—	Agoramoorthy and Rudran 1993.
Cercopithecidae	<i>B. arachnoides</i>	—	+	—	Strier 1994.
	<i>Chlorocebus aethiops</i>	+	—	—	Struhsaker 1967.
	<i>Colobus polykomos</i>	—	+	—	Korstjens and Nijssen 2005.
	<i>Colobus guereza</i>	+	—	—	Oates 1977.
	<i>C. vellerosus</i>	—	+	—	Teichroeb and Sicotte 2009.
	<i>Erythrocebus patas</i>	+	—	—	Hall 2010
	<i>Macaca fascicularis</i>	+	—	—	van Noordwijk and Van Schaik 1985.
	<i>Macaca silenus</i>	+	—	—	Kumar 2001.
	<i>Papio ursinus</i>	+	—	—	Seyfarth 1976.
	<i>P. hamadryas</i>	—	+	—	Hammond RL et al. 2006.
	<i>P. badius</i>	—	+	—	Fashing 2011.
	<i>P. verus</i>	—	—	+	Fashing 2011.
	<i>Rachypithecus phayrei</i>	—	+	—	Borries et al. 2004.
	<i>Rhinopithecus roxellana</i>	+	—	—	Qi et al. 2009.
	<i>Semnopithecus entellus</i>	+	—	—	Sugiyama 1976.
<i>T. gelada</i>	—	—	+	Dunbar and Dunbar 1974.	
<i>T. phayrei</i>	—	+	—	Borries et al. 2004.	
Hylobatidae	<i>Nomascus concolor</i>	+	—	—	Hu et al. 2018.
Indriidae	<i>Propithecus verreauxi</i>	+	—	—	Richard 1974.

“+” indicates the main sex dispersal pattern. “—” Predominant dispersing sex.

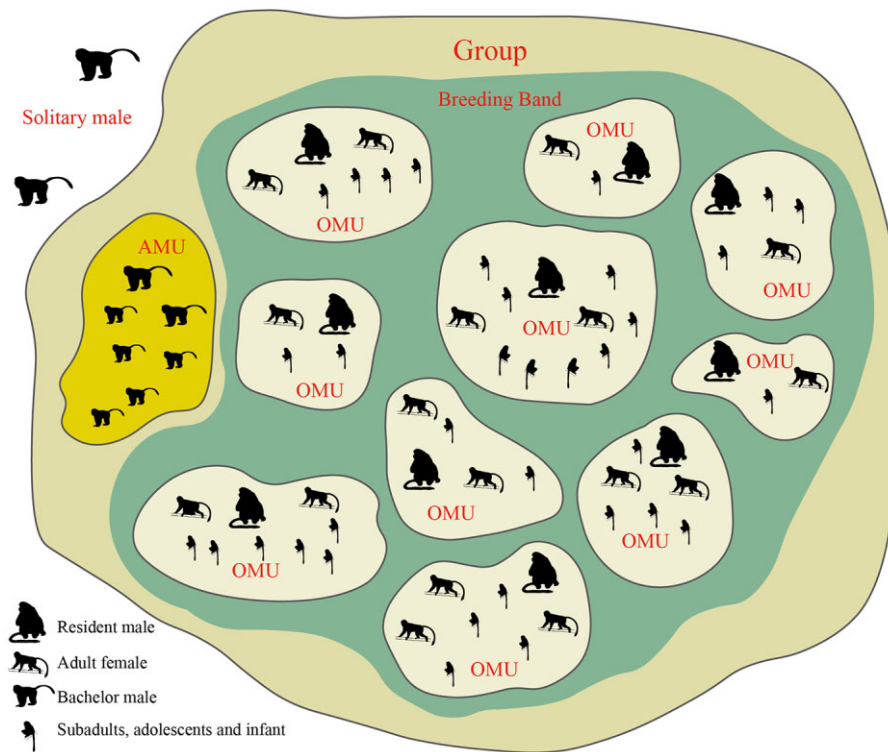


Figure 1. The social structure of Yunnan snub-nosed monkeys.

area between the Yangtze and Mekong Rivers (Xia et al. 2020a, 2020b, 2020c). *Rhinopithecus bieti* forms multilevel societies (Grueter et al. 2020) composed of many OMUs and at least one all-male unit (AMU; Ren et al. 2012; Grueter et al. 2020; Figure 1). In this type of social organization, there are clearly defined core units (OMUs and the AMU), but the boundary is not impermeable, and some individuals disperse across units (Grueter et al. 2020). Male dispersal is common in the genus *Rhinopithecus* (Qi et al. 2009; Yao et al. 2011; Chang et al. 2013; Huang et al. 2017), often accompanied by conflict and resident male takeover, but females in the genus *Rhinopithecus* have also been observed to disperse among OMUs (Qi et al. 2009). Whereas female dispersal is usually voluntary, it can also lead to conflicts between the original and the new resident male for females that are switching groups.

In this study, we spent 9 consecutive years following a habituated wild *R. bieti* group with multilevel social organization at close range in Xiangguqing, Baimaxueshan Nature Reserve. We aimed to (1) investigate sex-biased dispersal patterns in *R. bieti* specifically and species with multilevel social structure more generally and (2) explore the differences in both natal and secondary dispersal patterns between male and female individuals, including differences in proximate cause from other species with multilevel social structure.

Materials and Methods

Study site

We conducted this study at Xiangguqing (27°36'N, 99°15'E, elevation: 2,400–4,200 m) in Baimaxueshan Nature Reserve, Yunnan Province, China. The study site, located east of the Hengduan Mountains, encompasses an area of almost 90 km² (Li et al. 2014). The study area is affected by the plateau monsoon climate, so temperature and precipitation are strongly seasonal (Xia et al. 2016).

Study group and subjects

The focal group in this study is a habituated and provisioned wild *R. bieti* group (Xia et al. 2016). Since the end of 2009, all individuals have been identified (Xia et al. 2020b). From 2010 to 2018, a total of 22 OMUs and 1 AMU (158 individuals, including 83 males and 75 females) were recorded in the focal group (Xia et al. 2020c). Each year, the focal group consisted of 5–10 OMUs and 1 AMU, ranging from 45 to 93 individuals (Xia et al. 2020c).

Behavior sampling

In 2008 and 2009, not all individuals could be reliably identified, so data from those 2 years were only used to calculate the age of known individuals. The age of unknown individuals was assessed by body color, body size, and the thinning of white hairs on the back (Xia et al. 2020c). Accurate and detailed dispersal data were recorded over 9 years (1 January 2010 to 31 December 2018) for this group as part of long-term population monitoring. Each day at feeding time (9:00–10:00 and 17:00–18:00), we and the staff in the reserve counted the number of individuals in each OMU and AMU, then recorded information such as (1) demographic changes and composition of OMUs and the AMU, including birth, death and dispersal and (2) details of the dispersal process (name, time, age, and dispersal path). All dispersal events were confirmed to have occurred within 1–3 days.

When individuals that immigrated into an OMU or AMU were accepted by the members in the unit, these were considered successful dispersal events. We were unable to follow individuals out of the study group, so we assumed that all monkeys that disappeared had emigrated out of the focal group, with the exception of individuals that stayed away for younger than 2 years old and severely injured individuals (Hu et al. 2018).



Figure 2. Female individual dispersal patterns from 2010 to 2018. Capital letters in front of each navy-blue horizontal bar represent the codes of the OMU. The number in front of F represents the number of dispersal individuals.

Statistical analyses

All statistical tests in this study were performed using SPSS version 23.0 (SPSS Inc., Chicago, IL). Fisher's exact test was used to determine whether individual dispersal was sex-biased, and a binomial test was used to detect the difference between male and female individuals in parallel and single spread. Independent sample *t*-tests were used to compare the age difference of natal dispersal and secondary dispersal between females and males. All tests were 2-tailed with $P \leq 0.05$ as the threshold for significance. Average values are expressed as Mean \pm Standard Deviation (*SD*).

Results

Dispersal paths

A total of 192 dispersal events were recorded during the study period, including 95 female dispersal events (34 natal dispersal events and 61 secondary dispersal events) and 97 male dispersal events (25 natal dispersal events and 72 secondary dispersal events).

There are 2 paths for female dispersal: dispersal among OMUs (26 natal dispersals and 29 secondary dispersals), and dispersal between the OMUs and the wild group (8 natal dispersals and 32 secondary dispersals), in which 3 events were female secondary dispersals from the wild group to an OMU and 29 events were female secondary dispersals into the wild group (Figures 2 and 4).

The male dispersal paths are more complicated, with 4 potential paths for male dispersal: (1) 3 male offspring followed their mothers to a new OMU for natal dispersal; (2) dispersal between OMUs and

the AMU, with 12 natal dispersals to the AMU and 25 secondary dispersals (15 from the AMU to OMUs and 10 from OMUs to the AMU); (3) dispersal from OMUs to the wild group, with 10 natal dispersals and 8 secondary dispersals (no male individuals immigrated directly into an OMU from the wild group); and (4) dispersal between the AMU and the wild group (secondary dispersal only), with 29 dispersals from the AMU into the wild group and 10 dispersals from the wild group into the AMU (Figures 3 and 4).

Age of natal and secondary dispersal

A total of 59 natal dispersal events were recorded during the study period, 25 by males and 34 by females. There was no significant difference in the average age of natal dispersal for females (Mean \pm *SD* = 39.2 \pm 23.7 months, $n = 34$) and males (mean \pm *SD* = 32.4 \pm 17.5 months, $n = 25$) (independent samples *t*-test, $F = 0.58$, $P = 0.226$). Among the 133 secondary dispersal events recorded, the average age of females at secondary dispersal (mean \pm *SD* = 88.8 \pm 42.0 months, $n = 61$) was significantly younger than that of males (mean \pm *SD* = 116 \pm 47 months, $n = 72$) (independent samples *t*-test, $F = 1.312$, $P < 0.01$; Figure 5).

Sex-biased dispersal patterns

In our *R. bieti* study group, 43 males were born during the study period. Five died before dispersal. The mean age of natal dispersal (32 months) was used to estimate when males should be expected to disperse. Of the 26 males that survived at least 32 months, 25 had

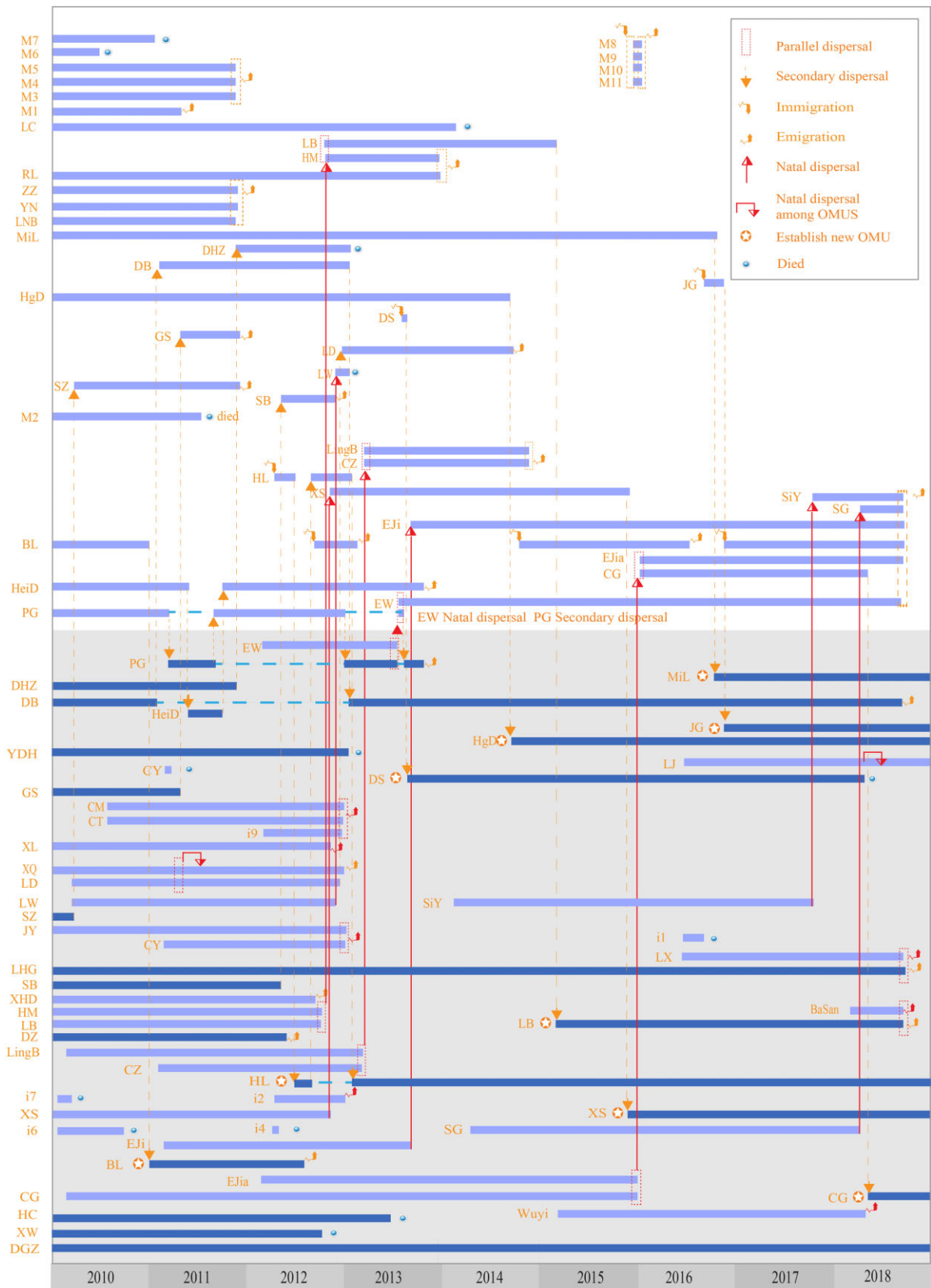


Figure 3. Male individual dispersal patterns from 2010 to 2018. Each horizontal bar represents the social history of a single bachelor male, and dark blue horizontal bars represent resident males of OMU. The gray area represents the breeding band, and the white patch represents the AMU. Capital letters in front of each horizontal bar represent the codes of the male.

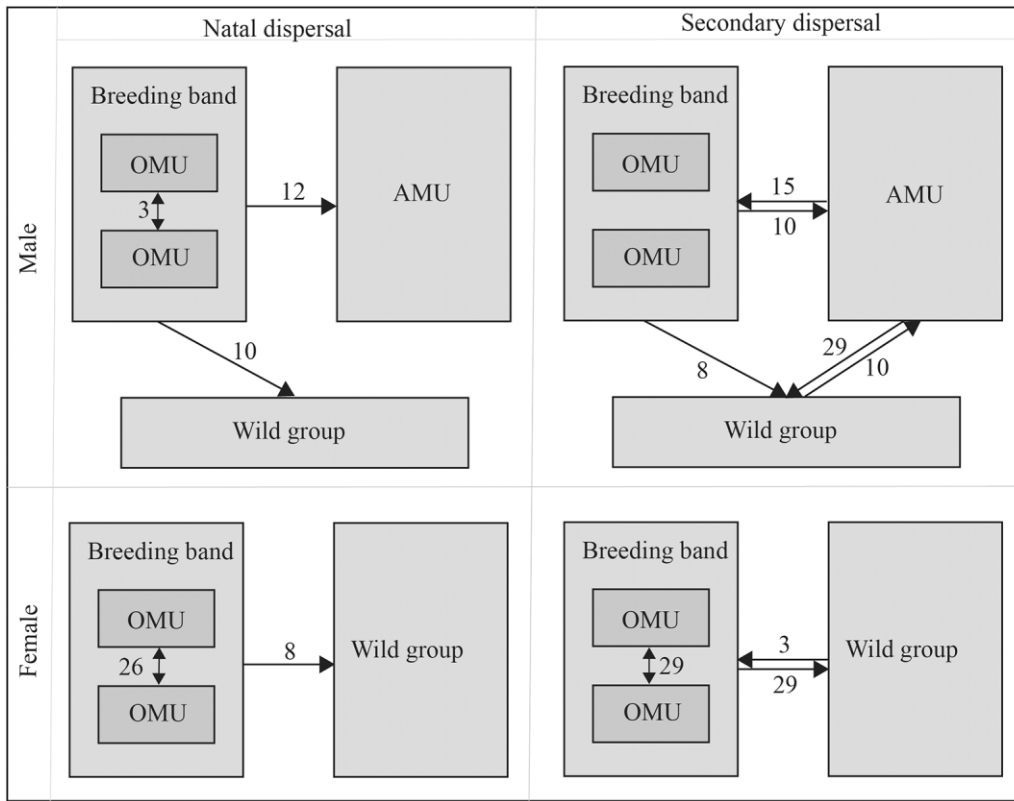


Figure 4. Dispersal path schematic diagram of Yunnan snub-nosed monkey.

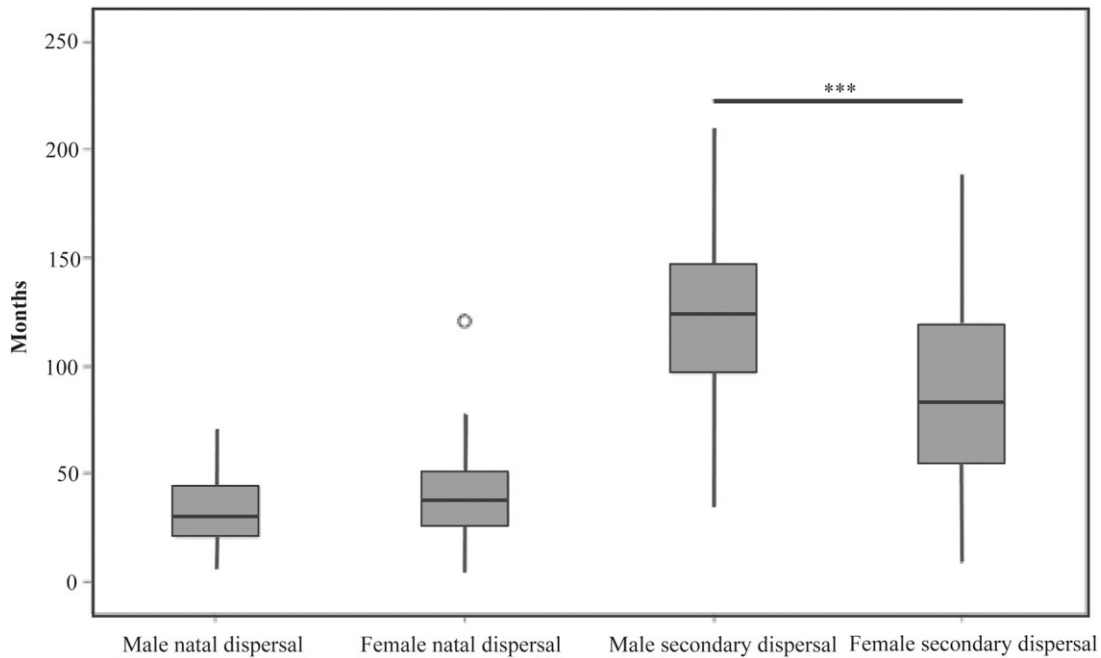


Figure 5. Age comparison of natal dispersal and secondary dispersal by sex class.

dispersed by the end of the study, accounting for 96%. Forty-one females were also born during the study period. Thirty-four of the 36 females older than 39 months dispersed out of their natal OMU,

accounting for 94%. These results show a bisexual dispersal pattern, with no sex bias in natal dispersal (Fisher's Exact test, $P = 0.999$).

Parallel dispersal and single dispersal

Among 192 dispersal events, the 80 single dispersal events (41.7%) were significantly fewer than the 112 parallel dispersal events (58.3%) (binomial test, $P=0.025$). Further analysis by sex showed that females were more inclined toward parallel dispersal (71 parallel events versus 24 single events, binomial test, $P<0.01$), whereas there was no significant preference in males (41 parallel events versus 56 single events, binomial test, $P=0.155$). Female parallel dispersal mostly occurred with female relatives (29 mother/daughter and 31 sisters or half-sisters). Only 11 parallel dispersals involved unrelated females. All male parallel dispersals involved male relatives (6 father/son, 11 brothers, or half-brothers) only in the breeding band. The individuals in the AMU were of unknown relation and were not included in this analysis.

Discussion

Previous literature suggested that male-biased dispersal and female philopatry was the predominant pattern in polygynous primates (Greenwood 1980; Clutton-Brock 1989), leading to harems comprised matrilineal and female kin (Qi et al. 2009). Recent publications suggest a more complicated dispersal pattern for polygynous species, and some polygynous species also display female-biased dispersal and bisexual dispersal (Table 1). In the current study of *R. bieti*, we find that nearly all offspring disperse from their natal OMU. The results also suggest a bisexual dispersal pattern without sex bias in *R. bieti*. Although female dispersal has previously been reported in the genus *Rhinopithecus*, those studies did not find near-universal female dispersal in the focal groups of *R. bieti* and *Rhinopithecus roxellana* (Qi et al. 2009; Yao et al. 2011; Huang et al. 2017).

Why are female *R. bieti* not rigidly philopatric, as might be predicted from their polygynous mating system? First, the tenure of resident males (mean \pm SD = 44 ± 28.83 , $n=18$) is long enough for their female offspring to mature, and female offspring will disperse in order to avoid inbreeding (Clutton-Brock 1989; Nagy et al. 2007). In our study group, a large number of subadult females dispersed from their natal OMUs, consistent with the inbreeding avoidance hypothesis (Xia et al. 2020b). Second, groups of *R. bieti* are composed of OMUs and AMUs (Xia et al. 2016), a social structure in which resident males seldom care for offspring (Wang et al. 2017). In polygynous primates, females with high investment in offspring tend to disperse to select the best available mate (Johnstone et al. 1996; e.g., *Papio hamadryas*, Mori et al. 2007; *Nasalis larvatus*, Murai et al. 2007 and *R. roxellana*, Qi et al. 2009). Third, in the case of parallel dispersal, kin cooperation may provide a competitive advantage for access to scarce resources and successful reproduction (Le Galliard et al. 2006). Female offspring will disperse together with their female relatives likely to maintain alliances and improve their fitness.

In many mammalian species, dispersal is often limited to specific life history stages (Smale et al. 1997), and natal emigration occurs prior to sexual maturity. The results of this study showed the mean age of male natal dispersal was 32 months (2.7 years), slightly earlier than for females at 39 months (3.2 years). Although there was no statistically significant difference in the age of natal dispersal, male individuals reach sexual maturity at around 7 years old, relatively late compared with females that reach sexual maturity at 5 years old (Li et al. 2013). From a developmental perspective, then, males' natal dispersal occurs earlier than for females, which may be related to the different social roles between males and females. Unlike other

species without AMUs, male Yunnan snub-nosed monkeys have the option of natal dispersal to the AMU. Only after they reach sexual maturity in the AMU can they challenge the resident male and obtain mating opportunities. For female offspring, who are not evicted by the resident male, delaying dispersal is a strategy to avoid the high cost of dispersing at a young age (Marty et al. 2017a, 2017b). Furthermore, the age and developmental stage of dispersal are variable, affected by local demographic and environmental factors (Pusey and Packer 1987). The average natal dispersal age of male *R. bieti* was younger than for *P. hamadryas* (Chalmers 1986), *Papio cynocephalus* (Pusey and Packer 1987), and *Cebus capucinus* (Jack and Fedigan 2004b). On the other hand, female *R. bieti* are similar to other langurs at natal dispersal, and all tend to disperse after menarche (Sterck 1997).

Secondary dispersal can occur when individuals reach sexual maturity, at which time they have the ability to compete with local individuals and enter the group (Jack and Fedigan 2004a; van Noordwijk and Van Schaik 1985). Our results show that the secondary dispersal age of female *R. bieti* is significantly younger than males. First, dispersal is related to the developmental trajectories of different sexes, with females maturing earlier than males (Xia et al. 2020c). This skews average age at secondary dispersal for females earlier than for males. Second, almost all dispersing immature males enter the AMU until they reach sexual maturity before they have the opportunity to replace the resident male of an OMU. In general, males cannot obtain mates immediately after they reach sexual maturity due to the monopolization of females within the OMUs, thus increasing the age of male secondary dispersal.

Parallel dispersal is thought to be connected to coalition formation (Jack and Fedigan 2004b). Coalitions make individuals more successful in entering and maintaining membership in social groups (Fedigan 1993). Similar to female *R. roxellana* (Qi et al. 2009) and male *C. capucinus* (Jack and Fedigan 2004b), female *R. bieti* also prefer parallel dispersal to avoid the loss of allies. Female *R. bieti* may offset the risks of dispersal by maintaining a high frequency of parallel dispersal at all life stages (van Hooft 2000), although males do not. Serial single dispersal reduces the relatedness of females within OMUs (Qi et al. 2009). In contrast, parallel dispersal ensures that related females stay together as they enter or form new OMUs. Kin coalitions can improve competitive advantage in obtaining scarce resources, reduce infanticide risk, and increase reproductive success (Le Galliard et al. 2006). But for males, in polygynous mating systems, the resident male monopolizes mates within his OMU and refuses to share access during his tenure. This disposes adult males in the AMU to prefer single dispersal when looking for mating opportunities.

In summary, we find a predominantly bisexual dispersal pattern in *R. bieti*. At the same time, male and female offspring showed differences in dispersal paths, dispersal age, and dispersal pattern. Males have higher a variety of dispersal patterns than females. The mean male age of natal dispersal was younger than females from a developmental standpoint. Males prefer single dispersal, whereas females prefer parallel dispersal. The above 3 results suggest that Yunnan snub-nosed monkeys may still have a loose matrilineal social system.

Acknowledgments

We are grateful to the 4 anonymous reviewers whose comments refined the manuscript, our field assistants Tai Zhong, Jianhua Yu, Jiming Yu, Lizhong

Yu, and Xinming He. We also thank Baimaxueshan Nature Reserve for our work permit.

Funding

Financial supports were provided by the project of the National Natural Science Foundation of China (No. 32070454), the Second Tibetan Plateau Scientific Expedition and Research Program (No. 2019QZKK0501), the National Key Programme of Research and Development, Ministry of Science and Technology (No. 2016YFC0503200), the Biodiversity Survey and Assessment Project of the Ministry of Ecology and Environment, China (No. 2019HJ2096001006), and Sichuan Science and Technology Program (2021JDRC0024).

Authors' Contributions

W.C.X., B.P.R., and D.Y.L. conceived the ideas and methodology. W.C.X., B.P.R., F.W., D.L.W., C.Y., and D.Y.L. collected the data. W.C.X., B.P.R., and D.Y.L. analyzed the data and wrote the manuscript. D.Y.L. and A.K. revised the manuscript.

Competing Interests Statement

We declare we have no competing interests.

References

- Agoramoorthy G, Rudran R, 1993. Male dispersal among free-ranging red howler monkeys *Alouatta seniculus* in venezuela. *Folia Primatol* 61:92–96.
- Bengtsson BO, 1978. Avoiding inbreeding: at what cost? *J Theor Biol* 73: 439–444.
- Bogges J, 1980. Intermale relations and troop male membership changes in langurs *Presbytis entellus* in Nepal. *Int J Primatol* 1:233–274.
- Boinski S, 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii*, *S. boliviensis* and *S. sciureus*): III. Cognition. *Behaviour* 142:679–699.
- Borries C, Larney E, Derby AM, Koenig A, 2004. Temporary absence and dispersal in phayre's leaf monkeys *Trachypithecus phayrei*. *Folia Primatol* 75: 27–30.
- Bourke AFG, 2014. Hamilton's rule and the causes of social evolution. *Philos Trans Royal Soc B: Biol Sci* 369:20130362.
- Bowler DE, Benton TG, 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80: 205–225.
- Broquet T, Petit EJ, 2009. Molecular estimation of dispersal for ecology and population genetics. *Ann Rev Ecol Evol Syst* 40:193–216.
- Chalmers NR, 1986. On socialization in hamadryas baboons. *Int J Primatol* 7: 109–110.
- Chang Z, Yang B, Vigilant L, Liu Z, Ming L, 2013. Evidence of male-biased dispersal in the endangered sichuan snub-nosed monkey *Rhinopithecus roxellana*. *Am J Primatol* 76:72–83.
- Clutton-Brock TH, 1989. Female transfer and inbreeding avoidance in social mammals. *Nature* 337:70–72.
- Clutton-Brock TH, Lukas D, 2011. The evolution of social philopatry and dispersal in female mammals. *Mol Ecol* 21:472–492.
- Di Fiore A, Link A, Campbell CJ, 2010. *The Atelines: Behavioral and Socioecological Diversity in a New World Monkey Radiation*. Oxford: Oxford University Press.
- Diaz-Muñoz SL, Duval EH, Krakauer AH, Lacey EA, 2014. Cooperating to compete: altruism, sexual selection and causes of male reproductive cooperation. *Anim Behav* 88:67–78.
- Dobson FS, 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192.
- Dunbar RIM, Dunbar P, 1974. Behaviour related to birth in wild gelada baboons *Theropithecus gelada*. *Behaviour* 50:185–191.
- Fashing PJ, 2011. *African Colobine Monkeys: Their Behavior, Ecology, and Conservation*. Oxford: Oxford University Press.
- Fedigan L, 1993. Sex differences and intersexual relations in adult white-faced capuchins *Cebus capucinus*. *Int J Primatol* 14:853–877.
- Greenwood P, 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim Behav* 28:1140–1162.
- Grueter CC, Qi X, Zinner D, Bergman T, Li M et al., 2020. Multilevel organisation of animal sociality. *Trends Ecol Evol* 35:834–847.
- Hall KRL, 2010. Behaviour and ecology of the wild patas monkey *Erythrocebus patas* in Uganda. *J Zool* 148:15–87.
- Hammond RL, Handley LJJ, Winney BJ, Perrin BN, 2006. Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. *Proc Royal Soc B: Biol Sci* 273:479–484.
- Hu N, Guan Z, Bei H, Ning W, Kai H et al., 2018. Dispersal and female philopatry in a long-term, stable, polygynous gibbon population: evidence from 16 years field observation and genetics. *Am J Primatol* 80:e22922.
- Huang ZP, Bian K, Liu Y, Pan RL, Qi XG et al., 2017. Male dispersal pattern in golden snub-nosed monkey *Rhinopithecus roxellana* in Qinling mountains and its conservation implication. *Sci Rep* 7:46217.
- Jack KM, Fedigan L, 2004a. Male dispersal patterns in white-faced capuchins *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. *Anim Behav* 67:771–782.
- Jack KM, Fedigan L, 2004b. Male dispersal patterns in white-faced capuchins *Cebus capudnus*. Part 1: patterns and causes of natal emigration. *Anim Behav* 67:761–769.
- Johnson ML, Gaines MS, 1996. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480.
- Johnstone RA, Reynolds JD, Deutsch JC, 1996. Mutual mate choice and sex differences in choosiness. *Evolution* 50:1382–1391.
- Koenig WD, Walters EL, Haydock J, 2011. Variable helper effects, ecological conditions, and the evolution of cooperative breeding in the *Acorn woodpecker*. *Am Nat* 178:145–158.
- Korstjens AH, Nijssen ECRN, 2005. Intergroup relationships in western black-and-white colobus *Colobus polykomos polykomos*. *Int J Primatol* 26: 1267–1289.
- Kumar A, 2001. The lion-tailed macaque *Macaca silenus*: life history, ecology, distribution and conservation. *Assessment* 1:40–48.
- Le Galliard JF, Gundersen G, Andreassen HP, Stenseth NC, 2006. Natal dispersal, interactions among siblings and intrasexual competition. *Behav Ecol* 17:733–740.
- Lehmann L, Perrin N, 2003. Inbreeding avoidance through kin recognition: choosy females boost male dispersal. *Am Nat* 162:638–652.
- Li YH, Li DY, Ren BP, Hu J, Li BG et al., 2014. Differences in the activity budgets of Yunnan snub-nosed monkeys *Rhinopithecus bieti* by age-sex class at Xiangguqing in Baimaxueshan nature reserve, China. *Folia Primatol* 85:335–342.
- Li Y, Ren BP, Li YH, Li DY, Hu J, 2013. Behavior ethogram and PAE coding system of *Rhinopithecus bieti*. *Sichuan J Zool* 32: 641–650.
- Marty PR, Hodges K, Agil M, Engelhardt A, 2017a. Alpha male replacements and delayed dispersal in crested macaques *Macaca nigra*. *Am J Primatol* 79: e22448.
- Marty PR, Hodges K, Heistermann M, Agil M, Engelhardt AJH et al., 2017b. Is social dispersal stressful? A study in male crested macaques *Macaca nigra*. *Hormones Behav* 87:62–68.
- McNutt JW, 1996. Sex-biased dispersal in african wild dogs *Lycaon pictus*. *Anim Behav* 52:1067–1077.
- Moore J, Ali R, 1984. Are dispersal and inbreeding avoidance related. *Anim Behav* 32:94–112.
- Mori A, Yamane Y, Sugiura H, Shotake T, Boug A et al., 2007. A study on the social structure and dispersal patterns of hamadryas baboons living in a commensal group at Taif, Saudi Arabia. *Primates* 48:179–189.
- Murai T, Mohamed M, Bernard H, Mahedi AP, Saburi R et al., 2007. Female transfer between one-male groups of proboscis monkey *Nasalis larvatus*. *Primates* 48:117–121.
- Nagy M, Heckel G, Voigt CC, Mayer F, 2007. Female-biased dispersal and patrilocal kin groups in a mammal with resource-defence polygyny. *Proc Royal Soc B: Biol Sci* 274:3019–3025.

- Oates JF, 1977. The social life of a black-and-white colobus monkey, colobus guereza. *Zeits Für Tierpsychol* 45:1–60.
- Packer C, Gilbert DA, Pusey AE, O'Brien SJ, 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562–565.
- Packer CR, 1979. Inter-troop transfer and inbreeding avoidance in *Papio anubis*. *Anim Behav* 27:1–36.
- Perrin N, Mazalov M, 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am Nat* 155:116–127.
- Prugnolle F, de Meeus T, 2002. Inferring sex-biased dispersal from population genetic tools: a review. *Heredity* 88:161–165.
- Pusey AE, 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends Ecol Evol* 2:295–299.
- Pusey AE, Packer C, 1987. *Dispersal and Philopatry*. Chicago (IL): University of Chicago Press.
- Qi XG, Li BG, Garber PA, Ji W, Watanabe K, 2009. Social dynamics of the golden snub-nosed monkey *Rhinopithecus roxellana*: female transfer and one-male unit succession. *Am J Primatol* 71:670–679.
- Ren BP, Li DY, Garber PA, Li M, 2012. Fission - fusion behavior in Yunnan snub-nosed monkeys *Rhinopithecus bieti* in Yunnan, China. *Int J Primatol* 33:1096–1109.
- Richard A, 1974. *Patterns of Mating in Propithecus Verreauxi Verreauxi*. London: Duckworth.
- Ridley AR, 2012. Invading together: the benefits of coalition dispersal in a cooperative bird. *Behav Ecol Sociobiol* 66:77–83.
- Riehl C, 2013. Evolutionary routes to non-kin cooperative breeding in birds. *Proc Royal Soc B: Biol Sci* 280:20132245.
- Ronce O, 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Ann Rev Ecol Syst* 38:231–253.
- Rudran R, 1973. Adult male replacement in one-male troops of purple-faced langurs *Presbytis senex* and its effect on population structure. *Folia Primatol* 19:166–192.
- Schoof V, Jack K, Isbell L, 2009. What traits promote male dispersal in primates? *Behaviour* 146:701–726.
- Seyfarth C, 1976. *The Social Development of Immature Male and Female Baboons*. Cambridge: University of Cambridge.
- Smale L, Nunes S, Holekamp KE, 1997. Sexually dimorphic dispersal in mammals: patterns, causes, and consequences. *Adv Study Behav* 26:181–250.
- Snyder-Mackler N, Alberts SC, Bergman TJ, 2014. The socio-genetics of a complex society: female gelada relatedness patterns mirror association patterns in a multilevel society. *Mol Ecol* 23:6179–6191.
- Stådele V, Doren VV, Pines M, Swedell L, Vigilant L, 2015. Fine-scale genetic assessment of sex-specific dispersal patterns in a multilevel primate society. *J Hum Evol* 78:103–113.
- Sterck EHM, 1997. Determinants of female dispersal in *Thomas langurs*. *Am J Primatol* 42:179–198.
- Strier KB, 1994. Myth of the typical primate. *Am J Phys Anthropol* 37:233–271.
- Struhsaker TT, 1967. Social structure among vervet monkeys *Cercopithecus aethiops*. *Behaviour* 29:83–121.
- Sugiyama Y, 1976. Life history of male Japanese monkeys. *Adv Study Behav* 7:255–284.
- Teichroeb JA, Sicotte WP, 2009. Female dispersal patterns in six groups of ursine colobus *Colobus vellerosus*: Infanticide avoidance is important. *Behaviour* 146:551–582.
- van Hooff J, 2000. *Relationships among Non-Human Primate Males: A Deductive Framework*. Cambridge: Cambridge University Press.
- van Noordwijk MA, Van Schaik CP, 1985. Male migration and rank acquisition in wild long-tailed macaques *Macaca fascicularis*. *Anim Behav* 33:849–861.
- Wang GM, Liu W, Wang YN, Wan XR, Zhong WQ, 2017. Restricted dispersal determines fine-scale spatial genetic structure of *Mongolian gerbils*. *Curr Zool* 63:687–691.
- Waser PM, Keane AB, 1986. When should animals tolerate inbreeding? *Am Nat* 128:529–537.
- Wey TW, Spiegel O, Montiglio PO, Mabry KE, 2015. Natal dispersal in a social landscape: considering individual behavioral phenotypes and social environment in dispersal ecology. *Curr Zool* 61:543–556.
- Wikberg EC, Jack KM, Campos FA, Fe Digan LM, Sato A et al. 2014. The effect of male parallel dispersal on the kin composition of groups in white-faced capuchins. *Anim Behav* 96:9–17.
- Xia WC, Zhang C, Zhuang HF, Ren BP, Zhou J, 2020a. The potential distribution and disappearing of Yunnan snub-nosed monkey: Influences of habitat fragmentation. *Glob Ecol Conserv* 21:e00835.
- Xia WC, Ji SN, Ren BP, He XM, Zhong T et al., 2020b. Proximate causes of dispersal for female Yunnan snub-nosed monkeys. *Zool Res* 41:80–85.
- Xia WC, Ren BP, Zhou H, Feng H, He XM et al., 2020c. Reproductive parameters of wild *Rhinopithecus bieti*. *Folia Primatol* 91:202–218.
- Xia WC, Ren BP, Li YH, Hu J, He XM et al., 2016. Behavioural responses of Yunnan snub-nosed monkeys *Rhinopithecus bieti* to tourists in a provisioned monkey group in Baimaxueshan nature reserve. *Folia Primatol* 87:349–360.
- Yao H, Liu XC, Stanford C, Yang J, Huang TP et al., 2011. Male dispersal in a provisioned multilevel group of *Rhinopithecus roxellana* in shennongjia nature reserve, China. *Am J Primatol* 73:1280–1288.
- Zhao Q, Borries C, Pan W, 2011. Male takeover, infanticide, and female counter-tactics in white-headed leaf monkeys *Trachypithecus leucocephalus*. *Behav Ecol Sociobiol* 65:1535–1547.