Dispersal patterns in Yunnan snub-nosed monkeys

Wancai XIAa,b, Fan WANGa,b, Dali WANGa,b, Xiaoqin ZENGa,b, Chan YANGa,b, Ali KRZTONc, Baoping REND,e,* and Dayong LIA,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, 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

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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.
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 2011). In addition, male dispersal is often linked to eviction by resident males, such as in *Presbytis senex senex* (Zhao et al. 2011). Atelidae such as *Alouatta seniculus* (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; 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 species, 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* (Boories et al. 2004), *Theropithecus gelada* (Snyder-Mackler et al. 2014), *Colobus vellerosus* (Teichroeb and Sicotte 2009), and *Piliocolobus badius* (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 (Stadele et al. 2015).

Dispersal is often accompanied by substantial benefits, but can also be costly, with risks to the individual involved (Martý 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 Hooft 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                          |
|-------------------|--------------|---------------------------|-------------------------------------|
| Atelidae          | A. palliata  | —                         | —                                   |
|                   | A. pigra     | —                         | —                                   |
|                   | Alouatta seniculus | +                         | —                                   |
|                   | B. arachnoides | —                         | —                                   |
|                   | Chlorocebus aethiops | +                         | +                                   |
|                   | Colobus polykomos | —                         | +                                   |
|                   | Colobus guereza | +                         | —                                   |
|                   | C. vellerosus | —                         | +                                   |
|                   | Erythrocebus patas | +                         | —                                   |
|                   | Macaca fascicularis | +                         | +                                   |
|                   | Macaca silenus | +                         | —                                   |
|                   | P. ursinus   | +                         | —                                   |
|                   | P. hamadryas | —                         | +                                   |
|                   | T. badius    | —                         | +                                   |
|                   | T. verus     | —                         | +                                   |
|                   | Rhachytpithecus phayrei | +                         | —                                   |
|                   | Rhinopithecus roxellana | +               | —                                   |
|                   | Semnopithecus entellus | —               | +                                   |
|                   | T. gelada    | —                         | +                                   |
|                   | T. phayrei   | —                         | +                                   |
| Hylobatidae       | Nomascus concolor | +                         | —                                   |
| Indriidae         | Propithecus verreauxi | +                     | —                                   |

“+” indicates the main sex dispersal pattern. “—” Predominant dispersing sex.
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).
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 $P < 0.05$ 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, $t = 0.58$, $P = 0.226$). 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, $t = 1.312$, $P < 0.01$; 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.
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 of matriline 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 a 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 ± 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; Ngy 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 dispersal 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, 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 Hooff 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.

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**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**

Agoramouorthy 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.

Boggs J, 1980. Intermale relations and troop male membership changes in langurs Presbytis entelus 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.

Brookes C, Larney E, Derby AM, Koenig A, 2004. Temporary absence and dispersal in phaye’s leaf monkeys Trachypithecus phayrei. Folia Primatol 75: 27–30.

Bourque 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. Am Nat 162:45–63.

Breen J, Ali R, 1984. Are dispersal and inbreeding avoidance related. Anim Behav 32: 117–121.

Chalmers NR, 1986. On socialization in hamadryas baboons. Ann Rev Ecol Syst 17:39–65.

Chambers JR, 2004. Behavioral and sociocultural 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 RJM, 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.

Fugden L, 1993. Sex differences and intersexual relations in adult white-faced capuchins Cebus capucinus. Int J Primatol 14:853–877.

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 248:15–37.

Hammond RL, Handley JLJ, 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.

Huang ZP, Jian 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, Fugden 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, Fugden L, 2004b. Male dispersal patterns in white-faced capuchins Cebus capucinus. Part 1: patterns and causes of natal emigration. Anim Behav 67:761–769.

Johnson ML, Ganes 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 Acom woodpecker. Am Nat 178:145–158.

Korstjens AH, Nijssen ECMN, 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, Andreason 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 choosiness. Evolution 50:1382–1391.

Li Y, Ren BP, Li YH, Li DY, Hu J, 2013. Behavior ethogram and PAE coding system of 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, Heistermann M, Agil M, Engelhardt AJH et al., 2017b. Intragroup relationships in western black-and-white colobus Colobus polykomos polykomos. Int J Primatol 26: 1267–1289.

Marty PR, Hodges K, Heistermann M, Agil M, Engelhardt AJH et al., 2017b. Intragroup relationships in western black-and-white colobus Colobus polykomos polykomos. Int J Primatol 26: 1267–1289.

Moore J, Ali R, 1984. Are dispersal and inbreeding avoidance related. Am J Primatol 32: 1067–1077.

Moore J, Ali R, 1984. Are dispersal and inbreeding avoidance related. Am J Primatol 32: 1067–1077.

Mori A, Yamane Y, Sugiura H, Shotake T, Boug A et al., 2007. A study on the inbreeding avoidance among the Rhinopithecus bieti. 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 complex society: female gelada relatedness patterns mirror association patterns in a multilevel society. Mol Ecol 23:6179-6191.

Stădele 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.

Sterier KB, 1994. Myth of the typical primate. Am J Phys Anthropol 37:233-271.

Strubhsaker 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 ur- sine 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 33:489-491.

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 61:453-356.

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 shennongia 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 65:1335-1547.