

Proximate causes of dispersal for female Yunnan snub-nosed monkeys

DEAR EDITOR,

Individual dispersal trends, unquestionably important for species ecology and evolution, are affected by multiple factors. Understanding the factors that influence female dispersal strategies offers important insight into primate dispersal mechanisms and female choice. To investigate the proximate causes of dispersal in female Yunnan snub-nosed monkeys (*Rhinopithecus bieti*), we observed and analyzed nine years of detailed dispersal and demographic data from a population of *R. bieti* in Xiangguqing, Baimaxueshan Nature Reserve, Yunnan Province, China. Results showed that females who lived long-term in a one-male unit (OMU), without giving birth and with few or no relatives, were more likely to leave that OMU. In addition, an OMU led by an outgroup male and containing more female relatives was significantly more likely to be chosen for immigration. Conversely, greater male age, longer male tenure, and more potentially fertile females discouraged immigration into an OMU. These results suggest that reproduction, male quality, and kin cooperation play the largest roles in female Yunnan snub-nosed monkey dispersal.

Dispersal, defined as the movement of an individual or group between the natal site and another location, is an important factor in the ecology and evolution of many species (Kautz et al., 2016; Nathan, 2001). Over the past four decades, dispersal has been alternately described in terms of mating systems, dispersal patterns, social behaviors, and ecological factors (Dunbar, 1983; Greenwood, 1980; Sterck, 1998; Stokes et al., 2003; Wrangham, 1980). Complex social and ecological dynamics have provided considerable empirical support for explanations of individual dispersal choices in primates and other mammalian taxa (Stokes et al., 2003). Potential factors include infanticide avoidance (Smuts & Smuts, 1993; Stewart & Harcourt, 1987), mate competition (Lawler et al., 2003; Stewart & Harcourt, 1987), inbreeding

prevention (Clutton-Brock, 1989; Packer, 1979; Pusey & Packer, 1987), kin cooperation (Radespiel et al., 2003), local resource competition (Clobert et al., 2001), local resource defense (McNutt, 1996), and dispersal costs (Bonte et al., 2012).

Individual dispersal is ubiquitous among animals, with males typically dispersing more often than females (Greenwood, 1980). Models that account for the benefits to females from dispersal depend on the assumption that females voluntarily move among social groups (Swedell et al., 2011), which they do under certain circumstances (Bowler & Benton, 2005). For example, immigration into a new group can provide access to better resources (Pusey & Packer, 1987; Sterck, 1998). In addition, the competition hypothesis predicts that individuals will disperse if competition is stronger in their current territory than elsewhere (Dobson, 1982). In polygynous primate species, females choose the best available male as a mate due to the high costs of reproduction (Johnstone et al., 1996). Thus, dispersal is often associated with sexual selection and kin cooperation because females can join the group led by their preferred male with lower reproductive investment (Höner et al., 2007).

Long-term studies on the social and ecological mechanisms of dispersal have indicated that the causes of these behaviors in primates and other mammals are multifactorial. As such, it can be difficult to determine the specific reasons for any given dispersal event in non-human primates. However, interaction among these factors undoubtedly influences dispersal. Given the limited information on adult and sub-adult female dispersal events in Yunnan snub-nosed monkeys, we examined the influence of several variables on individual dispersal, including OMU composition, indicators of male quality, and demographic factors. Based on dispersal data collected over nine years of observation, we addressed the following

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questions: (1) What factors differ between adult females that emigrated from their OMU and co-resident adult females that did not? (2) What characteristics differentiate females that emigrated from their OMUs from co-resident adult females that did not?

This study was carried out at Xiangguqing in Baimaxueshan Nature Reserve, located on the southern slopes of the Hengduan Mountains (N27°36', E99°15'), Yunnan Province, China. The study site encompasses an area of almost 90 km² and is characterized by a plateau monsoon climate, where temperature and precipitation are strongly seasonal (Li, 2010). Yunnan snub-nosed monkeys are endangered colobines that inhabit high-altitude temperate forests in northwestern Yunnan and southeastern Tibet (Long et al., 1994). This diurnal primate species subsists on lichens and leaves of angiosperms (Li, 2010). They also form large, multilevel social groups consisting of many OMUs and an associated all-male unit (AMU) (Li et al., 2014). Here, the study group consisted of 5–10 OMUs and one AMU each year. Monkeys were individually identifiable using distinctive physical characteristics such as body size, hair pattern, scars, facial features, and pelage color (Ren et al., 2011). As the monkeys were provisioned, they were usually observable through binoculars at distances between 10 m and 20 m. Every day at 0900h and 1700h from 1 January 2010 to 31 December 2018, reserve staff provided food including lichen, carrots, apples, peanuts, and lacquer tree fruit. During those times, we counted the number of individuals in each OMU and AMU (Xia et al., 2016).

In 2008 and 2009, individuals could not yet be reliably identified, so data for those two years were only used to assess age of dispersal for each individual and kinship (mother, daughter, and sister) among individuals within the group. Accurate and detailed records of dispersal, reproduction, and individual mortality were kept from 2010–2018 as part of long-term population monitoring efforts. At every feeding time, in addition to counting the number of individuals in each OMU and AMU, we recorded demographic data including (i) population composition and demographic changes for OMUs and AMU, including births, deaths, and dispersals, and (ii) details of dispersal such as dispersal type, identity of dispersing female, time of dispersal, female age at time of dispersal, age of past and present mates, fertility (female older than four years) before and after dispersal, and number of females relatives in past and present OMUs. Age was assessed by body color, body size, and thinning of white hairs on the back. All dispersal events were confirmed within 1–3 d. The ages of outgroup individuals were estimated using body size and hair color. Females younger than three years and not sexually mature typically migrated with their mothers, and thus were excluded from the scope of this paper. Natal dispersal is primarily considered to be an inbreeding avoidance mechanism and was also excluded from the emigration study.

To explore factors correlated with the likelihood of female dispersal, we divided dispersal into emigration and

immigration. Individuals that emigrated were classified as the Experimental Emigration Group (EEG) and individuals in the same OMU that did not emigrate were classified as the Control Emigration Group (CEG). Similarly, the OMUs chosen by immigrant females were identified as the Experimental Immigration Group (EIG) and OMUs not joined by immigrant females were classified as the Control Immigration Group (CIG). We used stepwise binary logistic regression (BLR) to predict female dispersion using reproduction, competition, male/female quality, and kin variables (Table 1). The predictor variables for modelling female emigration included WB (whether female has given birth in the OMU), HLB (length of time female did not breed), FA (female age), FLT (female length of tenure), NR1 (number of relatives), and WOD (whether offspring died within the first year). The predictor variables for modelling female immigration included AM (new alpha male age), MT (new alpha male length of tenure), NFF (number of potentially fertile females in new OMU), NI (total number of individuals in new OMU), OGM (outgroup male became alpha), and NR2 (number of relatives). We included EEG and CEG adult and sub-adult females from the same OMU in the same analyses. We used the Hosmer-Lemeshow goodness-of-fit test and Nagelkerke R^2 measures to determine model fit and significance. We assessed the contribution of predictor variables using the Wald statistic, and the odds ratio ($\exp(B)$) for interpreting the regression models. Significance was set at 0.05 and mean values are presented with standard deviations ($\pm SD$). We completed all statistical analyses using SPSS 19.0.

From January 2010 through to December 2018, we recorded a total of 92 female emigration events from 22 OMUs. After excluding dispersal involving individuals younger than three years (19 events), natal dispersal (19 events), and emigration of the whole OMU (13 events), a total of 41 cases of emigration were included in the EEG. Forty-three non-emigration cases occurring in the same OMU at the same time were included in the CEG. The Hosmer-Lemeshow goodness-of-fit test was not significant ($\chi^2=6.21$, $P=0.624$), indicating that the observed data frequencies did not violate the assumptions of the model, and the model was well-fitted (Nagelkerke $R^2=0.521$). The FLT variable was a significant positive predictor of female emigration (BLR: $\beta \pm SE=0.790 \pm 0.036$, $P=0.026$), whereas the WB ($\beta \pm SE=-2.468 \pm 0.923$, $P=0.007$) and NR1 ($\beta \pm SE=-1.938 \pm 0.537$, $P<0.001$) variables were indicative of a significantly reduced chance of female emigration (Table 2). Using the coefficient values from the final logistic regression output (Table 2), we obtained the logistic regression equation: $Y=0.79(FLT)-1.938(NR1)-2.468(WB)$.

A total of 55 cases of between OMU immigration and three cases of immigration by outgroup individuals were recorded. In eight cases, individuals were younger than three years old and were thus excluded, with the remaining 50 cases used here. The Hosmer-Lemeshow goodness-of-fit test was not significant ($\chi^2=2.489$, $P=0.962$), indicating that the observed data frequencies did not violate the assumptions of the model,

Table 1 Coding and description of variables used in binary logistic regression modelling

Group	Variable type	Variable	Variable description
Emigration Group	Reproduction	WB	Whether female has given birth in OMU (0: no, 1: yes)
		HLB	Length of time female did not breed (after age four)
		WOD	Whether offspring died within first year (0: no, 1: yes)
	Female quality	FLT	Female length of tenure
		FA	Female age
Immigration Group	Kin	NR1	Number of relatives (mother, daughter, and sister)
	Male quality	AM	New alpha male age
		MT	New alpha male length of tenure
		OGM	Outgroup male became alpha (0: no, 1: yes)
	Competition	NFF	Number of potentially fertile females in new OMU
		NI	Total number of individuals in new OMU
	Kin	NR2	Number of relatives (mother, daughter, and sister)

For abbreviations, see text.

Table 2 Binary logistic regression modelling for female emigration and immigration

	Variable type	Variable	Binary logistic regression model						95.0% CI for Exp(B)	
			B	SE	Wald	df	Sig	Exp(B)	Lower	Upper
Emigration	Reproduction	WB	−2.468	0.923	7.150	1	0.007**	0.085	0.014	0.517
		HLB	−0.022	0.055	0.156	1	0.693	0.979	0.879	1.090
		WOD	0.051	1.226	0.002	1	0.967	1.053	0.950	11.638
	Female quality	FA	0.021	0.012	2.993	1	0.084	1.021	0.997	1.046
		FLT	0.79	0.036	4.971	1	0.026*	1.083	1.010	1.161
	Kin	NR1	−1.938	0.537	13.04	1	<0.001**	0.144	0.050	0.412
	Intercept		−0.532	0.881	0.365	1	0.546	0.587	–	–
Immigration	Male quality	AM	−0.036	0.018	3.838	1	0.049*	0.965	1.001	1.079
		MT	−0.106	0.037	8.009	1	0.005**	0.900	0.836	0.968
		OGM	2.048	0.710	8.314	1	0.004**	7.7521	1.927	31.190
	Competition	NFF	−0.991	0.374	7.021	1	0.008**	0.371	0.178	0.773
		NI	0.090	0.181	0.250	1	0.617	1.095	0.768	1.560
	Kin	NR2	4.135	1.016	16.573	1	<0.001**	62.503	8.536	457.662
	Intercept		4.833	2.171	4.954	1	0.026*	125.536	–	–

For abbreviations, see text. B: Logistic coefficient; SE: Standard error of estimate; Wald: Wald chi-square values; df: Degrees of freedom; Sig: Significance; Exp(B): Exponentiated coefficient. CI: Confidence interval. –: Not available. *: $P < 0.05$; **: $P < 0.001$.

and the model was well-fitted (Nagelkerke $R^2=0.872$). Stepwise analysis of the best-fitting model identified five variables that significantly predicted female immigration (Table 2). In the model, the OGM (BLR: $\beta \pm SE=2.048 \pm 0.710$, $P=0.004$) and NR2 ($\beta \pm SE=4.135 \pm 1.016$, $P < 0.001$) variables had a significant positive effect on female immigration, whereas the AM ($\beta \pm SE=-0.036 \pm 0.018$, $P=0.049$), MT ($\beta \pm SE=-0.106 \pm 0.037$, $P=0.005$), and NFF ($\beta \pm SE=-0.991 \pm 0.374$, $P=0.008$) variables were significant negative predictors of female immigration (Table 2). Using the coefficient values from the final logistic regression output (Table 2), we obtained the logistic regression equation: $Y=2.048(OGM)+4.135(NR2)-0.036(AM)-0.106(MT)-0.991(NFF)$.

Our results showed that *R. bieti* females who have resided within an OMU for a longer period of time, have not given birth, and have few female relatives within the OMU are more likely to emigrate. Female age, length of time without

breeding, and whether an infant died in its first year had no significant effect on emigration. For factors pertaining to reproduction, only whether a female had given birth determined the likelihood of emigration. Adult females without offspring may be less constrained in their dispersal because there is no risk that the male in a new OMU will kill their existing dependent infant (Smuts & Smuts, 1993; Stewart & Harcourt, 1987). Females who had not given birth for a long time (dispersed and undispersed: 17.1 months vs. 16.5 months) were not more likely to disperse. The average inter-birth interval for *R. bieti* is two years (Cui et al., 2006), and mating is seasonal, occurring between July to October (Xiang & Sayers, 2009). It is possible that the relatively long reproductive cycle in *R. bieti* reduces their sensitivity to the length of time since birth. In regard to the influence of infant loss on dispersal, first-year infant mortality during the study period was 15.5% (unpublished data), which may have been

too small to produce significant results. Additionally, as mothers are the primary caregivers of infants, resident males in OMUs may have no direct influence on infant survival apart from infanticide.

Female tenure length and female age were used to explore the relationship between female quality and likelihood of emigration. Only tenure length had a significant effect on female emigration, with a female increasingly likely to emigrate as her tenure in an OMU increased. Longer female tenure in an OMU is correlated with longer tenure of its resident male; for example, longer tenure in western lowland gorillas (*Gorilla gorilla gorilla*) increases the probability of transfer (Stokes et al., 2003). Once they reach an advanced age, the social rank of an alpha male decreases; generally, lower-ranking individuals cannot compete as effectively for resources (Murray et al., 2007; Vogel, 2005). In addition, lower-ranking resident males are more susceptible to displacement by challengers (Zhu et al., 2016). Thus, females may leave an OMU with an older resident male to protect themselves from accidental injury or their infant from infanticide.

Females with more relatives in an OMU were less likely to disperse. In most polygynous non-human primate societies, females exhibit strong kin bonds, often forming matrilineal societies (Pusey & Packer, 1987). The importance of kin in determining offspring dispersal has been demonstrated in multiple species (e.g., *Microtus oeconomus*, Gundersen & Andresassen, 1998; *Microtus townsendii*, Lambin, 1994; *Lacerta vivipara*, Léna et al., 1998). In western gorillas (*Gorilla gorilla*), nearly half of adult females have adult female relatives living in the same group, despite the fact that females disperse out of their natal groups (Bradley et al., 2007). In the absence of female philopatry, continued associations with female kin into adulthood may be the result of choices made during dispersal. Indeed, related female western gorillas live in the same group more frequently than would be expected by chance (Bradley et al., 2007). Our results in *R. bieti*, which exhibit bisexual dispersal similar to other snub-nosed monkeys such as *Rhinopithecus roxellana* (Qi et al., 2009), further support the observation that female kin bonds can be important to social organization, even in primate species without female philopatry and strong matrilinealities.

Immigration is a selective process, requiring an adult female who has left her OMU to prefer a new, more satisfactory OMU with a high-quality male (Bowler & Benton, 2005). The high cost of reproduction means that in polygynous primates, females are expected to be choosy (Johnstone et al., 1996). In this study, three variables related to male quality (i.e., AM, MT, and OGM) had a significant influence on whether females immigrated into their OMU. Females preferred younger males with a shorter tenure as the OMU leader, as well as outgroup males. Younger resident males had less time to build their OMU, translating to fewer resident females and less female-female competition. Females may prefer mating with outgroup males to enhance genetic diversity (Lehmann & Perrin, 2003). Females also generally avoid mating with familiar males who

were members of their natal group to reduce the chance of costly inbreeding (Höner et al., 2007).

Competition appears to be the primary reason for individual dispersal between social groups. Increasing population density can reduce individual fitness, thus becoming a driving force for dispersal (Bowler & Benton, 2005). Types of competition that emerge as group size increases include kin, resource, and mating competition (Clobert et al., 2001). In this study, the dispersal behavior of *R. bieti* was not consistent with the resource competition hypothesis because the total number of individuals in an OMU (NI) had no significant effect on whether a female immigrated into it. However, the number of fertile females in an OMU (NFF) had a significant negative relationship with female immigration, indicating that females preferred to join OMUs with reduced mating competition, consistent with the mating competition hypothesis. Similar results have been reported for *R. roxellana* (Qi et al., 2009). Yunnan snub-nosed monkey social groups consist of many OMUs and an associated AMU (Li et al., 2014). If the females in an OMU mate exclusively with the single resident male, this creates intense mating competition among them. Additionally, sexual maturity occurs relatively late in *R. bieti* females. Field records indicate that they do not reproduce before the age of five (unpublished data). Considering these facts, in addition to the two-year average inter-birth interval (Cui et al., 2006; Kirkpatrick et al., 1998) and four-month window for conception (Xiang & Sayers, 2009), females in this species must invest considerable effort into reproduction. Therefore, the opportunity for enhanced reproductive success would provide strong motivation for dispersal. Many other primates have been observed to disperse to improve their chances of reproduction (Glander, 1980, 1992; Moore & Ali, 1984; Stewart & Harcourt, 1987; Watts, 1990; Wrangham, 1980). Finally, our results were inconsistent with the predation hypothesis, which predicts that individuals would choose larger OMUs to reduce the risk of predation (Cadet et al., 2003). One reason for this could be the reduced predation pressure due to the decline in monkeys' natural enemies in the families Felidae and Accipitriformes (Li, 2010).

Kin may cooperate to acquire or defend mates or resources, and to prevent unrelated competitors from joining the group (Le Galliard et al., 2003). Choosing an OMU with female relatives allows females to form kin-based alliances, potentially improving their fitness (Dunbar, 1983). Although *R. bieti* females preferentially join OMUs with female relatives, females within OMUs are not strongly genetically related outside of mother, daughter, and sister relationships. This lack of genetic similarity among females is also found in *R. roxellana* (Qi et al., 2009). Kin-based coalitions of female primates can better compete for patchy resources, such as high-quality food and habitat (Wrangham, 1980). Yunnan snub-nosed monkeys inhabit high-altitude temperate forests (Long et al., 1994) and subsist on lichens and mature leaves for much of the year, both of which are of low nutritional value (Li, 2010). In summer and autumn, when higher-quality foods such as fruits and bamboo become available, they are

uniformly distributed (Li, 2010). This helps to explain why this species does not form matrilineal groups to monopolize resources.

In conclusion, our study indicated that multiple factors influenced female dispersal in Yunnan snub-nosed monkeys. These factors were associated with reproduction, infanticide, mate competition, inbreeding avoidance, and kin cooperation but not with local resource defense. The likelihood of female emigration from an OMU increased with her length of tenure and decreased with the number of relatives in the group or if she had given birth. Whether an OMU was led by an outgroup male or contained more female relatives had a significant positive impact on female immigration. In contrast, the chance of female immigration declined with increasing male age, male tenure, and number of fertile females. We argue that female mate choice, inbreeding avoidance, and kin cooperation primarily governed female dispersal in *R. bieti*. In addition, in contrast to other Asian colobines, *R. bieti* does not organize around strong matrilineal due to the abundance of low-quality food year-round and uniform distribution of seasonally available high-quality food resources.

SCIENTIFIC FIELD SURVEY PERMISSION INFORMATION

This field experiments were approved by the State Forestry and Grassland Administration of China (the Second National Survey on Terrestrial Wildlife Resources in China).

COMPETING INTERESTS

The authors declare that they have no competing interests.

AUTHORS' CONTRIBUTIONS

W.C.X., S.N.J., Y.T., and D.Y. L. wrote the manuscript; W.C.X., D.Y.L., X.M.H., and T.Z. collected field data; B.P.R. and A.K. revised the manuscript. All authors read and approved the final version of the manuscript.

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