Original Article

Impact of Group Size on Female Reproductive Success of Free-Ranging *Rhinopithecus roxellana* in the Qinling Mountains, China

Dapeng Zhao[a, c]   Baoguo Li[a, b]   Kunio Watanabe[d]

[a]College of Life Sciences, Northwest University, and [b]Institute of Zoology, Shaanxi Academy of Sciences, Xi'an, and [c]Institute of Zoology, Chinese Academy of Sciences, Beijing, China; [d]Primate Research Institute, Kyoto University, Inuyama, Japan

Abstract

Group size influences female reproductive success through scramble/contest feeding competition, predation pressures and infanticide risks in primates. The Sichuan snub-nosed monkey *(Rhinopithecus roxellana)* is an endangered folivorous colobine species living in a multilevel society. From 2002 to 2008, we studied a free-ranging band of *R. roxellana* in the Qinling Mountains of China to examine the effect of group size on female reproductive success. During our observation period, the number of monkeys in the study band fluctuated from 61 to 108, and the number of one-male/multi-female groups within it varied from 7 to 10. A significant negative linear relationship was found between group size and birth rate, but group size was not significantly correlated with infant survival rate or interbirth interval. These results suggest that group size influences female reproductive success via within-group scramble competition in this folivorous species.

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Introduction

Animals face a variety of potential costs and benefits when living in groups, which vary across species and habitats [Krause and Ruxton, 2002; Silk, 2007]. In the primate socio-ecological model, it has been suggested that group size is one important factor regulating female reproductive success, mainly through feeding competition, predation pressures and infanticide risks [Wrangham, 1980; van Schaik, 1983,

1989; Janson and Goldsmith, 1995; Sterck et al., 1997; Isbell and Young, 2002; Koenig, 2002; Snaith and Chapman, 2007]. For example, female reproductive success is generally expected to be higher in larger groups, in which group members experience lower predation pressure [van Schaik, 1983, 1989], whereas in some species with one-male/multi-female groups, infanticide following male takeovers is more likely to occur in larger groups, and these events will decrease female reproductive success [van Schaik and Janson, 2000; e.g. *Semnopithecus entellus:* Agoramoorthy, 1994; *Theropithecus gelada:* Beehner and Bergman, 2008].

Group-living primates endure contest or scramble feeding competition [Nicholson, 1954; Lomnicki, 1988] within or between social groups, yielding four basic modes of competition: within-group scramble, within-group contest, between-group scramble, and between-group contest [Janson and van Schaik, 1988; van Schaik, 1989; Sterck et al. 1997; Koenig, 2002]. Among these, within-group scramble and between-group contest competition are dependent on group size, while the effects of within-group contest depend on dominance rank [Janson and van Schaik, 1988; van Schaik, 1989]. According to the socio-ecological model, the density, quality and distribution of food resources determine the mode and strength of feeding competition, which, in turn, affects female reproductive success [Sterck et al., 1997]. Although it is generally thought that clumped fruit is often associated with within-group contest competition, while foliage may be associated with within-group scramble competition [Wrangham, 1980; van Schaik, 1989; e.g. *Colobus vellerosus:* Saj et al., 2007; Teichroeb and Sicotte, 2009; *Procolobus rufomitratus:* Snaith and Chapman, 2008], accumulating evidence suggests that folivores may not differ from frugivores in the type and level of food competition they face [Snaith and Chapman, 2007; Majolo et al., 2008; e.g. *S. entellus:* Borries, 1993; Koenig et al., 1998; Koenig, 2000]. In other words, folivorous and frugivorous primates may experience similar ecological pressures [Snaith and Chapman, 2007; Majolo et al., 2008].

Given the strong asymmetry in the reproductive effort of mammalian females and males, resource competition over food within groups has more impact on females [Trivers, 1972], and differences in styles of feeding competition would lead to variation in female reproductive success and social relationships [Koenig, 2002]. In scramble competition, any individual has the potential to alter the net energy gain of all others in the population, and as a consequence, reproductive success is equal for all individuals [Nicholson, 1954; Lomnicki, 1988]. Within-group scramble competition prevails when group members equally share small, dispersed resources of low quality or small patches [van Schaik, 1989; Koenig, 2002], and females have inconsistent dominance relationships, female alliances are absent, and females frequently disperse [Sterck et al., 1997]. Increasing group size results in decreased net energy intake per individual, thus reducing female reproductive success [Janson and Goldsmith, 1995; Sterck et al., 1997; Koenig, 2002]. One thing to be noted here is that some primate species may, to a certain extent, mitigate scramble competition by temporal or regular fission and fusion in response to variable food availability [e.g. *Ateles geoffroyi:* Klein and Klein, 1977; Chapman, 1990; *Brachyteles arachnoids:* Strier, 1986; de Moraes et al., 1998; *Cacajao calvus ucayalii:* Bowler and Bodmer, 2009; *Nasalis larvatus:* Yeager, 1990; *Pan paniscus:* Kano, 1982; *Pan troglodytes:* Nishida, 1968; Lehmann et al., 2007; *Procolobus gordonorum:* Struhsaker et al., 2004; *P. rufomitratus:* Snaith and Chapman, 2008]. Considering that fission-fusion is a highly flexible system, reacting rapidly to environmental changes, investigating the female repro-

ductive success correlates of group size in a fission-fusion species could shed further light on the primate socio-ecological model.

The Sichuan snub-nosed monkey *(Rhinopithecus roxellana)* lives in temperate montane forests in Sichuan, Shaanxi, Gansu, and Hubei provinces in China. The species exhibits seasonal ranging patterns [Li et al., 2000; Tan et al., 2007] and shows seasonal variation in diets [Li, 2006; Guo et al., 2007] in response to temporal and spatial distribution in food resources. In the Qinling Mountains, it ranges in deciduous broadleaf and mixed deciduous broadleaf/conifer forests. Its overall diet consists of 29.4% fruit/seeds, 29.0% lichens, 24.0% leaves, 11.1% bark, 4.2% buds, 1.3% twigs and 1.0% unidentified items [Guo et al., 2007]. The species is a strict seasonal breeder; the mating season is September to December, and the birth season is March to May [Li and Zhao, 2007]. The social organization is characterized by multilevel societies with one-male/multi-female groups as the basic social structure; group size is variable, and both sexes disperse [Chen et al., 1983; Zhao et al., 2008a]. Female dominance relationships within the group are unstable and relaxed [Li et al., 2006; Zhang et al., 2008]. Several one-male/multi-female groups together constitute one band, the second level of the species' social organization. The band size fluctuates, with different numbers of one-male/multi-female groups foraging together in different seasons. Groupings in the band are semi-cohesive, suggesting a fission-fusion social system within the band [Tan et al., 2003; Grueter and Zinner, 2004].

To our knowledge, there has been no investigation on how group size impacts individual fitness in *Rhinopithecus* spp. In this paper, we analyse demographic data accumulated over a 7-year period from one free-ranging band of Sichuan snub-nosed monkeys in the Qinling Mountains to evaluate the effect of group size on female reproductive success. Three measures are applied in the analysis of female reproductive success: birth rate (BR), infant survival rate, and interbirth interval (IBI). We compare the relationship between group size and each measure with the expectation that, as a folivorous species, *R. roxellana* undergoes decreased net energy intake due to within-group scramble competition and females in larger groups pay a price on their reproductive efficiency. Consequently, we make the following predictions: (1) BR decreases with increasing group size, and (2) IBI shortens with increasing group size. Furthermore, it is generally believed that larger primate groups benefit from lower predation pressures [van Schaik, 1983]; therefore, we predict that (3) infant survival rate increases with increasing group size.

Methods

Study Sites and Species
We collected demographic data from 2002 to 2008 from a provisioned, free-ranging band of *R. roxellana* in the Zhouzhi National Nature Reserve, on the northern slope of the Qinling Mountains, in Shaanxi Province of China [for further details of the habitat and the provisioned band, see Zhao et al., 2005; Zhao, 2009]. The main potential predator of the monkeys would seem to be the goshawk *(Accipiter gentilis)* [one predation case reported by Zhang et al., 1999b]. During our observation period, the number of one-male/multi-female groups in the study band varied from 7 to 10, and the total number of monkeys fluctuated from 61 to 108 (table 1).

One provisioning site was set up at Sanchakou (1,646 m above sea level) in Gongnigou Valley (33°48′68′′N, 108°16′18′′E). Field assistants searched for monkeys of the focal band and herded them to the provisioning site at approximately 9.00 a.m. every day when research was

Table 1. Group size and composition in *R. roxellana*

Group name	Observation years	Mean group size (excluding infants)	Mean female number
BZT	7	11 ± 3 (8–15)	5 ± 1 (3–7)
CL	1	8 (8)	4 (4)
CM	4	9 ± 1 (8–11)	5 ± 1 (4–6)
DB	6	13 ± 2 (9–16)	7 ± 2 (5–9)
DZ	3	8 ± 2 (6–10)	5 ± 1 (4–6)
FP	2	8 ± 1 (7–8)	4 ± 1 (3–5)
HD	1	7 (7)	5 (5)
HT	3	5 ± 2 (4–7)	3 ± 1 (3–4)
JB	5	9 ± 2 (7–11)	5 ± 1 (4–6)
JZT	6	9 ± 2 (6–11)	5 ± 1 (3–6)
LP	5	16 ± 2 (14–19)	8 ± 3 (5–11)
PK	5	6 ± 2 (4–9)	4 ± 1 (3–6)
RX	3	7 ± 1 (6–7)	4 ± 1 (3–4)
TT	2	7 ± 1 (6–8)	5 ± 1 (4–6)
XN	1	7 (7)	6 (6)
Total	54	9 ± 3 (4–19)	5 ± 2 (3–11)

Figures in parentheses indicate ranges.

being conducted [Zhao et al., 2008a, b]. Apples, radishes, and corn were provided three times per day (10.00 a.m., 12.00 p.m., and 2.00 p.m.), approximately 200 g per monkey per day in total, a small proportion of their total daily diet. The focal monkeys would leave the provisioning site on their own initiative after feeding and resting briefly.

During the study period, distances between the monkeys and the observers typically vary between 0.5 and 50 m. Within the focal band, individuals were recognized via their prominent physical characteristics [Zhao et al., 2008a, b, 2010]. One-male/multi-female groups were easily identified by their close and continuous spatial association during daily activities and by their alliances during intergroup conflicts. Based on their estimated ages and physical characteristics we classified individuals as infants (0–1 year old), juveniles (estimated at 1–3 years old), sub-adults (females: estimated at 3–4 years old; males: estimated at 5–7 years old), and adults (females: estimated at more than 5 years old; males: estimated at more than 7 years old) [Zhao, 2009]. Our research complied with protocols approved by the Zhouzhi National Nature Reserve and adhered to legal requirements in China.

Data Collection and Analysis
In each observation year, demographic data collection was conducted from March to May and from September to November, i.e. the birth season and the mating season, respectively. Data on group size and composition were determined monthly and then averaged for each observation year. On average, there were 10 days per observation month. Observation records among different groups are uneven because several groups disappeared from or entered the focal population during our observation period (fig. 1). Birth data were gathered during each birth season, as described by Zhao et al. [2008a]; the typically close observation distances made it possible to observe mother-infant pairs closely.

For purposes of including effective feeding competitors, the group size included all juveniles and adults, but excluded infants (as argued by Zhao et al. [2008a]). For the analysis of fe-

Group name	Observation year						
	2002	2003	2004	2005	2006	2007	2008
BZT	gray	gray	gray	gray	gray	gray	gray
CL						gray	
CM	gray	gray	gray	gray			
DB		gray	gray	gray	gray	gray	gray
DZ	gray	gray	gray				
FP					gray	gray	gray
HD	gray						
HT	gray	gray					gray
JB			gray	gray	gray	gray	gray
JZT	gray	gray	gray	gray	gray		gray
LP			gray	gray	gray	gray	gray
PK			gray	gray	gray	gray	gray
RX					gray	gray	gray
TT	gray	gray	gray				
XN						gray	

Fig. 1. One-male/multi-female groups in the band during observation years. Gray boxes indicate that the group was present in the population. White boxes indicate that the group was not present in the population.

male reproductive success, we measured BR, infant survival rate and IBI. These measures were tallied on an annual basis for a given one-male/multi-female group. BR in any one observation year was calculated as the number of new infants in the birth season divided by the average numbers of females in one group within that year (adult plus subadult females: see van Belle and Estrada [2008]). Infant survival rate was calculated as the number of infants who survived to at least one year of age divided by the total number of births in that group over one observation year. IBI was counted from the birth date of the previous surviving offspring to the birth date of the next offspring. The measurement of IBI is restricted to intervals in which a mother gives birth successively in the same one-male/multi-female group, so avoiding the influence of female transfer between groups [Zhao et al., 2008a] on IBI, and a group is counted at the time of the earlier birth.

Group sizes for the same group in different observation years were similarly treated as independent data points, following Stokes et al. [2003] and Zhao et al. [2008a]. We used regression analysis to evaluate the influence of group size on BR, infant survival rate and IBI. To test for interdependence among births, we checked the relationship between consecutive births of the same mother, which would be the most probable conditions for which one birth could influence another [Robbins et al., 2007]. All statistical analyses were conducted in SPSS 16.0 at a significance level of $p < 0.05$.

Results

The mean ($\pm$ SE) size of one-male/multi-female groups in the study population was 9 ± 3 individuals (range: 4–19), the average number of females being 5 ± 2 (range: 3–11) during our observation period (tables 1, 2). A highly significant correlation was found between group size and number of females in the group ($r = 0.769$, $p < 0.001$).
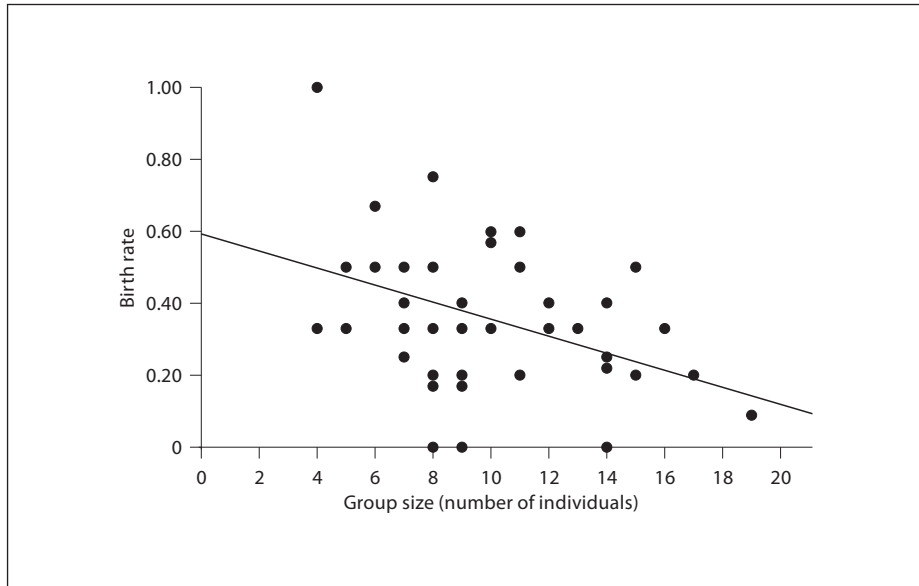
Fig. 2. Effect of group size on BR.

Table 2. Mean (±SE) of female number, BR, infant survival rate and IBI with different group sizes

| Group size	Number of observation years	Female number	Birth rate	Infant survival rate	Interbirth interval months
4	2	3 ± 0	0.7 ± 0.5	0.8 ± 0.2	–
5	2	4 ± 1	0.4 ± 0.1	1.0 ± 0.0	–
6	4	4 ± 1	0.6 ± 0.1	0.8 ± 0.5	12.3
7	10	4 ± 1	0.4 ± 0.1	0.9 ± 0.3	23.6 ± 0.4
8	10	5 ± 1	0.4 ± 0.2	1.0 ± 0.1	23.9 ± 0.4
9	6	6 ± 1	0.2 ± 0.1	1.0 ± 0.0	21.4 ± 5.4
10	3	6 ± 1	0.5 ± 0.2	0.8 ± 0.3	23.5
11	4	5 ± 1	0.5 ± 0.2	0.9 ± 0.2	16.1 ± 6.6
12	2	6 ± 1	0.4 ± 0.1	1.0 ± 0.0	24.4
13	1	3	0.3	1.0	–
14	5	8 ± 2	0.2 ± 0.2	0.8 ± 0.3	25.2 ± 4.1
15	2	6 ± 1	0.4 ± 0.2	1.0 ± 0.0	23.7
16	1	9	0.3	1.0	–
17	1	10	0.2	1.0	18.6 ± 7.8
19	1	11	0.1	1.0	23.4 ± 4.8
Total	54	5 ± 2	0.4 ± 0.2	0.9 ± 0.2	22.5 ± 4.8
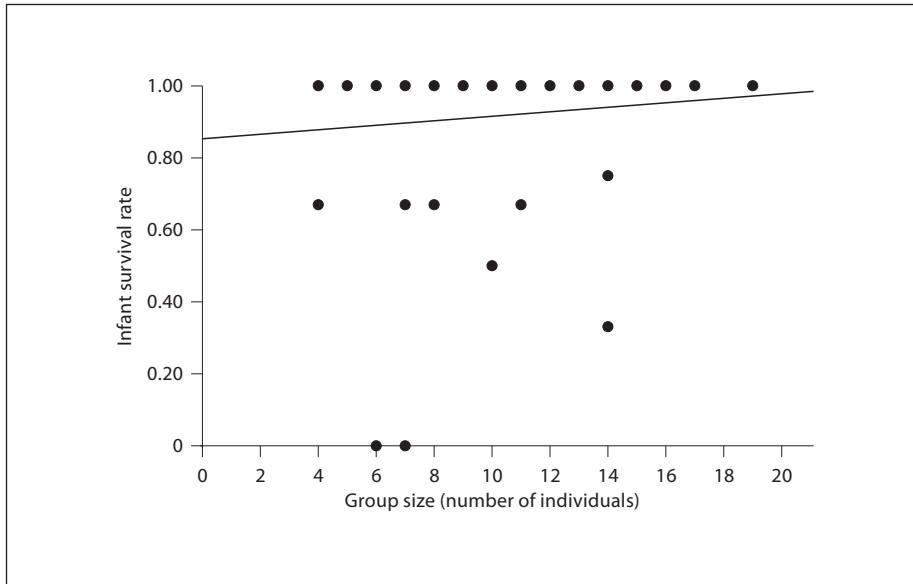
Fig. 3. Effect of group size on infant survival rate.

The BR ranged from 0.0 to 1.0 (mean = 0.4, SD = 0.2) (table 2). A significant negative linear relationship was found between BR and group size (y = 0.592 – 0.024x; $R^2 = 0.161$, $F_{52, 1} = 9.988$, p = 0.003; fig. 2).

The mean infant survival rate was 0.9 ± 0.2 (range: 0.0–1.0) (table 2). Infant survival rate was not significantly correlated with group size ($R^2 = 0.009$, $F_{52, 1} = 0.462$, p = 0.500; fig. 3). Infant mortality was 11.6% (11 of 95 infants) during our observation periods. The 11 cases of infant mortality include 7 cases in which we were able to observe the carcass directly, and 4 cases in which the infant simply disappeared, for unknown reasons. None of these cases seems to have been directly related to food scarcity.

Forty IBI, involving 27 females, could be measured under our criteria, ranging from 11.4 to 36.1 months (mean = 22.5, SD = 4.8) (table 2). There were 8 females with more than 1 IBI; the length of 1 IBI did not depend on the length of the previous IBI for the same mother ($R^2 = 0.110$, $F_{10, 1} = 1.237$, p = 0.292). This gives no indication that one birth can influence another, so supporting the treatment of each IBI as an independent data point. We found that IBI was not significantly correlated with group size ($R^2 = 0.012$, $F_{38, 1} = 0.447$, p = 0.508; fig. 4).

Discussion

This is the first investigation of how group sizes affect female reproductive success in *Rhinopithecus* spp. Our findings partly validate our predictions. On the one hand, the first prediction is supported, i.e. that there is a significant negative linear
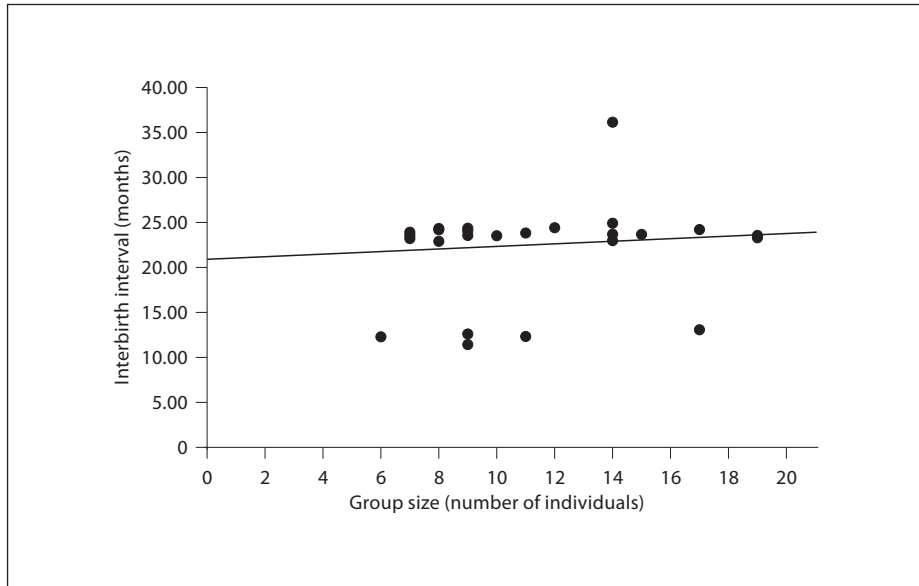
Fig. 4. Effect of group size on IBI.

relationship between group size and BR. On the other hand, contrary to what we expected, group size is not significantly correlated with IBI and infant survival rate.

Our results should be treated with caution because of the potential influence of food provisioning on female reproductive success, although only a very limited amount of provisioned food was available, during only a short period of time each day. Diets of folivorous primate species are generally widely distributed in space and time, allowing group members to spread out while foraging [Snaith and Chapman, 2007]. In the study area, the availability of food resources shows pronounced seasonal fluctuation, and snub-nosed monkeys in the Qinling Mountains exhibit distinct seasonal ranging patterns [Li et al., 2000; Guo et al., 2007; Tan et al., 2007]. The provisioning protocol used in the present study probably somewhat disturbed the normal ranging pattern since the animals could partly rely on provisioned food within the observation period, and this may have increased feeding competition and disturbed natural energy intake and thus possibly influenced female fecundity. It will be necessary in the future to compare this provisioned population with a non-provisioned population to evaluate provisioning effects on female reproductive success in this folivorous species.

It was found that BR is negatively related to group size in a one-male/multi-female group in *R. roxellana*. This accords with a basic assumption of the predation-intragroup feeding competition hypothesis [van Schaik, 1983], that within-group scramble competition influences female reproductive success. In conjunction with reports that females in other folivorous species also experience reduced reproductive success with an increasing number of females [e.g. *P. rufomitratus:* Snaith and Chapman, 2008; *Trachypithecus phayrei*: Borries et al., 2008], these results suggest that

feeding competition may play a more important role in the reproductive success of folivorous primate females than previously thought [Snaith and Chapman, 2007].

Besides feeding competition, predation and infanticide risks also influence female reproductive success [van Schaik, 1989; van Schaik and Janson, 2000]. The main predator of *R. roxellana* is a raptor [Shi et al., 1982; Zhang et al., 1999b; Grueter and Zinner, 2004], which was recorded to prey upon a juvenile *R. roxellana* in the study area in the 1990s [Zhang et al., 1999b], but no other case of predation has been observed since then, although these raptors are still active within the study area [D.Z., pers. observation]. In addition, there is no direct evidence for infanticide under natural conditions in *R. roxellana,* although its occurrence in conjunction with resident male changes has been reported in captive situations [Zhang et al., 1999a]. We conclude that there seems to be little apparent effect of predation and infanticide on female reproductive success in *R. roxellana,* and this may be one possible reason why the infant survival rate is relatively high; however, further investigation is required on this question.

Births must be timed to ensure that there are enough food resources available to support the high metabolic demands of lactation and growth of the offspring [Davies and Oates, 1994]. *R. roxellana* in the Qinling Mountains exhibits a seasonal breeding pattern and the peak of births (April) occurs during the time of year with the most favourable environmental conditions including food resource availability [Chen et al., 1983; Li and Zhao, 2007]. What is more, female *R. roxellana* start to wean their infants when they are 170 days old and infants are not independent of their mothers until they are at least 1 year old [Li et al., 2005]. It is likely that seasonal availability of food resources and continuance of maternal care together serve, to a great extent, to constrain females' reproductive rate and IBI for a given group size. It should be noted that, in some primate species, IBI may also be affected by other factors [Fedigan et al., 2008], such as female dominance rank and maternal age [e.g. *Gorilla beringei beringei*: Robbins et al., 2006, 2007]. Further studies should explore these potential influences in this species.

A series of adaptive behaviours may mitigate the cost of scramble competition in folivorous primates [Snaith and Chapman, 2008]. For example, females may disperse when within-group scramble competition begins to reduce the cost of their fitness [Koenig, 2002]. Given that adult female *R. roxellana* prefer to transfer into significantly smaller groups [Zhao et al., 2008a], it is likely that within-group scramble competition operates as a potential driving force behind adult female dispersal, in addition to mate competition [Zhao et al., 2008a]. In addition, some folivorous species may exhibit temporary fission-fusion to reduce scramble competition [Snaith and Chapman, 2007]. For *R. roxellana* in the Qinling Mountains, fission-fusion of the focal band is seasonal [Tan et al., 2003; Grueter and Zinner, 2004], with a larger band size in the mating season and a smaller one in the birth season [D.Z., unpubl. data]; this is plausibly an adjustment in response to seasonal reproductive patterns, which may ameliorate scramble competition within bands and increase female reproductive success within a group.

Clutton-Brock et al. [2001] point out that a positive relationship between group size and female reproductive success is common in social mammals whose young are reared by helpers. Although allomothering is a prominent feature of *R. roxellana* [Xi et al., 2008] and many other colobine species [Maestripieri, 1994], in the present study, there was no positive relationship between group size and female reproductive

success such as was proposed by Clutton-Brock et al. [2001]. This result is consistent with some reports for other social mammals [e.g. *Malurus cyaneus:* Nias and Ford, 1992]. It may be that benefits of allomothering are uniform across one-male/multi-female groups in *R. roxellana*. More data are needed to further explore how the existence of helpers impacts female reproductive success across different group sizes in this species.

Overall, we found clear evidence that *R. roxellana* in the Qinling Mountains experience within-group scramble competition and BR decreases linearly with increasing group size. It should be admitted that our study focused mainly on within-group scramble competition, and the results reported here may be influenced by between-group feeding competition, which will require further investigation in future research. Some open questions remain concerning socio-ecological constraints on female reproductive success in *R. roxellana*. For instance, group size in our study population was smaller than that observed in the Shennongjia National Nature Reserve [Ren et al., 2000] and the population density at Shennongjia was five times higher than at our study site [Chen et al., 1989; Ren et al., 2000]. Feeding competition among one-male/multi-female groups in the Qinling Mountains may therefore be weaker than that in Shennongjia. Comparative research with multipopulation demographic data in different habitats is needed to improve our understanding of the relationship between group size and female reproductive success in this species.

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