SOCIAL INTERACTION AND DISPERSAL PATTERNS OF GOLDEN SNUB-NOSED MONKEYS (*RHINOPITHECUS ROXELLANA*) LIVING IN MULTI-LEVEL SOCIETIES

BY

CAIE YAN

DISSERTATION

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy in Anthropology
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2012

Urbana, Illinois

Doctoral Committee:

Professor Paul Garber, Chair
Associate Professor Ripan Malhi
Associate Professor Rebecca Stumpf
Associate Professor Larissa Swedell, Queens College

ABSTRACT

This study aimed to explore the benefits that individuals gain from group living and the role of kin and nonkin affiliation and cooperation in the formation of social networks in primates by investigating the multi-level social structures exhibited by Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). The multi-level social network of snub-nosed monkeys composed of over 100 individuals, in which individuals form one-male breeding units (OMUs, which include one adult male, several adult females, and their offspring), all male units (AMUs), and bands (several OMUs that travel, feed and rest together). Given the fact that the majority of Asian colobines exhibit a harem social organization, multi-level societies of *R. roxellana* are proposed to have evolved through the aggregation of individual one-male groups. The specific objectives of this study are to explore 1) the social factors that help to maintain the stability of multilevel societies, 2) the benefits to individuals of forming a higher level social structure, 3) the presence and complexity of kinship networks and dispersal patterns in *R. roxellana* based on genetic data, and 4) the behavioral mechanisms regulating social interactions within multi-level social networks, and whether these are most consistent with kin selection theory, reciprocity theories, or biological market theory.

Behavioral observations for this study were conducted at Zhouzhi National Natural Reserve, Shaanxi, China. A habituated band of snub-nosed monkeys was followed from September 2007 to August 2008. Along with behavioral observations, fecal samples were collected from the focal band and two neighboring bands. DNA was extracted from the fecal samples. The d-loop region of the mitochondrial DNA was amplified and sequenced for each sample.

The behavioral data indicate that OMUs were socially and sexual independent since the

majority of social and sexual interactions were restricted to members of the same OMU. Both direct affiliative and agonistic interactions between members of different OMUs were infrequent. Compared to the harems formed by other Asian colobines, the OMUs of *R. roxellana* were more cohesive. Leader males played a critical role in maintaining the cohesion of his OMU by actively threatening or chasing both adult and juvenile members of other OMUs that were within 5 meters of his harem. It is likely that the formation of multi-level societies in *R. roxellana* is the result of social and spatial tolerance among harem males in response to the foraging requirements associated with the exploitation of highly seasonal and low productive habitat.

Three distinct haplotypes were found among 99 samples collected from the three neighboring bands. Based on the assumption that individuals with less frequent haplotypes represent immigrants from other bands, it was estimated that approximately 17-21% of females and 8-15% of males immigrated from neighboring bands. The genetic data also indicated that females transfer between OMUs within the same band since females with the same haplotype were present in different OMUs. In other words, OMUs appear to be not grouped by maternal lineages. Behavioral data suggested that female choice played a critical role in dispersal decision because females were voluntarily leave their natal OMUs.

Within OMUs, both kin and non-kin dyads formed long-term grooming partners. Therefore, kin selection is not sufficient to explain the formation of social bonds in snub-nosed monkeys. In contrast to the prediction of biological market theory, dyads did not evenly exchange grooming within short-time frames such as within bouts or during the same day. There is no evidence that females or males exchanged grooming for sex. However, dyads balanced grooming exchanged over lone-time period. In conclusion, long-term reciprocity appears to offer the strongest explanation for the social interactions of snub-nosed monkeys.

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my advisor Dr. Paul Garber. He has always been extremely supportive throughout my graduate training. I am honored to be his student. I am also very grateful to my other committee members Drs. Tony Goldberg, Ripan Malhi, Rebecca Stumpf, and Larissa Swedell. They read numerous drafts of my proposal and dissertation and provided me valuable comments. Dr. Jonathan Beever kindly taught me genetic analysis skills in his lab.

I want to thank Professor Baoguo Li for allowing me to do my dissertation project at his filed site. I would also like to thank all my field guides. Without their help this research could not be done. Mr. Qiangguo Li deserves special mention for being the head of field guides. I relied heavily on him for tracking the monkeys and collecting fecal samples. His extensive experience with the monkeys made my work so much easier and more fruitful.

Finally, I want to thank my parents and my husband, Xiangyu Tang, for their unconditional support.

This research was supported by a doctoral dissertation improvement grant from National Science Foundation, Lewis and Clark Fund for Exploration and Field Research, American Society of Primatologists General Small Grant, a dissertation travel grant from the Graduate college of University of Illinois, Freeman Fund from Center for East Asian and Pacific Study at University of Illinois, Cognitive Science/Artificial Cognition Award, Beckman Institute at University of illinois, and two summer reaearch grant from the department of Anthropology at University of Illinois. IDEA WILD provided the equipments needed for field work.

TABLE OF CONTENTS

LIST OF TABLES ..... **vi**

LIST OF FIGURES ..... **vii**

CHAPTER 1: INTRODUCTION AND SUMMARY OF CHAPTERS **1**

CHAPTER 2: MULTI-LEVEL SOCIETIES IN PRIMATES **24**

CHAPTER 3: SOCIAL INTERACTIONS AMONG MALE AND FEMALE *R. ROXELLANA* **51**

CHAPTER 4: DISPERSAL PATTERNS OF *R. ROXELLANA* AS INDICATED BY OBSERVATIONAL AND GENETIC DATA **88**

CHAPTER 5: TESTING THEORIES EXPLAINING THE GROOMING RECIPROCATION IN *R. ROXELLANA* **114**

CHAPTER 6: CONCLUSIONS AND FUTURE DIRECTIONS **146**

REFERENCES **153**

APPENDIX A: Affiliative interactions between members of different OMUs **183**

APPENDIX B: Sequences of three mtDNA haplotypes **184**

APPENDIX C: Satellite image of the home ranges of the three bands **185**

APPENDIX D: Case numbers and corresponding dyads **186**

LIST OF TABLES

Table 2.1 Group composition of baboon species and annual rainfall at different sites 46

Table 2.2 Group composition of Asian colobines, home range, and annual temperature at different sites..... 48

Table 3.1 Social time of Asian colobines..... 74

Table 3.2 Distribution of allogrooming among group members in Asian colobines..... 75

Table 3.3 Sexual behaviors in Asian colobines..... 76

Table 3.4 Inter-group encounters of Asian colobines 77

Table 3.5 Age and sex composition of the habituated band at Zhouzhi Natural Reserve, Shaanxi, China. May 2008..... 78

Table 3.6 Observation period for each focal OMU..... 80

Table 3.7 Sexual behaviors observed during the observation period..... 81

Table 3.8 Allogrooming between leader males and adult females of the same OMU..... 82

Table 3.9a Allogrooming occurred between adult members within each focal OMU..... 83

Table 3.9b Percentage of grooming provided by females to each possible partner within OMUs 84

Table 3.10 Agonistic interactions between members of different OMUs..... 85

Table 4.1 Primer sequences and annealing temperatures for the d-loop region of mtDNA 111

Table 4.2 Sequences, annealing temperatures, and length of amplicons of nested primers for SRY and amelogenin genes.....111

Table 4.3 The distribution of mtDNA haplotypes among *band 19, 20,* and *21* and detailed distribution pattern within Band 20..... 112

Table 4.4 Female transfer events between OMUs 113

Table 5.1 The impact of kinship on grooming distribution..... 136

Table 5.2 Allogrooming between leader males and adult females and reproduction record 144

Table 5.3 Grooming exchanged during the days when females and the lead male had intercourses 145

LIST OF FIGURES

Figure 2.1 Habitat, sexual dimorphism and harem size of snub-nosed monkeys and other Asian colobines 43

Figure 4.1 Bands distributed in Qinling Mountains (adapted from Li et al. 2003) 110

Figure 5.1a Length distribution of both reciprocal and unilateral grooming bouts 134

Figure 5.1b Length distribution of unilateral grooming bouts 134

Figure 5.1c Length distribution of reciprocall grooming bouts 134

Figure 5.2 The time of allogrooming occurred between each dyad 135

Figure 5.3 Within bout grooming reciprocation 137

Figure 5.4 Grooming reciprocation within bouts and a day 138

Figure 5.5 Grooming reciprocity over the entire observation period 139

Figure 5.6a Grooming frequency of each dyad 140

Figure 5.6b The impact of partner preference on within-bout reciprocation 140

Figure 5.7a The impact of kinship on within-bout reciprocation in JB OMU 141

Figure 5.7b The impact of kinship on within-bout reciprocation in LP OMU 142

Figure 5.8 The impact of sex on within-bout reciprocation 143

CHAPTER 1: INTRODUCTION AND SUMMARY OF CHAPTERS

1.1 Introduction

This study aimed to explore the benefits that individuals gain from group living and the role of kin and non-kin affiliation and cooperation in the formation of social networks in primates by studying the social interactions in the Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*). Snub-nosed monkeys are reported to form a multi-level social network composed of over 100 individuals, in which individuals form one-male breeding units (OMUs, which include one adult male, several adult females, and their offspring), all male units (AMUs), and bands (several OMUs that travel, feed and rest together) (Ren et al. 2000, Zhang et al. 2006). Multi-level societies refer to large social networks within which group members interact at different spatial, temporal, and social levels to form independent and cohesive subunits. This type of social system is rare in primates, but is reported in geladas (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*), and snub-nosed monkeys (*Rhinopithecus bieti*, Kirkpatrick 1998, Grueter 2009; *R. roxellana*, Ren et al. 2000, Zhang et al. 2006; *R. brelichi*, Bleisch et al. 1993, Bleisch and Xie 1998; *R. avunculus*, Boonratana and Le 1998). Little is known, however, concerning the set of social and ecological factors that promote and maintain stability and tolerance among members of a multi-level social system, the degree to which individuals residing in the same subunit and band are related, and the benefits to individuals of forming multilevel societies. The objectives of this study are to investigate the social interaction pattern of snub-nosed monkeys, examine evidence of kinship networks and dispersal patterns, and identify behavioral mechanisms that serve to regulate social interactions within a multi-level social network. In the first chapter, I review the current theories designed to explain the benefits

to individuals of residing in a stable, affiliative, and cohesive social unit and then briefly introduce the hypotheses examined in subsequent chapters.

1.2 Kin Selection

Kinship has been widely accepted as a major factor shaping primate affiliative and cooperative behavior (Chapais 2001, Chapais and Belisle 2004, Silk 2002, 2006). Kin selection theory helps to explain the presence of affiliative and cooperative behaviors under conditions in which initiators and recipients are closely related, and the initiator benefits through increased inclusive fitness (Hamilton 1964). Inclusive fitness includes two parts: direct benefits derived through ones own reproductive success and indirect benefits derived through the reproductive success of close relatives, because close relatives (full siblings, half siblings, and cousins) share 12.5-50% of their genome in common (Hamilton 1964). Kin selection theory proposes that if the indirect benefits gained by initiators are greater than the cost to their direct fitness, kin biased affiliative and cooperative behaviors are favored (Hamilton 1964).

1.2.1 Evidence of Kin Selection

Kin biased affiliative behaviors such as coalition support, co-feeding, allogrooming, spatial proximity, and nearest neighbor preferences have been reported in several cercopithecine primates (Gouzoules 1984, Gouzoules and Gouzoules 1987, Walters 1987, Silk 2001, Chapais 2006), such as Japanese macaques (*Macaca fuscata*) (e.g. Mori 1975, Kurland 1977, Belisle and Chapais 2001, Chapais et al. 2001), rhesus macaques (*M. mulatta*) (e.g. Missikian 1972, Sade 1965, 1972, Kapsalis and Berman 1996, Widdig et al. 2001, 2002), vervet monkey (*Cercopithecus aethiops sabaeus*) (Hunte and Horrocks 1986); baboons (*Papio spp.*) (e.g. Smith et al. 2003, Silk et al. 2004, Silk et al 2006ab, Silk et al. 2010a), New World monkeys such as

white-faced capuchins (*C. capucinus*) (Manson et al 1999, Perry 2008), red howler monkeys (*Alouatta seniculus*, Pope 1990, Pope 2000), marmosets and tamarins(*Saguinus Oedipus and Callithrix jacchus*, Harrison and Tardif 1988) and great apes (*gorilla gorilla*, Watts 1994, Harcourt and Stewart 1987,1989). For example, Silk et al (2006a) investigated partner preferences in 118 female baboons (*P. cynocephalus*) living in 2-4 habituated groups from 1984 to 1999 in the Amboseli Basin, Kenya. These females comprised 1,430 possible dyads. They measured the degree of preference by the frequency of grooming and proximity between two individuals. Their results indicated that baboon females prefer close relatives such as mothers, daughters, maternal sisters, and paternal sisters as partners. However, if close relatives were unavailable within the group, they chose individuals of the same age cohort or similar rank as substitutes. In another study, Silk et al. (2006b) compared the stability of social bonds formed by different types of dyads. They found that 90% of mother-daughter dyads (N=63 dyads), 70% of maternal sister dyads (N=63 dyads), and 35% of unrelated dyads (N=1,052 dyads) lasted for more than 1 year. Fourteen dyads formed by close kin remained stable for more than 5 years. The authors also found that 13 dyads formed by non-kin lasted more than 3 years. However, these dyads counted for less than 1% of the total unrelated dyads, and therefore the majority of unrelated dyads were less stable than related dyads.

Associations with kin can have a direct impact on long-term fitness benefits, such as increased longevity, reproductive success, and infant survival rates (Pope 1990, 2000, Silk et al. 2009, Silk et al 2010b). For example, Pope (1990) reported that in red howler monkeys, multi-male groupsformed by related males had longer tenure (8.2 yrs, N=14) than those formed by unrelated males (2.3 yrs, N=18). The results suggested that males can increase their reproductive success by forming groups with close same-sex relatives. Pope (2000) found that

red howler monkey females who left their natal group and established a new group with un-related females had a significantly lower rate of infant survival than those females who remained in their natal group and formed coalitions with their maternal relatives (45% vs 16%). Taken together, these data support the contention that in some primate species kinship is a primary factor promoting social bonds.

In contrast, studies of other cercopithecines such as tonkean macaques (*M. tonkeana*, Demaria and Thierry 2001), stump-tailed macaques (*M. arctoides*, Butovskaya, 1993), blue monkeys (*C. mitis stuhlmanni*, Rowell et al 1991), as well as New World monkeys including wedge-capped capuchins (*Cebus olivaceus*, O'Brien 1993, O'Brien and Robinson 1993), common marmosets (*Callithrix jacchus*, Nievergelt et al 2000, Faulkes 2003, Huck et al 2005), and golden lion tamarins (*Leontopithecus rosalia*, Dietz 2004) failed to identify a positive relationship between affiliative and cooperative behavior and relatedness in females. In addition, recent studies using molecular genetic markers to estimate relatedness among chimpanzees (*Pan troglodytes*) and banobos (*Pan paniscus*) also have failed to find strong evidence for kin biased behaviors (e.g. chimpanzees: Goldberg and Wrangham 1997, Mitani, et al., 2000, Mitani et al, 2002, Langergraber et al. 2007, 2009; bonobos: Hashimoto et al., 1996; Parish 1996). For example, Mitani et al. (2002) investigated relatedness and affiliative behaviors among male chimpanzees living in the Ngogo community, Uganda. They examined six different types of behaviors including: association, proximity, coalition formation, meat sharing, grooming, and patrolling behavior. Their results indicate that affiliative interactions occurred more frequently among non-relatives of similar age and rank than among maternal relatives. The relatedness estimates used in this study were based on mtDNA, which can only specify maternal kinship. It is possible that individuals of the same age were paternal siblings. In a following study,

Langergraber et al. (2007) investigated the same six behaviors, but estimated relatedness through sequencing mtDNA and genotyping 13 X-linked, 13 Y-linked, and 44 autosomal microsatellite loci, in order to account for both maternal and paternal relatedness. Their results indicate that although male chimpanzees showed a preference to affiliate with maternal brothers, the majority of dyads (on average greater than 85%) who affiliated and cooperated at a higher degree than expected by chance were formed by unrelated or distantly related individuals ($r<0.125$). Using similar methods, Boesch et al (2006) found that at Tai forest, Ivory Coast, male chimpanzees with closest rank tend to cooperatively hunt, and that kinship and age similarity have no effect on hunting partners. In the case of bonobos (*Pan paniscus*), based on mitochondrial haplotypes, females did not preferentially immigrate into communities containing maternal relatives (Hashimoto et al. 1996; Parish 1996). Even in those cases in which female bonobos immigrated into groups with maternal relatives, they did not maintain proximity or groom kin at a higher frequency than nonkin (Hashimoto et al., 1996). Thus, affiliation with non-relatives is prevalent in many primates.

1.2.2 Kin recognition

A basic assumption of kin selection theory is that primates have the ability to recognize their relatives. Preferences towards paternal siblings over non-relatives were used as a comparative measure to demonstrate kin recognition in primates (Erhart et al 1997, Widdig et al. 2001, Smith et al. 2003, Chapais and Berman 2004, Perry et al 2008). However, Chapais and Berman (2004) also pointed out that for studies showing a significantly greater preference towards paternal siblings than non-relatives, the preferences were not at the same level as the preference towards maternal siblings. For example, in a study of rhesus macaques (Widdig et al. 2001), preferences towards paternal siblings were significantly lower than for maternal siblings

(affiliation index: 10.77 vs. 1.745). The discrepancy between the degree of preference is contradictory to that expected by kin selection theory. Given equal relatedness, paternal and maternal siblings should be preferred to the same degree (Chapais and Berman 2004). Chapais and Berman (2004) pointed out that some of the preferences toward paternal siblings over non-relatives may be explained by age similarity. This is supported by a study by Smith et al. (2003). Smith et al. (2003) initially reported that female baboons (*P. cynocephalus*) biased a greater proportion of affiliative behaviors such as grooming, greeting, embracing, approaching, and lipsmacking towards both paternal and maternal half sisters than towards non-kin. However, the preference toward paternal sisters was not significant after controlling for age similarity (Smith et al. 2003).

In addition, a series of experimental studies indicated that pigtailed macaques failed to identify kin (MacKenzie et al .1985, Sackett and Frederickson 1987, Welker et al 1987, Martin 1997). For instance, Sackett and Frederickson (1987) separated infant pigtailed macaques (N=201) from their mother when they were 5-6 months of age, and then raised infants of similar age together. After the infants reached one year of age, Sackett and Frederickson (1987) compared their reactions to familiar relatives, non-familiar relatives, familiar non-relatives, and non-familiar non-relatives. Contrary to the predictions of kin selection theory, they found that the macaques reacted identically to both unrelated-unfamiliar individuals and related-unfamiliar individuals (measured by the amount of time spending in front of the cage of stimulus individuals). However, in the presence of related-unfamiliar individuals and unrelated-familiar individuals, the macaques significantly preferred familiar individuals. Overall, familiar individuals were preferred over unfamiliar individuals regardless of relatedness. They argued that kinship alone could not generate preference. Consequently, researchers argued that

familiarity, not genetic relatedness played a more important role in shaping social behaviors in these primates (Sackett and Frederickson 1987, Martin 1997, Widdig et al.2001). Relatedly, in rhesus macaques, paternal siblings of the same age, who are assumed to be more familiar with each other, associated more frequently than those of different ages (affiliation index: 1.745 vs.0.063) (Widdig 2001), suggesting that age similarity or cohort was a stronger factor than kinship in shaping the social behaviors in rhesus macaques.

In sum, difficulties in separating the effects of familiarity, age, cohort, and rank in influencing social interactions have led some researchers to call into question the direct importance of kin-selection in understanding primate social behavior (Silk 2002, Chapais 2006, Langergraber et al. 2007). In those cases in which kinship is not the primary factor in social interactions, studies have examined reciprocity theories, mutualisms, partner competence, and biological market theories, which emphasize the importance of direct benefits that individuals receive through affiliative interactions.

1.3 Theories of Reciprocity

Theories of reciprocity have been proposed to explain affiliative interactions among both kin and non-kin (Triver 1971, 2006, de Waal 2000, de Waal and Brosnan 2006). Reciprocity assumes that under certain conditions individuals gain direct benefits through affiliative and cooperative behavior with conspecifics. Clutton-Brock (2002) argued that kin selection theory may "overestimate" the cost of cooperation and "underestimate" the direct benefits that individuals gain through affiliative and cooperative interactions. If cooperation is cost-free and provides benefits to participants, or if the cost is relatively low and the direct benefits are high, the advantages of cooperative or collective action can result in increased sociality and group

cohesion (Clutton-Brock 2002).

Reciprocity or exchange of the same behaviors such as grooming, coalition support, or food sharing between unrelated individuals has been reported in some primate species (*M. fuscata* Muroyama 1991, Schino et al. 2003; *M. radiate* Silk 1992; *C. mitis stuhlmanni* Rowell et al 1991; *C. apella*, de Waal 2000; *C. apella*, Schino et al 2009; *Saguinus oedipus*, Hauser et al. 2003; *P. hamadryas*, Leinfelder et al. 2001; *M. sphinx*, Schino and Pellegrini 2009; *G. gorilla*, Watts 1997; *P. troglodytes*, Gomes et al. 2009). However, the reciprocal exchange of different social benefits, such as exchanging grooming for coalitionary support remains controversy. Studies conducted on non-ape primates yield inconsistent results (non-support: Silk 1992, Rapaport 2001, Matheson and Bernstein 2000, Leinfelder et al. 2001, Daniel et al. 2004, Ventura et al. 2006; support: Muroyama 1994, Schino 2007, Schino et al. 2007). For example, Ventura et al. (2006) investigated the interchange of grooming for reduced aggression, cofeeding, and agonistic support in wild adult female Japanese macaques (N=20). They developed a matrix for each agonistic and affiliative behavior and ran matrix correlation tests to determine whether one type of behavior was correlated with another. They found a positive relationship between grooming and tolerance at the food patch, and a positive relationship between grooming and agonistic support. However, the relationship between grooming and agonistic support became nonsignificant after controlling for kinship. This suggests that Japanese macaques might exchange grooming for tolerance but not for agonistic support. However, a similar study conducted in a captive group of Japanese macaques found a significant positive relationship between grooming and coalition support in adult females even after controlling for kinship, rank, and time spent in proximity (Schino et al. 2007). This study indicated that Japanese macaques exchanged grooming for coalitionary support.

The majority of evidence supporting an exchange of different social behaviors in primates is based on studies of chimpanzees (Hemelrijk and Ek 1991, de Waal 1997, Mitani and Watts 2001, Watts 2002, Koyama et al. 2006, Mitani 2006, de Waal and Brosnan 2006, Gomes and Boesch 2009, 2011). For example, Gomes and Boesch (2009) examined whether male and female chimpanzees trade meat for sex. They recorded the frequency of copulations and meat sharing between 5 adult males and 14 adult females from 2003 to 2006. They also considered other factors that may influence copulatory behaviors such as female and male rank, female age, female begging behavior, and female reproductive condition. They used generalized linear mixed model to identify factors that predict the number of copulations between each female-male dyad. Their results indicated that only the relationship between meat sharing and copulations was significant. In other words, female chimpanzees were more likely to copulate with males who shared meat with them. Compared to many other primates, chimpanzees exhibit a broader range of cooperative behaviors such as food sharing, hunting, patrolling, and coalition support (Gomes and Boesch 2011). This may be a reason why the interchange of social behaviors is more prevalent in chimpanzees.

Models of reciprocity require that the direct benefits gained by each partner through cooperative and affiliative interactions are fairly equal overtime (Trivers 2006). This is supported by many studies (e.g. Schino et al. 2007, Frank and Silk 2009, Schino and Pellegrini 2009, Tiddi et al. 2010, Gomes et al. 2009, Schino et al. 2009). For example, Frank and Silk (2009) compared the degree of grooming reciprocity in female baboons within two different time frames, within grooming bouts and over the entire observational period. They recorded grooming interactions among 16 adult female baboons living in a wild group of 60 individuals over 15 months. They analyzed their grooming data using linear regression models, which generate a

slope of 1 if reciprocity is perfectly balanced. When considering grooming exchanged between dyads within bouts, the slope generated by the linear regression model was 0.32. However, the slope was 0.86 for overall grooming exchanged over a 15 month period. The differences between the two slopes suggested that grooming in female baboons was more symmetrically exchanged within dyads over the long-tem than over the short-term.

Since most studies support long-term reciprocity in primates, several cognitive mechanisms have been proposed to explain how long-term reciprocity is maintained between two partners. The first "calculated reciprocity" requires that individuals have the cognitive ability to keep precise score of the benefits exchanged during previous interactions (de Waal and Luttrell 1988, Brosnan and de Waal 2002, de Waal and Bosnan 2006). Some researchers questioned that most primates, except possibly apes and humans, do not have the ability to finely calculate this type of information or separate it from other behavioral interactions that partners engage in (Stevens and Hauser 2005). Conversely, the second mechanism, "attitudinal reciprocity", does not require individuals to remember the precise interaction history between partners (de Waal 1997, 2000; Brosnan and de Waal, 2002; Hauser et al. 2003). The main argument of attitudinal reciprocity is that previous interactions influence the subject's attitude towards the partner in their next interaction. If the partner provided support or cooperated last time, the subject would be more willing to be supportive or cooperative this time. If not, the subject is more likely to refuse to cooperate with his partner. In this way, long-term detailed memory is not required.

1.4 Biological market theory

Biological market theory assumes that partner choices are based on the direct benefits

partners receive, regardless of relatedness (Noë and Hammerstein 1995, Noë 2001, Barrett and Henzi 2006). Different from reciprocity theories, biological market theory proposes that partners calculate the immediate costs and benefits of particular social interactions, and trade social benefits based on the current market value of the services to each partner (e.g. grooming for grooming or grooming for food). The value of each interaction varies based on local conditions, such as the motivation, experiences, and needs of each partner (Henzi and Barrett 1999, Barrett and Henzi 2006). In a biological market, if affiliative interactions with non-kin are more beneficial and impart a lower cost than with kin, non-kin bonds will be favored (Colmenares et al. 2002).

The major difference between biological market and reciprocity theories is that using the biological market model, social interaction patterns are dynamic and individuals are able to adjust their partner choice and effort according to the current social and ecological circumstances. Thus, reciprocity involves persistent interactions with a consistent set of patterns whereas biological markets involve an assessment of changing costs and benefits of goods, services, and affiliative interactions with any group member (Noë 2001).

Studies designed to test biological market theories have focused on time-matching within grooming bouts and how other factors such as rank, food competition, sexual behavior, and infant handling impact the degree of grooming reciprocity within bouts (*Papio anubis*, Frank and Silk 2009; *P. cynocephalus ursinus*, Barrett et al. 1999, Barrett et al. 2002, Henzi and Barrett 2002; *P. hamadryas hamadryas*, Leinfelder et al. 2001; *C. capucinus* and *M. radiate*, Manson et al. 2004; *M. fascicularis*, Gumert 2007a,b; *Lophocebus albigena*, Chancellor and Isbell 2008; *Ateles geoffroyi yucatanesis*, Slater et al. 2007; *Eulemur fulvus rufus*, Port et al. 2009, *Chlorocebus pygerythrus*, Fruteau et al. 2009, 2011; *Cebus apella nigritus*, Tiddi et al 2010).

These studies assume that without other influences, grooming should only be traded for grooming, and evenly exchanged between two partners within each grooming bout. However, under conditions in which grooming is used as a currency to exchange for other benefits, such as food, sex, rank increasing, and infants handing, grooming duration will be skewed in favor of the more valuable partners (e.g. individuals with higher rank and mothers with infants).

For example, Barrett et al (2002) studied how changes in the cost of feeding competition impact grooming reciprocity in a group of chacma baboons. Due to a flood, the study group had abandoned their original home range, a dry lake bed, and moved to a sand dune area. When feeding in the dry lake bed, the baboons foraged for subterranean food items such as sedge roots and corms. In order to access these types of food, they dig large holes. Competition over access to exiting holes is intense (2.19±0.21 agonistic events/female per hour) and result in a linear hierarchical relationships among adult females. While in the sand dunes area, baboons fed more on Mediterranean scrub, which is characterized by widely dispersed food items that cannot be monopolized by a single individual. As a result, feeding competition decreased (0.77±0.01 agonistic events/female per hour). Differences in agonistic interactions over food at these two sites provided Barrett and her colleagues an opportunity to investigate whether the baboons adjusted their grooming behaviors according to different social environments. They predicted that when foraging at the sand dune area, grooming was less favored towards high ranking females as the food resources they can control were reduced. The authors used linear regression models to analyze grooming exchanged during each grooming bout and obtained a time-matching regression equation for each habitat. Although they did not provide the exact slope of each equation, the regression figure indicated that the slope was steeper when foraging at the sand dunes area compared to the slope when foraging at dry lake bed. In other word, under

conditions in which higher ranking females control access to feeding holes, they received more grooming than they gave within each grooming bout. However, when rank relationships became less critical in access to resources, grooming was more evenly distributed between partners. These changes suggested that the values of individuals vary under different social environments, and female chacma baboons had the ability to adjust their behaviors accordingly.

In a related study, Henzi and Barrett (2002) examined grooming bouts directly associated with infant handling in chacma baboons. They found that 77% of grooming bouts (N=30) immediately prior to infant handling were unidirectional, and potential handlers groomed mothers. They then analyzed the amount of grooming handlers provided to the mothers. They divided mother-handler dyads into two categories: mothers outranked handlers and handlers outranked mothers, because rank distance could affect the amount of grooming exchanged between dyads. Their results indicated that if there was only one infant within the group, lower ranked handlers provided 500 seconds of grooming to higher ranked mothers in order to handle their infants, and higher ranked handlers provided 150 seconds of grooming to lower ranked mothers. However, for both categories, the amount of grooming that handlers provided to mothers reduced to 200 and 20 seconds respectively, when there were three infants within the group. These results are consistent with the predictions of biological market theory: as the supply increases the price for each item was reduced.

Similarly, Slater et al. (2007) reported that female spider monkeys trade embraces for infant handling. They did not include grooming in their analysis, because female spider monkeys spent very little time grooming (less than 0.2% of observation time). They compared the embraces that 15 females received immediately before their infants were handled by other females with those received at other times. Their results indicated that all embraces followed by

infant handling were initiated by handlers and females received more embraces when they were mothers than at other times (1.1 vs. 0.2 per hour). As predicted by biological market theory, Slater et al. (2007) found that the embraces that each mother received decreased with an increase of infants residing in the group. Ninety percent of embraces received by mothers were followed by infant handling when there were four infants within the group. Whereas only 10% of embraces received by mothers were followed by infant handling when there was one infant within the group.

However, Tiddi et al (2010) failed to find the market effects in tufted capuchin monkeys. They compared grooming received before and after giving birth by 10 mothers living in 3 groups. Although the mothers received more grooming after giving birth, the amount of grooming received by the mother did not decrease significantly when the number of infants within group increased. Similarly, studies examining the effect of rank distance on grooming reciprocation within bouts in other primates yield inconsistent results. A positive relationship between rank distance and grooming discrepancy within bouts has been found by some studies (Leinfelder et al. 2001, Barrett et al. 2002, Manson et al. 2004, Fruteau 2011), but not in others (Schino et al. 2003, Chancellor and Isbell 2008, Frank and Silk 2009). In grey-cheeked mangabeys, the effect of rank distance on within bout reciprocity varied across different groups (Chancellor and Isbell 2008). Taken together, the role of market forces in shaping social interactions in primates is still an open question. Tiddi et al (2010) pointed out that we need to be cautious when using the market theory to explain social interactions in primates because the biological market theory assumes that primates possess the cognitive ability to understand how a market is operating. In other words, individuals are required to have the cognitive abilities to assess the values of other group members, track the changes of other group members' values, and be aware of the supply/demand

ratio. However, this assumption has not been verified by empirical studies in nonhuman primates.

1.5 Theory of Partner Competency

The theory of partner competency proposed by Chapais (2006) is quite similar to the biological market theory since both theories considered partner pools as a market. However, partner competency theory takes kinship into consideration in choosing partners. Chapais (2006) divided cooperative behaviors into two categories: low-competence cooperation which includes huddling, co-sleeping, allogrooming, and allomothering; and competence-dependent cooperation which include grooming for tolerance and support, coalition support, group hunting, and meat-sharing. Chapais (2006) argued that all individuals are equally qualified as a partner for low-competence cooperation. Under these situations, relatives are often preferred because partners can gain both direct and indirect benefits. In contrast, for competence-dependent cooperation, individuals have different values as a partner. Individuals with higher rank or higher levels of predictability are of higher competence and therefore preferred regardless of relatedness, because the direct benefits received outweigh the indirect benefits obtained through cooperating with kin (Chapais 2006). Nevertheless, Chapais (2006) acknowledged that competence is a continuous variable. His dichotomous classification is a simplified model of social interactions.

1.6 By-product mutualism and collective action

By-product mutualism argues that individuals perform certain types of behavior, such as predator vigilance and searching for food regardless of living alone or in a group, and group members gain benefits as a by-product of such actions (Dugatkin 1997). By-product mutualism

may represent the simplest type and most common form of cooperation because neither kinship nor "scorekeeping" mechanisms are needed for its development (Dugatkin 1997, Sussman and Garber 2011).

According to by-product mutualism, there exist many benefits of living in a group, including reduced vigilance towards predator. Reduced vigilance has been reported in birds and ungulates (Elgar 1987, Caro 2005). In primates, most evidence in support of a group-size effect on vigilance come from studies of mixed species groups (*Cercopithecus mitis* & *C. ascanius*, Cords 1990, *Saguinus labiatus* & *S. fuscicollis*, Hardie and Buchanan-Smith 1997; *S. mystax* and *S. fuscicollis*, Stojan-Dolar and Heymann 2010). These studies found that individuals spent less time vigilant when in mixed species than in single species groups. However, many studies of single species groups failed to find a negative relationship between vigilance and group size (e.g. *A. pigra*, Treves et al. 2001; *C. ascanius*, Treves 1997, 1998; *C. capucinus*, Rose and Fedigan 1995; *Procolobus badius*, Treves 1998; *Cebus apella*, Hirsch 2002; P*an troglodytes*, Kutsukake 2007). For example, Treves et al (2001) investigated vigilance behavior in 6 groups of black howlers (group size range from 2 to 10 individuals). Heads up with eyes open was considered vigilant behavior. According to their results, vigilance did not relax as group sizes increased. However, individuals with one or two neighbors were less vigilant than isolated individual (52% scan vs. 40%) although the difference between one and two neighbors were not significant. Conversely, Hirsch (2002) found that brown capuchin monkeys spent more time vigilant when they were surrounded by neighbors than when alone (25% time spent vigilant when having 17 neighbors within 10m of a focal animal vs. 8% time when alone). Similar results have also been reported in chimpanzees (Kutsukake 2007). Kutsukake (2007) found that male chimpanzees spent more time vigilant (80 seconds/2min) when there were 4 individuals within 3 meters than

when they were alone (70 seconds/2min). The results of these two studies suggest that in contrast to the prediction of group-size effect, individuals increased their vigilance levels when they had neighbors compared to when they were alone. The increased vigilance was explained by increased social monitoring towards conspecific neighbors rather than vigilance toward predators. In other words, the increased vigilance or attentiveness was a response to the presence of nearby social partners. Given that factors such as social monitoring (Kutsukake 2007, Hirsch 2002, Caine and Marra 1988, Jack 2001), mate defense (Treves 1999a), and infant protection (Treves 1999b; Steenbeek 1999; Kutsukake 2007) also influence vigilance behaviors, it is difficult to detect the effect of group-size and nearest neighbor proximity on vigilance and social attentiveness in primates.

Nunn (2000) applied the concept of **collective action** to the study of cooperation and affiliation in primates. Similar to by-product mutualism, collective action theory argues that under many circumstances individuals may benefit from the joint or coordinated actions of others. However, collective action can result in a free-rider problem. Nunn (2000) used territorial defense as an example to explain the concept of collective action. For group living species, if one individual can successfully defend a territory, other individuals also gain benefits from accessing resources within the territory, even if they do not participate in territorial defense. These individuals are called free-riders. Nunn (2000)'s main argument is that cooperation is expected to continue as long as the benefits to the cooperating individual(s) exceed the benefits obtained by free-riders. Studies attempting to detect free riders have found considerable variation among individuals in participation in territorial defense (Nunn and Deaner 2004, Cords 2007, Kitchen and Beehneer 2007). However, these variations did not likely result from free-riders, because they could be explained by the asymmetrical benefits of group living gained by different

individuals and the asymmetrical costs to different individuals by joining in territorial defense (Steenbeek 1999, Kitchen et al. 2004, Majolo et al. 2005, Cords 2007, Kitchen and Beehneer 2007). For example, higher-ranking individuals have more access to food than lower-ranking individuals, thus, they are more aggressive during inter-group encounter (Nunn and Lewis 2001, Majolo et al. 2005). Nunn and Deaner (2004) found that in ring tailed lemurs (*Lemur catta*), females with young offspring tended to be further away from intergroup aggression compared to females without young offspring. Thus, similar to by-product mutualism, the impact of other factors such as rank, age, sex, relatedness, and with/without infants on participation in territorial defense make it difficult to distinguish the costs and benefits to both free-riders and cooperators (Kitchen and Beehneer 2007).

Finally, deception represents a form of competitive behavior in which one individual intentionally misleads another in order to obtain social and ecological benefits. Deception has been anecdotally reported in anthropoid primates, however the greatest number of possible instances has been reported in apes (Byrne and Whiten 1990, 1992; Byrne and Corp 2004). Deception is extremely difficult to measure in the field due to the fact that the specific intension of individuals is not easy to identify, and therefore recording deception in snub-nosed monkeys was not an objective of this study.

To sum, theories of kin selection, mutualism, reciprocity, biological markets, and partner competency have been proposed to explain the social interactions in group living species. Biological market theory is a particular model of reciprocity, in which the values of certain social services vary according to local circumstances (Noë 2001). Partner competency theory combines aspects of biological market theory and kin selection. Detailed data on relatedness, and the frequency, context, and cost and benefits of social interactions can be used to identify whether a

behavioral pattern is consistent with one or more of these theories. One of the main objectives of this research is to explore the role of kinship, reciprocity, and biological markets in regulating the multi-level societies of Sichuan snub-nosed monkeys.

1.7 Outlines of Chapters

Chapter 2. Multi-level societies in primates

Although the multi-level social structures in different primate species are superficially similar, the composition, dispersal pattern, and social interaction patterns within OMUs and bands differ across species. The aim of chapter II is to review the structure of multilevel societies formed by hamadryas baboons, gelada baboons, and snub-nosed monkeys. This chapter also discusses hypotheses proposed to explain the evolution of multilevel societies in primates. Multilevel societies are assumed to have evolved independently in different primate lineages, and different hypotheses have been proposed to explain the evolution of multi-level societies in Asian colobines and baboons.

Chapter 3. Social interactions among male and female *R. roxellana*

Given that the majority of Asian colobines exhibit a harem social organization, multi-level societies of *R. roxellana* are proposed to have evolved through the aggregation of individual one-male groups. The aim of chapter III is to identify the set of social and ecological factors that promote and maintain stability and tolerance among members of a multi-level social system. I accomplish this by comparing behavioral similarities and differences between snub-nosed monkeys and other Asian colobines. In the first part of this chapter, I reviewed the published literature on affiliation, sexual behavior, intrasexual social tolerance, inter-group encounters, and the process by which Asian colobines form new harems. In the second part of this chapter, I present the results of a detailed 8-month observational study investigating social interactions,

sexual interactions, inter-OMU associations, and the process of forming new OMUs in snub-nosed monkeys. Data collection was conducted by following a habituated band living at Zhouzhi National Natural Reserve, China. The primary research questions addressed in this chapter are: 1) What are the social and sexual interaction patterns within OMUs? 2) What are the affiliative and agonistic interaction patterns between members of different OMUs? 3) What is the process of forming new OMUs? 4) Are the social interaction patterns of *R. roxellana* different from other Asian colobines? And, 5) What are the benefits to group members of forming multi-level societies?

Chapter 4. Dispersal patterns of *R. roxellana* as indicated by observational and genetic data

Unlike other Asian colobines in which females are philopatric and males disperse, both female and male snub-nosed monkeys are reported to disperse from their natal OMU. Behavioral observations indicate that juvenile males of snub-nosed monkeys leave their natal OMUs and join an all-male group associated with their natal band. However, adult males were observed to immigrate into new bands and attempt to establish new OMUs. Recent behavioral evidence indicates that females also disperse between OMUs and bands.

Given the fact that dispersal is a process that takes months or years to accomplish, a combination of observational studies and genetic studies are required to provide a more complete picture of the dispersal process. Observational studies provide information on the social and ecological context under which dispersal occurs, such as age of dispersal, timing of dispersal, challenges faced when entering a new group, and the interactions of resident group members before dispersal. Genetic data can be used to calculate dispersal rates and dispersal distances. The main objective of this chapter is to present new information on the distribution patterns of mtDNA haplotypes among the focal band and two neighboring bands of snub-nosed monkeys.

The following questions are addressed: 1) Do females and males preferentially disperse long-distances to join non-neighboring bands? (If so, we expect the mtDNA haplotypes among individuals within the same band to show a high degree of sequence variation.); 2) Do females and males transfer equally among bands? (If so, we expect a relatively equal proportion of males and females residing in different bands to share the same mtDNA haplotypes.); and 3) Do females transfer between OMUs within the same band? (If so, we expect adult females residing in the same OMU to exhibit different haplotypes, whereas females with identical haplotypes are expected to reside in different OMUs.) Combined with behavioral observation, we discuss the potential factors affecting dispersal decisions in snub-nosed monkeys.

Chapter 5. Testing theories explaining the grooming reciprocation in *R. roxellana*

Studies investigating the mechanisms underlying within group affiliative and cooperative behaviors of primates have concentrated on allogrooming, because allogrooming is the most common affiliative behavior in primates and is assumed to be of beneficial value to both the groomer and the recipient. This chapter explores the roles of kin selection, reciprocity, and biological markets in shaping the social interactions of snub-nosed monkeys by investigating the distribution of allogrooming among OMU members, the time frame of grooming reciprocation between dyads, and the effects of other factors such as kinship, partner preference, and sex on the degree of grooming reciprocation within grooming bouts.

The specific hypotheses addressed in this chapter are: according to kin selection theory, (1.1) within the same OMU, allogrooming occurs more frequently between close relatives than between non-kin dyads; (1.2) related females living in different OMUs engage in allogrooming more frequently than unrelated females living in different OMUs; (1.3) grooming bouts between related dyads are not time-matched, because the direct benefits exchanged between relatives are

not expected to be reciprocal. According to reciprocity theory, (2.1) the grooming exchanged between both un-related and related partners is roughly equal over the entire observation period. According to biological market theory, (3.1) among male and female dyads, grooming given and received is not equal, if grooming bout is followed or preceded by sexual interactions.

Chapter 6 summarized the main conclusions of this study and suggested future research directions.

The main conclusions are:

1) Although the *Rhinopithecus* multilevel society is best regarded as a stable socially interdependent unit, OMUs within bands are socially and sexually independent because the majority of sexual and affiliative behaviors are limited to member of the same OMU. Spatial tolerance among leader males is a primary behavioral mechanism underlying the aggregation of independent OMUs.

2) Compared to the single harem group formed by other Asian colobines, the OMUs of snub-nosed monkeys are more cohesive as indicated by three lines of evidence: a) OMU members spent more time grooming each other; b) males actively participated in allogrooming with females; c) females provided help to males during inter-OMU aggression. These last two behaviors are rare in other Asian Colobines.

3) The distribution of mitochondrial haplotypes indicates that both males and female snub-nosed monkeys disperse between bands. The dispersal rates of both sexes are relatively low (♀:17-21%, ♂:8-15%) compared to other primates characterized by bisexual dispersal such as mantled howler monkeys (79-94%), but at a level similar to that of hamadryas baboons (♀: 30%, ♂: <8%).

4) Genetic data also indicate that females disperse between OMUs of the same band. Behavioral data suggest that the majority of female dispersal events (10 out of 11) were triggered by the presence of new solitary males in the band, and females voluntarily leave their leader males and follow new males.

5) The distribution of allogrooming among adult members of snub-nosed monkey was not determined by kinship. In addition, the results of this study show no evidence of individuals exchanged grooming for sex as predicted by biological market theory. Grooming exchanged between non-related dyads was consistent with long-term reciprocity rather than short-term reciprocity.

CHAPTER 2: MULTI-LEVEL SOCIETIES IN PRIMATES

The main objectives of this chapter are to compare the similarities and differences of multilevel societies formed by different primate species, as well as examine hypotheses proposed to explain the evolution of multilevel societies in different primate lineages.

2.1 Multi-level societies in primates

Multi-level societies refer to large social networks within which group members interact at different spatial, temporal, and social levels to form independent, cohesive, and stable subunits. Multi-level societies are reported to be rare in primates and only have been confirmed in hamadryas baboons (*Papio hamadryas*, Kummer 1990, Swedell 2006), gelada baboons (*Theropithecus gelada*; Dunbar and Dunbar 1975, Dunbar 1984), and snub-nosed monkeys (*Rhinopithecus bieti*, Kirkpatrick 1998, Grueter 2009; *R. roxellana*, Ren et al. 2000, Zhang et al. 2006; *R. brelichi*, Bleisch et al. 1993, Bleisch and Xie 1998; *R. avunculus*, Boonratana and Le 1998). Mandrills (*Mandrillus sphinx*) have been reported to live in multi-level societies (Hoshino et al. 1984, Rogers et al. 1996). However, a more recent four-year study indicates that mandrills are better described as living in sexually segregated social units with adult males aggregating with females and juveniles only during the mating season (Abernethy et al. 2002). Although the fission-fusion societies of chimpanzees (Boesch 1996), bonobos (Hohmann and Fruth 2002), and spider monkeys (Symington 1990, Chapman et al.1995) exhibit certain similarities to multilevel societies of baboons and *Rhinopithecus,* they differ in several ways including the fact that the composition of chimpanzee and spider monkey subunits is fluid, and it is rare for all community

members to coordinate their activities (Symington 1990, Chapman et al.1995, Boesch 1996, Hohmann and Fruth 2002).

Long-term studies indicate that the basic and most stable subunit within these multi-level societies is the one-male unit (OMU, composed of one adult male, several adult females, and their offspring). The OMU is best described as a breeding unit since sexual interactions are primarily restricted to individuals within an OMU (Kummer 1968, 1990, Dunbar and Dunbar 1975, Kirkpatrick et al. 1998, Zhang et al. 2006). OMUs are also socially independent because affiliative interactions are principally restricted to members within the OMU and affiliative interactions between individuals of different OMUs are rare (Swedell 2006, Dunbar 1983ab, Zhang et al. 2006). Despite being socially and sexually distinct units, OMUs that reside in the same band travel, forage, and rest together throughout the entire year. In species that form a multilevel society, the social and ecological function of a band is comparable to the "group" or "troop" of other monkeys (Kummer et al. 1968, Kawai et al. 1983, Swedell 2006, Kirkpatrick 2007, Zhang et al. 2006).

2.2 Social structure, interactions, and dispersal patterns of multi-level societies

Although the multi-level social structures in hamadryas baboons, gelada baboons, and snub-nosed monkeys are superficially similar, the composition, dispersal pattern, and social interaction patterns within OMUs and bands differ.

2.2.1Hamadryas baboons

In hamadryas baboons, OMUs belonging to the same band travel, forage, and rest together as a coordinated unit (Kummer 1968, 1990, Swedell 2002). The average size of hamadryas baboon bands is approximately 135 (range: 9 to 300) individuals (Kummer, 1968;

Sigg and Stolba, 1981; Biquand et al. 1992ab; Zinner et al. 2001; Swedell 2006). On average, each band consists of 15 OMUs. Each OMU consists of 2.8 (range: 1 to 9) adult females. Twenty five to thirty percent of OMUs have one to two follower males (Kummer 1968, Abegglen 1984, Swedell 2006). Followers are defined as sub-adult males or old former leader males who follow a particular OMU but are rarely allowed to mate or groom adult females (Kummer 1968). Several bands using the same sleeping cliffs are referred as a troop (Abegglen 1984, Kummer 1984). However, the composition of troops is flexible because bands are able to change sleeping cliffs independently (Kummer 1984). The size of a troop gathering at a sleeping cliff can reach 800 individuals (Zinner et al. 2001).

In hamadryas baboons, some OMUs form an intermediate layer of social structure between OMUs and bands, which is called a clan (Abegglen 1984, Clomenares et al. 2006, Schreier and Swedell 2009). OMUs of the same clan are spatially close to one another during traveling and resting (Abegglen 1984), more tolerant of each other at feeding sites (Clomenares et al. 2006), and occasionally travel as independent subunits (9 out of 105 days, Schreier and Swedell 2009). Each clan includes from two to thirteen OMUs (Abegglen 1984, Clomenares et al. 2006, Schreier and Swedell 2009). Abegglen (1984) assumed that leader males residing in the same clan were genetically related due to their similar facial color. A study conducted of a captive band with birth records confirmed that leader males within the same clan were father/sons, full brothers, or maternal brothers, although not all OMUs led by related males formed clans (Colmenares 1992). Colmenares (1992) argued that female kinship and familiarity also played a role in the formation of clans based on the fact that related females and females belonging to the same OMUs tended to interact with each other even after they migrated into different OMUs.

The cohesion of hamadryas OMUs appears to be maintained by the leader males' herding behavior (Kummer 1968, 1995; Swedell and Schreier 2009; Colmenares et al. 2006). Herding behavior occurs when leader males use threatening behaviors, such as neckbiting to control female movement patterns (Kummer 1968, 1995, Swedell and Schreier 2009). Hamadryas baboon are believed to exhibit a star like social structure in which males form the center of all social interactions, and interactions between adult females of the same OMU are infrequent (Kummer 1968). A recent study indicated that as the number of females in an OMU exceeded three, females spent more time sitting in close proximity, grooming and were groomed more by female members than by leader males (32% vs.17%, Swedell 2002). Swedell (2002) also pointed out that females vary considerably in the time they spend interacting with other female members. For example, among three OMUs that consisted of 3 females, the time females spent allogrooming ranged from 4% to 32% of social time. Swedell (2002) proposed that variation among females might be due to kinship. In other words, females that groomed each other most frequently also were close relatives. She argued that although hamadryas females disperse from their natal unit, related females may end up in the same OMUs if recruited by the same male. However, at present, genetic studies have not been conducted to determine whether kinship plays a significant role in hamadryas female social interactions.

Direct social interactions between members of different OMUs are rare in hamadryas baboons (Abegglen 1984, Swedell 2006, Schreier and Swedell 2009). Swedell (2006) observed only 13 cases of social interactions between females of different OMUs over two years of observation. Seven of these interactions were infant inspection. Three cases involved allogrooming. The grooming lasted between 15 to 20 minutes. In the remaining three cases, two females sat in proximity with each other for a period of less than 20 seconds. Schreier and

Swedell (2009) observed 17 cases of interactions between females of different OMUs over one year of observation. Direct social interactions between leader males were rarely observed (Swedell 2006).

Since interactions between OMUs are rare, it raises a question of how OMUs of multilevel societies coordinate their behavior. In the case of hamadryas baboons, communication between different OMUs is assumed to involve the "notifying" behavior of leader males (Kummer 1968, Abegglen 1984). Notifying is defined as behaviors in which actors approach recipients, stare, suddenly turn and present their back, and then run away rapidly (Kummer 1968). Abegglen (1984) assumed that notifying that occurred during travel marches functioned to inform other leader males of the travel direction and served to coordinate the activity of the band.

Different from other baboon species in which males disperse from their natal group and females are philopatric, both male and female hamadryas baboons are reported to disperse (Abegglen 1984, Swedell and Wooley-Barker 2001, Phillips-Conroy and Jolly 2004, Mori et al. 2007, Swedell et al 2011). Given the fact that hamadryas baboons form multi-level social structures, females have the opportunity to transfer across OMUs, clans, and bands. However, the majority of female transfer events (70%) are within bands (Sigg et al. 1982, Swedell 2011). Among the within-band transfer events, approximately 77% occurred within clans (Sigg et al. 1982, Swedell 2011). Dispersal within bands and clans results in changes in membership within the larger social unit, but does not result in increased gene flow. Therefore, across-band dispersal of hamadryas baboons is more comparable to between-group dispersal in other primates (Swedell et al. 2011).

Hamadryas females did not leave their natal OMU voluntarily. They were forced to leave by solitary males or followers who aggressively herded them in an attempt to establish an OMU

(Kummer 1984, Swedell 2006, Schreier and Swedell 2009, Pines et al. 2011, Swedell et al. 2011). Followers and solitary males obtain females through: a) herding one or two immature females from existing OMUs; b) taking over some (not all) mature females through challenging leader males; c) obtaining females without challenging leader males; and d) inheriting females from leader males who are injured, old, or disappear (Pines et al 2011). In each of these different strategies, females are reluctant to leave former leaders and follow the new leaders. Followers and solitary males force females to leave using aggressive herding behavior (Abegglen 1984, Pines et al. 2011, Swedell and Schreier 2009).

Hamadryas males have been observed to obtain females from the same band or a different band (Sigg et al. 1982, Phillips-Conroy and Jolly, 2004). Quantitative data concerning across-band dispersal rates of males, however, have not been published. Genetic date suggest that female dispersal rates are significantly higher than male dispersal rates (Hapke et al 2001, Hammond et al. 2006). Hammond et al. (2006) sampled 298 individuals from 4 populations distributed across an area of 1000 km. They calculated both male and female biased Fst based on the genotypes of 17 autosomal microsatellite loci, one Y-chromosome loci, and the sequence of the mtDNA d-loop region. Their results indicate that female biased gene flow between populations was four times greater than male biased gene flow between bands. According to behavioral evidence, the across-band dispersal rate of females is approximately 30% (Swedell et al. 2011). The across-band dispersal rate of males is estimated to be less than 8%. In other words, the majority of males remain in their natal bands. Compared to other bisexual dispersal species such as mantled howler monkeys (*Alouatta palliate*), in which 79-94% of adult males and adult females disperse from their natal groups (Glander 1992), the dispersal rates of both sexes of hamadryas baboons are low.

2.2.2 Gelada baboons

Gelada OMUs and all-male units that share a common range and forage together are defined as a band (Ohsawa 1979, Kawai et al. 1983, Dunbar 1993). Compared with hamadryas baboons, gelada bands are less cohesive since some OMUs may leave the band, join another band for several days, and then return to the original band (Ohsawa 1979). Mori et al. (1999) suggest that the cohesion of the band is influenced by environmental factors such as food supply. Under conditions with lower food availability, the bands become less cohesive and OMUs tend to forage more independently (Mori et al. 1999).

The average size of gelada bands is about 136 individuals (range: 27 to 262) (Iwamoto and Dunbar 1983, Shotake and Nozawa 1984, Ohsawa and Dunbar 1984, Mori et al. 1999). On average, each band consists of 11 OMUs (range: 2 to 25). Each OMU consisted of 3 adult females (range: 1 to 10). Fifteen percent of OMUs have one to two follower males (Ohsawa and Dunbar 1984, Mori et al. 1999). However, bachelor males also formed all-male units (an average of 10 individuals, N=7) (Dunbar and Dunbar 1975, Shotake and Nozawa 1984, Ohsawa 1979). All-male units may attach themselves to a band or range independently (Dunbar and Dunbar 1975, Ohsawa 1979).

Different from hamadryas baboons, gelada females remain in their natal OMUs their entire life (Dunbar, 1984, Le Roux et al. 2010). Males disperse from their natal OMUs after puberty, and join an AMU for two to four years (Dunbar and Dunbar 1975, Mori 1979). Based on the gene flow rate between bands (14%) estimated by blood protein polymorphism (Shotake and Nozawa 1984) and the assumption that female are philopatric, Dunber (1984) suggest that 70% of males return to the natal band to establish their OMUs.

Unlike hamadryas baboons, the cohesion of gelada OMUs appears to be maintained by

female-female bonds (Dunbar and Dunbar 1975, Dunbar 1984, 1993). The aggressive herding behavior adopted by male hamadryas baboons was rarely observed in geladas (Mori 1979, Dunbar 1983b). Leader males of geladas maintain strong grooming relationship (spending more than 10% of his social time) with an average of two adult females in his harem regardless of the size of his harem (Dunbar 1983b). In other words, there is a large variance in the frequency of social interactions between the leader male and individual females in his harem. Females "preferred" as social partners by the leader male were young and did not have other female grooming partner (Dunbar 1983b). Similarly, adult females did not distribute their social time evenly among potential female partners. They tended to interact with a small portion of adult females (on average 2.45 out of 4.84 females) within the OMU (Dunbar 1983a). Dunbar (1983a) assumed that female grooming partners were matrilineal relatives such as mothers, daughters, and sisters. However, as in the case of hamadryas baboons, genetic studies have not been carried out to confirm this prediction.

Similar to hamadryas baboons, affiliative interactions between adult members of different OMUs were rare in geladas (Mori 1979). However, juveniles of different OMUs occasionally form play groups (Mori 1979). Behaviors designed to coordinate band movement, such as "notifying" have not been observed in geladas bands (Mori 1979). How gelada OMUs coordinate with each other remains unknown.

2.2.3 Snub-nosed monkeys

Multi-level social structures have been reported in four of the five species of the genus *Rhinopithecus* (*R. bieti*: Kirkpatrick 1998, Grueter 2009; *R. roxellana*: Ren et al. 2000, Zhang et al. 2006; *R. brelichi*: Bleisch et al. 1993, Bleisch and Xie 1998; *R. avunculus*: Boonratana and Le 1998). There are no behavioral studies of the recently identified *R. strykeri* (Geissmann et al.

2011). In snub-nosed monkeys, OMUs of the same band were reported to rest, forage, and travel together as a single social unit (Kirkpatrick et al. 1999, Ren et al 2000, Zhang et al. 2006). Followers are rarely observed in snub-nosed monkeys. Instead, bachelor males form all-male units which are attached to the band (Kirkpatrick 1996, Bleisch and Xie 1998, Boonratana and Le 1998, Ren et al. 2000, Tan et al. 2007). The band size of *R. bieti* is more than 200 individuals belonging to about 19 OMUs and one AMU on average (the references for demographic information are listed in Table 2). Each OMU contains approximately 3.8 adult females. The band size of *R. roxellana* is more than 200 individuals and contains on average 11 OMUs and one AMU. Each OMU has an average of 5.4 adult females. The band size of *R. brelichi* is reported to be 225 individuals belonging to some 15 OMUs and one AMU. Each OMU has an average of 2.2 adult females. The band size of *R. avunculus* is smaller (85 individuals), and generally contains only two to three OMUs and one or two AMUs. Each OMU is composed of approximately 4.8 adult females.

Compared with other snub-nosed monkeys, the bands of *R. avunculus* were reported to be loosely organized (Boonratana and Le 1998). Based on a preliminary study, Boonratana and Le (1998) reported that OMUs of *R. avunculus* frequently leave and rejoin the band. However, no long-term study has been conducted to determine the rate at which OMUs move between bands. In other snub-nosed monkeys, the movement of OMUs between bands is uncommon (Kirkpatrick 1996, Grueter 2008, Ren et al. 2000, Guo et al. 2007, Tan et al. 2007, Bleisch et al. 1993, Bleisch and Xie 1998, Kirkpatrick et al. 1999). For example, Kirkpatrick (1996) observed only 7 cases of band fission in *R. bieti* in 650 hrs of observation over a 12 month period. In all 7 cases, OMUs reunited with the band within 25 hours (median=19 hrs) (Kirkpatrick 1996). Based on 1,444 hrs of observation over a period of two years, Grueter (2009) observed one case in

which his focal band of *R. bieti* split into two sub-bands for several weeks. Grueter (2009) argued that the fission was likely due to food scarcity because it occurred during winter when food availability was assumed to be lowest. Kirkpatrick et al. (1999) reported one case of a *R. roxellana* band splitting into two sub-bands for more than 2 days. However, other long-term observations have not reported band fission in *R. roxellana* (Ren et al. 2000, Guo et al. 2007, Tan et al. 2007).

Among the four studied species of genus *Rhinopithecus*, detailed data on dispersal patterns as well as social behavior have only been collected in *R. roxellana*, mainly through observations of a single habituated band (known as West Ridge band) living at Zhouzhi National Natural reserve (ZNNR), China (Zhao et al. 2005, Zhang et al. 2006, Zhang et al. 2008, Qi et al. 2009). Based on data from this group, I describe published reports of *R. roxellana* dispersal and social behavior.

Different from other Asian colobines in which females are philopatric and males disperse, both female and male *R. roxellana* are reported to disperse from their natal OMU (Zhang et al. 2008, Qi et al. 2009). Juvenile males (aged 3 to 5 years) have been observed to leave their natal OMU and join an all-male group associated with their natal band (Qi personal communication). Based on behavioral data collected from the habituated band at ZNNR, it appears that adult males immigrate into new bands and attempt to establish new OMUs (Qi et al. 2009). Qi et al. (2009) recoded 9 adult males immigrating into their study band from 2000 to 2008. However, whether these males were from the AMU associated with this band or from a different band remains unclear. Four out of the 9 males established their OMUs through attracting females from existing OMUs. Four become the harem males due to the disappearance of previous harem males. One took over an OMU through aggression. A recent study reported a higher takeover rate

within a provisioned band of *R. roxellana* residing at Shennongjia National Natural reserve (SNNR) (Yao et al. 2011). They observed 4 cases of violent takeovers and one case of attracting females from an existing OMU from 2006 to 2010. The higher takeover rate at SNNR might be due to the greater amount of food provided there than at ZNNR. At SNNR, 1,200g of fruit per individual per day were provided every day during spring and summer. In fall and winter, 1,000g of lichen, 1,000g fruit, and 500g pine seeds per individuals per day were provided every day. While at ZNNR, the amount of food provided was less than 200g per adult individual per day. On average, food was provided only 10 days every month from September to December and from March to May. Larger amount of food supply at SNNR might have attracted more solitary males, which may have led to greater takeover rates (Yao et al. 2011).

In addition, Qi et al. (2009) recorded 73 female dispersal events over eight years from the habituated band at ZNNR. During this eight year period, 26 sub-adult females, 64 adult females, and 16 adult males resided in the band. In 10 of the 73 dispersal events (9 adult females and 1 sub-adult female), females immigrated into the habituated band. In 33 cases (28 adult females and 5 sub-adult females), females were observed to leave the band and presumably transfer to a neighboring band. In 30 cases (27 adult females and 3 sub-adult females), females transferred between OMUs within the same band. Fifteen adult females were observed to disperse more than once. Overall, 31% of sub-adult females (8 out of 26) left their natal OMUs, and 53% of adult females (33 out of 64) dispersed at least once during their life time. Thus, it appears that dispersal in *R. roxellana* is bisexual.

Data on social interactions within and between OMUs of *R. roxellana* are based principally on observations of this habituated band when visiting a provisioned area (approximately 20m by 20m) located in a valley within their home range (Zhao et al. 2005,

Zhang et al 2006, Zhang et al 2008). The size of the band changed slightly every year. On average, the band was composed of about 100 individuals, 8 to 11 OMUs, and one all-male unit (Zhang et al 2006, this study). Based on 197 days of observation, Zhang et al. (2006) suggested that 92% of sexual behavior was restricted to individuals of the same OMU, and 8% involved individuals from different OMUs. More than 92% of allogrooming occurred among OMU members and 7.6% occurred between adult females from different OMUs (Zhang et al. 2006). Further investigation of the distribution of social interactions indicated that females spent more time interacting with other OMU females (grooming: 15% of observation, proximity: 28% of observation) than with their leader male (grooming: 5%, proximity: 8%). In this regard, Zhang et al (2008) classified *R. roxellana* as a female-bonded species which suggested that OMUs contained females of the same matriline.

Building on these previous studies, I investigated dyadic social interactions among male and female *R. roxellana* when traveling, feeding, foraging, and resting in their natural habitat. The goal of this research is to investigate behavioral strategies used by *R. roxellana* to cope with the challenges of living in a multi-level society, including the role of kin selection, reciprocity, and biological market theory in explaining dyadic social interactions within and between OMUs. Combined with genetic analysis, this research also investigated *R. roxellana* dispersal patterns and the dispersal rate between bands.

2.3 Hypotheses explaining the evolutionary history of multi-level societies

Researchers have suggested that multi-level societies evolved independently in different primate lineages (Kawai et al.1983, Grüeter et al. 2004, 2009). In the case of African cercopithecoids, multi-level societies of *T. gelada* and *P. hamadryas* appear to be derived from multi-male/multi-female groups that became less cohesive and split into OMUs for reproduction,

but the entire group remained cohesive (Swedell and Saunders 2006, Table 2.1). Given that most Asian colobines form one-male harems (Table 2), it has been argued that the multi-level social structure of snub-nosed monkeys evolved through the aggregation of small one-male groups in to a large band (Kirkpatrick 2007, Grueter and van Schaik 2010). Factors that may have led to such a social and spatial pattern of aggregation include coping with hash habitats characterized by low food productivity and cooperatively defending against threats posed by predators or bachelor males (Kirkpatrick 1996, Grueter and van Schaik 2010).

However, it is difficult to draw a direct path between multi-level societies and their ancestral social structures in either baboon species or Asian colobines. This is due to the fact that some species form an intermediate social structure (Kirkpatrick 2007, Jolly 2007, Grueter 2009). For example, OMUs of proboscis monkeys (*Nasalis larvatus*) are reported to aggregate and form a larger subgroup composed of several OMUs at sleeping sites along the river (Bennett and Sebastian 1988, Yeager 1991). These OMUs forage separately during the day (Yeager 1991). Thus, compared to *Rhinopithecus spp,* sets of proboscis monkey OMUs are spatially and socially less cohesive. Similarly, Guinea baboons (*P. papio*) are reported to form one-male units within larger multi-male/multi-female groups (65 individuals per group on average, range 10-249, N=134) based on spatial proximity during resting, foraging, and traveling (Boese 1973, Galat-Luong et al. 2006, Patzelt et al. 2011). However, the group sizes of Guinea baboons vary greatly within a day and across seasons, which suggest that their group composition is more flexible than hamadryas baboons (Patzelt et al. 2011). To date, no studies of wild Guinea baboon groups were able to identify individuals. Therefore, these studies provided very limited information on dyadic patterns of individual social interactions. Our current understanding of the social interactions of Guinea baboons is based principally on captive studies (Boese 1973,

Maestripieri et al. 2007). These studies indicate that similar to hamadryas baboons, most Guinea baboon females mate exclusively with only one male and maintain spatial proximity with that male (Boese 1973, Maestripieri et al. 2007). However, extra-OMU copulations do occur. For instance, among the 23 females studied by Maestripieri et al. (2007), one mated with two different males during the 12 week observation period. However, unlike hamadryas baboons who rarely affiliate with extra-OMU members, interactions between members of different OMUs were more tolerant in Guinea baboons (Boese 1973, Maestripieri et al. 2007). Boese (1973) observed that about 30% of these interactions involved grooming and embracing members of different OMUs. Taken together, these results indicate that although most Guinea baboon females mated exclusively with one male, they were socially less cohesive and had an increased frequency of affiliative social interactions with nonharem members than reported for hamadryas baboons.

2.3.1 Ecological constraints hypothesis in snub-nosed monkeys

Snub-nosed monkeys, except for *R. avunculus*, live in high altitude forests characterized by marked seasonal variation in food supply and periods of marked food scarcity in winter (*R. roxellana*: 1,500-3,300m, Li et al. 2002, Ren et al 2000; *R. bieti*: 2,700-4,600m, Kirkpatrick, 1998, Grueter 2008; *R. brelichi*: 1,400-2,300m; *R. avunculus*: 200-1200m, Boonratana and Le 1998). Therefore some researchers have argued that forming multi-level social structures is a strategy used by snub-nosed monkeys to deal with habitats characterized by large patches of low quality food that varies considerably in seasonal availability (Kirkpatrick 1998, Bleisch et al. 1993, 1998, Kirkpatrick and Grueter 2010). In order to test this hypothesis, I compared the average annual temperature, home range area per individual, and population density at each habitat occupied by Asian colobines (Table 2). I used these three measures as indirect indicators

of food availability. I assumed that lower average annual temperature, larger home range/individual, and lower population density indicate a more limited food supply.

The average annual temperatures at the habitats of *R. roxellana, R. bieti* and *R. brelichi* are below 11ºC degree (Table 2, Figure 2.1a). *R. avunculus* lives in forests at lower altitudes (200-1200m) with higher average annual temperature (22 ºC degree) (Boonratana and Le 1998). However, the multi-level social structures of *R. avunculus* are reported to be less cohesive than the other snub-nosed monkeys (Boonratana and Le 1998). The average annual temperature for the majority of other Asian Colobines is 24.5 ºC degree (Figure 2.1a), except for some populations of Nepal grey langurs (*S. schistaceus*) living at high altitude in the mountains of Nepal (above 3000m, Boggess 1980, Sayers and Norconk 2008). The annual temperature at these sites is 9.6-13.5 degree (Boggess 1980, Sayers and Norconk 2008). However, instead of forming a multi-level society, Nepal grey langurs form multi-male/multi-female groups (Boggess 1980, Sayers and Norconk 2008) that are similar to those reported for grey langurs distributed in warmer habitats.

The home range area/per individual for snub-nosed monkeys is larger (11.5 hectare/individual) than the average home range/individual for other Asian colobines (6 hectare/individual, Figure 2.1b). The population density of snub-nosed monkeys is lower (8.3 individuals/km^2) than the average population density of other Asian colobines (45 individuals/km^2, Figure 2.1c). Taken together, the results suggest that the habitats of *R. roxellana, R. bieti,* and *R. brelichi* appear to be less favorable in terms of food availability and distribution than other Asian colobines. It suggests that resource availability may play a critical role in the formation of multi-level societies. However, how exactly multi-level social structures help snub-nosed monkeys to cope with habitats of low food availability is still unclear.

2.3.2 Bachelor male threat hypothesis in Asian colobines

Grüeter (2009) proposed that the benefits that leader males gained through cooperatively repelling bachelor males was the driving force of forming a multi-level social structure in Asian colobines. Since there is not sufficient data on male takeovers, Grüeter (2009) used sexual dimorphism in body size and the number of adult females within an OMU as indirect indicators of threats faced by leader males. They assumed that increased sexual dimorphism in body mass indicated more severe male/male competition, and that the larger number of adult females within an OMU indicated that there were more bachelor males who posed a threat to leader males. They predicted that species forming multi-level societies should have a higher degree of sexual dimorphism and larger number of adult females within OMUs compared to other Asian colobines. Their results supported their predictions.

However, Grüeter (2009) used a very broad definition of multi-level societies. They classified Asian colobines that have overlapping home range (>40%) as species forming multi-level societies. Besides snub-nosed monkeys, this included species such as *Trachypithecus geei*, *Nasals larvatus*, *Pygathrix nigripes, Presbytis sizmensis* and *P. pileata*. However, OMUs of these species do not coordinate their activities. They do not feed, forage, travel or rest together although OMUs of these species do encounter each other frequently (Mukherjee and Saha 1974, Bennett and Sebastian 1988, Yeager 1991, Stanford 1991). For example, the home ranges of *P. pileata* OMUs were reported to overlap 84% (Stanford 1991). On average, OMUs encountered each other once a day (Stanford 1991). However, encounters between OMUs were characterized by aggressive male displays (Stanford 1991). In this regard, home range overlap is not a suitable measure of OMU coordination.

I re-analyzed Grüeter (2009)'s data but considered snub-nosed monkeys as the only Asian colobines to form multi-level societies. My results indicate that the number of females within OMUs (4.1) of snub-nosed monkeys is not significantly different from that of other Asian colobines (3.7, Figure 2.1d). The average ratio of male to female body weight of snub-nosed monkeys (1.76) is significantly greater than that of other Asian colobines (1.23, Figure 2.1e). However, *N. larvatus* exhibits the greatest sexual dimorphism (2.09) among Asian colobines. Taken together, there is no strong support for the hypothesis that the threat of takeover by bachelor males is a primary factor in the evolution of multi-level societies in Asian colobines.

2.3.3 Ecological constraints hypothesis in hamadryas baboons

Swedell and Saunder (2006) argued that the evolution of multi-level societies in hamadryas baboons represents an adaptation to their semi-desert habitats. I compared the total annual rainfall as a proxy measure of food availability at different sites inhabited by baboon species (Table 2.1). The annual rainfall at different habitats of hamadryas baboons is below 560 mm (Biquand et al 1992b, Zinner et al. 2001, Swedell 2006). However, although most other baboon species live in wetter habitats, some populations of *P. cynocephalus* live in habitats with only 335 mm of annual rainfall (Bronikowski and Altmann 1996), some populations of *P. ursinus* live in even drier habitats with less than 100mm annual rainfall (Hamilton et al. 1976, Cowlishaw 1997. Using rainfall as a proxy for food availability and habitat seasonality, the evolution of multi-level societies in baboons cannot be explained exclusively by their use of arid environments.

2.3.4 Evolution of herding behaviors in hamadryas baboons

The herding behavior of male hamadryas baboons plays a critical role in maintaining the cohesion of OMUs. Bergman (2006) explored the evolution of multi-level social structure in

hamadryas baboons through investigating the evolutionary origin of males' herding behavior. He investigated three potential behavioral precursors: herding by males during intergroup encounters, male-female "friendship", and consortships in a hamadryas/anubis hybrid group. These three types of behaviors have been reported in yellow baboons, olive baboons, and chacma baboons (Smuts 1985, Henzi et al. 1998, Palombit et al. 1997). Bergman (2006) assumed that the behaviors of hybrid males represent a transitional state of hamadryas' herding behavior. Bergman (2006) did not observe aggressive herding behaviors in hybrid males except for those phenotypically very hamadryas-like. He also found that hybrid males did not provide paternal care towards infants, and females did not follow hybrid males. These two behaviors have been considered important elements of male-female "friendship" in baboons. Thus, herding behavior does not appear to have evolved from male-female "friendships". However, Bergman (2006) did report that hybrid males consorted with estrous females for a longer period (15.6±3.39 days, N=17 estrous cycles) than did chacma (3.5±2.1 days, Seyfarth 1978) and anubis baboons (5.6±2.5 days, Bercovitch 1991). Hybrid males also followed non-estrous females frequently (0.5 times per hour, N=14), while non-hamadryas baboon males rarely followed non-estrous females (Bergman 2006). Based on these results, Bergman (2006) speculated that the herding behavior of hamadryas males evolved as extension of consortship observed in non-hamadryas baboons. In other words, the hamadryas males "permanently" consort with females (Bergman 2006). Female mate choice appears to play a limited role in the formation and maintenance of stable OMUs within the mutli-levels social structure of hamadryas baboons.

In summary, several hypotheses have been proposed to explain the evolution of multilevel societies in primates. However, our understanding of the set of factors resulting in the evolution of multi-level societies remains unclear, and it appears that multi-level societies have

evolved independently and serve different functions across Old World primates. The present study is not designed to test hypothesis concerning the origin and evolution of *R. roxellana* multilevel societies. However, this study examines detailed information on patterns of social interaction and kinship within and between OMUs and bands, which will help to shield light on the set of factors promoting multi-level social structures in *R. roxellana*.

Figure 2.1 Habitat, sexual dimorphism and harem size of snub-nosed monkeys and other Asian colobines.
(In figure a, b, c, and d, each data point represents a site, not a species. In figure e, each point represents a species. Data of figure a-d are adapted from Kirkpatrick 2007, data of figure e are adapted from Grueter 2009)

a: Average annual temperature of their habitats (the data point with a circle represents *R. avunculus*).

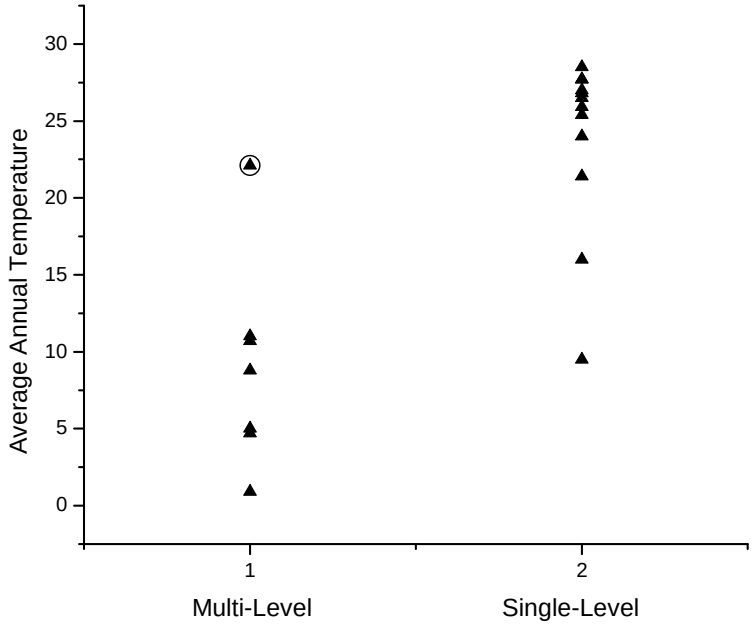
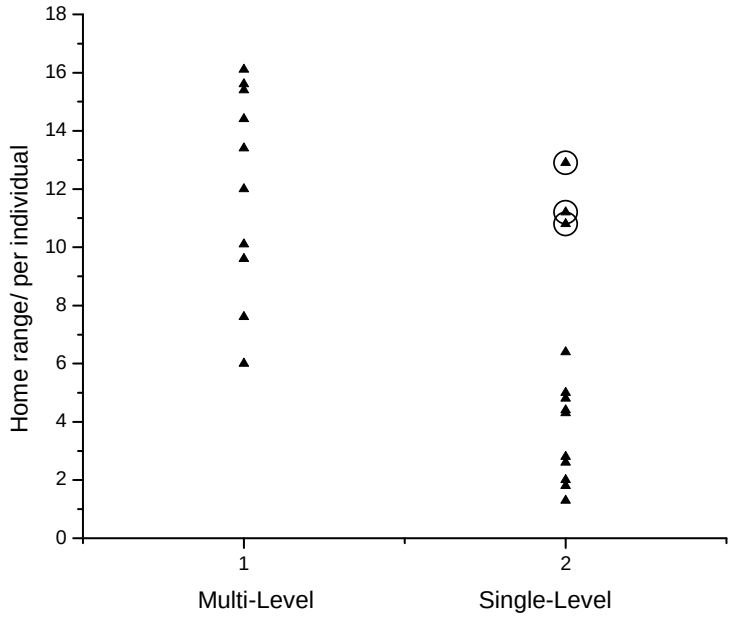


Figure 2.1 (cont.)
b: Home range/individual (data points with a circle indicate home range ovelapping)



c: Population density (individual/km^2)

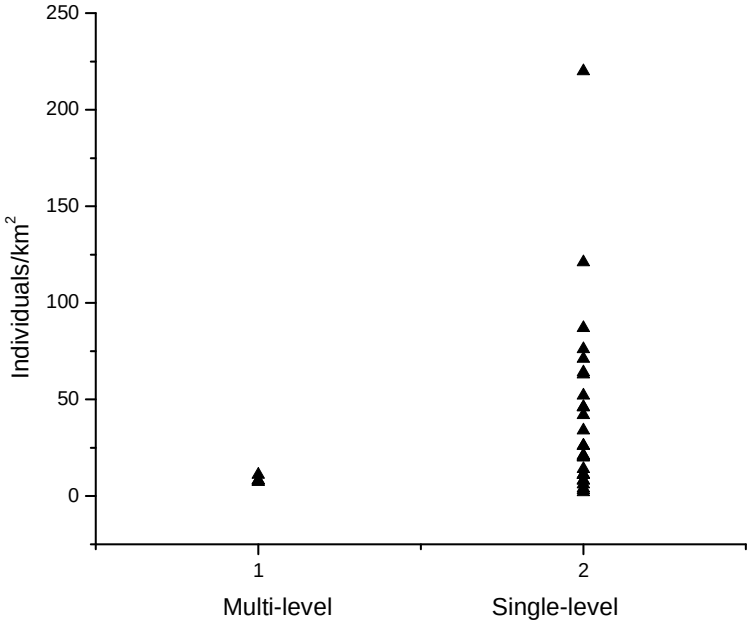
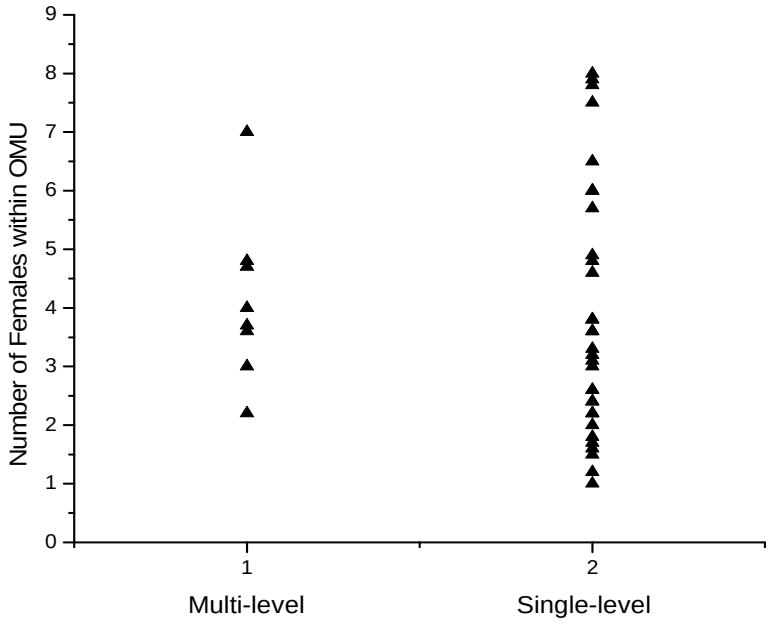


Figure 2.1 (cont.)
d: Number of adult females within OMUs



e: Ratios of male to female body size

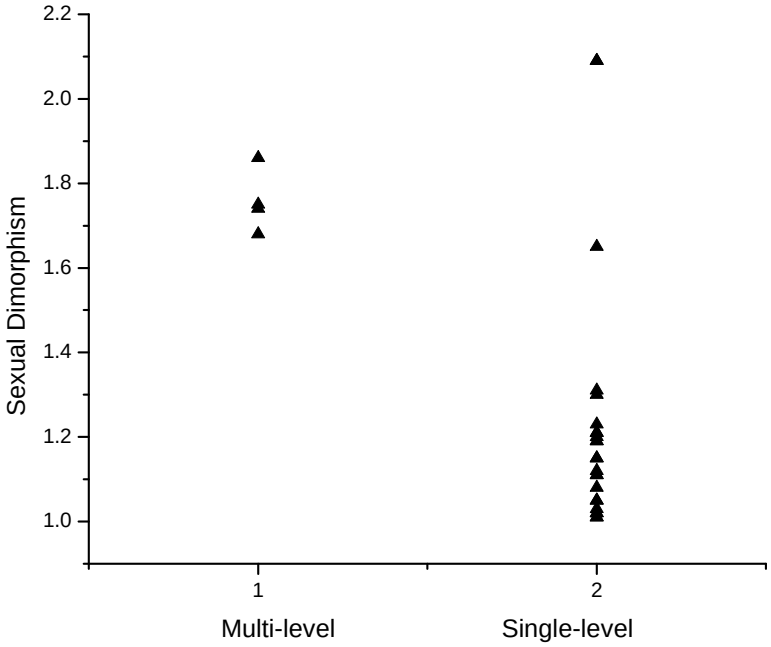


Table 2.1 Group composition of baboon species and annual rainfall at different sites.

Species	Site	Group Size	AF:AM	Annual Rainfall (mm)	References
Papio anubis	Gilgil, Kenya	84(n=1)	6:19	595-756	
	Gilgil, Kenya	45(n=3)	3.7:12	595-756	Eley et al. 1989
	Awash Valley, Ethiopia	48(n=6) (14-87)		654	Aldrich-Blake et al. 1971
	Gilgil, Kenya	49(1)		733	Harding 1976
	Eritrea	6-29?		544	Zinner et al. (2001)
	Laikipia Plateau	103(n=1)	female>26	550	Barton and Whiten 1993
	Bole Valley, Ethiopia	20(n=7)		2000	Dunbar & Dunbar 1974
P. cynocephalus	Amboseli, Kenya	28(n=3)		335	Stacey 1986
	Amboseli	39(n=7)	7:12	335	Samuels & Altmann 1991
	Amboseli	60(n=3)		335	Bronikowski & Altmann 1996
	Tana River, Kenya	75(n=1)		400	Wahungu 1998
	Mikumi, Tanzania	52(n=3) (17-71)		842	Norton et al. 1987
P. ursinus	Giants Castle Game, South Africa	20(n=27)	Male>2	630	Henzi et al. 1990
	Drakensberg	21(n=14)		1197	Whiten et al. 1987
	Tsaobis Leopard Park, Namibia	34(n=4)	3.2:11.7	85	Cowlishaw 1997
	Drakensberg	24.6(n=25)		1197	
	Transvaal	46(n=6)			Stoltz and Saayman 1970
		48(n=4)			Saayman 1971
	Moremi Game, Botswana	54	14:18		Bulger and Hamilton 1987
	Kuiseb River canyon, Namib	26(n=3)		18.1	Hamilton et al. 1976
	Okavango Swamp, Botswana	79(n=7)		457	Hamilton et al. 1976

Table 2.1 (cont.)

Species	Site	Group Size	AF:AM	Annual Rainfall (mm)	References
	Moremi, Botswana	43(n=5)	6.4:13	200-1400	Hamilton and Bulger 1992
P. papio	Niokolo Koba	62(n=111) 22-249		1000-1300	Galat-Luong et al. 2006
	Niokolo Koba	84(n=5) 10-193	5:15	1000-1300	Boese 1973
P. hamadryas	Awash, Ethiopia	136 (n=19)	1:2.5 (OMU)		Kummer (1968)
	Eritrea	139 (n=6)	1:2.9 (OMU)	499	Zinner et al. (2001)
	Saudi Arabia	37.8(n=48) (range 9-102)	1:2.6 (OMU)	100-559	Biquand et al 1992b
	Erer Gota, Ethiopia	78(n=2)			Sigg and Stolba 1981
	Filoha, Ethiopia	160(n=5)	1:2.2 (OMU)	550	Swedell 2006
Theropithecus gelada	Arsi	81(n=2)	1:2.7 (OMU)		Mori et al. 1999
	Bole	62.5(n=2)		1100	Iwamoto and Dunbar 1983
	Sankaber	206(n=3)		1385	Iwamoto and Dunbar 1983
	Gich	139(n=2)		1465	Iwamoto and Dunbar 1983
	Selale District, Ethiopia	203(n=4)	1:5.5 (OMU)		Shotake and Nozawa 1984
	Sankaber	131(n=11) (30-262)	1:2.8 (OMU)		Ohsawa and Dunbar 1984
	Gich	107 (n=6) (27-170)	1:2.4 (OMU)	1465	Ohsawa and Dunbar 1984

Table 2.2 Group composition of Asian colobines, home range, and annual temperature at different sites.
Adapted from Kirkpatrick (2007) and Grueter (2008) with some modifications. (Numbers with a * indicate home range overlapping)

Species	Site	Group size	AM/AF	Home range (Ha)	Range /per individual	Population density (individual/ km^2)	Annual T (ºC)	Reference
Simias Concolor	Pagai island	4	1:1.8	7-20	5	21		Tenaza and Fuentes 1995
	Sarabua /Grukna	5	1:1.7	13	2.6	8		Watanabe 1981
	Grukna			3.5		220	28.5	
Nasalis Larvatus	Kinabatangan -Sukai	17	1:7.5	220	12.9*	34	27	Tenaza and Fuentes 1995
	Tanjung Putting	12	1:3.6	130	10.8*	63		Yeager 1989, 1990
	Samunsam	9(n=12)	1:3.8			6	26.5	Bennett and Sebastian 1988
	Sukau	21(n=1)	1:8	220.5	10.5*		28	Boonratana 2000
	Menanggul	16(n=1)	1:6	138.3	8.7*		24	Matsuda et al. 2009
Presbytis femoralis	Perawang	11	1:4.8	22	2	42	26.5	Megantara 1989
P. siamensis	Kuala lompat	15	1:7.8	27	1.8		27.7	Bennett 1983, Davies et al 1988
		16	1:2.6	21	1.3			Curtin 1980
P. comata	Kamojang	8	1:3.0	38	4.8	11	16	Ruhiyat 1983
	Kutai					20		Ruhiyat 1983
P. thomasi	Bohorok	8	1:3.0	35	4.4	21	26.7	Gurmaya 1986
P. rubicunda	Sepilok	6	1:2.0	67	11.2*		27.2	Davies 1991, Davies et al. 1988
P. hosei	Lipad			35		26	27.1	Mitchell 1994
P. potenziani	Sarabua	3	1:1.0	13	4.3	14		Watanbe 1981
	Betumonga		1:1.0	34		11	29.4	

Table 2.2 (cont.)

Species	Site	Group size	AM/AF	Home range (Ha)	Range /per individual	Population density (individual/ km^2)	Annual T (ºC)	Reference
Trachypith-ecus pileatus	Madhupur	8	1:3.6	22	2.8*	52	24.9	Stanford 1991
	Manas	10	1:3.3	64	6.4*			Mukherjee 1978
T. auratus	Pangadaran	14	1:6.5					Kool 1993
T. cristatus	Rantau /Panjang	35	1:4.6					Furuya 1961
T. geei	Goalpara	12.5 (n=10)	1:4.9				25	Mukherjee and Saha 1974
	Ripu		1:2.2			46		Srivastava et al. 2001
	Chirrang		1:1.5			64		Srivastava et al. 2001
	Manas 01		1:2.2			20		Srivastava et al. 2001
	Manas 02		1:3.8			8		Srivastava et al. 2001
T. obscurus	Kuala Lompat	17	1:2.4	17-33	1-1.9	87	27.7	Curtin 1976, 1980
T. johnii	Nilgiri district	9	1:1.2	65-250 ?	7.2			Poirier 1970
	Kakachi	17		24	1.4	71		Oates et al. 1980
Semnopithec us dussumieri	Orcha	19	1:1.6	375?	20.0?	3-6?	21.4	Dolhinow 1972
	Kaukori	54	1:3.2	775		3?	25.9	Dolhinow 1972
	Kanha	22	1:7.9	74	3.4	46		Newton 1992
	Gir	28	1:6.0	20	0.7	121	26.8	Starin 1978
	Dhawar		1:3.1	149		11	24	Sugiyama 1964
	Dhawar			19		76	24	Sugiyama 1964
	Raipur	29	1:5.7					Sugiyama 1964
S. schistaceus	Nepal	10.5 (n=6)	1:2.4	660	6.6		10.0	Boggess 1980

Table 2.2 (cont.)

Species	Site	Group size	AM/AF	Home range (Ha)	Range /per individual	Population density (individual/ km^2)	Annual T (ºC)	Reference
	Nepal	42.5 (n=2)	3:10				13.6	Sayers 2008
S. ajax	Ramnagar	18	1:2.6			26	25.4	Borries et al. 2001
S. entellus	Jodhpur	38.5 (n=27-29) (range:7-93)	All male 11.8 (n=13) Range: 2-47				360(rain fall)	Rajpurohit and Sommer 1993
Rhinopithecus. bieti	Fuhe	80		1070	13.4			Liu et al. 2004
	Jinsichang	180		1730	9.6			Ren et al. 2004
	Longma	80		956	12.0		8.8	Huo 2005
	Semage	410	1:3	2475	6.0			Grueter 2008
	Wuyapiya	175	1:3.6	2525	14.4	7	0.9	Kirkpatick et al 1998
	Xiaochangdu	210		2125	10.1		4.7	Xiang 2005
	Xiangquaing	366	1:4.7					Ding and Zhao 2004, Liu et al. 2007
	Deqing	146(n=6)	1:4					Cui et al. 2008
R. roxellana	Yuhuangmiao	112(n=1)	1:3.7	1800	16.1	7.2	8.6	Tan et al. 2007, Qi et al. 2008
	Shennongjia	269(n=5)	1:7			8	5	Ren et al 1998
	Shennongjia	100(n=3)						Li. 2002
R. brelichi	Fanjinshan	225(n=1)	1:2.2	3500, 1275	5.7-15.6	11	11	Bleisch et al. 1993 Bleisch and Xie 1998
R. avunculus	Ta Ke/ Nam Trang	65(n=2)	1:4.8				22.1	Boonratana and Le 1998

CHAPTER 3: SOCIAL INTERACTIONS AMONG MALE AND FEMALE *R. ROXELLANA*

3.1 Introduction

Independent OMUs are believed to be the ancestral condition for Asian colobines, since most Asian colobines live in small unimale or harem social groups (Newton and Dunbar 1994, Kirkpatrick 2007, Grüeter and van Schaik 2010). The multi-level societies of *R. roxellana* are proposed to have evolved through the aggregation of several independent one-male units (OMU) in response to exploring habitats of low productivity and/or due to the threats of bachelor males who attempt to take over breeding units (Kirkpatrick 1999, Grüeter and van Schaik 2010). Individuals living in multi-level societies face different social challenges than those living in one-male/multi-female groups. These challenges include 1) maintaining a large and stable social network composed of several distinct reproductive and social subunits, 2) coordinating movement and activities between different OMUs, 3) developing affiliative or tolerant social bonds with members of different OMUs that function to reduce agonistic interactions, and avoiding reproductive competition, and 4) processing a potentially large amount of social information concerning the identity, partner competency, and intentions of many band members (Barton and Dunbar 1997). The main objective of this chapter is to examine patterns of sexual, affiliative, and agonistic interactions within and between OMUs in *R. roxellana*. In addition, through a comparison with other Asian colobines, I try to identify specific behavioral strategies that *R. roxellana* adopt to cope with the challenges of living in a multi-level society. The primary research questions addressed in this chapter are: 1) What are the social and sexual interaction patterns within OMUs? 2) What are the affiliative and agonistic interaction patterns between members of different OMUs? 3) What is the process of forming new OMUs? 4) Is the social

interaction patterns of *R.* rox*ellana* different from other Asian colobines? And, 5) What are the benefits to group members of forming multi-level societies?

3.2 Social structures and social behaviors of Asian colobines

3.2.1 Social structures of Asian colobines

Most species of Asian colobines live in small unimale or harem social groups (Newton and Dunbar 1994, Kirkpatrick 2007). The primary exceptions are some populations of Hanuman langurs (*Presbytis entellus*, Newton 1987, Vasudev et al. 2008) and Phayre's leaf monkeys (*P. phayrei*, Borries et al. 2004, Gupta and Kumar 1994). Some Hanuman langurs are reported to live in multi-male units of more than 40 individuals with as many as eight adult males (Newton 1987, Vasudev et al. 2008). Similarly, Phayre's leaf monkeys are reported to live in multi-male units of 17 individuals with as many as three adult males (Borries et al. 2004, Gupta and Kumar 1994). Proboscis monkeys (*Nasalis larvatus*) also have been reported to form multi-level troops (Bennett and Sebastian 1988, Yeager 1991). Proboscis OMUs with overlapping home range are reported to rest together along river sides at night, but forage separately in inland forests during the day (Bennett and Sebastian 1988, Yeager 1990, 1991, Boonratana 2000, Matsuda et al. 2009). Inter-OMU encounters are assumed to occur frequently during foraging and traveling because the home ranges of proboscis OMUs overlap by more than 95% (Bennett and Sebastian 1988, Yeager 1990, 1991, Boonratana 2000). In this species, sleeping sites along the river side were not randomly distributed (Yeager 1991). Yeager (1991) investigated the sleeping sites of 11 OMUs. She defined OMUs sleeping less than 100m apart as in association. According to her results, OMUs were in association in 58.2% of sightings and an OMU associated with an average of 1.8 other OMUs. In about 46.3% of these associations (ranging from 23-96.6%) the focal OMU's

nearest neighbor was the same OMU. According to these results, proboscis monkeys are considered to form a secondary level of social grouping at sleeping sites in which affiliated OMUs maintain proximity with each other (Bennett and Sebastian 1988, Yeager 1991). However, compared to *Rhinopithecus spp*, sets of OMUs of proboscis monkeys are spatially and socially less cohesive.

3.2.2 Social interactions among group members

Asian colobines spend between 0.1-11.0 percent of their day engaged in allogrooming (Table 3.1). Allogrooming is reported to occur primarily between adult females (*S. entellus*, Borries et at. 1994; *N. larvatus*, Yeager 1990, 1991; *Trachypithecus francoisi*, Zhou et al. 2006). In *N. larvatus*, males never groomed other group members, and only received grooming in 1 out of 252 scans (Yeager 1990, 1991). In *S. entellus*, grooming between females and males was less frequent (3% vs. 97%, N= 6655 episodes) and of shorter duration (2.4min vs. 5.9min) than female-female grooming bouts (Borries et al.1994). During intersexual grooming bouts, female *S. entellus* groomed males more frequently than males groomed females (1006 vs. 176 episodes, Borries et al. 1994). A captive study of one adult male and three adult female *T. francoisi* conducted over 27 days indicated that 29.9% of grooming bouts (N=198) occurred between adult males and females, and 61.7 % (N=464) occurred between adult females (Zhou et al. 2006). Table 3.2 summarizes the allogrooming distribution patterns of these three species. Overall, these Asian colobines spend a limited amount of time allogrooming compared to African cercopithecines and males groom females less than females groom males.

3.2.3 Sexual behavior

Copulations in Asian colobines are preceded by ritualized solicitations (Kavanagh 1978, Bishop 1979, Newton 1987, Ren et al. 1995, Murai 2006) except for *Simias concolor,* which is

the only species of Asian colobines in which females exhibit a sexual swelling (Tenaza 1989). Solicitations are generally initiated by females except for proboscis monkeys (*Nasalis larvatus,* Murai 2006). According to Murai (2006)'s observation, male proboscis monkeys initiated 172 out of 259 solicitations. The solicitation behavior of male proboscis monkeys begins with a vocalization followed by a pouting face directed towards a female (Murai 2006). Female solicitation behaviors vary slightly across Asian colobines but overall they share a similar pattern (Table 3.3). Females initiate sexual behavior by approaching an adult male, making eye contact, or head shaking. A female prostrates on the ground or branch and presents her hind quarters to the leader male. While waiting for the male to approach, the female frequently looks back at the male. Female solicitations appear to be a common feature of Asian colobine sexual interactions.

3.2.4 Inter-group encounters

Inter-group or OMU encounters in most Asian colobines are described in terms of aggression or avoidance (Table 3.4, Poirier 1968, Tenaza 1989, Stanford 1991, van Schaik et al. 1992, Steenbeek 1999, Wich and Sterck 2007). Only males are reported to engage in aggressive inter-group encounters (Table 3.4). Males also produce long calls to maintain or increase the distance between OMUs. Females rarely are involved in inter-group encounters. For example, in a 15-month study of capped langurs (*P. pileata*), females were reported to participate in only one of 106 inter-group encounters (Stanford 1991). In Thomas's langurs (*P. thomasi*), females were never observed to help males expel invading males unless these extra-group males attempted to attack their infants (Steenbeek 1999). Finally, in *P. pileata* and *P. thomasi*, males were found to herd females when encountering other groups (Stanford 1991, Steenbeek 1999). Herding was defined as leader males preventing females from moving towards other groups and forcing them to return to his group (Stanford 1991, Steenbeek 1999). In addition, in these two species, the

frequency of group encounters was negatively related to the number of male displays such as long calls and chasing, which indicates that males were less aggressive towards familiar groups than to unfamiliar groups (Stanford 1991, Wich and Sterck 2007, Wich et al 2002). Taken together, these data indicate that inter-group encounters in most Asian colobines are characterized by the harem male defending his females. Females rarely provided support or aid to the harem male in inter-OMU encounters. Therefore, the function of inter-group aggression in Asian colobines is proposed to be primarily mate-defense by males, rather than resource-defense by females (Stanford 1991, van Schaik et al. 1992, Wich and Nunn 2002).

3.2.5 Process of forming new one-male groups

Aggressive takeovers by extra-group males, which sometimes results in injury to both resident and invader males, are reported to be a common form of male replacement in Asian colobines (e.g. *P. entellus,* Rajpurohit et al 2003, Agoramoorthy 1994, Ross 1993; *Presbytis rubicunda* Davies 1987; *P. cristata,* Wolf and Fleagle 1977; *P. senex,* Rudran 1973; *N. larvatus,* Agoramoorthy and Hsu 2005). However, gradual replacement of the leader male has been observed in some populations of *P. entellus* exhibiting multi-male groups (Hrdy 1979, Boggess 1980). Based on 32-months of observation of 6 multi-male *P. entellus* groups, Boggess (1980) concluded that the gradual replacement of the harem male began when an extra group male followed a bisexual group from a distance (>150m). At the beginning, the extra group male received resistance, such as fighting, chasing and threatening from the resident males. However, if the extra group male persisted in entering the group, he was accepted. This process could take up to a month. During this process, adult females provided minimal assistance to resident males in driving off the extra group male. The new male resident had the lowest rank when he entered the group. After a period of 1 to 3 years, the immigrant male might ascend to the dominant

position and then either exclude long-term male residents or tolerate them (Boggess 1980). The social dynamics associated with changes in male group membership in OMUs and multimale *P. entellus* groups represent very different process.

Through a comparison of demographic data on *P. entellus* groups living at different sites, Boggess (1980) concluded that the ratio of bachelor males to males within bisexual groups is a main factor controlling the rate and pattern of male replacement. In populations with a low proportion of bachelor males (less than 25%), emigration is a gradual process (2 to 3 months). In populations with a higher proportion of bachelor males (greater than 40%), which might be the result of over crowding due to habitat reduction (Boggess 1980), male replacement was rapid (within one day).

3.3 Predictions tested in this chapter

In this chapter I investigate four types of behaviors in *R. roxellana*: sexual behavior, allogrooming, inter-unit interactions, and the formation of new OMUs. I test the following predictions:

1) OMUs of *R. roxellana* are best described as a breeding unit since most sexual behavior (92%) occurs between members of the same OMU (Zhang et al. 2006). If female choice plays a major role in restricting sexual behavior, female *R. roxellana* should solicit not only their leader male but also males from other OMUs. If, however, males are coercive and control females by preventing them from mating with extra-unit males, then virtually all copulations will involve resident females and the harem male.

2) If the cohesion of one-male units within multi-level societies is maintained through female-female bonds, allogrooming is expected to occur more frequently among female

members within OMUs than between females and the harem male. If OMU cohesion is maintained through female-male bonds, allogrooming is expected to occur more frequently between the harem male and adult females, or to increase during period of female sexual receptivity.

3) In order to maintain band cohesion and coordinate the movement of different OMUs, notifying behaviors are expected to occur between members of different OMUs. Notifying is defined as behaviors in which actors approach recipients, stare, suddenly turn and present their back, and then run away rapidly (Kummer 1968). Notifying behaviors have been reported in hamadryas baboons, which also form multi-level social structures (Kummer 1968, 1984, Abegglen 1984, Swedell 2006). Notifying behaviors are proposed as a way of coordinating the movement of different OMUs in hamadryas baboons (Abegglen 1984).

4) Grüeter (2009) proposed that coalition support of leader males against the threat of intruder or bachelor males is the driving force underlying the evolution of multilevel societies. Based on this hypothesis, harem leaders of several OMUs are expected to cooperate and act collectively to expel invading males (Grüeter 2009).

3.4 Methods

3.4.1 Field sites

Behavioral observations were conducted from September 2007 to August 2008 at Zhouzhi Natural Reserve (ZNR, 108°16´E, 33° 48´N) in China. ZNR is located on the northern slope of the Qinling Mountains, China. There are approximately 40 bands of *R. roxellana* distributed in the Qinling Mountains (Li et al 2003). Logging and hunting have been prohibited at ZNR since 1984. The habitat at ZNR consists of temperate broadleaf deciduous forest

(1,400-2,200m), conifer broadleaf mixed forest (2,200-2,600m), and coniferous forest at altitudes (above 2,600m) (Li et al. 2000). The average annual temperature is 10.7ºC with the highest temperatures in July (31.5ºC) and the lowest in January (-14.3ºC) (Qi et al. 2008). The average annual rainfall is 894 mm (Qi et al. 2008).

A research team from Northwest University, China, has been conducting studies of the ecology, demography, home range use, mating system, and social organization of *R. roxellana* at ZNR since the early 1990's (Li. et al. 2000, Li et al. 2003, Zhao et al. 2005, Zhang et al. 2006, Qi et al. 2008). In order to assist in habituation, individual identification, and behavioral observations, in 2001 researchers initiated a program of provisioning one band of about 100 individuals. This band is referred as the West Ridge band (Zhang et al. 2006). Food provided included corn and radishes, which can be obtained locally. In order to avoid making the band overly dependent on provisioning, the amount of food provided was less than 200g of food per adult individual per day (Zhang et al. 2006). The average weight of adult male *R. roxellana* is 19.8kg and the average weight of adult females is 12.4kg (Jablonski and Pan 1995). Thus, 200g represents approximately 1.6% of female weight and 1.0% of male weight. The provision site is located in a valley within their home range. Provisioning was concentrated in the fall and spring. On average, food is provided 10 days every month from September to December and from March to May. Food is provided two times a day, at 10 am and at 2pm. The band forages freely during other times of the day.

3.4.2 Behavioral observations

In this study, I chose the West Ridge band as my focal band. During the observation period (from September 2007 to August 2008), this band consisted of 11 OMUs and approximately 125 individuals. The age and sex composition of this band is given in Table 3.5.

Adult males are easily distinguished from adult females by their larger canines, longer back fur, and larger body size (Liang et al. 2001). In order to assist in individual identification, I spent the first month of my fieldwork marking as many individuals as possible using a nontoxic dye, Nyanzol-D. The dye was sprayed on the monkey's body using a water gun. This dye has been used to mark black-and-white colobus monkeys (*Colobus vellerosus*), and was found to have no effect on individual behavior (Teichroeb et al. 2005). The mark generally lasted more than 5 months, and I repeated the marking process when necessary. For the final six months of data collection, I was able to identify all focal individuals based on their individual physical characters, such as crown shape, fur color, and length of back fur.

Three OMUs were selected for intensive focal animal observations. They were JB OMU (having the most detailed pedigree information based on birth records, indicated in Table 3.5), PK OMU, and LP OMU. All OMUs were well habituated to the presence of observers. The adult males and females of these OMUs served as focal animals for this study (3 adult males, 13 adult females in total). Focal adult females were named by their leader male's name and a number, such as JB1, JB2, and LP1. Their nicknames used by observers at ZNR are indicated in Table 3.6.

During the observation period, one guide followed the focal band until dusk and located their sleeping site. Once I located the focal OMU, I started recording data. The total observation hours of JB OMU were 348 hours (58 days), the total observation hours of LP OMU were 240 hours (40 days), and the total observation hours of PK OMU were 228 hours (38 days) (Table 3.6). A field assistant helped in recording behavioral data. Behaviors were recorded using an instantaneous focal animal sampling method at 2 minutes intervals (Altmann 1974). The information collected included the identity of focal animal, time of the day, activity pattern (rest,

travel, forage, feed, and unknown), and location (canopy level, ground).

Social interactions (huddling, infant care, groom, coalition support, stare, chase, fight, displace, submit, solicitation, copulation, and unknown) were recorded *ad libitum*. I recorded the type of social interactions, the direction of the social interaction (e.g. A grooming B or B grooming A), and any change in direction. I also recorded the initiator of social interactions, and the starting and ending time of each grooming bout to the nearest half minute. Grooming bout length was timed using a stopwatch. The definitions of behaviors used in this project are list below:

Allogrooming: one individual grooming or being groomed by another individual

Initiator of grooming interactions: If two partners are sitting near each other before grooming, the individual that first grooms its partner was denoted as the initiator. If two partners were not sitting together before the grooming began, the individual who approached its partner was considered the initiator of grooming even if that individual was groomed first.

Grooming bout: A grooming bout began when one partner approached another and initiated grooming. Grooming interactions ended when the groomer stopped grooming or one partner left the area. Sometimes grooming ended but the two partners continued to sit near one another. If grooming resumed within 1 min, I considered this as a single grooming interaction. If grooming resumed after 1 min, I considered these as separate grooming interactions.

Huddle: Two or more individuals are in contact.

Alliance Support: One individual provides assistance to another who is involved in an aggressive interaction with a third group member

Stare: Move head toward the opponent's direction, and stare at it for several seconds

Chase: Run after another individual aggressively

Fight: Aggression with direct physical contact

Submission: Any gesture or posture showing submission to recipients. This included head bowing and neck bending.

Solicitation: An individual is observed to invite another individual to engage in sexual behavior. According to Ren et al. (2000) solicitation in Sichuan snub-nosed monkeys is characterized by head bowing, and bending the neck and body.

Copulation: Sexual intercourse

Other: Behaviors not listed above.

(Note: Submission and female solicitation do look similar. I distinguished them by context. Those that occurred after a conflict were considered submission. Those that were followed by a copulation are considered solicitation)

3.5 Results

3.5.1 Sexual behavior and birth record

I recorded 90 solicitations during my observation period (Table 3.7). In all cases a female solicited a leader male. Sixty-eight involved four adult females of the JB OMU (JB2, JB4, JB4, and JB5). Nine involved two adult females of the LP OMU (LP1 and LP2). Thirteen involved two adult females of the PK OMU (PK3 and PK4). The low frequency of solicitations in LP and PK OMUs is likely a result of the fact that these OMUs were observed principally from March to August or during nonmating periods. *R. roxellana* is a seasonal breeder, with the mating season from September to December (Yan and Jiang 2006, Qi et al. 2009).

Five females (JB3, JB4, JB5, PK1, and PK3) gave birth in March or early April 2008 (Table 3.7). Based on the birth dates and gestation length of *R. roxellana* (about 200 days, Yan and Jiang 2006), the conceptive date for each female was estimated. Based on the date of conception, all the solicitations observed by females JB3, JB4, JB5, and PK3 (PK1 was not observed to solicit males from March to August 2007) occurred after they were already pregnant. Thus, as reported in Qi et al (2011) female *R. roxellana* solicit copulations during both fertile and non fertile periods.

Six females did not give birth in 2008. These females had reproduced in 2007. Giving birth every two years is a common pattern in *R. roxellana* (Qi et al. 2008). However, if their infants died before they reached 5-months of age, females usually will give birth the following year. This occurred in adult female JB3 and PK1. The infants of JB3 and PK1 died in 2007 and both females gave birth in 2008. Two females (JB2 and PK2, >10 years old) didn't give birth in either 2007 or 2008. One female (JB4) gave birth in both years and both of her two offspring survived.

Virtually all solicitations (88 of 90) were initiated by females. In the two remaining cases the initiators were unclear. Coerced mating by males was not observed. Most solicitations (N=89) occurred between females and their leader males. In the remaining case, adult female JB3 solicited another leader male (the name of this male is uncertain because I did not have the opportunity to see his face and crown and I could not identify him). When JB3 solicited the extra-unit male, other members of the JB unit were approximately 30 meters away from JB3. The extra-unit male ignored JB3's solicitation. JB3 then quickly returned to her unit. None of the members of the JB OMU showed aggressive behavior toward JB3.

3.5.2 Allogrooming

Allogrooming principally occurred between members of the same OMU. On average, *R. roxellana* spent 9.5% (±3.7, N=16) of their time allogrooming adult members of the same OMU. In total, I recorded 1,768 grooming bouts. Mean grooming bout length was 7.3±8.6 min. Twenty-six percent of allogrooming occurred between adult females and the leader male (13 male/female dyads), and 74% occurred between adult females (22 female/female dyads). The average length of female-female grooming bouts was significantly longer than that of male-female grooming bouts (male-female grooming bout: 5.99±6.62min, n=461; female-female grooming bout: 7.78±8.94min, n=1302; T-test, $p<0.01$).

The leader male did not distribute his grooming evenly among female members of his OMU (Table 3.8). Leader males tended to interact extensively with two or three females in his OMU. For example, leader male JB spent 50% of allogrooming time (863.6 mins) with JB3 and 35% of allogrooming time (598.1 mins) with JB1 ($\chi^2=1527$, df=4, $p<0.001$). However, JB only spent 5.5% (97 mins), 4% (77.5 mins), and 5.5% (97mins) of this allogrooming time with JB2, JB4, and JB5 respectively. Leader male PK spent 35% of allogrooming time (199.7mins) with PK1 and 28% (157mins), 27% (155mins) and 10% (59.1mins) of allogrooming time with PK2, PK3, and PK4, respectively ($\chi^2=74$, df=3, $p<0.001$). Leader male LP spent 46% of allogrooming time (197.1mins) with LP4 and 26% (109mins), 16% (69.5mins) and 12% (51mins) of allogrooming time with LP2, LP3, and LP1, respectively ($\chi^2=119$, df=3, $p<0.001$). However, leader male allogrooming preferences towards a particular female were not correlated with the number of copulations that occurred between the leader male and the female (Pearson's correlation test, $p>0.05$). On average the leader male groomed females less than he was groomed by females (the ratio was 1: 0.63±0.34, one sample T test (one tailed) t=-3.57, df=12, $p<0.01$, Table 3.8).

Similarly, adult females did not distributed their grooming evenly among potential partners (Table 3.9a, chi-square test, $p<0.001$). For example, in the JB OMU, JB1 spent most of her allogrooming time (36%) with JB4, 26% with JB, 18% with JB5, 12% with JB3, and 11% with JB2. JB2 spent most of her allogrooming time (42%) with JB3, 19% with JB1, 17% with JB4, 16% with JB5 and 7% with JB. However, in some cases the preferred partner was the leader male. For instance, JB3 spent most of her allogrooming time (39%) with the leader male JB, 27% with JB2, 13% with JB1, 13% with JB5, and 8% with JB4. Similar patterns can be found in other females of the JB OMU and females of the LP and PK OMUs (Table 3.9b). Taken together, adult females were found to concentrate their grooming on one or two individuals within the OMU, either other adult females or the leader male.

3.5.3 Inter-unit interactions

Direct physical interactions between members of different OMUs, either affiliative or agonistic, were infrequent. This occurred despite the fact that OMUs were in close proximity. For example, the focal OMU had another OMU within a 15m distance during 100% of observations (N=816 hours). Nevertheless, I observed only 50 cases of inter-unit agonistic interactions (Table 3.10, agonistic interactions that occurred at the provision area were not included in this analysis because they are likely to have been the result of provisioning). Thus, the overwhelming nature of intra OMU social interactions was tolerant and peaceful. The rate of inter-OMU agonistic interactions was once every 16 hours of observation per OMU. Most cases (N=48) were initiated by leader males, and only two cases were initiated by adult females. In 13 cases (10 chasing and 3 fighting), females supported their leader male during inter-unit aggression.

Fighting between individuals from different OMUs occurred on only 9 occasions. Most of these fights (N=8) occurred between leader males over food (N=4) or due to members of

different OMUs coming into close proximity (less than 3m) (N=2). One fight occurred between a leader male (BZT) and two adult females (JB1, JB4) of JB OMU. The reasons for the remaining two fights are unknown. The remaining 41 cases of intergroup agonistic interactions included 2 cases of females chasing females, 18 cases of leader males chasing females, 8 cases of leader males chasing other leader males, 8 cases of leader males chasing juveniles, and 5 cases of leader males staring at juveniles. The reasons for these aggressive interactions were either over food (N=8) or due to members of different OMUs coming into close proximity (N=19). In 14 cases, the cause of aggression was unknown.

I observed six cases of affiliative interactions between members of different OMUs (once every 136 hours per OMU) (Appendix A). Among the 6 cases of affiliative interactions, one case involved allogrooming between adult female HG (BB unit) and her former leader male (LP). Two cases involved allogrooming between adult female HG (BB unit) and adult females ZT and KT (LP unit). These females had previously been members of the same unit. The other two cases involved allogrooming between adult female XC (HT unit) and adult females BJ (PK unit) and HJ (PK unit). Each of these grooming bouts started and ended peacefully without aggression between members of the two units. The remaining case involved an adult female of FP unit who was interested in the infant of another female (DB unit) and attempted to touch it. Both the mother and the infant screamed and the leader male FP threatened the female. She left the area.

3.5.4 Formation of new OMU

I did not observe the entire process of the formation of a new OMU. However, I observed different phases of this process.

Phase I: New males approach an OMU and attempt to bond with its female members

On August 13, 2008, an unknown adult male was observed to follow an adult female of

the LP OMU (LP3) at a distance of 4m. ZT was 5m away from other members of the LP unit, but followed their travel path. The harem male LP was not observed to attack the unknown male. My observation ended the next day. Subsequently, observation of BN20 was continued by the Northwest University research team and ZT was observed to leave the LP unit and follow the new male in September 2008 (S. Guo, personal communication).

Phase II: A lone male attempted to form a relationship with a harem female. However, the lone male was defeated by the resident male.

From May 16th to 20th, 2008, an unknown adult male followed adult female LP3 and maintained a distance of 5m from her. LP3 was 20-50m away from the LP unit. LP3's one year old juvenile traveled back and forth between LP3 and the LP unit. Other residents in the LP unit groomed the juvenile. On May 20, the harem male LP chased the unknown male. He left the area. The following day (May 21), LP3 was observed in close proximity with the other members of the LP unit, and groomed two adult females of the LP unit (LP1 and LP4).

Phase III: Females leave their former OMU and start following a new leader male.

In October 2007, four sub-adult females (unknown origin, because sub-adults females are difficult to recognize) were observed to follow a new adult male BB. BB was first observed in the vicinity of the all-male group at the beginning of September 2007. On November 2007, an adult female of LP's unit (HG) left her unit and began to following BB and became part of this OMU.

In both cases of lone males attempting to attract females from existing OMUs, leader males from different OMUs were not observed to cooperatively attack the invading male. However, the adult female who was attracted to these lone males was the same individual (LP3). During these events, LP OMU had 4 adult females, and was not the largest OMU (the JB OMU

had 5 adult females.). All adult females in the LP OMU, including LP3, had a one-year independent infant. The mtDNA haplotype of LP3 was **c** (detailed genetic data are presented in chapter 4), which is the same haplotype as LP, LP1, and LP4 (but different from LP2, **a**). Thus, avoidance of female mating competition and absence of maternal relatives within the OMU were unlikely to be reasons why LP3 chose to leave her resident OMU. Given limited information available and the small sample size, the driving force of female dispersal remains unclear.

3.6 Discussion

3.6.1 OMUs as independent breeding units

The results of this study are consistent with other behavioral observations that sexual behavior in *R. roxellana* was primarily restricted to females and the leader male of her OMU (Zhao et al. 2005, Zhang et al, 2006, Qi et al. 2011). Copulations were initiated by female solicitation, which is a common feature of Asian colobines (Kavanagh 1978, Newton. 1987, Ren et al. 1995, Murai 2006). Extra-OMU copulations were uncommon (Zhao et al. 2005, Qi et al 2011). In this study, I observed only one case of a female soliciting an extra-OMU male. The solicitation was not responded to by the extra-OMU male. The harem male did not observe this interaction. Qi et al. (2011) reported 29 cases of extra-OMU copulations within Band 20 during the mating season of 2007. However, in virtually all cases (27/29), either the female's leader male (17 cases) or adult females and juveniles from the non-resident OMU (10 cases) interfered with the copulation (Qi et al. 2011). Due to these interruptions, only 6 extra-OMU copulations were successful (Qi et al. 2011). As in the case of OMU copulations, extra-OMU copulations (28/29) were initiated principally by females (Qi et al. 2011). These results indicate that although females occasionally solicit copulations from extra-OMU males, these solicitations are generally

not successful as both the harem male and resident females actively attempt to disrupt the copulations.

Contrary to these behavioral observations, a recent genetic study suggests that among 21 immature individuals of Band 20 (6 sub-adults, 12 juveniles, and 3 infants), 57% of them (N=12) were sired by a male who was not currently the harem male (Guo et al. 2010). This result questions the idea that the OMU functions principally as a breeding unit. However, reasons other than extra-OMU copulations may explain some of these genetic results. For instance, immature individuals transfer between OMUs (Qi et al. 2009). Qi et al. (2009) reported that 34.6% of sub-adults (N=9) transferred between OMUs and 12.5% of females (N=9) dispersed from their natal OMUs with independent infants. This would result in the fact that juveniles and infants within the OMU were not sired by the leader male. Therefore, the effectiveness of extra-OMU copulation needs further investigation.

The results of this study also suggest that female snub-nosed monkeys continue to solicit/copulate with the leader male after they became pregnant. A captive study of 4 adult female *R. roxellana* living in one OMU indicates that the post-conceptive copulations were more frequent than pre-conceptive copulations and continued throughout the entire mating season (from September to December) (Yan and Jiang 2006). Post-conceptive copulations are not a unique feature of *R. roxellana*. It has been reported in many other primates including Asian colobines such as the Hanuman langur (*Semnopithecus entellus,* Sommer *et al.* 1992). Sommer et al (1992) proposed that post-conceptive copulations were a strategy adopted by female langurs to deplete the leader male's sperm and decrease the reproductive opportunities of other females within the same harem. However, the captive study of *R. roxellana* indicated that despite the high frequency of post-conceptive copulations, all of the four adult females conceived during their

first menstrual cycle of the mating season (Yan and Jiang 2006). Yan and Jiang (2006) proposed that post-conceptive copulations might be a way to enhance the bonding between females and leader males. This is likely to be important in wild populations because adult females may have increased opportunities to mate outside their OMU or to migrate into a new OMU.

3.6.2 OMUs as independent social units

Even though OMUs of the same band travel, forage, and rest together, OMUs of *R. roxellana* are best considered socially independent. During the course of this study, only 6 affiliative interactions occurred between members of different OMUs. Inter-unit agonistic interactions also were uncommon (N=50 cases). Although leader males do not aggressively herd females, they appeared to play an important role in maintaining the cohesion of the OMU. For instance, most aggressive interactions between members of different OMUs were initiated by the leader male when members of other OMUs, either adult females or juveniles, came into close proximity to members of his OMU.

Notifying behaviors reported in hamadryas baboons, which are proposed to coordinate the movement of different OMUs (Kummer 1968, Abegglen 1984) were never observed in *R. roxellana*. This raises the question of how different *R. roxellana* OMUs coordinate their behavior. In other Asian colobines, males exchange long calls during inter-group encounters, which can be heard 500m away (van Schaik et al. 1992, Steenbeek 1999). Play back experiments indicate that male pig-tailed langurs (*Simias concolor*) used long calls to maintain inter-group separation (Tenaza 1989). Adult male *R. roxellana* also make long calls, described as whining calls, according to a captive study (Tenaza et al. 1988). Although I did not collect systematic data on vocalizations in *R. roxellana*, long calls were frequently heard when the band was traveling and foraging. It is possible that *R. roxellana* use vocal communications to initiate and coordinate

traveling and foraging movements.

The majority of affiliative interactions in *R. roxellana* were restricted to members of the same OMU. Compared with most other Asian colobines (range: 0.1-11%, Table 3.1), *R. roxellana* spend more time (9.5%) engaged in direct social interactions. *R. roxellana* males also are actively involved in affiliative social interactions with adult females, which is not commonly reported in other Asian colobines (Table 3.2). Among the 1,768 grooming bouts observed in this study, 26% occurred between adult females and her leader male (♂ -> ♀ :15%, ♀ -> ♂ :59%, mutual: 26%). The average length of intersexual allogrooming bouts, however, was shorter than that of female-female allogrooming bouts (5.99 min vs. 7.78 min). In addition, *R. roxellana* females provided support to the leader males during inter-unit encounters. Such behavior has not been reported for other female Asian colobines (Table 3.4). During the course of this study, the focal females participated in one fourth of the inter-unit encounters (13 out of 50 cases) by forming a coalition with the leader male. In conclusion, OMUs of *R. roxellana* appear to be socially more cohesive than the harem groups formed by other Asian colobines.

3.6.3 Bachelor threaten hypothesis

Grüeter (2009) proposed that the collective benefits that leader males gain through cooperatively repelling bachelor males was the driving force of aggregation of OMUs in snub-nosed monkeys. He predicted that the leader males of different OMUs would cooperate and act collectively to expel bachelor males when they attempt to take over an OMU. However, the results of this study did not support his prediction. During the course of this study, I observed only two cases of new males attempting to attract females from an existing OMU. Coalitions among leader males acting against new males were not observed. In fact, the formation of a new OMU in *R. roxellana* is generally not the results of aggressive male takeovers. Band 20 has been

intensively studied since 2001. However, only one takeover has been documented and in this case the harem male did not receive coalitionary support from other leader males (Wang et al. 2004). Since 2001, five new OMUs (PK, RX, HT, BB, and an unnamed one) have formed in Band 20 through a gradual process (Guo 2007, Qi et al. 2009, this study). The gradual process began when a bachelor male approached and followed an OMU, and then some of the females left their former OMU and followed the new male (Guo 2007, Qi et al. 2009, this study). Observations of the formation of two OMUs suggest that the entire process may take only 9 to18 days (Guo 2007). Thus, current evidence of behavioral observation did not support the "bachelor male threat hypothesis".

3.6.4 Alterative hypothesis of forming multi-level societies

The results of this study indicate that the aggregation of socially and sexually independent OMUs in snub-nosed monkeys is facilitated by tolerance of spatial proximity by leader males. Harsh habitats are believed to play a critical role in tolerance among leader males (Kirkpatrick 1998, Bleisch et al. 1993, 1998, Kirkpatrick and Grueter 2010). Compared with other Asian colobines, the habitats of *R. bieti, R. roxellana,* and *R. brelichi* are characterized by significantly lower annual temperature (11ºC vs. 24.5ºC degree) and lower population density (8.3 vs. 45individuals/km2) (Chapter 2), which suggests the possibility of extreme seasonal variation in food availability and highly clumped feeding sites. *R. avunculus* live in forests at lower altitude (200-1200m) with higher average annual temperature (22 ºC degree) (Boonratana and Le 1998) than other *Rhinopithecus* species. Accordingly, the multi-level societies of *R. avunculus* are reported to be less cohesive than other snub-nosed monkeys (Boonratana and Le 1998). However, the mechanism of how a multi-level social structure facilitates the survival of snub-nosed monkeys in unfavorable habitats remains unclear.

Kirkpatrick (1998) proposed a hypothesis arguing that through foraging together, single OMUs could avoid visiting food patches that have already been depleted by other OMUs. The ranging patterns observed by Li et al (2010) are consistent with Kirkpatrick's prediction (1998). Li et al. (2010) observed that in summer, when the diet of *R. roxellana* is composed principally of young leaves, flowers, fruits, and mature leaves, the band never used the same area on consecutive days. Ranging in *R. roxellana* is characterized by a pattern of movement in which the entire home range is crossed about every 10 days. Grueter (2009) used the word "seminomadic" to describe this kind of ranging pattern. In winter, when lichen, bark, and oak acorns, and one plant species (*Quercus aliena*) were the major components of their diet (87%, Guo et al. 2007), the different sets of OMUs foraged in separated areas of the home range and stayed at the same areas for about 10 consecutive days and then traveled to another area to eat (Li et al. 2010). In addition, *R. roxellana* use different areas of the home range during summer and winter (Li et al. 2010). Li et al. (2010) reported that only 4.4% of summer habitats also were used during the winter. At present it is likely that in order to obtain enough food across the whole year, OMUs of *R. roxellana* have to occupy a large home range, some 20 km^2. In fact, the home range area/per individual for snub-nosed monkeys is the largest among Asian colobines (11.5 hectare/individual vs. an average of 6 hectare/individual, Chapter 2). Taken together, seasonal variation in food availability, low overall food productivity, but locally concentrated resources appear to play a critical role in the formation of multi-level societies in *R. roxellana.*

3.7 Conclusion

The results of this study indicate that the OMU of snub-nosed monkeys largely represents a socially and sexual independent unit within a multi-level society. Affiliative and sexual

interactions were principally restricted to members within the same OMU, although opportunities for female mate choice occur. Females do occasionally solicit other leader males. However, the majority of extra-OMU copulations were interrupted by the female's leader male or females of the extra-OMU male. Compared with the harems of other Asian colobines, the OMU of snub-nosed monkeys is highly cohesion. This is due to the fact that members of the OMU spend more time allogrooming than in other Asian colobines, leader males actively allogroom adult females, and females provide support to the leader male during inter-OMU conflicts. The leader male plays a critical role in maintaining the cohesion of OMU. He aggressively attempted to prevent extra-OMU copulations and was observed to attack and chase members of other OMUs if they get too close to OMU members.

The aggregation of independent OMUs to form a multi-level society is likely due to the tolerant of spatial proximity of harem males during feeding, traveling, and resting. The observational results of this study and others did not support the "bachelor male threat hypothesis", because coalitions among leader males against invading males were not observed. Seasonal variation in food availability and overall low food production are likely to play a critical role in evolution of multi-level social structure of snub-nosed monkeys.

Table 3.1 Social time of Asian colobines. (Adapted from Kirkpatrick (2007) and Grueter (2009))

Species	**Social time**
P. entellus	6% (Kanaha) 6.5% (Jodhpur) <2% (Gir)
P. femoralis	1.5%
P. siamensis	Rare
P. rubicunda	Rare
P. potenziani	<2%
P. achates	4%
P. schistaceus	7%
Trachypithecus. johnii	0.1%
T. pileatus	0.4% 1.9%
T. phayrei	7.2%
T. leucocephalus	11%
T. Francoisi	2%
N. larvatus	2.2% (Kinabatangan/Sukai) Rare (Tanjung Putting) Rare (Samunsam)
Pygathrix nigripes	2.4%
R. bieti	8.4%
R. avunculus	5.6%

Table 3.2 Distribution of allogrooming among group members in Asian colobines.

Species	M	F	% allogrooming	Reference
Nasalis larvatus	Male never groomed other individuals, and received grooming 1 out of 252 scans	Adult females direct their grooming toward other adult females (17.3%), juveniles (34.1%), and infants (48.6%) of grooming scans).	2.2	Yeager 1990ab Matsuda et al. 2009
Presbytis entellus	Male-female grooming bout every 900.8hr Female-male grooming every 39.4 hr. Male-female grooming length are shorter (2.4min)	Female-female grooming bout every 5.7 hour Females received 2.8% of their grooming from males Female-female grooming length are longer (5.9min)	6	Borries et al. 1994
Trachypithecus Francoisi	29.9% grooming bout	61.1% grooming bout	2	Zhou et al. 2006

Table 3.3 Sexual behaviors in Asian colobines.

Species	Sexual behaviors	Solicitation	Reference
Simias concolor	Female sexual swelling	-	Tenaza 1989
Pygathrix nemaeus	Females initiated sexual solicitations	"A female douc would sex-present by flexing all four limbs and pressing her ventrum against the substrate. The head was kept raised. The base of the tail was raised slightly, with the remainder of it hanging down. The peritoneum was oriented towards the partner."	Kavanagh 1978 p107
Nasalis larvatus	Solicitation M/F: 172/87	"A male would solicit a female with a pouted face, and when the female was more than 5 m away from him, he would often utter the sound ''aoh aoh'' prior to solicitation. A female would solicit a male with a pouted face, and sometimes shake her head from side to side. She would then approach him, turn her back, and wait for him, and while waiting she would frequently look back with a pouting face."	Murai 2006 P 834
Presbytis entellus	Females initiate solicitations	"A female presents her rump toward a male with or without concurrent rapid lateral head shaking,"	Newton. 1987 P204
R. roxellana	Females initiated 95% sexual solicitations in captivity	"solicitation began with the female glancing at the male for eye contact and running a short distance away. Usually the male responded with a typical facial expression characterized by a wide opening of the mouth. Then the female prostrated herself on the perch or on the ground. The posture of prostration entails lying on the perch ventrally with the head hanging down, the forearms stretched out or bent, the legs curled up and the tail dropping down freely. "	Ren et al. 1995 P837

Table 3.4 Inter-group encounters of Asian colobines (Adapted from van Schaik et al. 1992)

Species	Site	Home range over lap (%)	Encounter Frequency (#/hr)	Agonistic or Avoidance	Long Call (M/F)	Involvement of females	Reference
P. aygula	Kamojang	9	0.0352	+	M	-	Ruhiyat 1983
P. cristata	Pangandaran	23		+	M		Kool (1989)
	K. Selangor	2	0.0255	+	M	-	Bernstein (1968)
P. melalophos	K. Lompat	19	0.0020	+	M	-	Curtin (1980)
	S. Tekam	24			M		Johns (1983)
	Perawang	31	0.0550	+	M	-	Megantara (1989)
P. obscura	K. Lompat	3	0.0028	+	M	-	Curtin (1980)
P. rubicunda	G. Palung	12	0.0342	+	M	-	Salafsky (1988)
	T. Putting	14			M		Supriatna et al. (1986)
	Sepilok	10	0.0045	+	M	-	Davies (1984)
P. thomasi	W.Ketambe	28	0.0205	+	M	-	Assink & van Dijk (1990)
	Bohorok	23	0.0072	+	M		Gurmaya (1986)
	W. Ketambe	34	0.0251	+ (37%)	M 95%	-	Steenbeek (1999)
P. Johnii	Ootacamund		0.0784	+(86%)	M	-	Poirier 1968
P. pileata	Madhupur	84	0.96/12=0.06 Once per day	+	-	-	Stanford 1991
Simias concolor	Pagai Lslands			+ call	M	-	Tenaza 1989
Nasalis larvatus	Sarawak	100	At least once per day	-			Bennett and Sebastian 1988

Table 3.5 Age and sex composition of the habituated band at Zhouzhi Natural Reserve, Shaanxi, China. May 2008.
The first three OMUs are focal OMUs. Transfer records were adapted from Qi et al. (2009) and Guo (2007).

OMU	Adult male	Adult female	Sub-adult female	Juvenile (4yrs)		Juvenile (3yrs)		Juvenile (2yrs)		Infant (1 yr)	New Born	Total	Transfer records	Birth records
				M	F	M	F	M	F					
LP	1	4	0	1	0	2	2	0	1	4	0	15	Two adult females immigrated to Rui OMU at 2005	
JB	1	5	0	1	0	1	1	1	1	2	3	16	One adult female disappeared early 2007.	YL-XBC is mother-daughter. XBC and DBC are half siblings. YZM (8 yrs), XBC (7yrs), and DBC(7yrs) were born in this OMU, and reproduced.
PK	1	4	0	1	0	2	1	2	1	2	3-1	16	October 2003, Peng immigrated into the band as a solitary male.	
DB	1	4-1	0	2	0	0	1	2	2	3	1	15	One female disappeared in February 2008	
JZT	1	4-1	1	2	0	1	0	0	3	1	2	14	One female disappeared in February 2008	
BZT	1	3	0	3	1	1	1	1	1	2	1	15	Two adult females immigrated to Hei OMU at 2007	Two of the adult females (8 yrs) were born in this OMU and reproduced.
SY	1	2	1	0	0	0	0	0	0	0	0	4	OMU immigrated into the band in 2007.	

Table 3.5 (cont.)

OMU	Adult male	Adult female	Sub-adult female	Juvenile (4yrs)		Juvenile (3yrs)		Juvenile (2yrs)		Infant (1 yr)	New Born	Total	Transfer records	Birth records
				M	F	M	F	M	F					
BB	1	1	4	0	0	0	0	0	0	0	0	6	BB immigrated into the band in September 2007. Four sub-adult female join BB's OMU in September 2007, one female from Luo's unit join BB's unit in December, 2007	
HT	1	2	0	0	1	0	1	0	0	0	1	6	Two female from BZT emigrated into the Hei OMU in spring 2007	
FP	1	5	0	0	0	0	0	0	1	2	0	9		Two of the adult females (6 yrs) were born in this OMU and reproduced.
RX	1	3	1	0	0	0	0	1	1	1	2-1	9	Two adult females from Luo OMU joined this OMU in September 2005.	
Total	11	35	7	10	2	7	7	7	1	17	11	125		

Table 3.6 Observation period for each focal OMU.

OMU	OMU members	Observation days	Observation hours
JB	JB	2007 October 17-19; November 10-19; December 14-19 2008 January 14-19; February 28-29; March 1-4; April 2-7, 9; May 6-7, 15-16, 18, 20-21, 24; June 5, 10-12; July: 27-30; August 1, 5-6, 8	348 hours
	JB1(BD)		
	JB2(YL)		
	JB3(YZM)		
	JB4(DBC)		
	JB5(XBC)		
LP	LP	2008 March 15-19, 31; April 1, 2, 16-17, 29-30; May 1-2, 4-5; June 1-4, 6; July 27, 31; August 1-2, 4-6, 8, 11	240 hours
	LP1(KT)		
	LP2(JT)		
	LP3(ZT)		
	LP4(TH)		
PK	PK	2008 March 6-11; April 4-6, May 18-20, 25; June 1, 2-6, 10, 12; July 28-31; August 1-8, 11, 13-14	228 hours
	PK1(HJ)		
	PK2(BJ)		
	PK3(CM)		
	PK4(HS)		

Table 3.7 Sexual behaviors observed during the observation period.

OMU	Females	Date (copulations/solicitations)	Total (c/s)	Giving Birth in 2007	Birth date in 2008	Estimated date of conceiving
JB	JB1		0	Y	-	N
	JB2	Oct16 (2/2), Oct17(1/1) Nov10(2/2), Nov11 (1/1), Nov16(1/1)	8/8	-	-	N
	JB3	Oct17(1/1), Oct18(2/2) Nov13(1/1), Nov16(1/2), Nov17 (4/4), Nov18(0/unknown male), Nov19(2/2) Dec14(1/3), Dec 15 (1/1)	13/17	Y (infant died)	4/10	Sep.23rd± 15days/2007
	JB4	Nov16(0/1) Dec14 (1/2), Dec15(2/3), Dec16(1/1), Dec17(2/4), Dec18(3/3), Dec19(5/5)	14/19	Y	4/12-15	Sep.25th±15days/2007
	JB5	Nov10(1/1), Nov11(1/1), Nov12(1/1), Nov13(1/1), Nov14 (1/3), Nov 17(1/1), Nov18 (3/5), Nov19 (1/1) Dec15(2/2), Dec16(1/1), Dec17(3/3), Dec18(3/3), Dec19(0/1)	19/24	-	4/4	Sep.17th± 15days/2007
LP	LP1	May4(1/1), May5(1/2), Jun1(1/3)	3/6	Y	-	N
	LP2		0	Y	-	N
	LP3	Aug6(2/2), Aug8(0/1)	2/3	Y	-	N
	LP4		0	Y	-	N
PK	PK1		0	Y (infant died)	3/6-7	Aug.19th± 15days/2007
	PK2		0	-	-	N
	PK3	Jul28 (1/1), Jul 29(2/2), Jul30(1/1)	4/4	-	4/6	Sep.19th± 15days/2007
	PK4	Apr5(0/1), Apr6(0/1), Jun1 (0/1), Jun2(4/5), Jun3(0/1)	4/9	Y	-	N

Table 3.8 Allogrooming between leader males and adult females of the same OMU.

OMU	Female	Provide to male (min)	Receive from male (min)
JB	JB1	396.6	201.5
	JB2	80.1	17.1
	JB3	553.6	310
	JB4	47.5	30
	JB5	37	60
PK	PK1	144.2	55.5
	PK2	98	59
	PK3	87	68
	PK4	33.1	26
LP	LP1	26	25
	LP2	66	43
	LP3	31.5	38
	LP4	144.1	53

Table 3.9a Allogrooming occurred between adult members within each focal OMU.

JB OMU

	JB (min)	**JB1 (min)**	**JB2 (min)**	**JB3 (min)**	**JB4 (min)**	**JB5 (min)**	**Chi-square test (df=4)**
JB	-	598.1	97.2	863.6	77.5	97	χ^2=1527, p<0.001
JB1	598.1	-	263.5	291.5	775	216.5	χ^2=559, p<0.001
JB2	97.2	263.5	-	594.5	245	221.5	χ^2=482, p<0.001
JB3	863.6	291.5	594.5	-	169	298	χ^2=719, p<0.001
JB4	77.5	775	245	169	-	998.5	χ^2=1470, p<0.001
JB5	97	216.5	221.5	298	998.5	-	χ^2=1420, p<0.001

LP OMU

	LP	**LP1**	**LP2**	**LP3**	**LP4**	**Chi-square test (df=3)**
LP	-	51	109	69.5	197.1	χ^2=119, p<0.001
LP1	51	-	238.4	63.9	556.2	χ^2=730, p<0.001
LP2	109	238.4	-	404.3	403.5	χ^2=212, p<0.001
LP3	69.5	63.9	404.3	-	363.9	χ^2=451, p<0.001
LP4	197.1	556.2	403.5	363.9	-	χ^2=172, p<0.001

PK OMU

	PK	**PK1**	**PK2**	**PK3**	**PK4**	**Chi-square test (df=3)**
PK	-	199.7	157	155	59.1	χ^2=74, p<0.001
PK1	199.7	-	1474.5	370.5	430	χ^2=1625, p<0.001
PK2	157	1474.5	-	385	501	χ^2=1610, p<0.001
PK3	155	370.5	385	-	576.8	χ^2=240, p<0.001
PK4	59.1	430	501	576.8	-	χ^2=404, p<0.001

Table 3.9b Percentage of grooming provided by females to each possible partner within OMUs.

		Recipient (%)					
		JB	JB1	JB2	JB3	JB4	JB5
Provider	JB1	26%	–	11%	12%	**33%**	18%
	JB2	7%	19%	–	**42%**	17%	16%
	JB3	**39%**	13%	27%	–	8%	13%
	JB4	3%	34%	11%	7%	–	**44%**
	JB5	5%	20%	11%	15%	**49%**	–

		Recipient (%)				
		LP	LP1	LP2	LP3	LP4
Provider	LP1	6%	–	26%	7%	**61%**
	LP2	9%	21%	–	**35%**	**35%**
	LP3	8%	7%	**45%**	–	**40%**
	LP4	13%	**37%**	27%	24%	–

		Recipient (%)				
		PK	PK1	PK2	PK3	PK4
Provider	PK1	8%	–	**57%**	17%	18%
	PK2	6%	**57%**	–	15%	22%
	PK3	10%	25%	26%	–	**39%**
	PK4	4%	27%	32%	**37%**	–

Table 3.10 Agonistic interactions between members of different OMUs.

Case	Date	Time	Initiator	Coalition support	Receiver	Degree	Reason
1	5/20	13:10	LP unit		DB unit	avoid	LP unit passed by DB unit, DB unit retreat
2	5/20	14:57	LP		Unknown male	fight	Unknown males approach LP unit
3	5/20	15:03	PK		Juveniles of LP unit	chase	PK units pass by LP unit, PK chase juveniles of LP unit
4	5/16	14:06	JB	XBC	Juvenile of other unit	chase	Two units get two close (<6m) when traveling
5	5/15	13:47	LP		Unknown male	chase	Unknown males approach LP unit
6	5/16	11:54	LP		Unknown male	chase	Unknown males approach LP unit
7	5/16	12:39	LP		ZT	chase	ZT approach LP unit, (ZT follow unknown male since 5/15)
8	3/10	11:51	HS	PK	Females of nearest OMU	chase	Too close (<5m)
9	5/25	14:12	PK		Juveniles of BZT unit	stare	Over food
10	5/25	14:17	BZT		Females and juveniles of PK unit	chase	Over food
11	2/28	12:40	JB	YZM, XBC	Females of nearest unit (unclear)	chase	When feeding on oak seeds
12	2/28	10:58	JB		Females of nearest unit (unclear)	chase	When feeding on oak seeds
13	2/28	11:08	JB		Females of nearest unit (unclear)	chase	When feeding on oak seeds
14	2/28	11:10	Male of nearest Unit	Females of JB unit	JB	fight	When feeding on oak seeds
15	3/1	9:30	JB		Juveniles of BZT	chase	When feeding on oak seeds
16	3/1	9:57	JB		LP	fight	LP is too close to the females of JB unit
17	3/1	10:42	JB		BZT,JZT	chase	When feeding on oak seeds

Table 3.10 (cont.)

Case	Date	Time	Initiator	Coalition support	Receiver	Degree	Reason
18	3/3	8:51	JB	XBC	JZT	chase	Unknown
19	3/3	10:37	JB		JZT	chase	Unknown, JZT unit is JB unit's nearest neighbor
20	3/3	10:48	RX		DBC	chase	DBC got too close to RX unit.
21	3/3	13:49	JB		Juveniles of PK unit	chase	Foraging
22	3/4	9:34	BZT		BD,DBC	fight	BD and DBC got too close (3m) to BZT, resting
23	4/6	10:01	LP		JB units	stare	Feeding
24	4/6	13:45	JB		XC, HTP	chase	Traveling
25	6/10	16:46	JB		JZT	fight	Get too close on the feeding tree
26	6/11	11:05	JB		Juvenile of other OMU (unclear)	chase	Get too close
27	6/12	8:35	JB		FP	fight	Unknown
28	4/16	13:13	BZT		ZT	chase	Unknown
29	5/4	12:45	ZT		Juvenile of DB unit	stare	Get too close
30	5/4	14:36	BZT		KT	chase	Get too close (resting)
31	6/1	9:14	DB		Nearest OMU	chase	Get too close (resting <5m)
32	6/1	10:45	LP		Juveniles of DB unit	stare	Get too close
33	6/1	11:09	LP		PK	fight	Unknown
34	6/4	9:25	BZT	LP	TH, KT	chase	Unknown
35	6/4	16:39	JB	Females of JB	LP units	chase	Get too close
36	8/5	10:50	BZT	LP, TH, KT	Juveniles of LP	chase	Nearest unit
37	8/5	14:02	LP	TH,JT,KT	HT	chase	Get too close
38	8/8	11:17	HT		Juveniles of LP	stare	Get too close
39	8/8	14:20	JB	YL,DBC,XBC	HT	fight	Over food
40	6/2	16:25	Leader male (unclear)		CM	chase	Unknown

Table 3.10 (cont.)

Case	Date	Time	Initiator	Coalition support	Receiver	Degree	Reason
41	6/3	14:35	Females of PK unit		Females of other OMU(unclear)	Chase	
42	6/4	10:07	PK		Juvenile of other unit	chase	Get too close (<6m)
43	6/5	9:41	PK		Females of other unit	chase	Unknown
44	6/5	16:45	PK	Females of other unit	Male of other unit	fight	Over fruit tree
45	7/28	14:22	Leader male	PK, HJ, HS	BJ	chase	Unknown
46	11/14	16:42	JB		Juvenile of DB unit	chase	Unknown
47	11/17	16:35	JB		DB	chase	Get too close (when foraging, <5m)
48	11/18	16:17	JB		Females of DB	chase	Unknown
49	12/17	14:28	JB	BD,XBC,DBC	SY	chase	Get too close (traveling)
50	1/16	13:12	JB		Nearest OMU	chase	Unknown

CHAPTER 4: DISPERSAL PATTERNS OF *R. ROXELLANA* AS INDICATED BY OBSERVATIONAL AND GENETIC DATA

Unlike other Asian colobines in which females are philopatric and males disperse, both female and male *R. roxellana* are reported to disperse from their natal one-male unit (OMU) (Zhang et al. 2008, Zhao et al. 2008, Qi et al. 2009). The objective of this chapter is to present new information on the distribution patterns of mtDNA haplotypes among three neighboring bands of *R. roxellana*. Dispersal rates and dispersal distances of both male and female snub-nosed monkeys were estimated using genetic data. Combined with behavioral data, the social and environmental factors affecting dispersal decisions in snub-nosed monkeys are discussed.

4.1 Introduction

Dispersal represents a core feature of group living species because it is part of a process by which individuals that vary genetically move throughout the local population. Dispersal patterns also play a critical role in determining the degree to which kin and nonkin reside in the same social group (e.g. Hamilton 1964, Silk 2002). Depending on the distance traveled and the length of time it takes to successfully enter an established group, animals that disperse may face considerable costs associated with finding food and refuge in unfamiliar environments, increased predation risk by traveling alone, and injury associated with aggression received when attempting to join another group (Boinski et al. 2005, Ekernas and Cords 2007, Teichroeb et al. 2009). However, opportunities for dispersal also provide individuals with several benefits such as inbreeding avoidance, increased access to mating partners and mating opportunities, and a reduction in feeding and mating competition if the natal group contains a greater number of adults than is found in destination groups (Korstjens and Schippers 2003, Stokes et al. 2003, Jack

and Fegidan 2004ab, Boinski et al. 2005, Sterck et al. 2005, Stumpf et al. 2009, Teichroeb et al. 2009).

Although it has generally been assumed that among a majority of primate taxa, females are philopatric and males migrate from their natal group, there is a growing consensus that this is not the case (Jack and Isbell 2009). Dispersal is reported to female biased among many species of apes (e.g. *Gorilla gorilla*, Stokes et al. 2003, Robbins et al. 2009ab; *Pan troglodytes*, Stumpf et al. 2009; *P. paniscus*, Eriksson et al. 2006), and New World monkeys (*Brachyteles arachnoids*, Printes and Strier 1999, Strier and Ziegler 2000), or bisexual in some colobine monkeys (e.g. *Procolobus badius*, Struhsaker 1975, Marsh 1979; *Colobus vellerosus*, Teichroeb et al. 2009; *Presbytis spp,* Sterck 1997, 1998, Sterck et al. 2005; *Procolobus verus,* Korstjens and Schippers 2003; *Trachypithecus phayrei*, Koenig et al 2007, Borries et al. 2004; *Nasalis larvatus*, Murai et al. 2007), New World monkeys (e.g. *Saguinus mystax*, Garber et al. 1993; *Cebus capucinus*, Jack and Fedigan 2009; *Alouatta pigra*, Brockett et al. 2000; *A. palliata*, Clarke and Glander 1984, *A. caraya*, Glander 1992, Kowalewksi and Garber, 2010; *A. seniculus*, Pope 1992, Crockett and Pope, 1993; *Lagothrix poeppigii*, Di Fiore et al. 2009), and hamadryas baboons (*P. hamadryas*, Abegglen 1984, Hapke et al. 2001, Hammond et al. 2006). In contrast, female philopatry and male biased dispersal is common in several species of cercopithecine monkeys (Pusey and Packer, 1987) (e.g. *C. mitis stuhlmanni*, Ekernas and Cords 2007; *C. pygerythrus*, Cheney and Seyfarth 1983; *Macaca spp*. Melnick and Hoelzer 1992, Matsumura 1993, Kuester and Paul 1999; *P. cynocephalus*, Alberts and Altmann 1995), Asian colobines (*S. entellus*, Rajpurohit and Sommer 1993), and several species of lemurs (e.g. *Propothecus edwardsi*, Morelli et al 2009; *Microcebus ravelobensis*, Radespiel et al. 2009; *M. murinus*, Radespiel et al. 2003; *Lemur catta,* Parga and Lessnau 2008). Given species and population differences in sex-biased opportunities

of natal and secondary dispersal, a combination of behavioral observations and genetic data are needed to best understand the effects that particular dispersal patterns have on primate social organization, alliance formation, kin bonds, and partner preferences (Harris et al. 2009, Fuentes, 2011).

4.1.1 Observation studies

Studies examining dispersal patterns in primates can roughly be divided into two categories: observational studies and genetic studies. Observational studies provide detailed information on the age, timing, context, and number of dispersal events, as well as data on dispersal risk and the reaction of resident group members towards potential immigrants (e.g. *P. troglodytes*, Kahlenberg et al. 2008, Stumpf et al 2009; *G. gorilla*, Stoinski et al. 2009; *C. mitis stuhlmanni*, Ekernas and Cords 2007; *P. hamadryas*, Abegglen 1984, Swedell 2006; *P. cynocephalus*, Alberts and Altmann 1995; *A. palliata*, Clarke and Glander 1984, Glander 1992; *A. seniculus*, Pope 1992, Crockett and Pope 1993; *S. entellus*, Rajpurohit and Sommer 1993; *B. arachnoids*, Strier and Ziegler 2000; *C. capucinus*, Jack and Fedigan 2004ab, Jack and Fedigan 2009; *M. sylvanus*, Kuester and Paul 1999; *C. pygerythrus*, Cheney and Seyfarth 1983; *Lemur catta*, Parga and Lessnau 2008). According to these studies, emigration in nonhuman primates is generally characterized by three discrete patterns. These include: 1) noncoercive or voluntary dispersal; 2) coercive dispersal of juveniles, sub adults, or young adults by same sex adults; 3) dispersal in response to male takeover or attraction. In species such as chimpanzees (Stumpf et al 2009), blue monkeys (Ekernas and Cords 2007), Barbary macaques (Kuester and Paul 1999), Thomas langurs (Sterck 1997), grey-cheeked mangabeys (Olupot and Waser 2001), muriquis (Printes and Strier 1999, Strier and Ziegler 2000), white-faced capuchin (Jack and Fedigan 2004ab), and gorillas (Stoinski et al. 2009), dispersal appears to be voluntary or at least not the

result of coercion by other group members. Hormonal studies indicate that dispersing adult female chimpanzees and juvenile female muriquis do not exhibit higher cortisol levels than non-dispersing individuals (Stumpf et al 2009, Strier and Ziegler 2000). Given that increased cortisol levels are reported to be a marker of increased stress (Muller and Wrangham 2004), this suggests that in these species dispersing females may not be under greater physiological stress than resident females (Stumpf et al 2009, Strier and Ziegler 2000).

In contrast, in species such as mantled howlers (*A. palliata*, Clarke and Glander 1984, Glander 1992), red howlers (*A. seniculus*, Pope 1992, Crockett and Pope 1993), hanuman langurs (*Semnopitheaus entellus*, Rajpurohit and Sommer 1993), and Phayre's leaf monkeys (*Trachypithecus phayrei*, Koenig et al. 2006) juveniles are forced to leave their natal groups by the aggressive action of same sex adults. In hamadryas baboons, immature and mature females are reportedly forced to leave their natal one-male unit (OMU) by followers and solitary males (Pines et al. 2011 Swedell et al 2011).

Data on processes of immigration, including takeovers by invading males have been documented in many primate species (Rajpurohit et al. 2003, Davies 1987, Wolf and Fleagle 1977, Rudran 1973, Agoramoorthy and Hsu 2005). In many cases, resident individuals defend against same sex immigrants such as in female chimpanzees (*P. troglodytes*, Pusey et al. 2008, Kahlenberg et al. 2008, Pusey and Packer 1987, Nishida 1989), female mountain gorillas (*Gorilla gorilla beringei*, Watts 1991), male and female red howlers (*A. seniculus*, Pope 1992, Crockett and Pope 1993) and mantled howlers (*A. palliata*, Glander 1992). For example, during the process of attempting to join a new group, resident female mantled howlers were observed to chase, mob, and bite immigrant females (Glander 1992). Based on the observation of 31 immigrant events, Glander (1992) found that it took several months (6-12 months) until

immigrant females were accepted by resident females. The immigration process was aided by adult males who copulated with the immigrant female (Glander 1992). In contrast, in some species, immigrants are able to join a new group without resistance (Murai et al. 2007, Sterck 1997). For example, Murai et al. (2007) reported 4 cases of dispersal in female proboscis's monkeys (*Nasalis larvatus*) in which immigrants directly entered a new group without aggression. Similarly, Sterck (1997) reported one case of non-aggressive immigration of a female Thomas langur. Due to these limited number of cases, however, it remains unclear whether non-aggressive female immigration represents a common pattern among Asian colobines.

4.1.2 Genetic studies

Given that dispersal is a process that may take months or years to accomplish, a detailed understanding of the complete process is difficult to obtain using only behavioral information, especially on unmarked animals. In many cases, data on successful immigration and emigration events are based on opportunistic incidences of individuals entering an established group or the disappearance of group members. Genetic techniques offer a complementary tool to study dispersal processes, especially for estimating dispersal distances and rates (e.g. Hapke et al 2001, Kappeler et al. 2002, Wimmer et al. 2002, Bradley et al. 2004, Eriksson et al. 2006, Hammond et al. 2006, Douadi et al. 2007, Handley and Perrin 2007, Lappan 2007, Harris et al. 2009, Di Fiore et al. 2009). For instance, using data from 6 microsatellite loci located on the Y-chromosome and mtDNA sequences of 163 western gorillas from 6 sites distributed across an area of 6000 km^2 in the Republic of the Congo, Douadi et al. (2007) found that 59% of genetic variation among females occurred between sites, whereas all genetic variation among males occurred within sites. Although individuals of both sexes have been observed to disperse from their natal group

(Parnell 2002, Stokes et al. 2003), the results of Douadi et al. (2007) indicate that male gorillas disperse over longer distances (greater than 6 km), whereas female dispersal was more narrowly restricted to neighboring groups.

Similarly, Hammond et al. (2006) provide an example of how genetic analyses were used to estimate the degree of gene flow between social bands of hamadryas baboons. These authors sampled 298 individuals from 4 different populations distributed across Arabia. They calculated both male and female Fst values based on the genotypes of 17 autosomal microsatellite loci, one Y-chromosome loci, and the mtDNA d-loop sequence. Their results indicate that female biased gene flow was four times greater than male biased gene flow. This is consistent with behavioral observations indicating that female hamadryas baboons disperse between OMUs and bands whereas males are philopatric and remain within their natal bands (Sigg et al 1982, Abegglen 1984, Swedell et al 2011).

4.1.3 Behavioral evidence of female and male dispersal in R. roxellana

Sichuan snub-nosed monkeys (*R. roxellana*) represent one of five *Rhinopithecus* species (Geissmann et al. 2011). They are listed as endangered (IUCN, 2010), and are distributed in southwest China (Li et al. 2002). The current population size of Sichuan snub-nosed monkey is estimated to be between 15,000 and 16,000 individuals (Li et al. 2002). Due to deforestation and other forms of anthropogenic disturbance, these primates are restricted to three isolated mountainous areas (Li et al. 2002). The three isolated subpopulations are referred to as Sichuan-Gansu, Shaanxi, and Hubei subpopulations and contain approximately 11,000, 4,000, and 600 individuals respectively (Li et al. 2002). Li et al. (2007) investigated the genetic structure of these three subpopulations by comparing the first part of the d-loop region of mtDNA. They found no shared mtDNA haplotypes between any two subpopulations, which

suggests a long history of isolation and very limited gene flow across subpopulations.

Unlike other Asian colobine monkeys, in which males disperse and females are philopatric, both female and male snub-nosed monkeys disperse between bands, and females disperse between OMUs of the same band (Zhang et al. 2008, Qi et al. 2009). Most dispersal data concerning snub-nosed monkeys were collected through observing a habituated band living at Zhouzhi National Natural Reserve, Shaanxi (Zhang et al. 2008, Qi et al. 2009). Chapter 2 provided a detailed description of the results of these studies. In brief, juvenile males were observed to leave their natal OMU and joined an AMU at 3 or 4 years of age (Qi, personal comunication). From 2001 to 2008, nine adult males were observed to migrate into the habituated band to establish new OMUs, 31% of sub-adult females (8 out of 26) left their natal OMUs, and 53% of adult females (33 out of 64) dispersed at least once during their life time (Qi et al. 2009).

4.2 Hypothesis tested in this chapter

The objectives of this chapter are to present new data on mtDNA haplotype distribution patterns among three neighboring bands of *R. roxellana* and calculate the dispersal rate and distance of females and males between OMUs and bands using these genetic data. The following hypotheses are tested: 1) If females and males preferentially disperse to join non-neighboring bands, then mtDNA haplotypes among individuals within the same band are expected to show a high degree of sequence variation. 2) If females disperse among OMUs within the same band, then adult females residing in the same OMU are expected to exhibit different haplotypes whereas females with identical haplotypes are expected to reside in different OMUs. And, 3) if males and females transfer equally among bands, then a relatively equal proportion of males and females residing in different bands are expected to share the same mtDNA haplotypes. Shared

mtDNA haplotypes across bands also could reflect band fission events over the course of the species recent history. Combined with behavioral observation data, I discuss the social and environmental factors affecting dispersal decisions in snub-nosed monkeys.

4. 3 Methods

4.3.1 Study animals

This project focused on the Shaanxi subpopulation of *R. roxellana*. The Shanxi subpopulation is primarily distributed in the Qinling Mountains, and is composed of 39 social bands, each containing approximately 100 individuals. Fecal samples were collected from three neighboring bands, Band 19, Band 20, and Band 21 (also known as East Ridge band) as indicated in Figure 4.1. These three bands were located at the northeastern part of the *R. roxellana* distribution in Shaanxi province. The home ranges of Band 21 and Band 20 overlapped approximately 25% (Tan et al. 2007). The home ranges of Band 20 and Band 19 were assumed to overlap to a similar degree (Figure 4.1). Band 20 also was the subject of intensive behavioral observations from September 2007 to August 2008. Band 20 contained 11 OMUs and approximately 120 individuals during the observation period. Band 21 had approximately 110 individuals (Tan and Guo 2007). The group size of band 19 was estimated to be about 100 individuals.

Three out of 11 OMUs from Band 20 were observed regularly from October 2007 to August 2008 (observation time for each OMU is listed in Table 3.6). I conducted a census of the composition of the remaining 8 OMUs once each month. In order to assist with individual identification, I used a nontoxic dye, Nyanzol-D (Teichroeb et al. 2005) to mark the individuals from Band 20 at the beginning of behavioral observations in September 2007. The mark

generally lasted more than 5 months (personal observation). I repeated the marking process when necessary.

4.3.2 Fecal sample collection

Genetic data were obtained by extracting DNA from fecal samples collected from the ground. Along with behavioral observations, fresh feces from individuals in Band 20 were collected immediately after defecation and then labeled by date, time, location, as well as the name and sex of the individual. Fecal samples from bands 19 and 21 were collected by experienced field assistants. These two bands were not habituated to human observers. Field assistants followed them from a distance of about 200 meters and collected fresh feces left on the ground. Consequently, the age and sex of individuals voiding fecal samples from these two bands were not identified. For Band 19 and Band 21, fresh fecal samples separated by a distance of ≥2 meters were considered to be from different individuals. The feces were soaked in 15ml 97% ethanol right after collection (Nsubuga et al. 2004).

Forty five samples (11 harem males, 1 invading male, 27 adult females, and 6 sub-adult females) were collected from Band 20. I sampled all harem males, one of the 2 invading males, 27 out of 35 adult females, and 6 out of 8 sub-adult females. Twenty samples were collected from Band 21 (approximately 19% of individuals in the band). Thirty-four samples were collected from Band 19. Based on the assumption that Band 19 has 100 individuals, this represents approximately 34% of the individuals in Band 19.

4.3.3 Genetic analysis of the d-loop region of mtDNA

Samples were sent back to Zoological Institute of Beijing, China for genetic analysis. QIAamp DNA stool kits were used to extract DNA from fecal samples, following the protocol of isolation of DNA from stool for human DNA analysis (e.g. Morin et al. 2001). I designed three

pairs of primers to amplify the d-loop region of mtDNA, which is the most variable region of mtDNA (Kocher and Wilson 1991). The three pairs of primers can amplify a sequence of about 1000bp in total. The sequence, annealing temperature, and length of amplicon for each pair of primers are listed in Table 4.1.

PCR mixture (20ul) was composed of template DNA (2ul), dNTP mix (2ul, 4mM each), two primers (100uM, 0.1ul each), BSA (0.2ul), 1 unit DNA polymerase (Qiagen HotStarTaq Plus) with supplied 10×buffer (2ul), and nuclease-free water (14.5ul). PCR products were sent to Beijing Sinogen Company for purification and sequencing. Each sample was sequenced on both forward and backward strands. If the two sequencing results were not consistent, additional independent amplification and sequencing were conducted. The sequencing results were assembled and aligned using Sequencher 4.7.

4.3.4 Numts

In some species including primates, a part of the mitochondrial DNA inserts into the nuclear DNA, and this is called a Numt (Zhang and Hewitt 1996, Bensasson et al. 2001, Jensen-Seaman et al. 2004). Primers for real mitochondrial DNA can amplify the Numts during PCR (Bensasson et al. 2001). Numts can lead to false conclusions when inferring maternal lineages among individuals, because Numts can be inherited from either father or mother and the mutation rate of Numts is lower than mitochondrial DNA (Zischler et al. 1995).

Amplifying nuclear DNA from fecal material is possible, but difficult. In this project I tried to amplify microsatellite DNA from DNA extracted from fecal samples. However, using the protocol described above, it was virtually impossible to amplify useable PCR products for sequencing. For this reason, the sequences obtained through the protocol described above are assumed to be mitochondrial sequences, rather than Numts.

4.3.5 Sex determination

Sex of the individual voiding a fecal sample from Band 19 and 21 was determined through the Y-linked sex-determining region (SRY) gene (Di Fiore 2005). The amelogenin gene, which is located on both X and Y-chromosomes, serves as a control gene (Di Fiore 2005). I used two-step PCR reported by Arandjelovic et al. (2009) with slight modifications to amplify both the SRY gene and amelogenin gene. The PCR mixture of the first-step PCR is the same as the PCR mixture for amplifying the mtDNA d-loop region except I used a 5ul extraction production as template DNA. For the second-step PCR, I used 2ul of the first-step PCR product as template DNA and nested primers, which helped to increase the specificity of the PCR amplification. Then, the product of second-step PCR was run on an agarose gel. Since the SRY gene is located on Y-chromosome, only samples from male individuals have amplicons. However, samples from both males and females should have amplicons of the amelogenin gene. If a sample had no amplicons of either the amelogenin gene or the SRY gene, the sex of this sample was assigned as uncertain rather than female. The sequence, amplicon length, and annealing temperature of each pair of primers are listed in Table 4.2.

4.4 Results

4.4.1 Behavioral observation

During our observation period, there were 11 OMUs in Band 20 (Table 3.5). I observed one adult male (BB) from the all-male unit of Band 20 try to establish his own OMU. In October, four sub-adult females (unknown origin) were observed to follow BB. In November 2007, an adult female (HG) was observed to leave the LP OMU and follow BB. As a result, a new OMU was established. HG and the four sub-adult females remained in BB OMU until the observation

period ended in August 2008 (about 9 months).

I observed one solitary male (unknown origin) to join Band 20 in May 2008. From May 16 to May 20, 2008, this adult male followed an adult female (ZT) of the LP OMU, but maintained a 5m distance from her. At this time, ZT was 20-50m away from other members of the LP OMU. ZT's infant (about 1 year old) traveled back and forth between ZT and the LP OMU. Other resident females in the LP OMU groomed the infant. On May 20, the harem male of the LP OMU chased the male, who ran away. The following day (May 21), ZT was observed traveling and feeding with the LP OMU, and grooming two of its resident adult females (KT and TH).

I observed another solitary male (this could have been the same male, but since he was not marked, this cannot be determined) who joined Band 20 in August 2008. On August 13, 2008, this adult male was observed to follow ZT at a distance of 4m. At this time, ZT was only 5m away from other members of the LP OMU. The harem male LP was present, but was not observed to attack the intruder male. In September 2008, ZT was observed to leave LP OMU and follow the new male (Guo SG, personal communication).

Over the course of 9 months of field observations, I observed one case of female dispersal between OMUs of the same band (female HG from the LP OMU to the BB OMU). I observed four sub-females (4 years old) join the BB OMU (October 2007), and one sub-adult female (4 years old) join the PK OMU (August 2008). When these immigrantion events occurred, BB was a solitary male and the PK OMU contained 4 resident adult females. Since the origin of these sub-adult females remains unclear, I do not know if these were females natal to Band 20 or they were recent immigrants from another band. I also observed one adult female in the DB OMU to disappear from Band 20 in January 2008. There were four resident adult females in the

DB OMU before she left. She appeared healthy prior to her disappearance. Thus, I assumed she emigrated from Band 20 into another band. One adult female in the LP OMU disappeared in December 2007. Since that female had shed most of her back hair prior to her disappearance, I assumed she was ill and died. An adult female in the JZT OMU was found seriously injured in November 2007 and she died two days later. Since there was no evidence of bite marks on her, it is possible that her injures were the result of falling from a tree and landing on the rocks below. The composition of the remaining OMUs in Band 20 did not change during our observational period. Overall, the dispersal rate of adult individuals during our study was one male per year per band, 2 adult female per year per band, and 5 sub-adult female per year per band. These rates are similar to those found in other studies of *R. roxellana* (Zhang et al. 2008, Qi et al. 2009).

4.4.2 Distribution pattern of mtDNA haplotypes

Three distinct haplotypes were found among the 99 samples (DNA sequences for each haplotype are listed at Appendix B). These haplotypes, **a**, **b** and **c**, contain 3 variable sites, and the haplotype frequencies are 63% (n = 63), 29% (n = 28) and 8% (n = 8), respectively. All of the samples (N=20) from Band 21 were haplotype **a** (Table 4.3). Six samples (18%) from Band 19 were haplotype **a,** and the remaining 28 samples were haplotype **b**. Eight samples (18%) from Band 20 were haplotype **c** (including one adult male LP, three of the four adult females within the LP OMU, one of the three adult females of the BZT OMU, one sub-adult female of the PK OMU, as well as the adult female and one of the four sub-adult females of the BB OMU)**.** The remaining 37 samples were haplotype **a** (including 10 harem males, 1 invading male, 23 adult females of 10 different OMUs, and 3 of the four sub-adult females of the BB OMU).

Given the fact that only three mtDNA haplotypes were found from 29 males and 67 females sampled from three neighboring bands and the three haplotypes differ from each other

by only one to two mutation sites, male and female *R. roxellana* appear to migrate principally between neighboring bands. Hypothesis 1 is not supported

4.4.3 Females dispersal between OMUs

As indicated by the distribution of mtDNA haplotypes, adult and sub-adult females with haplotype **c** were found in four different OMUs (LP, BB, BZT, and PK OMU, Table 4.3) in Band 20. Furthermore, females residing in different OMUs did not group by maternal lineages. Both haplotypes **a** and **c** were found among adult and sub-adult females of these four units. The results support the hypothesis that both adult and sub-adult females transfer between OMUs of the same band. For example, an adult female (HG) in the BB OMU who migrated from the LP OMU has haplotype **c**. Three other females in the LP OMUs also were haplotype **c**, and one was haplotype **a.** A sub-adult female who joined the PK OMU was haplotype **c**, whereas the other 4 adult females in the PK OMU were all haplotype **a**. However, due to the low variation of mtDNA haplotypes within Band 20, the immigration rate of females between OMUs cannot be accurately calculated.

4.4.4 Female and male dispersal between bands

Of the 54 samples from Band 21 and Band 19, sex was successfully determined for 51 samples. The sex of samples from Band 20 was known when collecting. Overall, I sampled 4 males from Band 21, 12 males from band 20, and 13 males from Band 19 (Table 4.3). All 4 males from Band 21 were haplotype **a**. Ten of the 11 harem males from Band 20 were haplotype **a**. The remaining one harem male and one invading male were haplotype **c**. Two of the 13 males from Band 19 were haplotype **a**. The remaining 11 were haplotype **b**. Taken together, males with haplotype **a** were present in all three neighboring bands.

I sampled 16 females from Band 21, 33 females from Band 20, and 18 females from

Band 19 (Table 4.3). All 16 females from Band 21 were haplotype **a**. Twenty-six of the 33 females from Band 20, including three sub-adult females were haplotype **a**. The remaining 7 individuals, including 2 sub-adult females were haplotype **c**. Three of the 18 females from Band 19 were haplotype **a**, and the remaining 15 were haplotype **b**. Like males, females with the same haplotype were present in neighboring bands.

I estimated the dispersal rate between bands based on the assumption that individuals with less frequent haplotypes represent immigrants from other bands. If this assumption is correct, then based on haplotype **a**, the male immigration rate for Band 19 was approximately 15% (2 divided by 13 males), and the rate of female immigration for Band 19 was approximately 17 % (3 divided by 18 females). Based on data from haplotype **c**, male immigration rate for Band 20 was approximately 9% (1 divided by 11 males), and the female immigration rate for Band 20 was approximately 21 % (7 divided by 33 females). The results support hypotheses 3 that females and males transfer equally among bands. However, these values represent rough estimates and probably underestimate actual dispersal rates because these estimations overlooked the immigration of individuals with haplotype **a** into Band 20 and the immigration of individuals with haplotype **b** into Band 19.

4.5 Discussion

In this study, I collected fecal samples from three neighboring bands of *R. roxellana* and sequenced the d-loop region of the mtDNA. According to our results, both females and males with identical haplotypes were present in neighboring bands. This supports the hypothesis that both sexes disperse between bands. The distribution of mtDNA haplotypes within Band 20 (fecal samples collected from Band 20 have detailed OMU membership information) indicated that

females within the same OMU were not grouped by mtDNA haplotypes. In other words, females within the same OMU had different mtDNA haplotypes. This supports the hypothesis that females disperse between OMUs within the same band. These results are consistent with the results of observational studies (Zhang et al. 2008, Guo 2008, Qi et al. 2009). Due to the low variation of mtDNA haplotypes within Band 20, the immigration rate of females between OMUs cannot be accurately determined. Based on the assumption that individuals with less common haplotypes represent immigrants, rough estimates of dispersal rates indicated that 15%-21% percent of females and 9%-16% of males immigrated from neighboring bands. Dispersal rates of *R. roxellana* are relatively low compared to typical bisexual dispersal species such as mantled howlers (79% of males and 94% of females disperse from natal group, Glander 1992), but are similar to those reported in gelada baboons (Shotake and Nozawa 1984), which also form multi-level societies. Based on blood protein polymorphisms, gene flow between gelada baboon bands is estimated to be approximately 14% (Shotake and Nozawa 1984). Shorake and Nozawa (1984) assumed that all the gene flow was due to male dispersal because female dispersal was rarely observed in this population. Based on this assumption, Shorake and Nozawa (1984) argued that 70% of males return to their natal band to breed despite leaving their natal OMU as juveniles. All *R. roxellana* males leave their natal OMUs and join an AMU before puberty (Ren et al. 2000). However, based on current genetic and behavioral evidence it remains unclear whether these males return to their natal band to breed.

In addition, male and female *R. roxellana* appear to migrate between neighboring bands rather than travel distances of over 10 km (diameter of home range) to encounter more distant bands. This conclusion is based on the fact that only three mtDNA haplotypes were found from 28 males and 68 females sampled from three neighboring bands, and the three haplotypes differ

from each other by only one to two mutation sites.

The low genetic diversity among individuals of these three bands does not appear to be the result of low genetic diversity among the Shaanxi subpopulation of *R. roxellana*. Pan et al. (2009) sequenced the same region of mtDNA from 35 individuals randomly collected from the three remaining sub-populations of *R. roxellana* (Shanxi-Gansu, Sichuan, and Hubei). They found 15 haplotypes with 49 mutation sites in total. Six of these haplotypes were present in the Shaanxi subpopulation, which includes a total of 39 Bands including Bands 19, 20, and 21. Moreover, the haplotypes reported by Pan et al. (2009) only represented a subset of all possible mtDNA haplotypes because haplotype **c** reported in this study was not reported in their study. Therefore, it appears that overall genetic diversity in *R. roxellana* is not low. This has important conservation implications for the survivorship of this endangered primate species.

4.5.1 Comparison with R. bieti

Distribution patterns of mtDNA haplotypes also have been studied in a closely related species *R. bieti* (Liu et al. 2007). Liu et al. (2007) sampled 157 individuals from 11 of the remaining 15 bands. The number of individuals sampled per band ranged from 5 to 26. These authors sequenced the hyper-variable region of the d-loop region (401bp) and found 30 haplotypes with 52 mutation sites. The average number of haplotypes within a band was 4.5 (ranging from 2 to 8). Twenty-one haplotypes were present in only one band, and nine haplotypes were present in bands (2 to 5 bands) located over 100 km apart. The distribution pattern of mtDNA haplotypes of *R. bieti* reported by Li et al (2007) fits a two-dimensional stepping-stone model, in which individuals transfer between neighboring bands. Since both R. bieti and *R. roxellana* form multi-level societies, it is reasonable to assume that they share similar (although not necessarily identical) dispersal patterns. Given the quite fragmented nature

of the *R. bieti* population, it is surprising that the three focal bands of *R. roxellana* that I studied have fewer mtDNA haplotypes within each band compared to *R. bieti*. One possible explanation is that the current fragmentation of *R. bieti*'s habitat was a very recent event (Liu et al. 2007). High genetic diversity within *R. bieti* bands reflects high gene flow in the past. However, since I only sampled a small proportion (3 out of 40 bands) of the Shaanxi subpopulation of *R. roxellana*, the results of this study can not be used to estimate their fragmentation history and how fragmentation has impacted gene flow in *R. roxellana*. Further studies sampling additional bands of *R. roxellana* will yield more information on these issues.

4.5.2 Dispersal behavior of R. roxellana

During this study I observed one adult male join Band 20. He attracted one adult female from an established OMU in Band 20 plus four sub-adult females with unknown origin to form a new OMU. I observed one sub-adult female join an established OMU, and one adult female resident of an established OMU disappear/emigrate. I also recorded two cases in which a solitary male attempted to attract an adult female from an established OMU. Solitary *R. roxellana* males were not observed to use aggressive behaviors to force females to leave their OMU. In addition, aggressive behaviors directed towards females by the leader male and other females were not observed in the days prior to dispersal. Taken together, *R. roxellana* females appear to leave their natal OMUs voluntarily and to exercise mate choice in deciding which OMU to join. This is consistent with the results of other behavioral studies of *R. roxellana* (Guo 2008, Zhang et al. 2008, Qi et al. 2009). The dispersal pattern of *R.roxellana* females is different from that of hamadryas baboons, which also form multi-level societies. Hamadryas females are reported to be abducted by followers or solitary males attempting to establish an OMU or by leader males attempting to expand their harem during a takeover (Kummer 1984, Swedell 2006, Schreier and

Swedell 2009, Swedell et al. 2011). In hamadryas baboons, solitary males and leader males use aggressive herding behaviors such as neckbiting to coerce females to leave their natal OMU and join a new OMU (Swedell 2006). Female mate choice appears to not get expressed in Hamaryas baboons.

In *R. roxellana*, female transfer between OMUs within the same band has been well documented (Guo 2008, Qi et al 2009). Table 4.4 lists the published data on female inter-OMU transfer events as well as data collected by this study. All transfer events (N=11), except for one takeover, were triggered either by the presence of a solitary male who recently immigrated into the band or the disappearance of the leader male (Guo 2008, Qi et al. 2009, this study). Adult females voluntarily leaving an established OMU and joining another OMU within the same band have not been reported. However, immature females might transfer between two established OMUs of the same band. In his study, I observed one subadult female join PK OMU. This subadult female was not frightened by observers, so I assumed she was from the habituated band. However, immature individuals can not be reliably identified. So, the degree of immature females transfer within band remains unclear.

Although adult female transfer between exsiting OMUs within the same band has not been documented in *R. roxellana*, cases of extra-band adult females joining an established OMU and adult females disappearing/emigrating from an exsiting OMU have been reported (Zhang et al. 2008, Qi et al. 2009). Genetic data presented in this study provide evidence that females appear to transfer between bands. Since solitary females have never been observed in over 10 years of studying wild *R. roxellana* (Ren et al. 2000), female transfers between bands may occur principally during inter-band encounters.

4.5.3 Reasons for females to transfer

Inbreeding avoidance has been proposed to be one of the main factors that one or both sexes disperse (e.g. Jack and Fedigan 2004b, Boinski et al. 2005). In the case of *R. roxellana*, Qi et al. (2009) reported that sub-adult females were more likely to leave her natal unit if the leader male was her father (71.4% vs. 21.1%). However, daughter-father copulations do occur in *R. roxellana*. For example, two females in the BZT OMU were sired by BZT according to birth records. Both of them copulated and had offspring with BZT in the spring of 2007 and remained in the BZT OMU until the end of this study (August 2008). In addition, inbreeding avoidance could not explain the dispersal of adult females.

As seasonal breeders and polygamous species, female mate competition has been argued to play an important role in dispersal decision of *R. roxellana* females (Zhao et al. 2008). That fact that new solitary males were attractive to females provides supporting evidence to this argument. If reducing mate competition is also the reason for between-band transfer, a reasonable prediction is that females prefer to join OMUs with fewer adult females. In order to test this prediction, Zhao et al. (2008) assumed that healthy females that disappeared from the focal band immigrated into another band. They compared the number of adult females within OMUs that females disappeared (N=4) and OMUs that females immigrated into (N=9) with the average number of adult females within OMUs of the focal band. Their results did not support the prediction. In *T. phayrei*, aggression directed at dispersing adult and sub-adult females and resistance towards immigrants from resident females has been used to support the mate competition argument (Koenig et al. 2007). Although similar behavior has not been reported in *R. roxellana*, we could not rule out this possibility. Because between-band transfer events are infrequent, it is possible that current behavioral studies did not capture the beginning stage of females joining a new OMU.

Reducing food competition is another reason used to explain female dispersal behavior (e.g. Watts 1996). However, contests over food within bands of *R. roxellana* are extremely rare. Over the 816 hours of observation, I recorded only 7 cases of competition over food among the three focal OMUs (0.0005 time per adult per hour). This appears to reflect the fact that the *R. roxellana* diet is principally composed of scattered items such as fruit/seeds (29.4%), lichen (29%), leaves (24%), and tree bark (11.1%) (Guo et al. 2007). In this regard, OMU size appears to reflect factors such as female mate choice, female intrasexual tolerance, and a harem male's ability to defend his harem, rather than a constant pressure imposed by limited food availability.

To sum, given that females appear to voluntarily leave their natal OMU and approach a different leader male, it appears that female mate choice plays a critical role in dispersal decisions. However, the specific set of factors guiding female migration and female mate choice in *R. roxellana* still remain unclear and require additional study.

4.6 Conclusion

New genetic data support behavioral observations that both male and female *R. roxellana* transfer between bands. Based on mtDNA haplotypes, it appears that approximately 17%-21% percent of females and 9%-15% of males immigrated from neighboring bands. These dispersal rates are simaliar to those of hamadryas baboons, but relatively low compared with other bisexually dispersing primates such as mantled howler monkeys, in which 79-94% of adult males and adult females migrate (Glander 1992). Since the mtDNA haplotypes show limited variation within a band, I conclude that dispersing individuals join neighboring bands rather than travel long distances across mountainous terrain to encounter new bands. The genetic data also indicated that females transfer between OMUs within the same band. Behavioral observations

suggested that between-OMU transfers were triggered either by the presence of young solitary males trying to establish a harem or the disappearance of a harem leader. However, the benefits to females of joining a new solitary male or transferring into a different band remain unclear. Inbreed avoidance might play a role in the dispersal of immature females but not mature females. Feeding competition is unlikely to be the driving force in female dispersal because contests over food were rarely observed in *R. roxellana*. Mating competition was assumed to play an important role in dispersal. However, based on a limited number of transfers, females did not show preference to immigrate to OMUs with fewer adult females (Zhao et al. 2008). Since females voluntarily leave their natal OMU, it appears that female mate choice plays a critical role in dispersal decisions.

Figure 4.1 Bands distributed in Qinling Mountains (adapted from Li et al. 2003).
This figure also depicts potential barriers to dispersal such as large rivers, high altitude mountains (altitude greater than 2600m), roads, and human settlements. Fecal samples are collected from three neighboring bands (19, 20, and 21). Band 20 also is the focal band of behavioral observation.

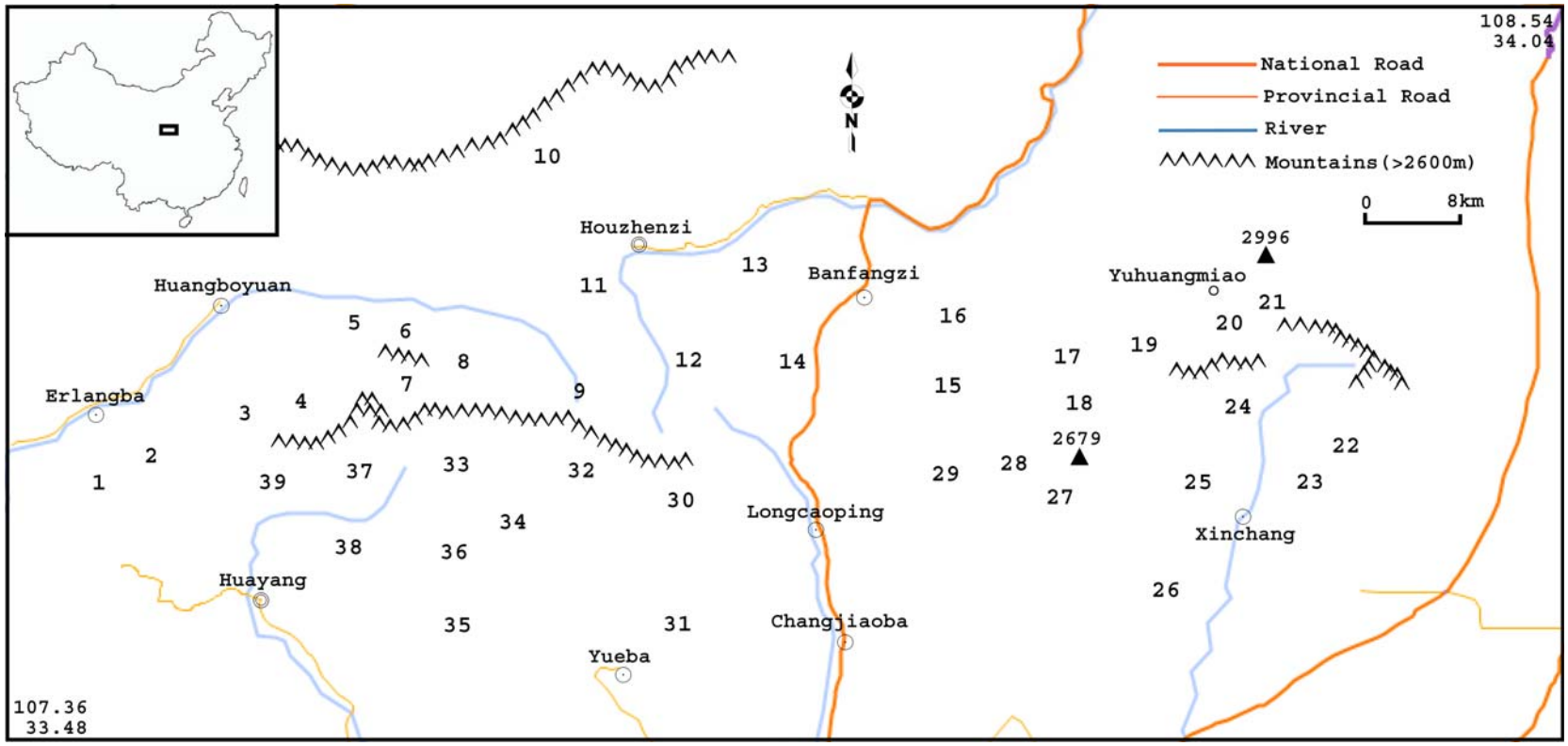


Table 4.1 Primer sequences and annealing temperatures for the d-loop region of mtDNA.

	Forward primer	**Backward primer**	**Annealing Temperature (°C)**
1	AACTGG CATTCTATTTAAACTAC	ATTGATTTCACGGAGGATGGT	56
2	TATATGCCCTTATGTAATTCGTGC	GTGTCAAGGGTGGCTAGTGAAATA	60
3	GCGCCTGTCTTTGATTCCTA	TGTGGGTCCGTCTAGACATTT	58

Table 4.2 Sequences, annealing temperatures, and length of amplicons of nested primers for SRY and amelogenin genes.

Genes	**Forward primer**	**Backward primer**	**Annealing Temperature(°C)**	**Length of Amplicons (bp)**
SRY	AGTGAAGCGACCCATGAACG	TGTGCCTCCTGGAAGAATGG	58	165
	CGCATTCATTGTGTGGTCTC (nested)	GCTTCGGTAAGCATTTTCCA (nested)	55	117
Amelogenin	ACCATCAGCTTCCCAGTTTA	CACCAGATGGGATAGAACCAA	55	204
	CTCAAGCCTGTGTTGTTCCA (nested)	GAACCAAGCTGGTCAGTCAGA (nested)	55	154

Table 4.3 The distribution of mtDNA haplotypes among *band 19, 20,* and *21* and detailed distribution pattern within Band 20. Numbers in the parenthesis are numbers of samples with certain haplotypes. (- denotes females without fecal samples, the letters in parentheses are an individual's initials, individuals without initials are those that cannot be confidently identified). Three haplotypes are found among three bands.

Band	**Haplotype distribution**											
BD 19 (n = 34)	♂: **a** (2), **b** (11) ♀: **a** (3), **b** (15) Unknown: **a** (1), **b** (2)											
BD 21 (n = 20)	♂: **a** (4) ♀: **a** (16)											
BD 20 (n = 44)	♂: **a** (11), **c** (1) ♀: **a** (26), **c** (7)											
		One-male units										Invading ♂
		LP	JB	PK	DB	JZT	BZT	SY	BB	HT	FP	RX	NN[a]
	Adult ♂	**c**	**a**	**a**	**a**	**a**	**a**	**a**	**a**	**a**	**a**	**a**	**a**
	Adult ♀	**a**(KT) **c**(JT) **c**(ZT) **c**(TH)	**a**(BD) **a**(YL) **a**(YZM) **a**(DBC) **a**(XBC)	**a**(HJ) **a**(BJ) **a**(CM) **a**(HS)	**a** **a** -	**a** **a** -	**a**(NZ) **a**(YQ) **c**(BT)	- -	**c**(HG)	**a**(HTP) **a**(XC)	**a** - - - -	**a**(HX) **a**(BHX) **a**(JD)	
	Subadult ♀			**c**					**a** **a** **a** **c**			**a**(KK)	

NN[a]: unnamed

Table 4.4 Female transfer events between OMUs. (Data after November 2007 were collected by this study, the remaining data was adapted from Qi et al. 2009, Zhang et al. 2008, and Guo 2008).

Year	New leader male	Status of new leader male	Previous leader male	Reason for transfer	Destiny of previous leader male	Number of transferring females	
						Adult female	Sub-adult female
Aug. 2002	DB	Solitary	HD	Presence of solitary male	Disappear	5	1
May 2003	JB	Solitary	HT	Take over	Disappear	2	1
Jul. 2003	LP	With females	TT	Disappearance of previous leader	Disappear	5	-
Jun. 2003	LP	With females	DZ	Disappearance of previous leader	Disappear	1	-
Jul. 2003	FP	Solitary	DZ*	Presence of solitary male	Disappear	4	
Oct. 2003	PK	Solitary	CM	Presence of solitary male	Leader of the remaining 3 females	-	3
Mar. 2004	PK	With females	CM	Disappearance of previous leader	Disappear	3	-
Sep. 2005	RX	Solitary	LP	Presence of solitary male	Leader of the remaining 6 females	2	-
Mar. 2007	HT	Solitary	BZT	Presence of solitary male	Leader of the remaining 3 females	2	
Nov.2007	BB	Solitary	LP	Presence of solitary male	Leader of the remaining 4 females	1	4(unknown origin)
Aug. 2008	NN[a]	Solitary	LP	Presence of solitary male	Leader of the remaining 3 females	1	-
Total						26	5

*: DZ disappeared from and reappeared in Band 20 for two times since June 2003 to March 2005. One of his females joined LP OMU. The remaining four females temporally associated with leader male FP, DB, and DZ during this period, and finally immigrated into FP OMU after DZ permanently disappeared from Band 20 in March 2005.

[a]: unnamed

CHAPTER 5: TESTING THEORIES EXPLAINING THE GROOMING RECIPROCATION IN *R. ROXELLANA*

The objective of this chapter is to explore the roles of kinship, reciprocity, and biological markets in shaping the social interactions of snub-nosed monkeys by examining patterns of allogrooming, the time frame of grooming reciprocation, as well as the impact of kinship, partner preference, and sex on time matching within grooming bouts.

5.1 Introduction

Most studies investigating the mechanisms underlying affiliative and cooperative behavior in primates have concentrated on allogrooming (e.g. Schino and Aureli 2009). This is because allogrooming is the most common overt affiliative behavior primates engage in (Goosen 1987, Dunbar 1991). Moreover, allogrooming provides benefits to both partners. The inherent hygienic function of allogrooming was confirmed by studies which demonstrate that allogrooming often focuses on body areas that cannot be reached on one's own (Barton 1985, Borries 1992, Reichard and Sommer 1994, Perez and Vea 2000), as well as on areas of the body having the highest parasite density (Zamma 2002). However, the social functions of allogrooming have attracted considerable attention and are believed to play a critical role in maintaining group stability and in the formation of dyadic social bonds. Grooming has been shown to reduce the heart rate of groomed rhesus macaques (*M. mulatta*, Boccia et al 1989, Aureli et al. 1999), and therefore has been proposed to serve a tension-reduction function for group living animals. A recent study in Barbary macaques (*M. sylvanus*) indicates that grooming also reduced the stress levels of groomers, as indicated by a negative correlation between the amount of grooming given and the fecal cortisol concentrations of the groomer (Shutt et al.

2007). Grooming also is reported to alleviate anxiety and distress of groomers in crested black macaques (*M. nigra*), as indicated by decreased self-scratching rates and reduced aggressive behavior after grooming a conspecific (Aureli and Yates 2010). Moreover, since the cost of grooming is mainly the time invested rather than the amount of energy invested (Dunbar 1992, Dunbar et al 2009), allogrooming represents an important low cost social investment that functions to establish strong social bonds. However, rather than grooming all potential partners, individual primates concentrate their grooming effort on a subset of all possible partners (e.g. Henzi et al. 1997, Lehmann et al. 2007, Berman and Thierry 2010). Therefore, studies exploring partner preferences can shed light on mechanisms underlying the social interactions and social bonds in primates.

Grooming also is considered a common currency in the social life of primates. In addition to exchanging grooming for itself, some primates are assumed to exchange grooming for other services such as coalition support, tolerance, food exchange, infant handling, and sex. This is referred to as interchange. The majority of evidence supporting interchange of grooming for other services comes from chimpanzees (Hemelrijk and Ek 1991, de Waal 1997, Mitani and Watts 2001, Watts 2002, Koyama et al. 2006, Mitani 2006, de Waal and Bosnan 2006, Gomes and Boesch 2009). Studies conducted in other primate species, however, have yielded inconsistent results (non-support: *Macaca radiate*, Silk 1992; *Leontopithecus rosalia*, Rapaport 2001; *M. mulatta*, Matheson and Bernstein 2000; *Papio hamadryas*, Leinfelder et al. 2001; *Cercopithecus aethiops*, Daniel et al. 2004; *M. fuscata*, Ventura et al. 2006; support: *Erythrocebus patas*, Muroyama 1994; *M. fuscata*, Schino et al. 2007; meta-analysis, Schino 2007). Compared to other primates, chimpanzees exhibit a broader range of cooperative behaviors such as hunting, food sharing, patrolling, and coalitionary support. This may be a

reason why the interchange of social behaviors is more prevalent in chimpanzees (Gomes and Boesch 2009).

Kinship has been widely accepted as a major factor influencing partner choice (Chapais 2001, Chapais and Belisle 2004, Silk 2002, 2005). Kin selection theory helps to explain the presence of affiliative and cooperative behaviors under conditions in which initiators and recipients are closely related, and the initiator gains benefits through increasing its inclusive fitness (Hamilton 1964). Recent studies on several species of primates, however, indicate that affiliative and cooperative behaviors also are common among unrelated or distantly related group members (*C. mitis stuhlmanni*, Rowell et al 1991; *Callithrix jacchus*, Faulkes et al. 2003; *Cebus olivaceus*, O'Brien and Robinson 1993; *M. arctoides*, Butovskaya 1993; *M. tonkeana*, Demaria and Thierry 2001; *Papio paniscus*, Hashimoto et al. 1996; Silk 2005, Chapais 2006; *Pan troglodytes*, Goldberg and Wrangham 1997, Mitani et al. 2000, Langergraber et al. 2007, 2009). In this regard, various forms of reciprocity have been proposed to explain the affiliative and cooperative behaviors among non-kin (Triver 1971, 2006, de Waal 2000, de Waal and Brosnan 2006).

Reciprocity theories assume that the direct benefits individuals gain through affiliative behavior with conspecifics are significant and function to maintain dyadic and group cohesion (Triver 1971, 2006, de Waal 2000, Clutton-Brock 2002, de Waal and Brosnan 2006). Thus, kinship is not a prerequisite for affiliative and cooperative behavior to occur. Theories of reciprocity require that the direct benefits gained by each partner through cooperative and affiliative interactions are relatively equal overtime and that individuals maintain predictable social relationships (Trivers 2006). Unrelated individuals forming long-term grooming bonds have been widely reported in primates (e.g. *M. fuscata* Muroyama 1991; *M. radiate* Silk 1992; *C.*

mitis stuhlmanni Rowell et al 1991; *C. apella*, de Waal 2000; *C. apella*, Schino et al 2009; *Saguinus oedipus*, Hauser et al. 2003; *P. hamadryas*, Leinfelder et al. 2001; *M. sphinx*, Schino and Pellegrini 2009; *G. gorilla* Watts 1997; *P. troglodytes*, Gomes et al. 2009).

Biological market theory is a particular model of reciprocity in which the value of services vary based on local conditions, such as the demand/supply ratios and the current motivation and experiences of each partner (Noë and Hammerstein 1995, Noë 2001, Barrett and Henzi 2006). As a result, social interaction patterns are dynamic. According to biological market theory, individuals are assumed to adjust their partner choice and the amount of service provided to partners according to the current social and ecological circumstances (Henzi and Barret 2002, Slater et al. 2007). For example, if food competition within a group changed from scramble competition to contest competition, grooming exchanged within bouts is expected to shift from more evenly balanced to being skewed in favor of higher ranking individuals, because they exercise greater control over access to food sources than do lower ranking individuals (Barrett et al. 2002). Similarly, under conditions in which grooming is used as a currency to obtain access to infants, food, and sex (i.e. interchange), favored partners (such as higher ranking individuals and mothers with infants) are expected to receive more grooming than they provide, especially if several group members are simultaneously vying for those same commodities (Barrett et al 1999, Manson et al. 2004, Gumert 2007ab, Chancellor and Isbell 2008, Port et al. 2009). In contrast, grooming is expected to be more evenly exchanged between partners during a given grooming bout if it is changed for itself under conditions when there are a large number of available partners (supply is high) and individual are of similar rank (Barrett et al. 1999, Barrett et al. 2002, Henzi and Barrett 2002, Manson et al. 2004, Gumert 2007ab, Slater et al. 2007, Chancellor and Isbell 2008, Frank and Silk 2009, Port et al. 2009).

5.2 Hypotheses tested in this chapter

The aim of this chapter is to explore the roles of kinship, reciprocity, and biological markets in shaping the social interactions of snub-nosed monkeys by examining the distribution pattern of allogrooming and the time frame of grooming reciprocation. Allogrooming is a major part of the social life of snub-nosed monkeys and on average, accounts for 9.5% of their daily activity budget (Chapter 4). It is the most common form of social interaction between adults. Social interactions in *R. roxellana* were extremely peaceful overall. I only recorded 13 cases of within-OMU aggression between resident adults during over 816 hours of observation. This may reflect, in part the fact that the diet of snub-nosed monkeys is composed principally of large patches of widely scattered food items such as seeds, leaves, lichen, and bark (Guo et al. 2007). These resources are not easily monopolized by any one or small set of individuals. Therefore, if feeding competition occurs in snub-nosed monkeys, it is expected to take the form of scramble competition. Social interactions in the snub-nosed monkeys are best described as egalitarian. Consequently, females are expected to principally exchange grooming for grooming. Cases in which females groom for other benefits such as tolerance at feeding site and coalition support are infrequent. However, the exchange of grooming for sex between the harem male and resident females may be an exception. Based on these assumptions, the specific hypotheses tested in this chapter include:

Hypotheses (1) kin selection theory,

1.1: Within the same OMU, allogrooming occurs more frequently between close relatives than between non-kin dyads.

1.2: Related females living in different OMUs engage in allogrooming more frequently than unrelated females living in different OMUs.

1.3: Grooming bouts between related dyads are not time-matched because the direct benefits exchanged between relatives are not expected to be reciprocal. The level of unevenness between dyads is expected to vary according to relatedness.

Hypotheses (2) of reciprocity theory,

2.1: The grooming exchanged between both kin and non-kin dyads is roughly equal over the entire observation period, but may vary over the short term.

Hypotheses (3) of biological market theory

3.1: Among male and female dyads, grooming given and received is not equal, if grooming bouts are followed or preceded by sexual interactions.

5.3 Data collection and analysis

Detailed descriptions of the field site, band composition, and observation methods are provided in Chapter 3. In brief, three out of 11 OMUs of a habituated band were selected for focal animal observations. These are JB OMU, PK OMU, and LP OMU. All adult males and females of these OMUs served as focal animals for this study (3 adult males, 13 adult females). Focal adult females were named by their leader male's name, and numbered sequentially, such as JB1, JB2, and LP1. The total observation period for JB OMU, LP OMU, and PK OMU was 348 hours (58 days), 240 hours (40 days), and 228 hours (38 days), respectively (Table 3.6).

5.3.1 Kinship data

Kinship data were obtained through birth records and genetic data. According to birth records, JB2 is the mother of JB5. JB4 and JB5 are half siblings. The relatedness of the remaining dyads in the JB OMU was less than 0.25 (based on birth records). In order to test kin selection theory, I use a χ^2 test to determine if females provide more frequent and longer

grooming to close relatives than to non-relatives within the JB OMU.

The pedigree of the LP OMU is unknown. However, according to genetic data the females of LP OMU belong to two different maternal lineages. LP2, LP3, and LP4 belong to the mtDNA haplotype c. LP 1 belongs to haplotype **a**. Using a χ^2 test, I determined if dyads belonging to the same haplotypes (N=3) spent more time grooming than dyads belonging to different haplotypes (N=3). The majority of females of the focal band belong to haplotype **a**. However, one adult female in the BZT OMU and one adult female in the BB OMUs belonged to haplotype **c**. I examined the degree to which these individuals affiliated more frequently with females in the LP OMU who also shared haplotypes **c**.

The pedigree of individuals in the PK OMU is unknown and all females of the PK OMU were characterized by the same haplotype (haplotype **a**). Thus, kin selection theory was not tested in the PK OMU.

The kinship data of this study is estimated using mtDNA haplotypes. I acknowledge that mtDNA haplotypes can only provide information on maternal lineages and may not represent actual relatedness. This is a limitation of this study.

5.3.2 Grooming data

Grooming interactions were analyzed using Frank and Silk (2009)'s method with some modifications. A grooming bout began when one partner approached another and initiated grooming. I recorded the direction of the allogrooming (e.g. A grooming B or B grooming A), and any changes in direction. The length of each grooming episode was timed using a stopwatch to the nearest half minute. Grooming bouts ended when the groomer stopped grooming or the recipient left the groomer.

Ordinary least square (OLS) regression was used to test the degree of grooming reciprocation. Female-female dyads and male-female dyads were analyzed separately so as to avoid the influence of sex. In order to test the time frame of grooming reciprocation, an OLS regression was performed on grooming exchanged within bouts, grooming exchanged between dyads during a day, as well as grooming exchanged over the entire observation period. Before performing OSL regression, grooming durations were square-root transformed to normalize the distribution. OLS regression generates a slope of 1 if allogrooming is well balanced between dyads. ANCOVA was used to compare whether the slopes of two OLS regression models were significantly different from each other.

5.3.3 Grooming reciprocity within different time frames

Both reciprocal and unilateral grooming bouts were included when testing grooming reciprocation within the same day and across several months. The grooming contributions of each partner during a given time frame were summed, and served as the independent and dependent variables when performing OSL regression. For each dyad, I picked the assignment of independent/dependent variables that generated a slope less than 1 for grooming exchanged during a day. This was done in order to avoid the situation in which the grooming data of one dyad generate a slope greater than 1 and the grooming data of another dyad generate a slope less than 1. After pooling different dyads together, a slope of 1 was generated. For comparative purposes, for each dyad, I used the same assignment of independent/dependent variables when estimating the degree of grooming reciprocity over the entire observation period. For male-female dyads, the grooming contributed by males was considered as the independent value in order to test if females provided more grooming than received from males.

When testing grooming reciprocation within bouts, only reciprocal grooming bouts were

included. This was done to increase the possibility of detecting time-matching within bouts. I ran two different OLS regression models. In Model 1, grooming contributed by the initiator was assigned as an independent variable and the grooming contributed by the partner was assigned as the dependent variable. This was done in order to test if initiators provided more grooming than recipients. In Model 2, for comparative purposes, independent/dependent variables were assigned to each partner the same way as when analyzing grooming reciprocation during a day. These two models were run on two different grooming data sets so as to test if the definition of grooming bout had an effect on the regression results. For the first data set, I considered grooming bouts that resumed within 1min as a single grooming bout. However, between the two grooming episodes, the two partners remained in close proximity. For the second data set, I considered grooming bouts that resumed within a 5 min period as a single grooming bout.

5.3.4 The effect of partner preference, kinship, and sex on the degree of within bout reciprocity

In order to determine preferred and non-preferred partners, I compared the grooming frequency of all 22 female-female dyads (Figure 5.6a, ID numbers and their corresponding dyads are listed in Appendix D). Nine dyads spent 0.26-0.99 min per hour grooming. These are considered as non-preferred partners including dyads 6, 7, 9, 11, 13, and 14 of JB OMU, dyads 5 and 6 of the LP OMU. The mother-daughter dyad, JB12, is not included in order to avoid the influence of kinship. Seven dyads spent between 1.51 and 1.89 min per hour grooming. They are considered as occasional partners including dyad 10 of JB OMU, dyads 8, 9, 10 of the LP OMU, and dyads 6, 7, 8 of the PK OMU. Six dyads spent 2.20-6.67min per hour grooming. These are considered as preferred partners including dyad 8 of the JB OMU, dyad 7 of the LP OMU, dyads 5, 9 and 10 of the PK OMU (the half sibling dyad, JB15, is not included). To increase the

possibility of detecting the impact of partner preference, I only compared the degree of within bout reciprocation between preferred and non-preferred dyads.

In order to estimate the impact of kinship on within-bout reciprocation for the JB OMU, I compared the within-bout reciprocation of the mother-daughter dyad (dyad 12), the half-sibling dyad (dyad 15), and non-relative dyads (all of the remaining dyads). For the LP OMU, I compared the within-bout reciprocation between dyads that two individuals shared the same matriline (dyads 8, 9, and 10) with individuals of different-matriline dyads (dyads 5, 6, and 7). I also estimated the impact of sex on within-bout reciprocation by comparing allogrooming bouts between female-female dyads and between male-female dyads.

In order to test whether females and males exchanged sex for grooming within a short time period, I recorded grooming interactions immediately prior to and after copulations. I also calculated the average daily grooming exchanged between male-female dyad during the days when copulations were observed between them. For each dyad, I tested whether the mean values for each male-female dyad were significantly greater than the average daily grooming exchanged between them during the entire observation period (one-sample t-test). All of the analyses were conducted using SPSS 16.0.

5.4 Results

I recorded 1,768 grooming bouts over the entire observation period (using 1min interval to separate grooming bouts). Mean grooming bout length was 7.3 ±8.6 min (Figure 5.1a). Sixty percent of grooming bouts (N=1054) were unilateral (Figure 5.1b), and forty percent (N=704) were reciprocal (Figure 5.1c). Mean length of reciprocal grooming bouts was significantly longer than that of unilateral bouts (13.2 ±10.6 min vs. 3.4 ±3.0 min, t-test, $p<0.01$).

5.4.1 The effect of kinship on grooming distribution (female-female grooming)

Females did not distribute their allogrooming evenly among OMU members (Figure 5.2). Female *R. roxellana* tended to concentrate their grooming efforts on one or two out of the 4.3 mean number of potential partners in their OMU (including the leader male, see also chapter 3). However, preferred partners were not necessarily their closest relatives. In the JB OMU, JB2 and JB5 represented a mother-daughter dyad, however, JB2 preferred to groom adult female JB3 (269 min) and groomed JB5 the least (108.5 min, χ^2 test, $p<0.01$, Table 5.1). However, JB4 and JB5 were paternal half siblings based on birth record (this assumes that the leader male sires all OMU offspring), and they were each others' preferred partners (χ^2 test, $p<0.01$, Table 5.1). In the LP OMU, LP1 belonged to a different maternal lineage than LP2, LP3, and LP4. However, LP 4 groomed LP1 the most (LP1: 386.6 min, LP2: 214 min, and LP3: 191 min, χ^2 test, $p<0.01$). While, LP2 and LP3 belong to the same matriline and also were each other's preferred partners. Taken together, there were 2 cases in which preferred grooming partners were kin, and there were 2 cases in which preferred grooming partners were not close maternal kin. Therefore, kin selection was not a necessary condition to explain female-female grooming relationships. A kin selection hypothesis was not supported by these data.

One female in the BZT OMU (BT) and one female in the BB OMU (HG) had the same mitochondrial haplotype as LP2, LP3, and LP4. Allogrooming was never observed between the adult females of LP OMU and BT during the 8 month observation period. However, allogrooming did occur once between HG and LP3 (same matriline) and once between HG and LP1 (different matriline). HG had previously been a resident in the LP OMU and migrated to BB OMU at the beginning of this study. Thus, familiarity rather than kinship may explain the observed grooming and social interactions between females of different OMUs.

5.4.2 Time frame of grooming reciprocation

For both models (Model 1: grooming contributed by initiators as independent variable or Model 2: assigned independent and dependent variables) and both grooming data sets (5 min break and 1 min interval), grooming given during a single grooming bout was significantly related to grooming received during that grooming bout. This was true for both male-female dyads and female-female dyads (Figure 5.3, female-female dyad: N=22, $p<0.001$, Model 1: slope=0.53, r2=0.31; Model 2: slope=0.60, r2=0.37; male-female dyads: N=13, $p<0.001$, Model 1, slope=0.49, r2=0.19; Model 2, slope=0.36, r2=0.15). There were no significant differences between the two models and two data sets (Figure 5.3, ANCOVA, female-female dyad: $p=0.176$; male-female dyad: $p=0.863$). Similarly, grooming was not evenly distributed between dyads during the course of a day (Figure 5.4, slope=0.53 and 0.40, respectively) although grooming provided was significantly correlated with grooming received between members of a given dyad (Figure 5.4, female-female dyad: N=508, r2=0.28, $p<0.001$; male-female dyads: N=225, r2= 0.16, $p<0.001$). The differences between grooming reciprocation during a single day and within a single bout are not significant (Figure 5.4, ANCOVA, female-female dyads: $p=0.955$; male-female dyads, $p=0.918$). However, the lower R square values (female-female dyads: 0.28-0.37, male-female dyads: 0.15-0.19) suggest that the linear regression model can only explain 30% of correlation between grooming provided and grooming received. The variation around the regression lines is considerable for both female-female dyads and male-female dyads.

Across the entire observation period, grooming exchanged between female-female dyads were positively correlated (female-female dyads: N= 22, r2=0.66, $p<0.001$, Figure 5.5). The slopes were significantly different from those found during within-bout reciprocation (0.83 vs 0.53, ANCOVA, $p<0.01$), which suggests that grooming was more evenly exchanged between

dyads over the long-term (8 months) than short-term (within bout and during a day). This is consistent with the expectations of the reciprocity hypothesis (hypothesis 2.1).

Although grooming exchanged between male-female dyads was also positively correlated over 8 months (male-female dyads: N=13, r2=0.86, p<0.001, Figure 5.5), the slope of male-female dyads was greater than 1 (1.36), which indicates that females provided more grooming to the harem male than they received from the harem male. Although the small sample size of this study does not allow any statistical analyses, current evidence (Table 5.2) suggests that the amount of grooming that female provided to the harem males cannot be explained by the number of copulations occurred between them, and whether or not females conceived or carried an infant that year.

5.4.3 The effect of partner preference, kinship, and sex on within bout reciprocity

Partner preference was found to have no significant impact on within-bout reciprocation (Figure 5.6b, ANCOVA, p=0.02). Preferred partners did not exchange grooming more evenly within bouts than non-preferred partners. Thus, hypothesis 3.1, which stated that preferred partners exchange grooming more evenly within bouts, was not supported.

The impact of kinship on grooming relationships appeared to be affected by the degree of relatedness. For the LP OMU, within bout reciprocation between same-matriline dyads (N=3) was not significantly different from that between different-matriline dyads (N=3) (Figure 5.7b, ANCOVA, p=0.096). For the JB OMU, within bout reciprocation between non-related dyads was not significantly different from the half sibling dyad (Figure 5.7a, ANCOVA, p=0.818). However, for all these dyads, grooming provided was significantly related to the grooming received within bouts (Figure 5.7ab). Whereas, between the adult mother-adult daughter dyad, grooming provided and grooming received within bouts was not significantly correlated (Figure

5.7a, N=18, r^2= 0.012, p=0.666). These results indicate that relatedness impacts within bout reciprocity. Thus, the Kin selection hypothesis 1.3, stating that grooming bouts between related dyads are not expected to be time-matched, is supported.

Within-bout reciprocation between female-female dyads was not significantly different from that of male-female dyads (Figure 5.8, ANCOVA, p=0.651). I recorded 90 copulations over the observation period. In none of these instances did grooming precede the copulation. In 15 cases females groomed the leader males after the copulations. The average length of these grooming bouts was 2.97±1.82 min (range from 30 seconds to 7 min), which was significantly shorter than the average duration of male-female grooming bouts (5.99±6.62min, N=461, T-test, p<0.01). Since each the copulations were initiated by females (Chapter 3), this could not be explained by the harem male exchanging sex for grooming. In addition, the average daily grooming exchanged between male-female dyads on days in which copulations were observed did not differ significantly from grooming exchanged between males and females on days in which copulations were not observed (Table 5.3, N=9 dyads, one-sample t-test, P>0.05). Thus, the biological market hypothesis 3.2 of trading grooming for immediate sex was not supported.

5.5 Discussion

In this chapter I tested a series of hypotheses to examine three theories to explain grooming partnerships in *R. roxellana*. Data presented were based on 1768 allogrooming bouts recorded from 23 female-female and 13 male-female dyads. Kin selection theory predicts that affiliation is expected to occur more frequently among close relatives than distant relatives and non-relatives, and grooming exchanged between relatives does not need to be reciprocal (Hamilton 1964). Reciprocity theory predicts that non-relatives form stable social bonds and

equally exchange social services (usually the same commodity) over time (Triver 1971, 2006, de Waal 2000, de Waal and Brosnan 2006). Biological market theory predicts that partners calculate the immediate costs and benefits of particular social interactions, and trade social benefits based on the current market value of the services to each partner (e.g. grooming for grooming or grooming for sex). The value of each interaction will vary based on local conditions, such as the motivation, experiences, and needs of each partner (Barrett and Henzi 2006). Therefore, we expect that the grooming bouts between leader male and females will be skewed if the grooming bouts is followed or preceded by sexual interactions.

5.5.1 Kin selection theory

The results of this study indicated that kinship was not the primary factor explaining affiliation and grooming interactions in snub-nosed monkeys. Although the two half siblings in the JB OMU were each other's preferred grooming partner, the adult mother-adult daughter dyad of the JB OMU groomed each other infrequently. In fact, the mother groomed her daughter least compare to other females in the OMU. In the LP OMU, three females belonged to the same matriline and one female belonged to a different matriline. Although two females from the same matriline groomed each other the most, one of these females devoted the majority of her grooming to a female of a different matriline. In addition, the occasional interactions between females of different OMUs are better explained by the familiarity between them rather than the same matriline shared by them. Although the sample size of closely related adult females in this study is small, the results suggest that female snub-nosed monkeys form strong bonds with both related and non-related OMU members, even in those cases in which they have close relatives within the OMU.

Thierry (1990) suggested that social styles, dominance hierarchies, and aggression

frequency play a critical role in kin biased affiliations in macaques. Although all macaque species are female philopatric and males disperse, the prevalence of kin biased affiliations varies across species (Thierry 1990, Berman and Thierry 2010). Affiliative behaviors were concentrated mainly between close relatives in macaque species characterized by a despotic female dominance hierarchy and frequent aggression (such as rhesus and Japanese macaques) (Kapsalis and Berman 1996, Majolo et al. 2005). In contrast, in those species having a more egalitarian dominance style and infrequent aggression (e.g. Tonkean macaques, moor macaques), females also maintained strong social bonds with nonrelatives (Thierry et al. 1994, Matsumura and Okomoto 1997, Berman and Thierry 2010). According to this pattern, the relatively egalitarian social style of female snub-nosed monkeys may help to explain the existence of strong non-kin grooming associations.

Even though relatedness cannot predict long-term reciprocity, the results of this study indicate that relatedness had an impact on within bout reciprocity. Unlike unrelated dyads, for the mother-daughter dyad, grooming provided and received within a single bout was not correlated. This is consistent with the kin selection theory which predicts that affiliation between relatives is not maintained through the reciprocation of direct benefits, but inclusive benefits (Hamilton 1964, Muroyama 1991). However, only the impact of relatedness of $R > 0.5$ is significant. Within-bout reciprocity between the half-sibling dyad was not significantly different from that of unrelated dyads. Due to the small sample size of this study, additional data are needed to confirm this pattern.

5.5.2 Biological market theory

There was no evidence that female and male snub-nosed monkeys traded grooming for immediate sex, although grooming was not evenly balanced within bouts between male-female

dyads. The mating unit of the snub-nosed monkey consists of one male and multiple females. According to biological market theory, females should compete over access to males. Thus, females were expected to trade grooming for sex. However, none of the copulations were preceded by grooming interactions. Seventeen percent of copulations were followed by females grooming males. However, given the fact that all copulations were initiated by females, post-copulatory grooming bouts were short, and females who mated more frequently did not groom the male longer than females who mated infrequently, male-female grooming relationships in snub-nosed monkeys cannot be explained by females grooming males to increase their access to copulatory partners. Males exchanging grooming for immediate sex was reported in long tailed macaques (Gumert 2007b) but not in chimpanzees (Gilby et al. 2010). However, male chimpanzees were reported to trade grooming for sex on a long-term basis (Gilby et al. 2010, Gomes and Boesch 2011). Similarly, over the entire observation period, snub-nosed monkey females provided more grooming to males than they received from males. This suggested that it is possible that female snub-nosed monkeys compete for access to the harem male by establishing a strong grooming bond. However, what types of benefits females could gain from bonding with the harem male remains unclear. The results of this study do not support that females exchanged grooming for copulations or infant protections from the harem male.

Many studies testing biological market theory assume that grooming should be time-matched within bouts irrespective of the impact of rank, sex, food competition, and infant handling because under those circumstances grooming is assumed to be exchanged for grooming itself (e.g. Henzi and Barrett 2002, Manson et al. 2004, Slater et al. 2007, Chancellor and Isbell 2008, Port et al. 2009, Fruteau et al. 2009, Frank and Silk 2009, Tiddi et al 2010). Time matching within bouts, in fact, has rarely been observed in primates. The slope of linear

regression for grooming exchanged within bouts was 0.32 (grooming duration was square-root transformed, SRT) for olive baboons (*P. anubis*, Frank and Silk 2009), 0.34 for white-faced capuchins, 0.12 for bonnet macaques (grooming duration was log transformed (LT), Manson et al. 2004), an average of 0.35 (LT) for gray-cheeked mangabeys (*Lophocebus albigena*, Chancellor and Isbell 2008), and 0.23 (LT) for chacma baboons (*P. ursinus*, Barrett et al. 2002). Skewed grooming bouts can be explained by exchanging grooming for other social benefits or changes in the costs based on supply and demand. Biological market theory predicts that higher ranked individuals should receive more grooming than they provide within bouts because they are able to 'charge' more for their services, such as tolerance at feeding site and coalition support than lower ranked individuals. In snub-nosed monkeys, the slope for grooming exchanged within bouts was 0.57 between female-female dyads and 0.49 between male-female dyads (SRT). However, the opportunities for coalitionary support in snub-nosed monkeys, especially among females, are limited due to infrequent aggressive interactions within and between OMUs (Chapter 3). In addition, the compositions of focal OMUs were stable for the entire observational period. In this regard, the grooming discrepancy within bouts in snub-nosed monkeys cannot be explained by exchanging grooming for rank related benefits or changes in supply and demand.

Studies examining the effect of rank distance on grooming reciprocation within bouts in other primates yield inconsistent results. A positive relationship between rank distance and grooming discrepancy within bouts has been found in white-faced capuchin, bonnet macaques, chacma baboons, sooty mangabeys, and vervet monkeys (Barrett et al. 2002, Manson et al. 2004, Fruteau 2011), but not in and gray-cheeked mangabeys (Chancellor and Isbell 2008) and olive baboons (Frank and Silk 2009). In grey-cheeked mangabeys, the effect of rank distance varied across different groups (Chancellor and Isbell 2008). Chancellor and Isbell (2008) found in one

of five groups, grooming discrepancy increased as rank distance increased. In one group, grooming discrepancy decreased as rank distance increased. In the remaining three groups rank distance had no significant effect on grooming discrepancy. However, even in these three groups, without the impact of rank, grooming was not time-matched within bouts. These results suggest that individuals may adopt different strategies under similar circumstances (Chancellor and Isbell 2008).

5.5.3 Theories of reciprocity

Even though the amount of time each member of the dyad was groomed varied considerably across bouts, over a period of several months, grooming within dyads was relatively balanced between female partners. This is consistent with the prediction of reciprocity theory. Even though similar results also have been reported in many other primates (e.g. *P. anubis*, Frank and Silk 2009, *Macaca fuscata*, Schino et al., 2007, *Cebus apella*, Schino and Pellegrini, 2009, and *Pan troglodytes*, Gomes et al 2009), the mechanisms of long-term reciprocity are controversial. One prediction of "attitudinal reciprocity" is that short-term reciprocation is a prerequisite for long-term reciprocation. However, the results of this study suggested that snub-nosed monkeys did not reciprocate grooming evenly within a short-time frame but did so in the long run. In addition, preferred partners, which are assumed to be more predicable and reliable partners, do not exchange grooming more evenly within bouts compared to non-preferred partners. Thus, attitudinal reciprocity is not supported by this study. It is possible that individual snub-nosed monkeys were able to keep score or track social interactions across a longer time period.

In conclusion, the results of this study provide evidence of the importance of both short-term and long-term grooming reciprocity between kin and nonkin dyads in female

snub-nosed monkeys. The mechanisms underlying long-term reciprocity are likely to be caculated reciprocity. However this will require additional study. Kin selection and biological market theories appear to play very limited roles in shaping grooming relationships and social interactions in snub-nosed monkeys.

Figure 5.1a Length distribution of both reciprocal and unilateral grooming bouts.

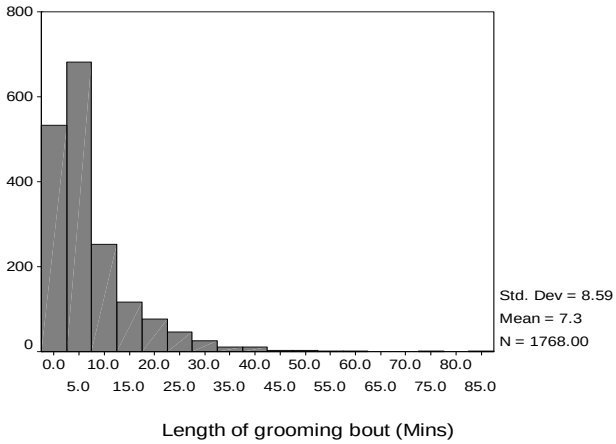


Figure 5.1b Length distribution of unilateral grooming bouts.

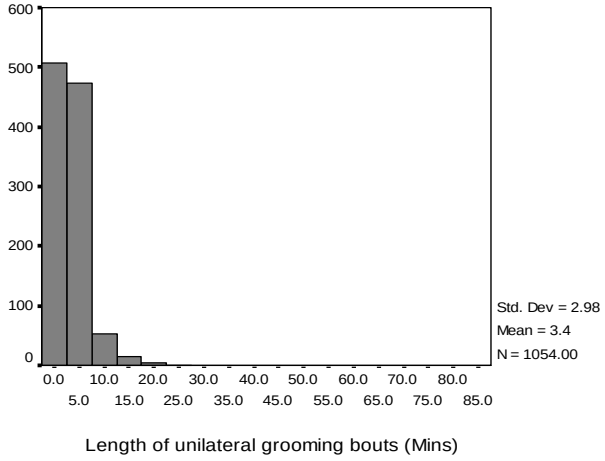


Figure 5.1c Length distribution of reciprocall grooming bouts.

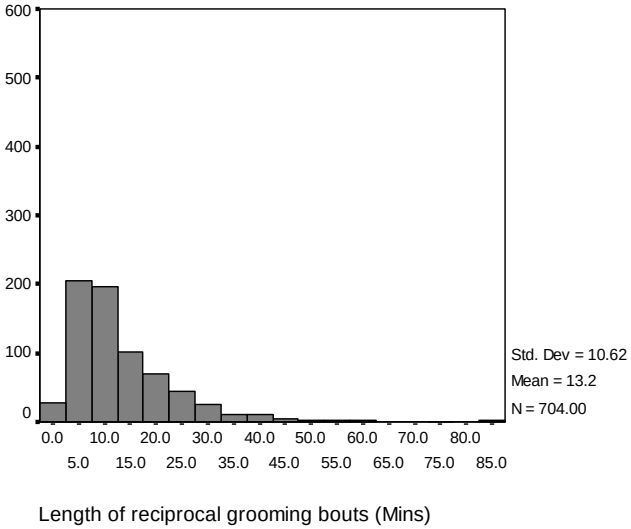
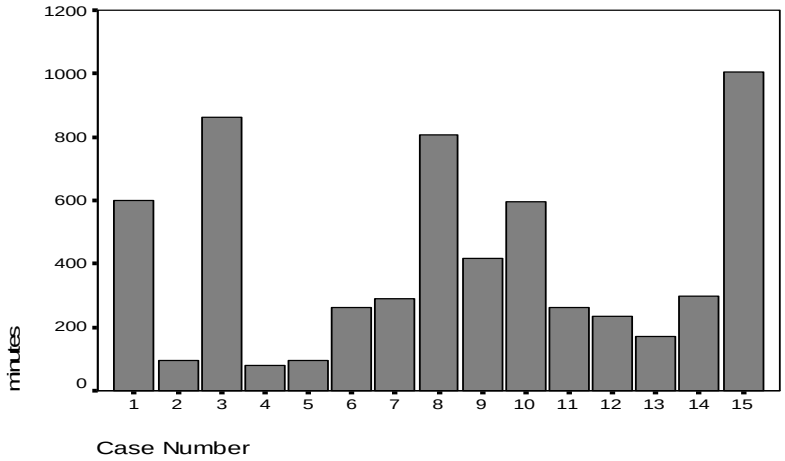
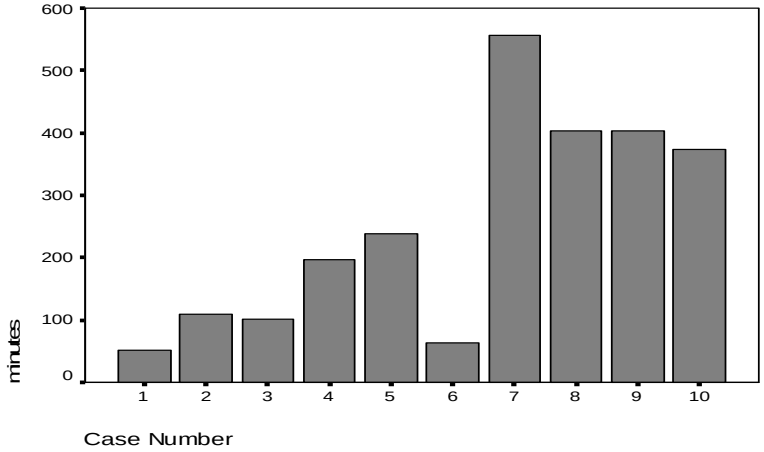


Figure 5.2 The time of allogrooming occurred between each dyad.
(Case numbers' corresponding dyads are listed in Appendix D)
JB OMU



LP OMU



PK OMU

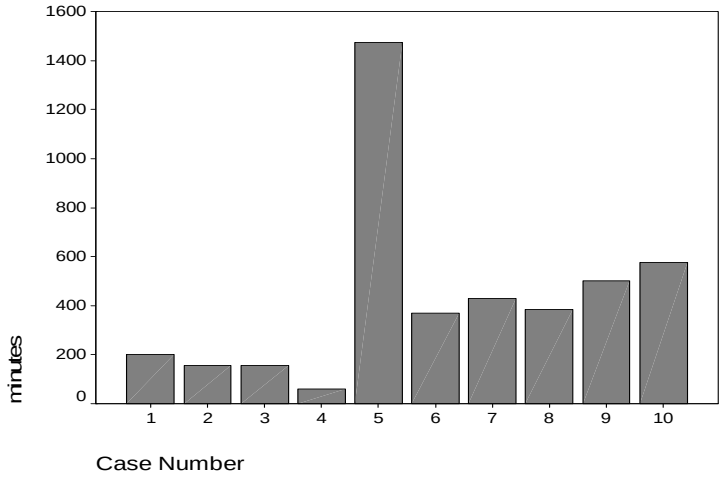


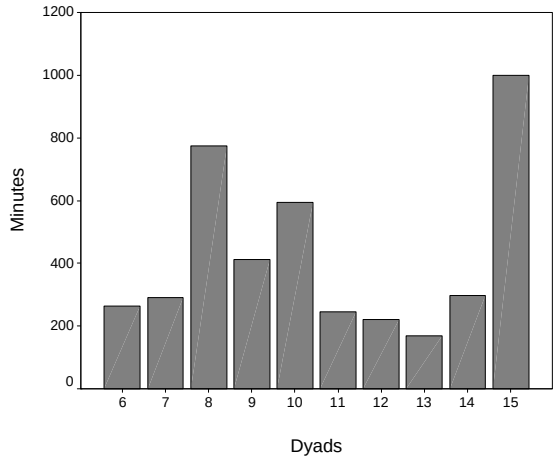
Table 5.1 The impact of kinship on grooming distribution. In JB OMU, JB2-JB5 is mother-daughter dyad. In LP OMU, LP2, 3, and 4 belong to the same matriline. LP1 belongs to a different matriline.

JB OMU:

	Recipient (min)					
		JB1	JB2	JB3	JB4	JB5
Provider	JB1	-	116.5	92	245	179.5
	JB2	147	-	**269**	156	108.5
	JB3	199.5	**325.5**	-	66	160.5
	JB4	530	89	103	-	**592**
	JB5	232.5	113	137.5	**406.5**	-

LP OMU:

	Recipient (min)				
		LP1	LP2	LP3	LP4
Provider	LP1	-	106.2	34.5	169.6
	LP2	132.2	-	**220.6**	189.5
	LP3	29.4	**183.7**	-	172.8
	LP4	**386.6**	214	191.1	-



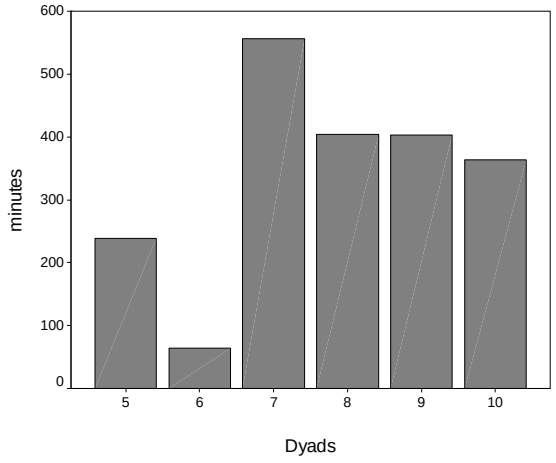
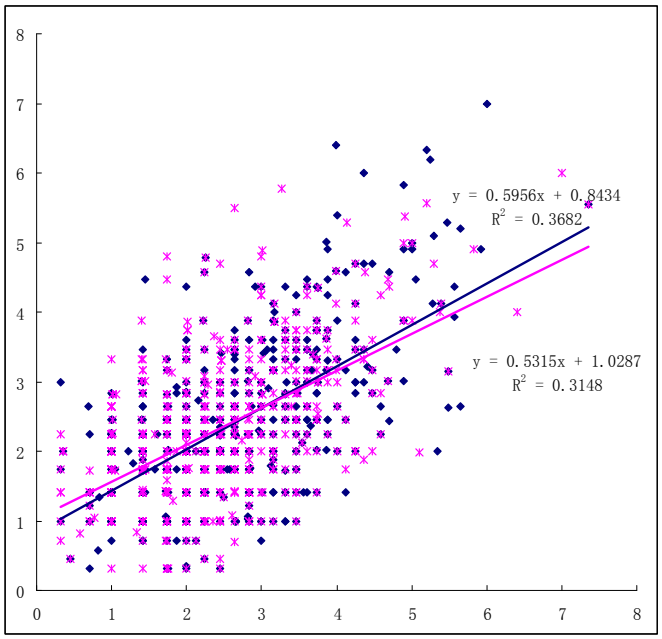


Figure 5.3 Within bout grooming reciprocation.
Blue squares represent grooming bouts separated using 5 minutes, and grooming contributed by the initiator was considered as independent values. Pink dots represent grooming bouts separated using 1 minute and independent and dependent values were assigned to each dyad. There is no significant difference between the two models (ANCOVA, female-female dyad, p=0.176; male-female dyad, p=0.863) (Grooming durations were square-root transformed to normalize the data distribution).

Female-female dyads:



Male-female dyads:

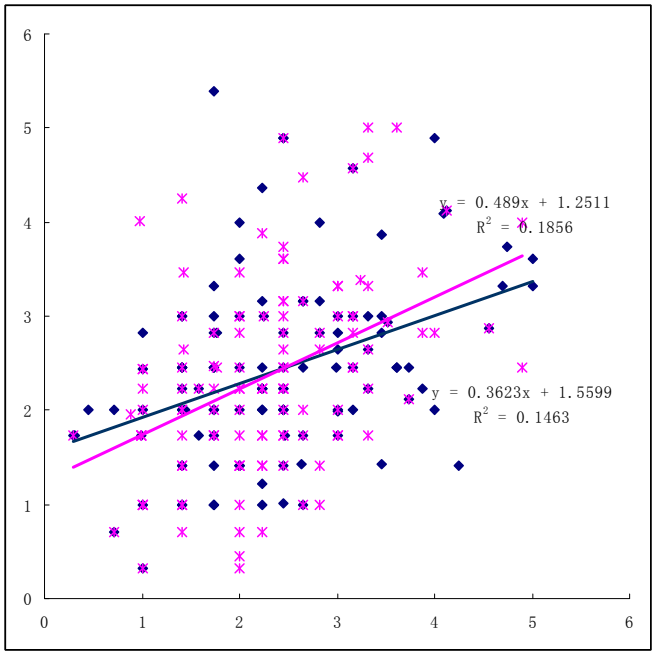
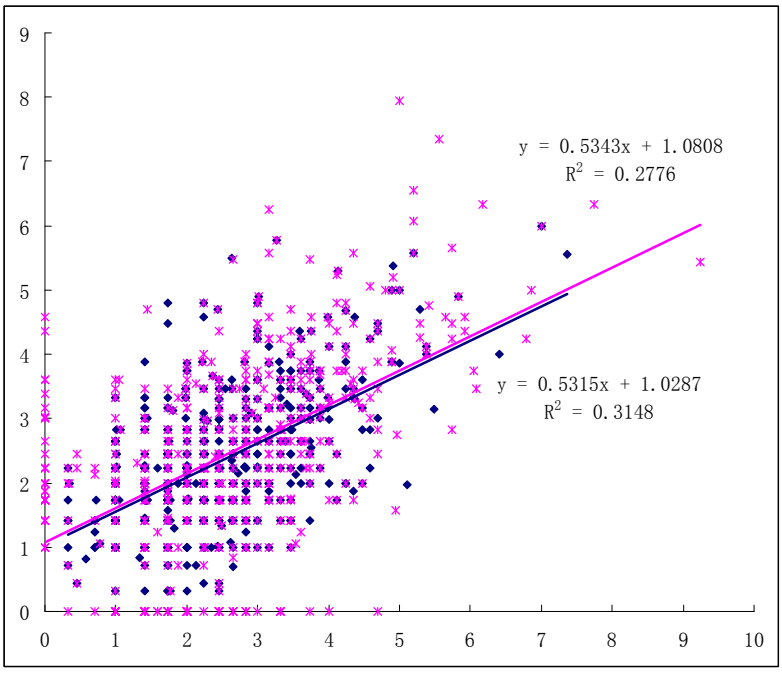


Figure 5.4 Grooming reciprocation within bouts and a day.
Each blue dot represents a reciprocal grooming bout. Each pink dot represents the grooming exchanged between a dyad within a day. There is no significantly difference between the two slopes for both female-female dyads and male-female dyads. male-female dyads, p=0.918)

Female-female dyads (Dyad=22, Allogrooming bout=582, ANCOVA, p=0.955)



Male-female dyads (Dyad=13, Allogrooming bout=119,)

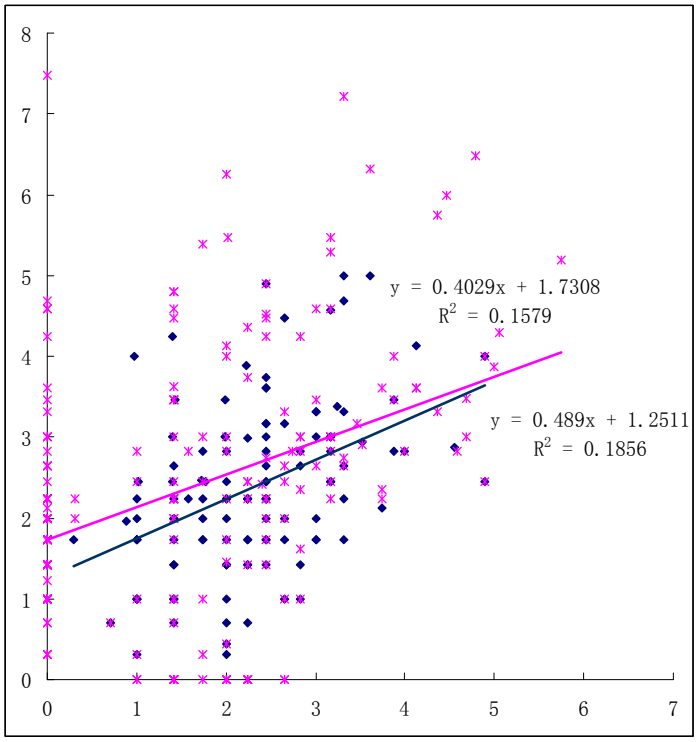
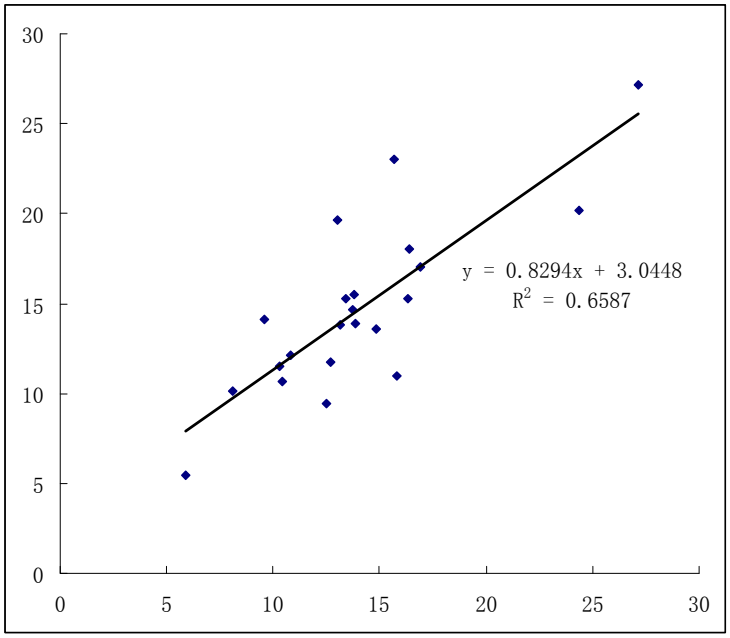


Figure 5.5 Grooming reciprocity over the entire observation period.
Each dot represents a dyad. (Grooming durations were square-root transformed to normalize the data distribution)

a: female-female dyad (N=22)



b: male-female dyad (N=13)

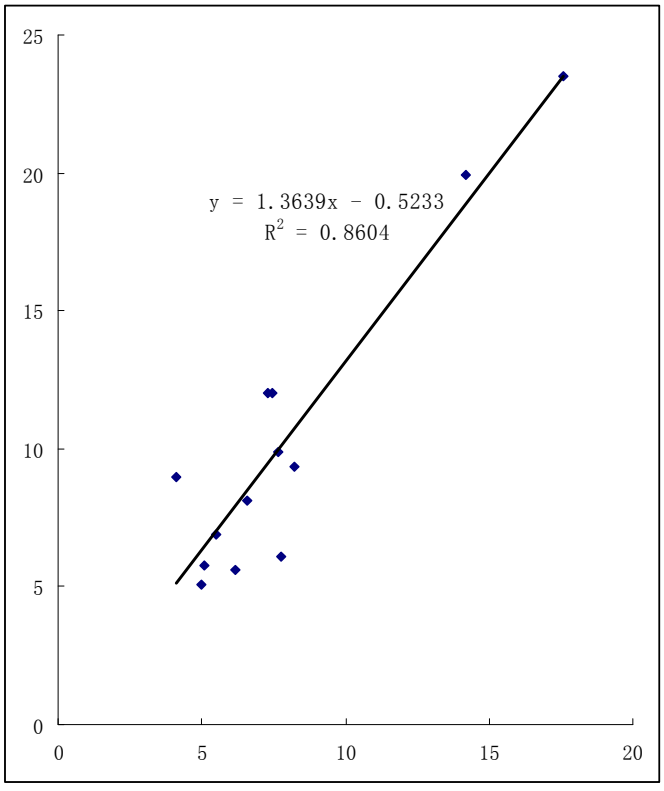


Figure 5.6a Grooming frequency of each dyad.
If grooming per hour is greater than 2min, the dyads are considered as preferred partners including dyad 8 of JB OMU, dyad 7 of LP OMU, dyad 5, 9 and 10 of PK OMU (half sibling dyad (JB15) is not included in order to avoid the influence of kin ship). If grooming per hour is less than 1min, the dyads are considered as non-preferred partners including dyad 6, 7, 9, 11, 13, and 14 of JB OMU, dyad 5 and 6 of LP OMU (mother-daughter dyad (JB12) is not included).

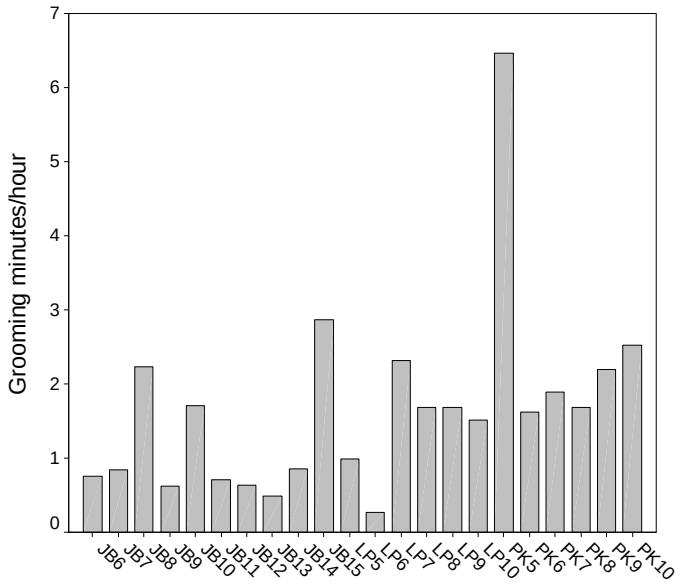


Figure 5.6b The impact of partner preference on within-bout reciprocation.
Pink squares represent allogrooming bouts between non-preferred partners. Blue squares represent preferred partners. The two slopes are not significantly different from each other (ANCOVA, p=0.02).

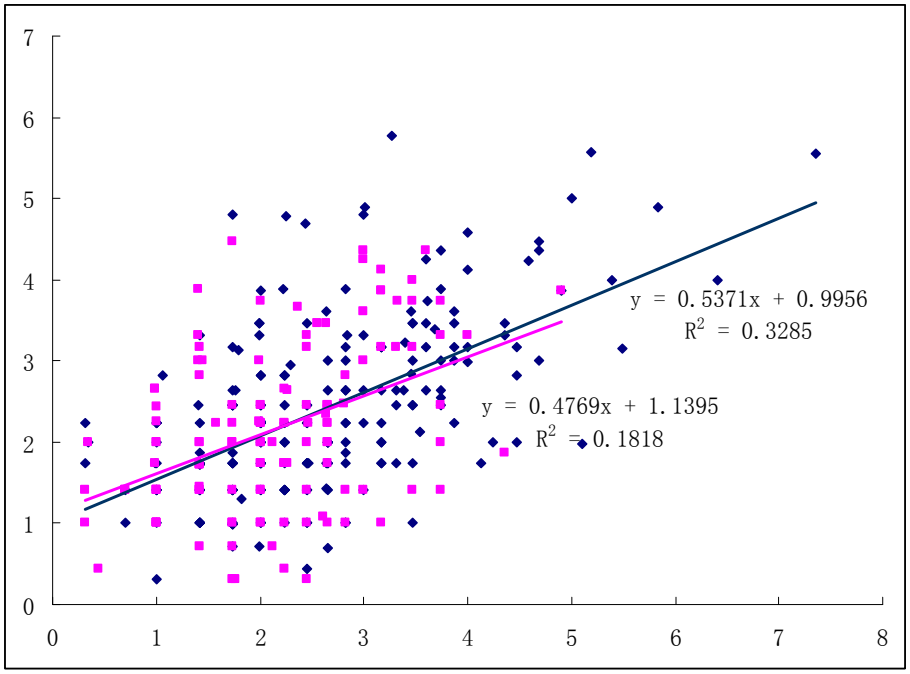


Figure 5.7a The impact of kinship on within-bout reciprocation in JB OMU.
Blue squares represent allogrooming between mother-daughter dyad (dyad 12). Pink squares represent those between half-sibling dyad (dyad15). Green crossings represent those between non-related dyads (dyad 6, 7, 8, 9, 10, 11, 13, and 14). There is no significant relationship between mother-daughter dyad (LSQ, $p>0.1$). The other two slopes are not significantly different from each other (ANCOVA, $p=0.818$). (Grooming durations were square-root transformed to normalize the data distribution.)

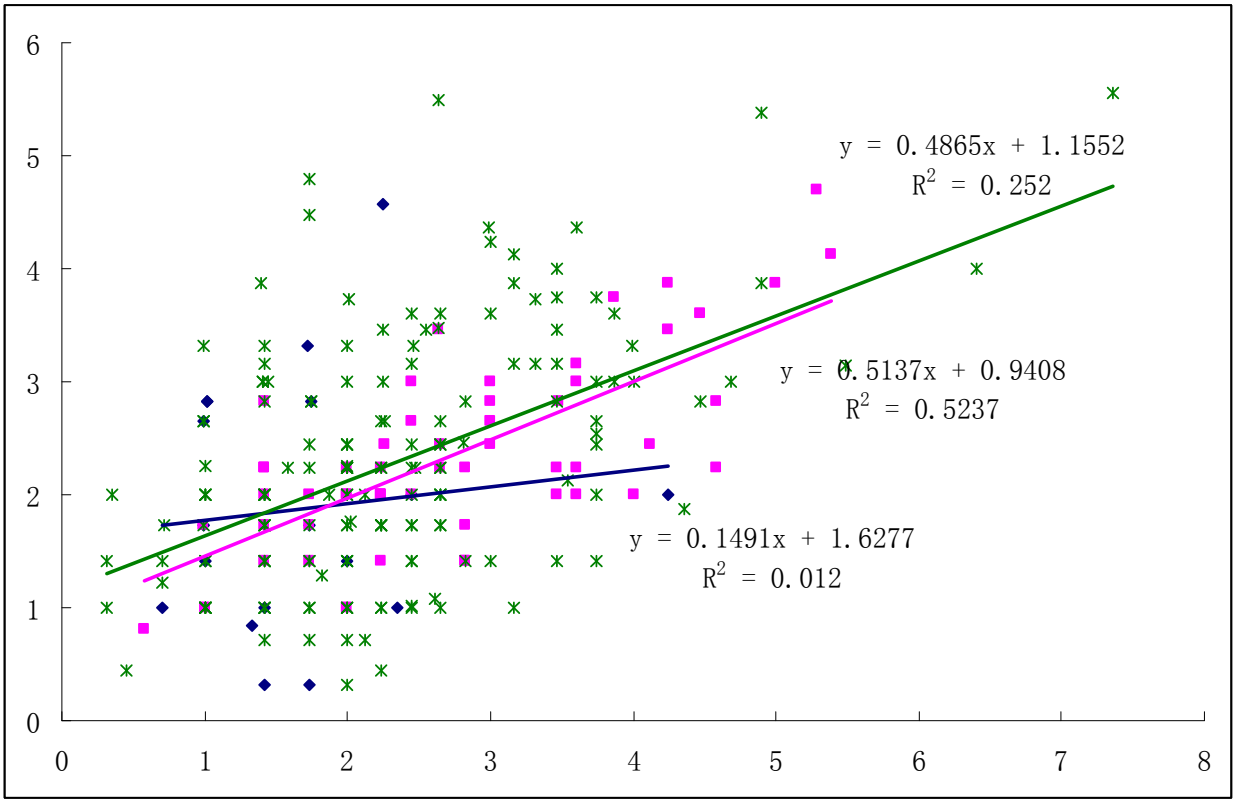


Figure 5.7b The impact of kinship on within-bout reciprocation in LP OMU.
Blue squares represent allogrooming between females belonging to the same matriline (dyad 8, 9, and10, N=68). Pink squares represent those between females belonging to different matrilines (dyad 5, 6, and 7, N=83). The two slopes are not significantly different from each other (ANCOVA, p=0.096). (Grooming durations were square-root transformed to normalize the data distribution.)

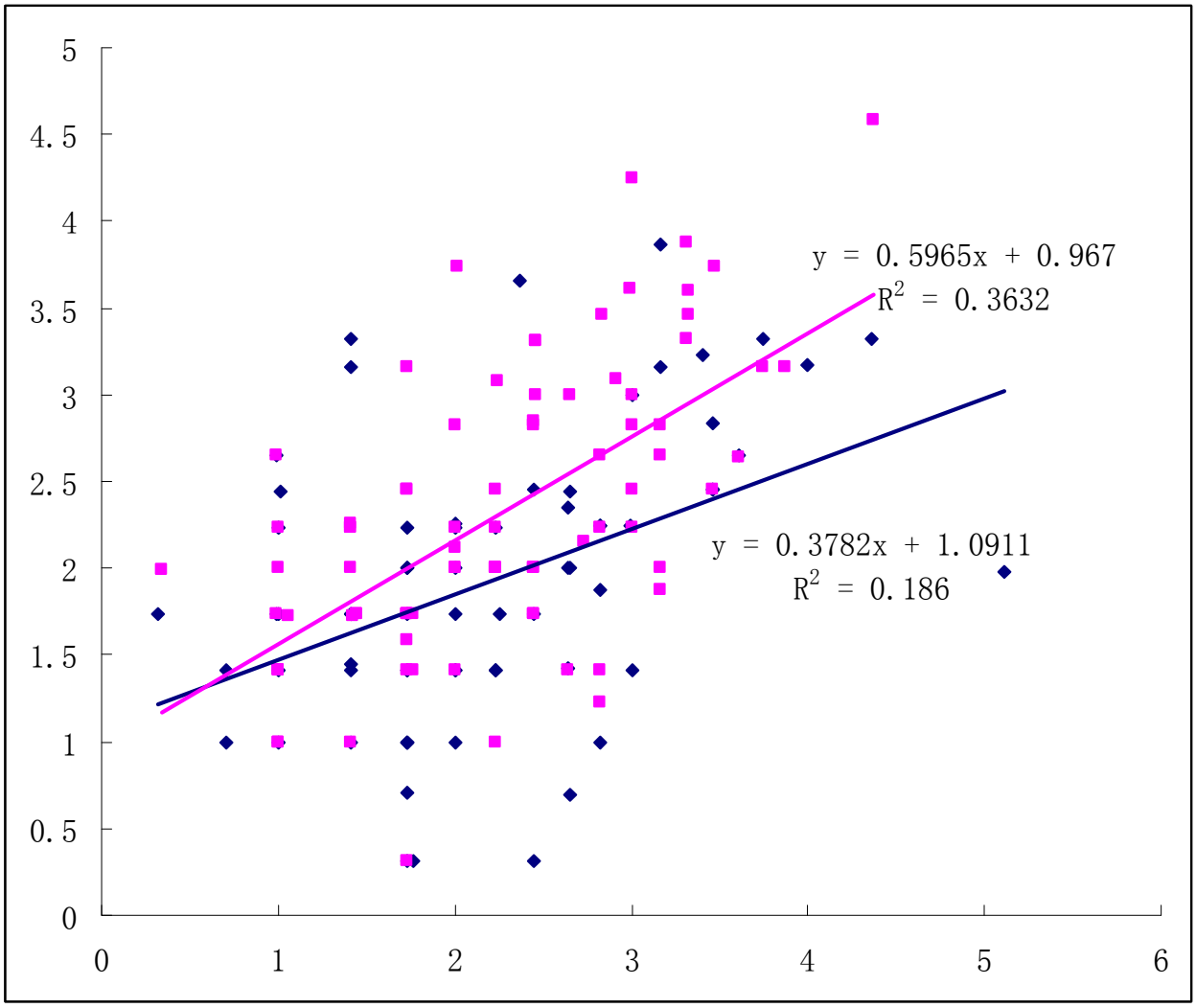


Figure 5.8 The impact of sex on within-bout reciprocation.
Blue squares represent the allogrooming bouts between females. Pink squares represent the allogrooming bouts between males and females. The two slopes are not significantly different from each other (ANCOVA, p=0.651). (Grooming durations were square-root transformed to normalize the data distribution.)

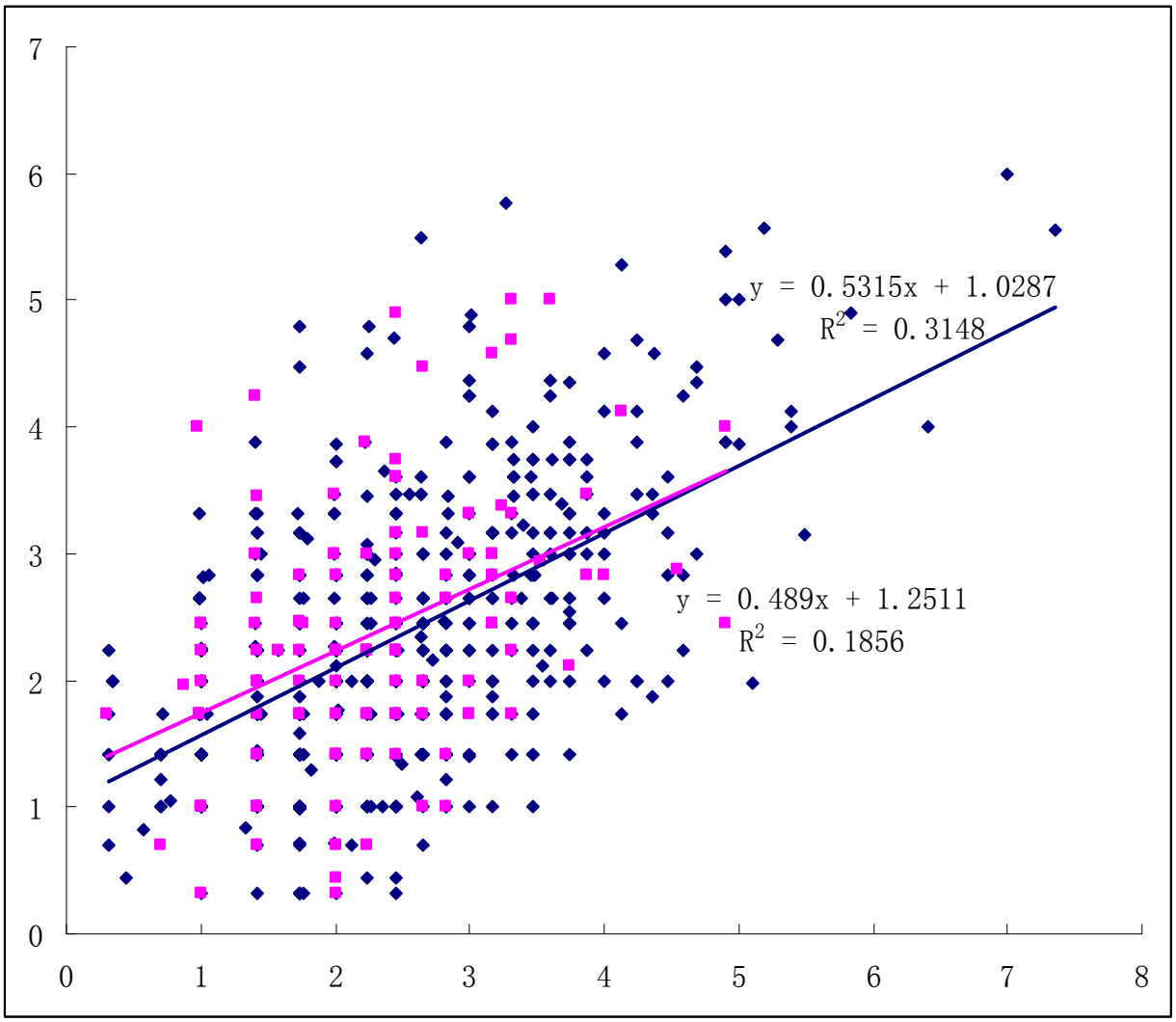


Table 5.2 Allogrooming between leader males and adult females and reproduction record.

OMU	Female	Provide to male (min)	Receive from male (min)	Living infant in 2007	Date of giving birth(2008)	Copulation/solicitation observed during this study
JB	JB1	396.6	201.5	Y	-	0
	JB2	80.1	17.1	-	-	8/8
	JB3	553.6	310	-	4/10	13/17
	JB4	47.5	30	Y	4/12-15	14/19
	JB5	37	60	-	4/4	19/24
PK	PK1	144.2	55.5	Y	-	3/6
	PK2	98	59	Y	-	0
	PK3	87	68	Y	-	2/3
	PK4	33.1	26	Y	-	0
LP	LP1	26	25	-	3/6-7	0
	LP2	66	43	-	-	0
	LP3	31.5	38	-	4/6	4/4
	LP4	144.1	53	Y	-	4/9

Table 5.3 Grooming exchanged during the days when females and the lead male had intercourses.

OMU	Dyad	Date	Grooming provided by male	Grooming provided by female	One sample T-test
JB	2	Nov 16, 2007	0	1	P>0.05
JB	2	Nov 11, 2007	0	0.5	
JB	2	Nov 10, 2007	0	8	
JB	2	Oct 17, 2007	0	4	
JB	3	Dec 15, 2007	6	18	P>0.05
JB	3	Dec 14, 2007	6	4	
JB	3	Nov 19, 2007	9	7	
JB	3	Nov 17, 2007	0	3	
JB	3	Nov 16, 2007	2	20	
JB	3	Nov 13, 2007	6	20	
JB	3	Oct 18, 2007	0	3	
JB	3	Oct 18, 2007	0	21	
JB	4	Dec 19, 2007	0	1	P>0.05
JB	4	Dec 18, 2007	1	8	
JB	4	Dec 15, 2007	7	0	
JB	5	Dec 19, 2007	0	1	P>0.05
JB	5	Dec 15, 2007	0	4	
JB	5	Nov 19, 2007	7	1	
JB	5	Nov 18, 2007	0	5	
JB	5	Nov 17, 2007	21	8	
JB	5	Nov 14, 2007	0.1	4	
JB	5	Nov 13, 2007	0	3	
LP	1	May 4, 2008	0	2	P>0.05
LP	1	May 5, 2008	0	1	
LP	1	Jun 1, 2008	0	1	
LP	3	Aug 6, 2008	0	3	P>0.05
LP	3	Aug 8, 2008	0	0	
LP	4	May 2, 2008	0	3	P>0.05
LP	4	Jun 1, 2008	0	0	
LP	4	Jun 2, 2008	2	0	
LP	4	Jun 4, 2008	6	7.5	
PK	3	Jul 28, 2008	0	1	P>0.05
PK	3	Jul 29, 2008	4	9	
PK	3	Jul 30, 2008	0	2	
PK	4	Apr 5, 2008	0	0	P>0.05
PK	4	Apr 6, 2008	0	0	
PK	4	Jun 1, 2008	0	0	
PK	4	Jun 2, 2008	0	0	
PK	4	Jun 3, 2008	0	0	

CHAPTER 6: CONCLUSIONS AND FUTURE DIRECTIONS

This study investigated the behavioral strategies that Sichuan snub-nosed monkeys adopt to cope with the challenges associated with living in a multi-level society, behavioral mechanisms underlying social interactions within an OMU, as well as male and female dispersal patterns. The goals of this chapter are to integrate the results of previous chapters and outline the directions of future studies.

6.1 Conclusions

6.1.1 Why form multilevel societies?

The results of this 8-month field study suggest that the formation of multi-level societies in *R. roxellana* is likely the result of social and spatial tolerance among harem males. As is the case of other primate species that form a multilevel society composed of several OMUs, newly formed OMUs of snub-nosed monkeys do not explore new home ranges or forage independently within the original home range. Instead, they maintain close proximity with other OMUs, coordinate their activities, and form a higher level social structure.

Two hypotheses have been proposed to explain the formation of multi-level societies in primates. The bachelor male threat hypothesis was proposed to explain that the benefits that leader males gained through cooperatively repelling bachelor males. It was argued that this is the driving force of forming a multi-level social structure in Asian colobines (Grüeter 2009). This hypothesis predicted that harem males would form coalitions when a solitary male attempted to takeover or extract females from existing OMUs. During my study, I observed two cases of invader males attempting to extract females from the LP OMU. However, harem males did not

respond by acting cooperatively to repel the invader males. Thus, my results do not support the bachelor male threat hypothesis.

Some researchers argue that the unfavorable habitat that snub-nosed monkeys live in is the primary driving factor in the formation of multi-level societies (Bleisch et al. 1993, 1998, Kirkpatrick et al.1998, Kirkpatrick and Grueter 2010). Snub-nosed monkeys, except for *R. avunculus*, live in extremely high altitude forests characterized by marked seasonal variation in food supply and heterogeneous distribution in space (Chapter 2, Boonratana and Le 1998, Kirkpatrick et al. 1998, Ren et al 2000, Li et al. 2002, Guo et al. 2007, Grueter et al. 2009, Li et al. 2010). Resources dispersion hypothesis (RDH, Johnson et al 2002), a hypothesis explaining the relationship between recourse distribution and group size, states that if resources are distributed heterogeneously in time and space, even a smallest-sized social unit has to occupy a large home range in order to satisfy the needs across time. However, at any given time, the amount of resources provided by the large home range can support more individuals. Therefore, group members will suffer little cost if adding additional individuals into the gorup. A testable prediction of the RDH is that there is no correlation between home range size and group size (Johnson et al. 2002). The habitats of snub-nosed monkeys fit perfectly with the scenario described by the RDH. Future studies comparing the home range size and group size of snub-nosed monkeys will help to demonstrate whether the aggregation of OMUs in snub-nosed monkeys can be explained by RDH.

6.1.2 Social interactions within and between OMUs

Although leader males show spatial tolerance towards each other, they do not allow individuals of other OMUs to interact with members of their OMU. Even though leader males of snub-nosed monkeys do not aggressively herd females, they actively chase away members of

other OMUs, both adult and juvenile males and females, if they come within 5 meters of OMU members. This type of agonistic interaction, however, rarely escalated into a fight. As a result, both affiliative and agonistic interactions between members of different OMUs were rare. Only 6 cases of affiliative interactions were recorded over an 8 month observation period. Occasionally, females have been observed to solicit other leader males, though in 93% of cases (N=29), solicitations and copulations were interrupted by the female's leader male or other resident females (Qi et al. 2011). Female choice, however, can play a key role in the formation of new OMUs. In general new OMU were formed when adult and sub-adult females of established OMUs are attracted by a solitary male and become part of his harem. Studies by Qi et al (2009) indicate that the formation of new OMUs occurs at a rate of roughly one OMU per year.

Compared to the harem groups formed by other Asian colobines, the OMU of snub-nosed monkeys are more cohesive. In this study, OMU cohesion was measured by the frequency of affiliative interactions that OMU members engaged in. Among the 1768 allogrooming bouts observed, 26% occurred between harem males and resident females (♂ -> ♀ :15%, ♀ -> ♂ :59%, mutual: 26%). In addition, females provided coalitionary support to males during inter-OMU aggressions. In 13 out of 50 inter-unit aggressive episodes observed, females assisted the leader male. These behaviors are uncommon in other Asian colobines (see Table 2 & 4 of Chapter 3). Overall, snub-nosed monkeys spent 9.5% of their daily activity budget allogrooming. This is greater than that reported in many but not all species of Asian colobines (see Table 1 of Chapter 3).

6.1.3 Behavioral mechanisms underling their social interactions

Further investigation of the distribution of allogrooming among OMU members suggested that kinship appeared to play a limited role in partner choice of snub-nosed monkeys,

because kin dyads did not spend more time allogrooming than non-kin dyads. In fact, the mother-daughter dyad in the JB OMU groomed each other the least compared to other females in the OMU (Table 1 of chapter 5). But relatedness influence within bout reciprocity. For unrelated and distantly related dyads, although grooming exchanged within bout is not time matched, it is statistically correlated. However, the grooming exchanged between the mother-daughter dyads was not correlated (Figure 7a of Chapter 5). This is consistent with the kin selection theory which states that direct benefits exchanged between relatives do not need to be balanced because individuals can gain indirect benefits. But this conculsion is based on one single dyad, interpretation of the results need to be cautious.

Contrary to the prediction of biological market theory, neither males nor females were found to exchange grooming for sex. Detailed examination of the time frame of grooming reciprocity indicate that although grooming exchanged between two partners was not time-matched in the short-term, such as within a grooming bout or during a day, it was evenly balanced over the course of several months (Figure 3, 4, and 5 of Chapter 5). Thus, long-term reciprocity provides a better explanation for the social interactions in Sichuan snub-nosed monkeys.

6.1.4 Dispersal pattern

The dispersal patterns of Sichuan snub-nosed monkeys were studied through analyzing the distribution pattern of mitochondrial haplotypes among three neighboring bands. Three haplotypes were found among the 99 samples collected from these bands. The three haplotypes differed from each other at one mutation site. The limited haplotypes and mutation sites indicated that snub-nosed monkeys prefer to join nearby bands when dispersing rather than traveling long distances. Based on the assumption that individuals with less frequent haplotypes

represent immigrants from other bands, it is estimated that approximately 17-21% of females and 8-15% of males immigrated from neighboring bands. Since all males leave their natal OMU before puberty, the low dispersal rate indicates that some males might return to their natal band to takeover or establish new OMUs. In terms of female dispersal, since solitary females were never observed, it is likely that female dispersals between bands takes place during inter-band encounters (Qi et al. 2009).

Genetic data also indicate that females disperse between OMUs within the same band because females in different OMUs shared the same haplotypes. However, adult females were not observed to transfer from one established OMU to another within the same band. Forming a new OMU with a solitary male appears to be the more common pattern to explain female dispersal. In addition to incest avoidance, female mate choice was also assumed to play a critical role in female dispersal based on the fact that females appeared to voluntarily leave their natal OMU (Qi et al. 2009, this study).

6.2 Future Directions

Among the five species of *Rhinopithecus*, *R. avunculus* live in sub-tropical regions. Their habitat is similar to that of other Asian colobines, such as *Nasalis larvatus,* with a higher average annual temperature (approximately 20^{o} C, Boonratana and Le 1998). Accordingly, the multi-level social structure of *R. avunculus* is reported to be less cohesive compared to other *Rhinopithecus* species (Boonratana and Le 1998). Unfortunately, within the genus of *Rhinopithecus*, social interactions have only been systematically studied in *R. roxellana*. Boonratana and Le (1998)'s study represents the only published information on the social organization, ranging pattern, and feeding ecology of *R. avunculus*. They identified three OMUs

at Ta Ke and two OMUs at Nam Trang-Ban Bung, Vietnam. However, due to the difficulty of following these OMUs in their natural habitat, they only collected 206 scan samples of the 5 OMUs. Their preliminary results indicate that *R. avunculus* OMUs within the same home range frequently separate and come together, representing an intermediate state from independent harem groups to unified multi-level societies. In the future, detailed studies concerning the ranging patterns, fission-fusion patterns, and ecological factors that affect their fission-fusion patterns of *R. avunculus* may provide critical insight into the evolution of multi-level societies in snub-nosed monkeys.

In this study I used mithochondrial haplotype data to estimate dispersal rates of both sexes and kinship between individuals. However, mitochondrial data can only provide information on maternal lineages, which do not accurately reflect the relatedness between two individuals. In order to obtain a more accurate relatedness network, it is necessary to amplify polymorphic STR loci for each individual. STRs have a high mutation rate (10-2—10-6 per generation, Schlötterer, 2000), which makes them suitable for individual identification, even among closely related individuals (Di Fiore, 2003). However, only limited polymorphic STR loci data have been published for *R. roxellana.* Traditionally, identifying polymorphic STR loci for a new species required building a microsatellite-enriched library or using cross-species amplification of a set of STR loci from a well-studied and closely related species (e.g. Smith et al. 2000, Newman et al. 2002, Muniz and Vigilant 2008). These methods are time consuming and labor intensive. In a recent project, we took advantage of the next generation sequencing technology, which can generate thousands to millions of sequence reads (up to 400 base pair per read) in one run, and sequenced a partial genome of *R. roxellana*. Combined with bioinformatic technology, we detected about 347 candidate STR loci specific to *R. roxellana* (unpublished

data). These STR loci make relatedness analyses possible.

Another obstacle in studying relatedness among wild primate groups is the low success rate of amplifying nuclear DNA from non-invasive samples, such as feces and shed hair (Taberlet et al. 1996). However, the protocol of two-step PCR proposed by Arandjelovic et al. (2009) significantly enhanced the success rate. In this study, I used this protocol to amplify SRY and amelogenin genes for the purpose of sex determination. The successful rate was above 90% (N=54). In this regard, a promising future project would be to amplify polymorphic STR loci for all of the 99 samples collected during this study and obtain a more detailed kinship network within the focal band and between the three neighboring bands. This kinship network will allow more accurate estimates of dispersal rates between OMUs and bands. It will also provide more information on how multi-level societies develop and how kinship influences *R. roxellana* social behavior.

REFERENCES

Abegglen JJ. 1984. On Socialization in Hamadryas Baboons: a field study. Bucknell University, Lewisburg. Cranbury, NJ: Associated University Presses.

Abernethy KA, White LJT, Wickings EJ. 2002. Hordes of mandrills (*Mandrillus sphinx*): Extreme group size and seasonal male presence. J Zoology 258(1):131-137.

Agoramoorthy G, Hsu MJ. 2005. Occurrence of infanticide among wild proboscis monkeys (*Nasalis larvatus*) in Sabah, Northern Borneo. Folia Primatol 76(3):177-179.

Agoramoorthy G. 1994. Adult male replacement and social change in two troops of Hanuman langurs (*Presbytis entellus*) at Jodhpur, India. Int J Primatol 15(2):225-238.

Alberts SC, Altmann J. 1995. Balancing costs and opportunities: Dispersal in male baboons. Am Nat 145(2):279-306.

Aldrich-Blake FPG, Bunn TK, Dunbar RIM, Headley PM. 1971. Observations on baboons, *Papio anubis*, in an arid region in Ethiopia. Folia Primatol 15:1-35.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour. 49:227-267.

Arandjelovic M, Guschanski K, Schubert G, Harris TR, Thalmann O, Siedel H, Vigilant L. 2009. Two-step multiplex polymerase chain reaction improves the speed and accuracy of genotyping using DNA from noninvasive and museum samples. Mol Ecol Res 9(1):28-36.

Assink PR, van Dijk, IF. 1990. Social organization, ranging and density of Presbytis Thomasi at Ketambe (Sumatra), and a comparison with other Presbytis species at several Southeast Asian locations. MSc. thesis, Rjiksuniversiteit Utrecht, the Netherlands.

Aureli F, Preston SD, de Waal FBM. 1999. Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): A pilot study. J Comp Psych 113(1):59-65.

Aureli F, Yates K. 2010. Distress prevention by grooming others in crested black macaques. Biol Lett. 6(1):27-9.

Barrett L, Gaynor D, Henzi SP. 2002. A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. Anim Behav 63:1047−1053.

Barrett L, Henzi SP, Weingrill T, Lycett JE, Hill RA. 1999. Market forces predict grooming reciprocity in female baboons. Proc Roy Soc Lond B266(1420):665-670.

Barrett L, Henzi SP. 2006. Monkeys, markets and minds: biological markets and primate sociality. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolutions. Springer, New York, pp:209-232.

Barton R. 1985. Grooming site preferences in primates and their functional implications. Int J Primatol 6(5): 519-532.

Barton RA, Dunbar RIM. 1997. Evolution of the social brain. In: Whiten A, Byrne RW (eds) Machiavellian Intelligence II. Cambridge Univ. Press, Cambridge, UK, pp:240–63.

Barton RA, Whiten A. 1993. Feeding competition among female olive baboons, *Papio anubis*. Anim Behav 46(4):777-789.

Belisle P, Chapais B. 2001. Tolerated co-feeding in relation to degree of kinship in Japanese macaques. Behaviour. 138(4):487-509.

Bennett EL, Sebastian AL. 1988. Social organization and ecology of proboscis monkeys (*Nasalis larvatus*) in mixed coastal forest in Sarawak. Int J Primatol 9:233-255.

Bennett EL. 1983. The Banded Langur: Ecology of a Colobine in West Malaysian Rain-Forest, PhD dissertation, Cambridge: Cambridge University.

Bensasson D, Zhang DX, Hartl DL, Hewitt GM. 2001. Mitochondrial pseudogenes: evolution's misplaced witnesses. Trends Ecol Evol 16:314-321.

Bercovitch FB. 1991. Mate selection, consortship formation, and reproductive tactics in adult female savanna baboons. Primates. 32(4):437-452.

Bergman TJ. 2006. Hybrid baboons and the origins of the hamadryas male reproductive strategy. In: Swedell L, Leigh SR (eds) Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. Springer, New York, pp:81-103.

Berman CM, Thierry B. 2010. Variation in Kin Bias: Species Differences and Time Constraints in Macaques. Behaviour. 147:1863-1887.

Bernstein IS. 1968. The lutong of Kuala Selangor. Behavior. 32:1-16.

Biquand S, Biquand-Guyot V, Boug A, Gautier JP. 1992a. Group composition in wild and commensal hamadryas baboons: A comparative study in Saudi Arabia. Int J Primatol 13(5):533-543.

Biquand S, Biquand-Guyot V, Boug A, Gautier JP. 1992b. The distribution of Papio hamadryas in Saudi Arabia: Ecological correlates and human influence. Int J Primatol 13(3):223-243.

Bishop NH. 1979. Himalayan langurs: Temperate colobines. J Hum Evol 8:251-281.

Bleisch W, Cheng A, Ren X, Xie J. 1993. Preliminary results from a field study of wild Guizhou snub-nosed monkeys (*Rhinopithecus brelichi*). Folia Primatol 60:72-82.

Bleisch W, Xie J. 1998. Ecology and behavior of the Guizhou snub-nosed langur (*Rhinopithecus brelichi*). In: Jablonski N (ed) The Natural History of the Doucs and Snub-Nosed

Monkeys. World Scientific Press, Singapore, pp:217-241.

Boccia ML, Reite M, Laudenslager M. 1989. On the physiology of grooming in a pigtail macaque. Phys Behav 45(3):667-670.

Boesch C, Boesch H, Vigilant, L. 2006. Cooperative hunting in chimpanzees: kinship or mutualism? In: Kappeler PM, van Schaik CP (eds) Cooperation in Primates and Humans: Mechanisms And Evolutions. Springer, New York, pp:139-150.

Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge Univ Press, Cambridge, pp:101-113.

Boese G.K, 1973, Behavior and social organization of the Guinea baboon (*Papio papio*). PhD dissertation. Baltimore: Johns Hopkins University.

Boggess J. 1980. Intermale relations and troop male membership changes in langurs (*Presbytis entellus*) in Nepal. Int J Primat 1:233-274.

Boinski S, Kauffman L, Ehmke E, Schet S, Vreedzaam A. 2005. Dispersal patterns among three species of squirrel monkeys (*Saimiri oerstedii, S. boliviensis and S. sciureus*): I. Divergent costs and benefits. Behaviour 142(5):525-632

Boonratana R, Le XC. 1998. Preliminary observations of the ecology and behavior of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in Northern Vietnam. In: Jablonski N (ed) The Natural History of the Doucs and Snub-Nosed Monkeys. World Scientific Press, Singapore. pp 207-217.

Boonratana R. 2000. Ranging behavior of proboscis monkeys (*Nasalis larvatus*) in the lower Kinabatangan, northern Borneo. Int J Primatol 21(3):497-518.

Borries C, Koenig A, Winkler P. 2001. Variation of life history traits and mating patterns in female langur monkeys (*Semnopithecus entellus*). Behav Ecol Sociobiol 50(5):391-402.

Borries C, Larney E, Derby AM, Koenig A. 2004. Temporary absence and dispersal in Phayre's leaf monkeys (*Trachypithecus phayrei*). Folia Primatol 75(1):27-30.

Borries C, Sommer V, Srivastava A. 1994. Weaving a tight social net: Allogrooming in free-ranging female langurs (*Presbytis entellus*). Int J Primatol 15(3):421-443.

Borries C. 1992. Grooming site preferences in female langurs (*Presbytis entellus*). Int J Primatol 13(1): 19-32.

Bradley BJ, Doran-Sheehy DM, Lukas D, Boesch C, Vigilant L. 2004. Dispersed male networks in western gorillas. Curr Biol 14(6):510-513.

Brockett RC, Horwich R, Jones CB. 2000. Female dispersal in the Belizean black howling monkey (*Alouatta pigra*). Neotropical Primates 8(1):32-34.

Bronikowski AM, Altmann J. 1996. Foraging in a variable environment: Weather patterns and the behavioral ecology of baboons. Behav Ecol Sociobiol 39(1):11-25.

Brosnan SF, de Waal FBM. 2002. A proximate perspective on reciprocal altruism. Hum Nat 13(1):129-152.

Bulger J, Hamilton WJ III. 1987. Rank and density correlates of inclusive fitness measures in a natural chacma baboon (*Papio ursinus*) troop. Int J Primatol 8(6):635-650.

Butovskaya, M. 1993. Kinship and different dominance styles in groups of three species of the genus Macaca (*M. arctoides, M. mulatta, M. fascicularis*). Folia Primatol 60:210–224.

Byrne RW, Corp N. 2004. Neocortex size predicts deception rate in primates. Proc Roy Soc Lond B271(1549):1693-1699.

Byrne RW, Whiten A. 1990. Tactical deception in primates: The 1990 database. Primate report. (27):1-101.

Byrne RW, Whiten A. 1992. Cognitive evolution in primates: Evidence from tactical deception. Man. 27(3):609-627.

Caine NG, Marra SL. 1988. Vigilance and social organization in two species of primates. Anim Behav 36(3):897-904.

Caro T. 2005. Antipredator Defenses in Birds and Mammals, University of Chicago Press

Chancellor RL, Isbell LA. 2008. Female grooming markets in a population of gray-cheeked mangabeys (*Lophocebus albigena*). Behav Ecol 20(1):79-86.

Chapais B ; Berman CM. 2004. Variation in nepotistic regimes and kin recognition: A major area for future research. In: Chapais B, Berman CM (eds) Kinship and Behavior in Primates. Oxford University Press, Oxford, pp:477-489.

Chapais B, Belisle P. 2004. Constraints on kin selection in primate groups. In: Chapais B, Berman C (eds) Kinship and Behaviour in Primates. Oxford University Press, New York, pp:365-386.

Chapais B, Savard L , Gauthier C. 2001. Kin selection and the distribution of altruism in relation to degree of kinship in Japanese macaques (*Macaca fuscata*). Behav Ecol Sociobiol 49(6):493-502.

Chapais B. 2001. Primate nepotism: What is the explanatory value of kin selection? Int. J. Primatol. 22(2):203-229.

Chapais B. 2006. Kinship, competence and cooperation in primates. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolutions. Springer, New York, pp:47-64.

Chapman CA, Wrangham RW, Chapman LJ. 1995. Ecological constraints on group size: An analysis of spider monkey and chimpanzee subgroups. Behav Ecol Sociobiol 36(1):59-70.

Cheney DL, Seyfarth RM. 1983. Nonrandom dispersal in free-ranging vervet monkeys: Social and genetic consequences. Am Nat 122(3):392-412.

Clarke MR, Glander KE. 1984. Female reproductive success in a group of free-ranging howling monkeys (*Alouatta palliata*) in Costa Rica. In: Small MF (ed) Female Primates: Studies by Women Primatologists. Alan R. Liss Inc, New York, pp:111-126.

Clutton-Brock TH. 2002. Breeding together: kin selection and mutualism in cooperative vertebrates. Science 296:69-72.

Colmenares F ; Zaragoza F ; Hernandez-Lloreda MV. 2002. Grooming and coercion in one-male units of hamadryas baboons: Market forces or relationship constraints? Behavior. 139(11-12):1525-1553.

Colmenares F, Esteban MM, Zaragoza F. 2006. One-male units and clans in a colony of hamadryas baboons (*Papio hamadryas hamadryas*): effect of male number and clan cohesion on feeding success. Am J Primatol 68(1):21-37.

Colmenares F. 1992. Clans and harems in a colony of hamadryas and hybrid baboons: Male kinship, familiarity and the formation of brother-teams. Behavior. 121(1-2):61-94.

Colmenares F. 2004. Kinship structure and its impact on behavior in multilevel societies. In: Chapais B, Berman CM (eds) Kinship and behavior in primates. Oxford University Press, Oxford, pp:242-270.

Cords M. 1990. Vigilance and mixed-species association of some East African forest monkeys. Behav Ecol Sociobiol 26(4): 297-300.

Cords M. 2007. Variable participation in the defense of communal feeding territories by blue monkeys in the Kakamega Forest, Kenya. Behavior. 144(12): 1537-1550.

Cowlishaw G. 1997. Refuge use and predation risk in a desert baboon population. Anim Behav 54(2):241-253.

Crockett CM, Pope TR. 1993. Consequences of sex differences in dispersal for juvenile red howler monkeys. In: Pereira ME, Fairbanks LA (eds) Juvenile Primates: Life History, Development, and Behavior. Oxford University Press, New York, pp:104-118.

Cui LW, Huo S, Zhong T, Xiang ZF, Xiao W, Quan RC. 2008. Social organization of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Deqing, China. Am J Primatol 70:169-174.

Curtin SH. 1976. Niche separaion in sympatric Malaysian leaf-monkeys (*Presbytis obscura* and *Presbytis melalophos*). Yearbook of Physical Anthropology. 20: 421-439

Curtin SH. 1980. Dusky and banded leaf monkeys. In: Chivers DJ (ed) Malayan forest primates---Ten years' study in tropical forest. Plenum Press, New York, pp:107-145.

Daniel J, Santos AJ, Vicente L. 2004. Affiliative behaviour among captive adult female vervet monkeys (*Cercopithecus aethiops*): lack of interchange of grooming for support. Folia Primatol 75(S1):367-368.

Davies AG., Bennett EL, Waterman PG. 1988. Food selection by two south-east Asian colobine monkeys (*Presbytis rubicunda* and *P. melalophos*) in relation to plant chemistry. Biol. J. Linn. Soc. 34:34-56.

Davies G . 1991. Seed-eating by red leaf monkeys (*Presbytis rubicunda*) in dipterocarp forest of Northern Borneo. Int J Primatol 12(2):119-144.

Davies G. 1987. Adult male replacement and group formation in Presbytis rubicunda. Folia Primatol 49(2):111-114.

Davies, A.G. 1984. An ecological study of the red leaf monkey (*Presbytis rubicunda*) in the dipterocarp forest of Northern Borneo. PhD. dissertation. University of Cambridge, UK.

de Waal FBM, Brosnan SF. 2006. Simple and complex reciprocity in primates. In: Kappeler PM, van Schaik CP (eds) Cooperation In Primates And Humans: Mechanisms And Evolutions. Springer, New York, pp:85-105.

de Waal FBM, Luttrell LM. 1988. Mechanisms of social reciprocity in three primate species: Symmetrical relationship characteristics or cognition? Ethol Sociobiol 9(2-4):101-118.

de Waal FBM. 1997. The chimpanzee's service economy: Food for grooming. Evol Hum Behav 18(6):375-386.

de Waal FBM. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. Anim Behav 60:253-361.

Demaria C, Thierry B. 2001. A comparative study of reconciliation in rhesus and Tonkean macaques. Behavior 138(3):397-410.

di Fiore A 2009. Genetic approaches to the study of dispersal and kinship in New World primates. In: Garber PA, Estrada A, Bicca-Marques JC, Heymann EW, Strier KB (eds) South American Primates: Comparative Perspectives in the Study of Behavior, Ecology, and Conservation. Springer, New York, pp:211-250.

di Fiore A. 2003. Molecular genetic approaches to the study of primate behavior, social organization, and reproduction. Yearbook Phys Anthropol. 46: 62-99.

di Fiore A. 2005. A rapid genetic method for sex assignment in non-human primates. Conserv Biol 6(6):1053-1058

Dietz JM. 2004. Kinship structure and reproductive skew in cooperatively breeding primates. In:

Chapais B, Berman CM (eds) Kinship and Behavior in Primates. Oxford University Press, Oxford, pp:223-241.

Ding W, Zhao Q. 2004. Rhinopithecus bieti at Tacheng, Yunnan: diet and daytime activities. Int J Primatol 25:583-598.

Dolhinow PJ. 1972. The North Indian langur. In: Dolhinow PJ (ed) Primate Patterns. Holt, Rinehart and Winston, New York. pp:181-238.

Dong HT, Boonratana R. 2006. Further observations on the ecology and behavior of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in Vietnam. Int J Primatol 27(Suppl 1). Abst #150

Douadi MI, Gatti S, Levrero F, Duhamel G, Bermejo M, Vallet D, Menard N, Petit EJ (2007) Sex-biased dispersal in western lowland gorillas (*Gorilla gorilla gorilla*). Mol Ecol 16(1):2247-2259.

Dugatkin, LA. 1997. Cooperation among animals: an evolutionary perspective. New York: Oxford University Press.

Dunbar RIM, Dunbar P. 1975. Social Dynamics of Gelada Baboons. Basel: Karger.

Dunbar RIM, Korstjens AH, Lehmann J. 2009. Time as an ecological constraint. Biological Reviews 84, 413–429.

Dunbar RIM. 1983a. Structure of gelada baboon reproductive units. II. Social relationships between reproductive females. Anim Behav 31(2):556-564.

Dunbar RIM. 1983b. Structure of gelada baboon reproductive units. III. The male's relationship with his females. Anim Behav 31(2): 565-575.

Dunbar RIM. 1984. Reproductive Decisions: an Economic Analysis of Gelada Baboon Social Strategies. Princeton: Princeton University.

Dunbar RIM. 1991. Functional significance of social grooming in primates. Folia Primatol 57(3):121-131.

Dunbar RIM. 1992. Time: A hidden constraint on the behavioural ecology of baboons. Behav Ecol Sociobiol 31(1):35-49.

Dunbar RIM. 1993. Social organization of the gelada. In: Jablonski, NG (ed) Theropithecus: the Rise and Fall of a Primate Genus. Cambridge University, Cambridge, pp:425-439.

Ekernas LS, Cords M. 2007. Social and environmental factors influencing natal dispersal in blue monkeys, *Cercopithecus mitis stuhlmanni*. Anim Behav 73(6):1009-1020.

Eley RM, Strum SC, Muchemi G, Reid GDF. 1989. Nutrition, body condition, activity patterns, and parasitism of free-ranging troops of olive baboons (*Papio anubis*) in Kenya. Am J

Primatol 18(3):209-219.

Elgar M. 1989. Predator vigilance and group size in mammals and birds: A critical review of empirical evidence. Biol Rev 64:13–33.

Erhart EM, Coelho A M Jr, Bramblett CA. 1997. Kin recognition by paternal half-siblings in captive *Papio cynocephalus*. Am J Primatol 43(2):147-157.

Eriksson J, Siedel H, Lukas D, Kayser M, Erler A, Hashimoto C, Hohmann G, Boesch C, Vigilant L. 2006. Y-chromosome analysis confirms highly sex-biased dispersal and suggests a low male effective population size in bonobos (*Pan paniscus*). Mol Ecol 15(4):939-949

Faulkes CG, Arruda MF, Cruz AOM. 2003. Matrilineal genetic structure within and among populations of the cooperatively breeding common marmoset, *Callithrix jacchus.* Mol Ecol 12:1101–1108.

Frank RE, Silk JB. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time-course of grooming exchanges in baboons. Behaviour 146(8):1123-1135.

Fruteau C, Lemoine S, Hellard E, van Damme E, Noë R. 2011. When females trade grooming for grooming: testing partner control and partner choice models of cooperation in two primate species. Anim Behav 81:1223–1230.

Fruteau C, Voelkl B, van Damme E, Noe R. 2009. Supply and demand determine the market value of food providers in wild Vervet monkeys. PNAS 106(29):12007-12012.

Fuentes A. 2011. Social systems and socioecology: understanding the evolution of primate behavior. In: Campbell CJ, Fuentes A, MacKinnon, CK, Bearder SK, and Stumpf RM (eds) Primates in Perspective. Oxford University Press, New York, pp: 500-511.

Furuya Y. 1961. The social life of silvered leaf monkeys, Trachypithecus cristatus. Primates 3(2):41-60.

Galat-Luong A, Galat G, Hagell S. 2006. The social and ecological flexibility of Guinea baboons: Implications for Guinea baboon social organization and male strategies. In: Swedell L, Leigh SR (eds) Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. Springer, New York, pp:105-121.

Garber PA, Pruetz JD, Isaacson J. 1993. Patterns of range use, range defense, and intergroup spacing in moustached tamarin monkeys (*Saguinus mystax*). Primates 34(1):11-25

Geissmann T, Lwin N, Aung SS, Augn TN, Augn ZM, Lha TH, Grindley M, Momberg F. 2010. A New Species of Snub-Nosed Monkey, Genus Rhinopithecus Milne-Edwards, 1872 (Primates, Colobinae), From Northern Kachin State, Northeastern Myanmar. Am J Primatol 73:96-107.

Gilby M. Thompson E, Ruane JD, Wrangham R. 2010. No evidence of short-term exchange of

meat for sex among chimpanzees. J Hum Evol 59:44–53.

Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey (*Procolobus badius*): an evaluation of the generality of the ecological-constraints model. Behav Ecol Sociobiol 50:329-338.

Glander KE. 1992. Dispersal patterns in Costa Rican mantled howling monkeys. Int J Primatol 13(4):415-436.

Goldberg, T. and Wrangham, R. 1997. Genetic correlates of social behaviour in wild chimpanzees: evidence from mitochondrial DNA. Anim Behav 54:559–570.

Gomes CM, Boesch C. 2009. Wild chimpanzees exchange meat for sex on a long-term basis. Plos One. 4(4): e5116(online 1-6)

Gomes CM, Boesch C. 2011. Reciprocity and trades in wild West African chimpanzees. Behav Ecol Sociobiol 65: 2183-2196.

Gomes CM, Mundry R, Boesch C, Gomes CM, Mundry R, Boesch C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. Proc Roy Soc (London) B276(1657): 699-706

Goosen C. 1987. Social grooming in primates. In: Mitchell G, Erwin J (eds) Comparative Primate Biology Vol. 2, Part B: Behavior, Cognition, and Motivation. Alan R. Liss, New York, pp:107-131.

Gouzoules S, Gouzoules H. 1987. Kinship. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp:299-305.

Gouzoules S. 1984. Primate mating systems, kin associations, and cooperative behavior: Evidence for kin recognition? Yearbook Phys Anthropol 27:99-134.

Grueter CC, Li D, Ren B, Wei F, van Schaik CP. 2009. Dietary profile of *Rhinopithecus bieti* and its socioecological implications. Int J Primatol 30(4):601-624.

Grueter CC, Li DY, van Schaik CP, Ren BP, Long YC, Wei FW. 2008. Ranging of Rhinopithecus bieti in the Samage Forest, China. I. Characteristics of range use. Int J Primatol 29(5):1121-1145.

Grueter CC, van Schaik CP. 2010. Evolutionary determinants of modular societies in colobines. Behav Ecol 21(1):63-71.

Grüeter CC, Zinner D. 2004. Nested societies. Convergent adaptations in snub-nosed monkeys and baboons? Primate Report 70:1-98.

Grueter CC. 2009. Determinants of Modular Societies in Snub-nosed Monkeys (*Rhinopithecus bieti*) and other Asian Colobines. PhD dissertation. Zurich, Switzerland: University of

Zurich.

Gumert MD. 2007a. Grooming and infant handling interchange in *Macaca fascicularis*: the relationship between infant supply and grooming payment. Int J Primatol 28(5): 1059-1074.

Gumert MD. 2007b. Payment for sex in a macaque mating market. Anim Behav 74(6):1655-1667.

Guo ST, Ji WH, Li M, Chang H, Li BG. 2010. The mating system of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*). Am J Primatol 72(1):25-32.

Guo ST, Li BG, Watanabe K. 2007. Diet and activity budget of Rhinopithecus roxellana in the Qinling Mountains, China. Primates 48:268–276.

Guo ST. 2007. Inbreeding avoidance, paternity exclusion and matting system of Sichuan snub-nosed monkey in Qinling, China. PhD dissertation. Xian, China: Northwest University.

Gupta AK, Kumar A. 1994. Feeding ecology and conservation of the Phayre's leaf monkey, Presbytis phayrei, in northeast India. Biol Conserv 69(3):301-306.

Gurmaya JK. 1986. Ecology and behavior of *Presbytis thomasi* in Northern Sumatra. Primates 27:151-172.

Hamilton WJ III, Bulger J. 1992. Facultative expression of behavioral differences between one-male and multimale savanna baboon groups. Am J Primatol 28(1):61-71.

Hamilton WJ III, Buskirk RE, Buskirk WH. 1976. Defense of space and resources by chacma (*Papio ursinus*) baboon troops in an African desert and swamp. Ecology 57:1264-1272.

Hamilton, WD. 1964. The genetical evolution of social behaviour. I & II. J Theor Biol 7:1–52.

Hammond RL, Lawson Handley LJ, Winney BJ, Bruford MW, Perrin N. 2006. Genetic evidence for female-biased dispersal and gene flow in a polygynous primate. Proc Roy Soc (London) B273(185):479-484.

Handley LJ, Perrin N. 2007. Advances in our understanding of mammalian sex-biased dispersal. Mol Biol 16(8):1559-1578.

Hapke A, Zinner D, Zischler H. 2001. Mitochondrial DNA variation in Eritrean hamadryas baboons (*Papio hamadryas hamadryas*): Life history influences population genetic structure. Behav Ecol Sociobiol 50(6):483-492.

Harcourt AH, Stewart KJ. 1987. The influence of help in contests on dominance rank in primates: Hints from gorillas. Anim Behav 35(1):182-190.

Harcourt AH, Stewart KJ. 1989. Functions of alliances in contests within wild gorilla groups.

Behavior 109(3-4): 176-190.

Hardie SM, Buchanan-Smith HM. 1997. Vigilance in single- and mixed-species groups of tamarins (*Saguinus labiatus* and *Saguinus fuscicollis*). Int J Primatol 18(2):217-234.

Harding RSO. 1976. Ranging patterns of a troop of baboons (*Papio anubis*) in Kenya. Folia Primatologica. 25: 143-185

Harris TR, Caillaud D, Chapman CA, Vigilant L. 2009. Neither genetic nor observational data alone are sufficient for understanding sex-biased dispersal in a social-group-living species. Mol Ecol 18(8):1777-1790.

Harrison ML, Tardif SD. 1988. Kin preference in marmosets and tamarins: *Saguinus oedipus* and *Callithrix jacchus* (callitrichidae, primates). Am J Primatol 77(3):377-384.

Hashimoto C, Furuichi T, Takenaka O. 1996. Matrilineal kin relationship and social behavior of wild bonobos (*Pan paniscus*): sequencing the D-loop region of mitochondrial DNA. Primates 37:305–318.

Hauser MD ; Chen MK ; Chen F ; Chuang E. 2003. Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. Proc Roy Soc (London) B270(1531):2363-2370.

Hemelrijk CK, Ek A. 1991. Reciprocity and interchange of grooming and `support' in captive chimpanzees. Anim Behav 41(6):923-935.

Henzi SP, Barrett L. 1999. The value of grooming to female primates. Primates. 40(1): 47-59

Henzi SP, Barrett L. 2002. Infants as a commodity in a baboon market. Anim Behav 63:915−921.

Henzi SP, Dyson ML, Deenik A. 1990. The relationship between altitude and group size in mountain baboons (*Papio cynocephalus ursinus*). Int J Primatol 11(4):319-325.

Henzi SP, Lycett JE, Weingrill T. 1997. Cohort size and the allocation of social effort by female mountain baboons. Anim Behav 54(5):1235-1243.

Henzi SP, Lycett JE, Weingrill T. 1998. Mate guarding and risk assessment by male mountain baboons during inter-troop encounters. Anim Behav 55(6):1421-1428.

Hirsch BT. 2002. Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). Behav Ecol Sociobiol 52(6):458-464.

Hohmann G, Fruth B. 2002. Dynamics in social organization of bonobos (*Pan paniscus*). In Boesch C, Hohmann G, Marchant L (eds) Behavioural Diversity in Chimpanzees and Bonobos. Cambridge University Press, Cambridge, pp:138-150.

Hoshino J, Mori A, Kudo H, Kawai M. 1984. Preliminary report on the grouping of mandrills (*Mandrillus sphinx*) in Cameroon. Primates 25(3):295-307.

Hrdy SB. 1979. Infanticide among animals: A review, classification, and examination of the implications for the reproductive strategies of females. Ethol Sociobiol 1:13-40.

Huck M, Loettker P, Boehle UR, Heymann EW. 2005. Paternity and kinship patterns in polyandrous moustached tamarins (*Saguinus mystax*). Am J Phys Anthropol 127(4):449-464.

Hunte W, Horrocks JA. 1986. Kinand non-kin interventions in the aggressive disputes of vervet monkeys. Behav Ecol Sociobiol 20:257-263.

Huo S. 2005. Diet and Habitat Use of *Rhinopithecus bieti* at Mt Longma, Yunnan, and Phylogeny of the Family Viverridae in China. Ph.D. dissertation. Chinese Academy of Sciences, Kunming Institute of Zoology, Kunming, China.

Iwamoto T, Dunbar RIM. 1983. Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. J Anim Ecol 52(2):357-366.

Jablonski NG, Pan Rl. 1995. Sexual dimorphism in the snub-nosed langurs (*Colobinae: Rhinopithecus*). American Journal of Physical Anthropology. 96(3): 251-272

Jack KM, Fedigan L. 2004a. Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 1: patterns and causes of natal emigration. Anim Behav 67(4):761-769.

Jack KM, Fedigan L. 2004b. Male dispersal patterns in white-faced capuchins, *Cebus capucinus*. Part 2: patterns and causes of secondary dispersal. Anim Behav 67(4):771-782.

Jack KM, Fedigan L. 2009. Female dispersal in a female-philopatric species, *Cebus capucinus*. Am J Primatol 146(4-5): 471-497.

Jack KM, Isbell LA. 2009. Dispersal in primates: advancing an individualized approach -- Preface. Behavior 146(4-5):429-436.

Jack KM. 2001. Effect of male emigration on the vigilance behavior of coresident males in white-faced capuchins (*Cebus capucinus*). Int J Primatol 22(5):715-732.

Jensen-Seaman MI, Sarmiento EE, Deinard AS, Kidd KK. 2004. Nuclear integrations of mitochondrial DNA in gorillas. Am J Primatol 63(3):139-147.

Johns, A.D. 1983. Ecological effects of selective logging in west Malaysian rainforest. Ph.D. dissertation. University of Cambridge, UK.

Johnson DP, Kays R, Blackwell PG, Macdonald DW. 2002. Does the resource dispersion hypothesis explain group living? Trends Ecol Evol 17:563 – 570.

Jolly CJ. 2007. Baboons, mandrills, and mangabeys: Afro-papionin socioecology in a phylogenetic perspective. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in Perspective. Oxford Univ Press, New York, pp:240-251.

Kahlenberg SM, Emery Thompson M, Muller MN, Wrangham RW. 2008. Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Anim Behav 76(5):1497-1509.

Kappeler PM, Wimmer B, Zinner D, Tautz D. 2002. The hidden matrilineal structure of a solitary lemur: Implications for primate social evolution. Proc Roy Soc (London) B269(1502):1755-1763.

Kapsalis, E. and Berman, C.M. 1996. Models of affiliative relationships among free-ranging rhesus monkeys (*Macaca mulatta*). II. Testing predictions for three hypothesized organizing principles. Behavior 133(15-16):135-1263.

Kavanagh M. 1978. The social behaviour of doucs (*Pygathrix nemaeus nemaeus*) at San Diego Zoo. Primates. 19: 101-114

Kawai, M, Dunbar, RIM, Ohsawa, H., Mori, U. 1983. Social organization of gelada baboons: Social units and definitions. Primates 24:13-24.

Kirkpatrick RC, Grueter CC. 2010. Snub-nosed monkeys: multilevel societies across varied environments. Evol Anthropol 19(3):98-113.

Kirkpatrick RC, Gu HJ, Zhou XP. 1999. A preliminary report on Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) at Baihe Nature Reserve. Folia Primatol 70(2):117-120.

Kirkpatrick RC, Long YC, Zhong T, Xiao L. 1998. Social organization and range use in the Yunnan snub-nosed monkey Rhinopithecus bieti. Int J Primatol 19(1):13-51.

Kirkpatrick RC. 1996. Ecology and behavior of the Yunnan snub-nosed langur (*Rhinopithecus bieti*, Colobinae). PhD dissertation, Davis, CA: University of California.

Kirkpatrick, RC. 2007. The Asian colobines: diversity among leaf-eating monkeys. In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M, Bearder SK (eds) Primates in Perspective. Oxford Univ Press, New York, pp:186-200.

Kitchen DM, Beehner JC. 2007. Factors affecting individual participation in group-level aggression among non-human primates. Behavior 144(12):1551-1581.

Kitchen DM, Horwich RH, James FA. 2004. Subordinate male black howler monkey (*A. pigra*) responses to loud calls: experimental evidence for the effects of intra-group male relationships and age. Behavior 141:703–723.

Kocher TD, Wilson AC. 1991. Sequence evolution of mitochondrial DNA in humans and chimpanzees. In: Evolution of Life: Fossils, Nucleotides and Culture, Springer, Tokyo. pp:391–413.

Koenig A, Larney E, Lu A, Borries C. 2007. Female dispersal in Phayre's leaf monkeys: competition for group membership and optimal groups. [Abstract] Am J Primatol 68(suppl 1):145.

Kool KM. 1989. Behavioural ecology of the silver leaf monkey, *Trachypithecus auratus* sondaicus, in the Pangandaran Nature Reserve, West Java, Indonesia. PhD dissertation, Australia: University of New South Wales.

Kool KM. 1993. The diet and feeding behavior of the silver leaf monkey (*Trachypithecus auratus sondaicus*) in Indonesia. Int J Primatol 14(5):667-700.

Korstjens AH, Schippers EP. 2003. Dispersal patterns among olive colobus in Tai National Park. Int J Primatol 24(3):515-539.

Kowalewski MM, Garber PA. 2010. Mating promiscuity and reproductive tactics in female black and gold howler monkeys (*Alouatta caraya*) inhabiting an island on the Parana River, Argentina. Am J Primatol 72(8):734-748.

Koyama NF, Caws C, Aureli F. 2006. Interchange of grooming and agonistic support in chimpanzees. Int J Primatol 27(5): 1293-1309.

Kuester J, Paul A. 1999. Male migration in Barbary macaques (*Macaca sylvanus*) at Affenberg Salem. Int J Primatol 20(1):85-106.

Kummer H. 1968. Social organization of hamadryas baboons. Basel: Karger.

Kummer H. 1984. From laboratory to desert and back: A social system of hamadryas baboons. Anim Behav 32(4):965-971.

Kummer H. 1995. In Quest of the Sacred Baboon: a Scientist's Journey. Princeton: Princeton University.

Kummer, H. 1990. The social system of hamadryas baboons and its presumable evolution. In: de Mello T, Whiten T, Byrne RW (eds) Baboons. Brasilia, pp:43-60.

Kurland JA. 1977. Kin selection in the Japanese monkey. Contributions to Primatology 12:1-145.

Kutsukake N. 2007. Conspecific influences on vigilance behavior in wild chimpanzees. Int J Primatol 28(4):907-918.

Langergraber KE, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. PNAS 104:7786-7790.

Langergraber KE, Mitani JC, Vigilant L. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). Am J Primatol 71:1-12.

Lappan S. 2007. Patterns of dispersal in Sumatran siamangs (*Symphalangus syndactylus*): preliminary mtDNA evidence suggests more frequent male than female dispersal to adjacent groups. Am J Primatol 69(6):692-698.

Le KQ, Nguyen AD, Vu AT, Wright BW, Covert HH. 2007. Diet of the Tonkin snub-nosed monkey (*Rhinopithecus avunculus*) in the Khau Ca area, Ha Giang Province,

Northeastern Vietnam. Vietnamese J Primatol 1(1):75-83.

le Roux A, Beehner JC, Bergman TJ. 2010. Female philopatry and dominance patterns in wild geladas. Am J Primatol 73(5):422–430.

Lehmann J, Korstjens AH, Dunbar RIM. 2007. Fission-fusion social systems as a strategy for coping with ecological constraints: a primate case. Evol Ecol 21(5):613-634.

Leinfelder I, de Vries H, Deleu R, Nelissen M. 2001. Rank and grooming reciprocity among females in a mixed-sex group of captive hamadryas baboons. Am J Primatol 55(1):25-42.

Li B, Pan R, Oxnard CE. 2002. Extinction of snub-nosed monkeys in China during the past 400 years. Int J Primatol 23: 1227-1244.

Li BG, Chen C, Ji WH, Ren BP. 2000. Seasonal home range changes of the Sichuan Snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling mountains of China. Folia Primatol 71:375–386.

Li BG, Jia ZY, Pan RL, Ren BP. 2004. Changes in distribution of the snub-nosed monkey in China. In: Marsh LK (ed) Primates in Fragments: Ecology and Conservation. Kluwer Academic/Plenum, New York, pp:29-51.

Li BG, Pan RL, Oxnard CE. 2002. Extinction of snub-nosed monkeys in China during the past 400 years. Int J Primatol 23(6):1227-1244.

Li M, Liu ZJ, Gou JX, Ren BP, Pan RL, Su YJ, Funk SM, Wei FW. 2007. Phylogeography and population structure of the golden monkeys (*Rhinopithecus roxellana*): inferred from mitochondrial DNA sequences. Am J Primatol 69(11):1195-1209.

Li Y. 2002. The seasonal daily travel in a group of Sichuan snub-nosed monkey (*Pygahrix roxellana*) in Shennongjia Nature Reserve, China. Primates 43:271-276.

Li YK, Jiang ZG, Li CW, Grüter CC. 2010. Effects of Seasonal Folivory and Frugivory on Ranging Patterns in *Rhinopithecus roxellana*. Int J Primatol 31(4):609-626.

Liang B, Qi HJ, Zhang SY, Ren BP. 2001. Developmental traits of captive Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) at different age stages. Acta Zool Sin 47(4):381-387.

Liu Z, Ding W, Grüter C. 2004. Seasonal variation in ranging patterns of Yunnan snub-nosed monkeys Rhinopithecus bieti a Mt. Fuhe, China. Acta Zoologica Sinica 50:691-696.

Liu ZH, Ding W, Grueter CC. 2007. Preliminary data on the social organization of black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) at Tacheng, China. Acta Theriologica Sinica 27:120-122.

Liu ZJ, Ren BP, Wei FW, Long YC, Hao YL, Li M. 2007. Phylogeography and population structure of the Yunnan snub-nosed monkey (*Rhinopithecus bieti*) inferred from mitochondrial control region DNA sequence analysis. Mol Ecol 16(6):3334-3349.

MacKenzie MM, McGrew WC, Chamove AS. 1985. Social preferences in stumptailed macaques (*Macaca arctoides*): effects of companionship, kinship, and rearing. Dev Psychobiol 18:115–123.

Maestripieri D, Mayhew J, Carlson CL, Hoffman CL, Radtke JM. 2007. One-male harems and female social dynamics in Guinea baboons. Folia Primatol 78:56-68.

Majolo B, Ventura R, Koyama NF. 2005. Sex, rank and age differences in the Japanesee macaque (*Macaca fuscata yakui*) participation in inter-group encounters. Ethol 111:455-468.

Manson JH, Navette CD, Silk JB, Perry S. 2004. Time-matched grooming in female primates? New analyses from two species. Anim Behav 67:493−500.

Manson JH, Rose LM, Perry S, Gros-Louis J. 1999. Dynamics of female-female relationships in wild *Cebus capucinus*: data from two Costa Rican sites. Int J Primatol 20:679–706.

Marsh CW. 1979. Female transference and mate choice among Tana River red colobus. Nature 281:568-569.

Martin DA.1997. Kinship bias: A function of familiarity in pigtailed macaques (*Macaca nemestrina*). PhD dissertation, Athens, GA: University of Georgia.

Matheson MD, Bernstein IS. 2000. Grooming, social bonding, and agonistic aiding in rhesus monkeys. Am J Primatol 51(3):177-186.

Matsuda I, Tuuga A, Higashi S. 2009. Ranging behavior of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. Int J Primatology. 30(2):313-325.

Matsumura S, Okamoto K. 1997. Factors affecting proximity among member of a wild group of moor macaques during feeding, moving, and resting. Int J Primatol 18(6):929-940.

Matsumura S. 1993. Intergroup affiliative interactions and intergroup transfer of young male Japanese macaques (*Macaca fuscata*). Primates 34(1):1-10.

Megantara EN. 1989. Ecology, behavior and sociality of *Presbytis femoralis* in East-central Sumatra. Comparative Primatology Monographs 2:171-301.

Melnick DJ, Hoelzer GA. 1992. Differences in male and female macaque dispersal lead to contrasting distributions of nuclear and mitochondrial DNA variation. Int J Primatol 13(4):379-393.

Missakian EA. 1972. Genealogical and cross-genealogical dominance relations in a group of free-ranging rhesus monkeys (*Macaca mulatta*) on Cayo Santiago. Primates 13:169–180.

Mitani J. 2006. Reciprocal exchange in chimpanzees and other primates. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolutions. Springer, New York, pp:107-120.

Mitani JC, Merriwether DA, Zhang CB. 2000. Male affiliation, cooperation and kinship in wild chimpanzees. Anim Behav 59(4):885-893.

Mitani JC, Watts DP. 2001. Why do chimpanzees hunt and share meat? Anim Behav 61(5):915-924.

Mitani, JC, Watts, DP, Pepper, JW, Merriwether, D.A. 2002. Demographic and social constraints on male chimpanzee behavior. Anim Behav 64:727–737.

Mitchell AH. 1994. Ecology of Hose's langur, *Presbytis hosei*, in mixed logged and unlogged dipterocarp forest of northeast Borneo. PhD dissertation, New Haven: Yale University.

Morelli TL, King SJ, Pochron ST, Wright PC. 2009. The rules of disengagement: takeovers, infanticide, and dispersal in a rainforest lemur, *Propithecus edwardsi*. Behavior 146(4-5):499-523.

Mori A, Iwamoto T, Mori U, Bekele A. 1999. Sociological and demographic characteristics of a recently found Arsi gelada population in Ethiopia. Primates 40(2):365-381.

Mori A, Yamane A, Sugiura H, Shotake T, Boug A, Iwamoto T. 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.

Mori, A. 1975. Intratroop spacing mechanism of the wild Japanese monkeys of the Koshima troop. In: Kondo S, Kawai M, Ehara A (eds) Contemporary Primatology. S. Karger, Basel, pp: 423–427.

Morin PA, Chambers KE, Boesch C, Vigilant L. 2001. Quantitative PCR analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). Mol Ecol 10:1835–1844.

Mukherjee RP, Saha SS. 1974. The golden langurs (*Presbytis geei* Khajuria, 1956) of Assam. Primates 15: 327-340.

Mukherjee RP. 1978. Further observations on the golden langur (*Presbytis geei* Khajuria, 1956), with a note to capped langur (*Presbytis pileatus* Blyth, 1843) of Assam. Primates 19: 737-747.

Muller MN, Wrangham RW. 2004. Dominance, cortisol and stress in wild chimpanzees (*Pan troglodytes schweinfurthii*). Behav Ecol Sociobiol 55(4):332-340.

Muniz L, Vigilant L. 2008. Isolation and characterization of microsatellite markers in the white-faced capuchin monkey (*Cebus capucinus*) and cross-species amplification in other New World monkeys. Mol Ecol Res 8:402–405.

Murai T, Mohamed M, Bernard H, Mahedi PA, Saburi R, Higashi S. 2007. Female transfer between one-male groups of proboscis monkey (*Nasalis larvatus*). Primates 48(2):117-121.

Murai T. 2006. Mating behaviors of the proboscis monkey (*Nasalis larvatus*). Am J Primatol 68(8):832-837.

Muroyama Y. 1991. Mutual reciprocity of grooming in female Japanese macaques (*Macaca fuscata*). Behavior 119(3-4):161-170.

Muroyama Y. 1994. Exchange of grooming for allomothering in female patas monkeys. Behavior 128(1-2):103-119.

Newman TK, Fairbanks LA, Pollack D, Rogers J. 2002. Effectiveness of human microsatellite loci for assessing paternity in a captive colony of vervets (*Chlorocebus aethiops sabaeus*). Am J Primatol 56:237–243.

Newton P. 1992. Feeding and ranging patterns of forest hanuman langurs (*Presbytis entellus*). Int J Primatol 13:245-285.

Newton PN, Dunbar RIM. 1994. Colobine monkey society. In: Davies AG, Oates JF (eds) Colobine Monkeys: Their Ecology, Behaviour and Evolution. Cambridge University Press, Cambridge, pp:311-346.

Newton PN. 1987. The social organization of forest hanuman langurs (*Presbytis entellus*). Int J Primatol 8(3):199-232.

Nievergelt CM, Digby LJ, Ramakrishnan U, Woodruff DS. 2000. Genetic analysis of group composition and breeding system in a wild common marmoset (*Callithrix jacchus*) population. Int J Primatol 21:1–20.

Nishida T. 1989. Social interactions between resident and immigrant female chimpanzees. In: Heltne PG, Marquardt LA (eds) Understanding Chimpanzees. Harvard University Press, Cambridge, pp:68-89.

Noë R, Hammerstein P. 1995. Biological markets. Trends Ecol Evol 10:336–339.

Noë R. 2001. Biological markets: partner choice as the driving force behind the evolution of mutualisms. In: Noë R, van Hooff JARAM, Hammerstein P (eds) Economics in Nature. Social dilemmas, mate choice and biological markets. Cambridge University Press, New York, pp:93-118.

Norton GW, Rhine RJ, Wynn GW, Wynn RD. 1987. Baboon diet: A five-year study of stability and variability in the plant feeding and habitat of the yellow baboons (*Papio cynocephalus*) of Mikumi National Park, Tanzania. Folia Primatol 48(1-2):78-120.

Nsubuga AM, Robbins MM, Roeder AD, Morin PA, Boesch C, Vigilant L. 2004. Factors affecting the amount of genomic DNA extracted from ape faeces and the dentification of an improved sample storage method. Mol Ecol 13(7):2089-2094.

Nunn CL, Deaner RO. 2004. Patterns of participation and free riding in territorial conflicts among ringtailed lemurs (*Lemur catta*). Behav Ecol Sociobiol 57(1):50-61.

Nunn CL, Lewis RJ. 2001. Cooperation and collective action in animal behaviour. —In: Noë R, van Hooff JARAM, Hammerstein P (eds) Economics in Nature. Social dilemmas, mate choice and biological markets. Cambridge University Press, New York, pp:42-66.

Nunn CL. 2000. Collective benefits, free-riders, and male extra-group conflict. — In: Kappeler P (ed) Primate males: causes and consequences of variation in group composition Cambridge University Press, Cambridge, pp:192-204.

Oates JF, Waterman PG, Choo GM. 1980. Food selection by the South Indian leaf-monkey, Presbytis johnii, in relation to leaf chemistry. Oecologia 45: 45-56.

O'Brien TG, Robinson JG. 1993. Stability of social relationships in female wedge-capped capuchin monkeys. In: Pereira ME, Fairbanks LA (eds) Juvenile Primates: Life History, Development, and Behavior. Oxford University Press, pp: 197-210.

O'Brien TG. 1993. Allogrooming behaviour among adult female wedge-capped capuchin monkeys. Anim Behav 46(3):499-510.

Ohsawa H, Dunbar RIM. 1984. Variations in the demographic structure and dynamics of gelada baboon populations. Behav Ecol Sociobiol 15(3):231-240.

Ohsawa H. 1979. Herd dynamics. Contributions to Primatology 16:46-80.

Olupot W, Waser PM. 2001. Correlates of intergroup transfer in male grey-cheeked mangabeys. Int J Primatol 22(2):169-187.

Palombit RA, Seyfarth RM, Cheney DL. 1997. The adaptive value of 'friendships' to female baboons: Experimental and observational evidence. Anim Behav 54(3):599-614.

Pan D, Hu HX, Meng SJ, Men ZM, Fu YX, Zhang YP. 2009. A high polymorphism level in Rhinopithecus roxellana. Int J Primatol 30(2):337-351.

Parga JA, Lessnau RG. 2008. Dispersal among male ring-tailed lemurs (*Lemur catta*) on St. Catherines Island. Am J Primatol 70(7):650-660.

Parish AR. 1996. Female relationships in bonobos (*Pan paniscus*): evidence for bonding, cooperation, and female dominance in a male-philopatric species. Hum. Nat. 7:61–96.

Parnell RJ. 2002. Group size and structure in western lowland gorillas (*Gorilla gorilla gorilla*) at Mbeli Bai, Republic of Congo. Am J Primatol 56(4):193-206.

Patzelt A, Zinner D, Fickenscher G, Diedhiou S, Camara B, Stahl D, Fischer J. 2011. Group Composition of Guinea Baboons (*Papio papio*) at a Water Place Suggests a Fluid Social Organization. Int J Primatol 32:652-668.

Perez AP, Vea JJ. 2000. Allogrooming behavior in Cercocebus torquatus: The case for the hygienic functional hypothesis. Primates 41(2):199-207.

Perry S ; Manson JH ; Muniz L ; Gros-Louis J ; Vigilant L. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, Cebus capucinus. Anim Behav 76(1):187-199.

Phillips-Conroy JE, Jolly CJ. 2004. Male dispersal and philopatry in the Awash baboon hybrid zone. Primate Report. 68:27-52.

Poirier FE. 1968. Nilgiri langur (*Presbytis johnii*) territorial behavior. Primates 9:351-364.

Poirier FE. 1970. The Nilgiri langur (*Presbytis johnii*) of South India. In: Rosenblum LA (ed) Primate behavior: developments in field and laboratory research, VOL. 1. Academic Press, New York, pp: 251-383.

Pope TR. 1990. The reproductive consequences of male cooperation in the red howler monkey: Paternity exclusion in multi-male and single-male troops using genetic markers. Behav Ecol Sociobiol 27(6):439-446.

Pope TR. 1992. The influence of dispersal patterns and mating system on genetic differentiation within and between populations of the red howler monkey (*Alouatta seniculus*). Evolution 46(4):1112-1128.

Pope TR. 2000. Reproductive success increases with degree of kinship in cooperative coalitions of female red howler monkeys (*Alouatta seniculus*). Behav Ecol Sociobiol 48:253–267.

Port M, Clough D, Kappeler PM. 2009. Market effects offset the reciprocation of grooming in free-ranging redfronted lemurs, *Eulemur fulvus rufus*. Anim Behav 77(1):29-36.

Printes RC, Strier KB. 1999. Behavioral correlates of dispersal in female muriquis (*Brachyteles arachnoides*). Int J Primatol 20(6):941-960.

Pusey AE, Packer C. 1987. Dispersal and philopatry. In: Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW, Struhsaker TT (eds) Primate Societies. University of Chicago Press, Chicago, pp 250-266.

Pusey AE, Wilson ML, Collins DA. 2008. Human impacts, disease risk, and population dynamics in the chimpanzees of Gombe National Park, Tanzania. Am J Primatol 70(8):738-744

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(8):670-679.

Qi XG, Li BG, Ji WH. 2008. Reproductive parameters of wild female Rhinopithecus roxellana. Am J Primatol 70:311-319.

Qi XG, Yang B, Garber P, Ji WH, Watanade K, Li BG. 2011. Sexual interference in the golden snub-nosed monkey (*Rhinopithecus roxellana*): a test of the sexual competition hypothesis in a polygynous species. Am J Primatol 73(4):366-377.

Radespiel U, Juric M, Zimmermann E. 2009. Sociogenetic structures, dispersal and the risk of inbreeding in a small nocturnal lemur, the golden-brown mouse lemur (*Microcebus ravelobensis*). Behaviour 146(4-5):607-628.

Radespiel U, Lutermann H, Schmelting B, Bruford MW, Zimmermann E. 2003. Patterns and dynamics of sex-biased dispersal in a nocturnal primate, the grey mouse lemur, *Microcebus murinus*. Anim Behav 65(4):709-719.

Rajpurohit LS, Chhangani AK, Rajpurohit RS, Mohnot SM. 2003. Observation of a sudden resident-male replacement in a unimale bisexual troop of Hanuman langurs, *Semnopithecus entellus*, around Jodhpur (India). Folia Primatol 74(2):85-87.

Rajpurohit LS, Sommer V. 1993. Juvenile male emigration from natal one-male troops in Hanuman langurs. In: Pereira ME, Fairbanks LA (eds) Juvenile Primates: Life History, Development, and Behavior. Oxford University Press, New York, pp 86-103

Rapaport LG. 2001. Food transfer among adult lion tamarins: mutualism, reciprocity or one-sided relationships? Int J Primatol 22(4):611-629.

Reichard U, Sommer V. 1994. Grooming site preferences in wild white-handed gibbons (*Hylobates lar*). Primates 35(3): 369-374.

Ren BP, Li M, Wei FW, Long YC. 2004. The Yunnan snub-nosed monkey (*Rhinopithecus bieti*). Chinese Journal of Zoology 39:111 & 104.

Ren RM, Su YJ, Yan KH, Li JJ, Zhou Y, Zhu ZQ, Hu ZL, Hu YF. 1988. Preliminary survey of the social organization of *Rhinopithecus roxellana* in Shennongjia National Natural Reserve, Hubei, China. In: Jablonski NG (ed) The Natural History of the Doucs and Snub-nosed Monkeys. World Scientific, Singapore, pp: 269-277.

Ren Rm, Yan Kh, Su Yj, Qi Hj, Liang B, Bao Wy, de Waal FBM. 1995. The reproductive behavior of golden monkeys in captivity (*Rhinopithecus roxellana*). Primates 36(1):135-143.

Ren RM, Yan KH, Su YJ, Zhou Y, Li JJ, Zhu ZQ, Hu ZL, Hu YF. 2000. A field study of the society of *Rhinopithecus Roxellana*. Beijing University, Beijing

Robbins AM, Stoinski T, Fawcett K, Robbins MM. 2009a. Leave or conceive: natal dispersal and philopatry of female mountain gorillas in the Virunga volcano region. Anim Behav 74(4):831-838

Robbins AM, Stoinski TS, Fawcett KA, Robbins MM. 2009b. Socioecological influences on the dispersal of female mountain gorillas - evidence of a second folivore paradox. Behav Ecol Sociobiol 63(4):477-489.

Rogers ME, Abernethy KA, Fontaine B, Wickings EJ, White LJT, Tutin CEG. 1996. Ten days in the life of a mandrill horde in the Lope Reserve, Gabon. Am J Primatol 40:297-313.

Rose LM, Fedigan LM. 1995. Vigilance in white-faced capuchins, *Cebus capucinus*, in Costa Rica. Anim Behav 49(1):63-70.

Ross C. 1993. Take-over and infanticide in South Indian Hanuman langurs (*Presbytis entellus*). Am J Primatol 30:75-82.

Rowell TE, Wilson C, Cords M. 1991. Reciprocity and partner preference in grooming of female blue monkeys. Int J Primatol 12(4):319-336.

Rudran R. 1973. Adult male replacement in one-male troops of purple-faced langurs (*Presbytis senex senex*) and its effect on population structure. Folia Primatol 19:166-192.

Ruhiyat Y. 1983. Socio-ecological study of Presbytis aygula in West Java. Primates 24(3):344-359.

Saayman GS. 1971. Behaviour of chacma baboons. African Wildlife 25:25-29.

Sackett GP, Fredrickson WT. 1987. Social preferences by pigtailed macaques: Familiarity versus degree and type of kinship. Anim Behav 35(2):603-606.

Sade, D. S. 1965. Some aspects of parent-offspring and sibling relations in a group of rhesus monkeys, with a discussion of grooming. Am J Phys Anthropol 23:1–18.

Sade, D. S. 1972. Sociometrics of Macaca mulatta. I. Linkages and cliques in grooming matrices. Folia Primatol 18:196–223.

Salafsky N. 1988. The feeding behavior and socioecology of the Kelasi (*Presbytis rubicundu*). Honors thesis, Harvard University, Cambridge, Massachusetts.

Samuels A, Altmann J. 1991. Baboons of the Amboseli Basin: Demographic stability and change. Int J Primatol 12(1):1-19.

Sayers K, Norconk MA. 2008. Himalayan Semnopithecus entellus at Langtang National Park, Nepal: Diet, activity patterns, and resources. Int J Primatol 29(2):509-530.

Schino G, Aureli F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions. Adv Study Behav 39:45–69.

Schino G, Di Giuseppe F, Visalberghi E. 2009. The time frame of partner choice in the grooming reciprocation of *Cebus apella*. Ethol 115(1):70-76.

Schino G, Pellegrini B. 2009. Grooming in mandrills and the time frame of reciprocal partner choice. Am J Primatol 71(10):884-888.

Schino G, Polizzi di Sorrentino E, Tiddi B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame reciprocation. J Comp Psychol 121(2):181-188.

Schino G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism.

Behav Ecol 18(1):115-120.

Schlötterer C. 2000. Evolutionary dynamics of microsatellite DNA. Chromosoma 109:365–371.

Schreier AL, Swedell L. 2009. The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. Am J Primatol 71(11):948-955.

Seyfarth RM. 1978. Social relationships among adult male and female baboons. I. Behaviour during sexual consortship. Behaviour 64:204-226.

Shotake T, Nozawa K. 1984. Blood protein variations in baboons. II. Genetic variability within and among herds of gelada baboons in the central Ethiopian plateau. J Hum Evol 13(3):265-274.

Shutt K, MacLarnon A, Heistermann M, Semple S. 2007. Grooming in Barbary macaques: better to give than to receive? Biology Letters 3(3):231-233.

Sigg H, Stolba A, Abegglen JJ, Dasser V. 1982. Life history of hamadryas baboons: Physical development, infant mortality, reproductive parameters and family relationships. Primates 23(4):473-487.

Sigg H, Stolba A. 1981. Home range and daily march in a Hamadryas baboon troop. Folia Primatol 36:40-75.

Silk JB, Alberts SC, Altmann J. 2004. Patterns of coalition formation by adult female baboons in Amboseli, Kenya. Anim Behav. 67(3):573-582.

Silk JB, Altmann J, Alberts SC. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. Behav Ecol Sociobiol 61(2):183-195.

Silk JB, Altmann J, Alberts SC. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*). II. Variation in the quality and stability of social bonds. Behav Ecol Sociobiol 61(2):197-204.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. Behav Ecol Sociobiol 64(11):1733-1747.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2010b. Strong and consistent social bonds enhance the longevity of female baboons. Current Biology 20(15):1359-1361.

Silk JB, Beehner JC, Bergman TJ, Crockford C, Engh AL, Moscovice LR, Wittig RM, Seyfarth RM, Cheney DL. 2009. The benefits of social capital: close social bonds among female baboons enhance offspring survival. Proc Roy Soc (London) B276(1670):3099-3104.

Silk JB. 1992. The patterning of intervention among male bonnet macaques: Reciprocity, revenge, and loyalty. Current Anthropology 33(3):318-325.

Silk JB. 2002. Kin selection in primate groups. Int J Primatol 23(4):849-875.

Silk JB. 2006. Practicing Hamilton's rule: kin selection in primate groups. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolutions. Springer, New York, pp:25-46.

Silk, J.B. 2005. The Evolution of Cooperation in Primate Groups. In: Gintis H, Bowles S, Boyd R, Fehr E (eds) Moral sentiments and material interests: on the foundations of cooperation in economic life. MIT Press, Cambridge, pp:43–73.

Slater KY, Schaffner CM, Aureli F. 2007. Embraces for infant handling in spider monkeys: evidence for a biological market? Anim behav 74(3):455-461.

Smith DG, Kanthaswamy S, Viray J, Cody L. 2000. Additional highly polymorphic microsatellite (STR) loci for estimating kinship in rhesus macaques (*Macaca mulatta*). Am J Primatol 50(1):1-7.

Smith, K, Alberts, SC, Altmann, J. 2003. Wild female baboons bias their social behaviour towards paternal half-sisters. Proc Roy Soc (London) B270:503-510.

Smuts BB. 1985. Sex and friendship in baboons. New York: Aldine.

Sommer V, Srivastava A, Borries C. 1992. Cycles, sexuality, and conception in freeranging female langurs (*Presbytis entellus*).Am J Primatol 28:1–27.

Srivastava A, Biswas J, Das J, Bujarbarua P. 2001. Status and distribution of golden langurs (*Trachypithecus geei*) in Assam, India. Am J Primatol 55(1):15-23.

Stacey PB. 1986. Group size and foraging efficiency in yellow baboons. Behav Ecol Sociobiol 18(3): 175-187.

Stanford CB. 1991. Social dynamics of intergroup encounters in the capped langur (*Presbytis pileata*). Am J Primatol 25(1):35-47.

Stanford CB. 1996. The hunting ecology of wild chimpanzees: Implications for the evolutionary ecology of Pliocene hominids. Am Anthropol 98(1):96-113.

Starin E. 1978. A preliminary investigation of home range use in the Gir Forest Langur. Primates 19:551-568.

Steenbeek R. 1999. Tenure related changes in wild Thomas's langurs. I: Between-group interactions. Behavior. 136(5): 595-625.

Sterck EHM, Willems EP, van Hooff JARAM, Wich SA. 2005. Female dispersal, inbreeding avoidance and mate choice in Thomas langurs (*Presbytis thomasi*). Behaviour

142(7):845-868.

Sterck EHM. 1997. Determinants of female dispersal in Thomas langurs. Am J Primatol 42(3):179-198.

Sterck EHM. 1998. Female dispersal, social organization, and infanticide in langurs: Are they linked to human disturbance? Am J Primatol 44(4):235-254.

Stevens JR, Hauser MD. 2005. Cooperative brains: psychological constraints on the evolution of altruism. In: Dehaene S, Duhamel JR, Hauser MD, Rizzolatti G (eds) From monkey band to human brain: a fyssen foundation symposium. MIT Press, Cambridge, pp: 159-187.

Stoinski TS, Vecellio V, Ngaboyamahina T, Ndagijimana F, Rosenbaum S, Fawcett KA. 2009. Proximate factors influencing dispersal decisions in male mountain gorillas, Gorilla beringei beringei. Anim Behav 77(5):1155-1164.

Stojan-Dolar M, Heymann EW. 2010. Vigilance of mustached tamarins in single-species and mixed-species groups—the influence of group composition. Behav Ecol Sociobiol 64(3): 325-335.

Stokes EJ, Parnell RJ, Olejniczak C. 2003. Female dispersal and reproductive success in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behav Ecol Sociobiol 54(4):329-339.

Stoltz LP, Saayman GS. 1970. Ecology and behaviour of baboons in the northern Transvaal. Annals of Transvaal Museum. 26:99-143.

Strier KB, Ziegler TE. 2000. Lack of pubertal influences on female dispersal in muriqui monkeys, *Brachyteles arachnoides*. Anim Behav 59(4):849-860.

Struhsaker TT. 1975. The red colobus monkey. The University of Chicago Press, Chicago

Stumpf RM, Emery Thompson M, Muller MN, Wrangham RW. 2009. The context of female dispersal in Kanyawara chimpanzees. Behaviour. 146(4-5):629-656

Sugiyama Y. 1964. Group composition, population density and some sociological observations of hanuman langurs (*Presbytis entellus*). Primates 5:7-37.

Supriatna J, Manullang BO, Soekara E. 1986. Group composition, home range, and diet of the Maroon leaf monkey (*Presbytis rubicunda*) at Tanjung Puting reserve, Central Kalimantan, Indonesia. Primates 27:185-190.

Sussman RW, Garber PA. 2011. Cooperation, collective action, and competition in primate social interactions. In: Campbell CJ, Fuentes A, MacKinnon KC, Bearder S, Stumpf R (eds) Primates in Perspective Vol 2. Oxford University Press, pp:587-599.

Swedell L, Saunders J, Schreier A, Davis B, Tesfaye T, Pines M. 2011. Female “dispersal” in hamadryas baboons: Transfer among social units in a multilevel society. Am J Phys Anthro 145(3):360-370.

Swedell L, Saunders J. 2006. Infant mortality, paternity certainty, and female reproductive strategies in hamadryas baboons. In: Swedell L, Leigh SR (eds) Reproduction and fitness in baboons: behavioral, ecological, and life history perspectives. Springer, New York, pp:19-51.

Swedell L, Schreier A. 2009. Male aggression toward females in Hamadryas baboon: conditioning, coercion, and control. In: Muller MN, Wrangham RW (eds) Sexual Coercion in Primates and Humans: an Evolutionary Perspective on Male Aggresion against Females. Harvard Univ Press, Cambridge, pp:244-268.

Swedell L, Wooley-Barker T. 2001. Dispersal and philopatry in Hamadryas baboons: A re-evaluation based on behavioral and genetic evidence. Am J Phys Anthropol Suppl (32): 146

Swedell L. 2002. Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). Int J Primatol 23:1205–1226.

Swedell L. 2006. Strategies of sex and survival in hamadryas baboons: through a female lens. Upper Saddle River, NJ: Pearson Prentice Hall.

Symington M.M. 1990. Fission-Fusion Social Organization in Ateles and Pan. Int J Primatol 11:47-61.

Taberlet P, Griffin S, Goossens B et al. 1996. Reliable genotyping of samples with very low DNA quantities using PCR. Nucleic Acids Research. 24:3189–3194.

Tan CL, Guo ST, Li BG. 2007. Population structure and ranging patterns of *Rhinopithecus roxellana* in Zhouzhi National Reserve, Shaanxi, China. Int J Primatol 28(3):577-591.

Teichroeb JA, Marteinson S, Sicotte P. 2005. Individuals' behaviors following dye-marking in wild black-and-white colobus (*Colobus vellerosus*). Am J Primatol 65(2):197-203.

Teichroeb JA, Wikberg EC, Sicotte P. 2009. Female dispersal patterns in six groups of ursine colobus (*Colobus vellerosus*): infanticide avoidance is important. Behaviour 146(4-5):551-582.

Tenaza RR, Fitch HM, Lindburg DG. 1988. Vocal behavior of captive Sichuan golden monkeys (*Rhinopithecus roxellana*). Am J Primatol 14:1-9.

Tenaza RR, Fuentes A. 1995. Monandrous social organization of pigtailed langurs (*Simias concolor*) in the Pagai Islands, Indonesia. Int J Primatol 16(2):295-310.

Tenaza RR. 1989. Intergroup calls of male pig-tailed langurs (*Simias concolor*). Primates 30(2):199-206.

Thierry B, Anderson JR, Demaria C, Desportes C, Petit O. 1994. Tonkean macaque behaviour from the perspective of the evolution of Sulawesi macaques. In: Roeder JJ, Thierry B, Anderson JR, Herrenschmidt N (eds) Current Primatology. VOL. II: Social Development,

Learning and Behaviour. Univ. Louis Pasteur, Strasbourg, pp:103-117.

Thierry B. 1990. Feedback loop between kinship and dominance: the macaque model. J Theor Biol 145:511–521.

Tiddi B, Aureli F, Schino G. 2010. Grooming for infant handling in tufted capuchin monkeys: a reappraisal of the primate infant market. Anim Behav 79(5):1115-1123.

Treves A. 1997. Vigilance and use of micro-habitat in solitary rainforest mammals. Mammalia. 61(4): 511-525.

Treves A. 1998. The influence of group size and neighbors on vigilance in two species of arboreal monkeys. Behaviour 135(4): 453-481.

Treves A. 1999a. Vigilance and spatial cohesion among blue monkeys. Folia Primatol 70(5):291-294.

Treves A. 1999b. Within-group vigilance in red colobus and redtail monkeys. Am J Primatol 48(2):113-126.

Trivers R. 2006. Reciprocal altruism: 30 years later. In: Kappeler PM, van Schaik CP (eds) Cooperation in primates and humans: mechanisms and evolutions. Springer, New York, pp:67-84.

Trivers RL. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46:25-57.

van Schaik CP, Assink PR, Salafsky N. 1992. Territorial behavior in southeast Asian langurs: Resource defense or mate defense? Am J Primatol 26(4):233-242.

Vasudev D, Kumar A, Sinha A. 2008. Resource distribution and group size in the common langur *Semnopithecus entellus* in southern India. Am J Primatol 70(7):680-689.

Ventura R, Majolo B, Koyama NF, Hardie S, Schino G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. Am J Primatol 68(12):1138-1149.

Wahungu GM. 1998. Diet and habitat overlap in two sympatric primate species, the Tana crested mangabey *Cercocebus galeritus* and yellow baboon *Papio cynocephalus*. Afr J Ecol 36(2):159-173.

Walters JR. 1987. Kin recognition in non-human primates. In: Fletcher DJC, Michener CD (eds) Kin Recognition in Animals. John Wiley & Sons Ltd, New York, pp:359-393.

Wang HP, Tan CL, Gao YF, Li BG. 2004. A takeover of resident male in the Sichuan snub-nosed monkey *Rhinopithecus roxellana* in Qinling Mountains. Acta Zoologica Sinica 50(5):859-862

Watanabe K. 1981. Variations in group composition and population density of the two sympatric

Mentawaian leaf-monkeys. Primates 22:145-160.

Watts DP (1996) Comparative socio-ecology of gorillas. In: McGrew WC, Marchant LF, Nishida T (eds) Great ape societies. Cambridge University Press, Cambridge, pp:16-28.

Watts DP. 1991. Harassment of immigrant female mountain gorillas by resident females. Ethol 89:135-153.

Watts DP. 1994. Social relationships of immigrant and resident female mountain gorillas, II: Relatedness, residence, and relationships between females. Am J Primatol 32(1):13-30.

Watts DP. 1997. Agonistic interventions in wild mountain gorilla groups. Behaviour 134(1-2):23-57.

Watts DP. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. Behaviour 139(2-3):343-370.

Welker C, Schwibbe MH, Schaefer-Witt C, Visalberghi E. 1987. Failure of kin recognition in Macaca fas*cicularis*. Folia Primatol 49(3):216-221.

Whiten A, Byrne RW, Henzi SP. 1987. The behavioral ecology of mountain baboons. Int J Primatol 8(4):367-388.

Wich SA, Assink PR, Becher F, Sterck EHM. 2002. Playbacks of loud calls to wild Thomas langurs (Primates; *Presbytis thomasi*): The effect of familiarity. Behavior 139(1):79-87.

Wich SA, Nunn CL. 2002. Do male "long-distance calls" function in mate defense? A comparative study of long-distance calls in primates. Behav Ecol Sociobiol 52(6):474-484.

Wich SA, Sterck EHM. 2007. Familiarity and threat of opponents determine variation in Thomas langur (*Presbytis thomasi*) male behaviour during between-group encounters. Behaviour 144(12):1583-1598

Widdig A, Nurnberg P, Krawczak M, Bercovitch FB. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. PNAS 98: 13,769–13,773.

Widdig A, Nurnberg P, Krawczak M, Streich WJ, Bercovitch F. 2002. Affiliation and aggression among adult female rhesus macaques: A genetic analysis of paternal cohorts. Behaviour 139(2-3):371-391.

Wimmer B, Tautz D, Kappeler PM. 2002. The genetic population structure of the gray mouse lemur (*Microcebus murinus*), a basal primate from Madagascar. Behav Ecol Sociobiol 52(2):166-175.

Wolf KE, Fleagle JG. 1977. Adult male replacement in a group of silvered leaf monkeys (*Presbytis cristata*) at Kuala Selangor, Malaysia. Primates 18:949-955.

Xiang ZF. 2005. The Ecology and Behavior of Black-and-White Snub-nosed Monkeys (*Rhinopithecus bieti*, Colobinae) at Xiaochangdu in Honglaxueshan National Nature Reserve, Tibet, China. Ph.D. thesis. Kunming Institute of Zoology, Kunming, China.

Yan C, Jiang ZG. 2006. Does estradiol modulate sexual solicitations in the female Sichuan Golden Monkey (*Rhinopithecus roxellana*)? Int J Primatol 27(4):1171-1186.

Yao H, Liu XC, Stanford G, Yang JY, Huang TP, Wu F, Li YM. 2011. Male dispersal in a provisioned multilevel group of *Rhinopithecus roxellana* in Shennongjia Nature Reserve, China. Am J Primatol 73(12):1280-1288.

Yeager CP. 1990a. Proboscis monkey (*Nasalis larvatus*) social organization: Group structure. Am J Primatol 20(2):95-106.

Yeager CP. 1990b. Proboscis monkey (*Nasalis larvatus*) social organization and ecology. PhD dissertation, Davis: University of California,

Yeager CP. 1991. Proboscis monkey (*Nasalis larvatus*) social organization: intergroup patterns of association. Am J Primatol 23:73-86.

Zamma K. 2002. Grooming site preferences determined by lice infection among Japanese macaques in Arashiyama. Primates 43(1):41-49.

Zhang DX, Hewitt GM. 1994. Nuclear integrations: challenges for mitochondrial DNA markers. Trends Ecol Evol 11(6):247-251.

Zhang P, Watanabe K, Li BG, Tan CL. 2006. Social organization of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains, Central China. Primates 47(4):374-382.

Zhang P, Watanabe K, Li BG. 2008. Female social dynamics in a provisioned free-ranging band of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains, China. Am J Primatol 70(11):1013-1022.

Zhao DP, Ji WH, Li BG, Watanabe K. 2008. Mate competition and reproductive correlates of female dispersal in a polygynous primate species (*Rhinopithecus roxellana*). Behavioral Process 79(3):165-170.

Zhao, DP, Li, BG, Li, YH, Wada, K. 2005. Extra-unit sexual behaviour among wild Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains of China. Folia Primatol 76(3):172-176.

Zhou QH, Huang CM, Li YB. 2006. Allogrooming of captive Francois langur (*Trachypithecus francoisi*). Acta Theriologica Sinica 26(3):221-225.

Zinner D, Pelaez F, Torkler F. 2001. Group composition and adult sex-ration of hamadryas baboons (*Papio hamadryas hamadryas*) in central Eritrea. Int J Primatol 22(3):415-430.

Zischler H, Hoss M, Handt O, von Haeseler A, van der Kuyl AC, Goudsmit J. 1995. Detecting dinosaur DNA. Science 268(5214):1192-1193.

APPENDIX A
Affiliative interactions between members of different OMUs

Case1: On **April 29**, at 11:00am, adult female HG (HG used to belong to LP's unit, and then immigrated into BB's unit during the winter of 2007) solicited adult male LP and LP mated with her for 10 second. HG continued to solicit, but LP ignored. At 11:02am HG started grooming LP. They are 10m away from LP's females and are within their sights, but none of the females showed any response. BB was out of the view. The grooming interactions lasted for 26mins (LP groomed HG 4mins, HG groomed LP 22mins). At 11:28am LP left HG. At the same time, TH approached HG and threatened HG. LP did not show any response. At 11:29am TH groomed LP 2 min, and then LP left TH.

Case 2: On **April 1** at 11:06am, adult female ZT (LP unit) was resting on the ground. Adult female HG (BB unit) was on this way leaving the provision area and approached ZT. HG groomed ZT for 3 mins and then left. At the same time LP and his three other females was eating corns at the provision area 25m away. The two females were out of the sight of LP. At the end of the grooming interaction, adult male BB approached HG and ZT. However, BB did not show any threaten to HG or ZT. ZT look scared and retreated. HG left ZT calmly and continued walking. BB followed ZT and both climbed to a tree and rest.

Case 3: On **May 18** at 15:56pm**,** one of FP's female (can't determine which one) get close to one of DB' female (can't determine which one), who was carrying an infant. FP's female get interested in the infant, and touched the infant. Both the mother and the infant screamed, DB threatened FP's female, and then FP's female retreated.

Case 4: On **August 4** at 14:00pm, adult female KT (LP unit) approached adult female HG (BB unit) and HG started grooming KT. At the same time, LP sit 15m away and BB is out of view. The grooming interaction between HG and KT lasted for 77 minutes (KT (44 mins): HG (33 mins)). In the end, KT left HG, followed LP and started eating. HG stayed at the same place.

Case 5: On **August 11** at 16:22pm. When most individuals of the band were resting, XC (belong to HT unit) approached BJ (belong to PK unit), and groomed BJ for 4 mins and then left BJ and sit alone 6m away. At the same time HT was 20m away from XC.

Case 6: On **August 11** at 17:16pm, XC approached HJ (belong to PK unit). HJ started grooming XC for 21 minutes, and then XC groomed HJ for 11 minutes. 17:48pm, XC went back to HT unit.

APPENDIX B
Sequences of three mtDNA haplotypes

```
a     1   AGTATAATCT AATTTTATAT GCCCTTATGT AATTCGTGCA TTACTGCTAG
b     1   ----------------------------------------------------------------------------------------------------
c     1   ----------------------------------------------------------------------------------------------------

     51   TCACCATGGA TATTATATAG TACTATAAAT GTTTTATCGT CCATAGGACA
     51   ----------------------------------------------------------------------C-----------------------------
     51   ----------------------------------------------------------------------T-----------------------------

    101   TAAACTTACA TATTTACTAG CAGATCTATC TAGAACATGC TTACAAGCAA
    101   ----------------------------------------------------------------------------------------------------
    101   ----------------------------------------------------------------------------------------------------

    151   GTACTTTACC AGAACACAAT AACTGTAACA CATATCAACT AAACACCCAA
    151   ------------------------------------------------------C-----------------------------------------------
    151   ------------------------------------------------------T-----------------------------------------------

    201   ATCACATGGT AGCACCCACC GGAATACCAA CCAACACGAG ATTTCCATCA
    201   ----------------------------------------------------------------------------------------------------
    201   ----------------------------------------------------------------------------------------------------

    251   GCGTACATAG TACATCACAT TCTTTACCGG ACATAGCACA TTTTAACCGA
    251   ----------------------------------------------------------------------------------------------------
    251   ----------------------------------------------------------------------------------------------------

    301   GCATCCATAA ACAATCCTAG ACAATACGGA TATTCCCGTC AATTAGGTGT
    301   ----------------------------------------------------------------------------------------------------
    301   ----------------------------------------------------------------------------------------------------

    351   CCCTTGATAA CCATCCTCC
    351   ---------------------------------------
    351   ---------------------------------------
```

APPENDIX C
Satellite image of the home ranges of the three bands

(Satellite image was download from google map. Home ranges of Band 21, 20 are from Tan et al. 2007 and Li et al. 2000, the home ranges of Band 19 is based on estimation).



APPENDIX D
Case numbers and corresponding dyads

Dyad	Case number
JB:BD	1
JB:YL	2
JB:YZM	3
JB:DBC	4
JB:XBC	5
BD:YL	6
BD:YZM	7
BD:DBC	8
BD:XBC	9
YL:YZM	10
YL:DBC	11
YL:XBC	12
YZM:DBC	13
YZM:XBC	14
DBC:XBC	15

Dyad	Case number
PK:HJ	1
PK:BJ	2
PK:CM	3
PK:HS	4
HJ:BJ	5
HJ:CM	6
HJ:HS	7
BJ:CM	8
BJ:HS	9
CM:HS	10

Dyad	Case number
LP:KT	1
LP:JT	2
LP:ZT	3
LP:TH	4
KT:JT	5
KT:ZT	6
KT:TH	7
JT:ZT	8
JT:TH	9
ZT:TH	10