

## Comparisons of Intraunit Relationships in Nonhuman Primates Living in Multilevel Social Systems

Ikki Matsuda · Peng Zhang · Larissa Swedell ·  
Umeyo Mori · Augustine Tuuga · Henry Bernard ·  
Cédric Sueur

Received: 20 October 2011 / Accepted: 18 April 2012 / Published online: 16 June 2012  
© Springer Science+Business Media, LLC 2012

**Abstract** Multilevel social systems have evolved in several species of cercopithecoid primates and appear to be an effective means of changing group size amid variation in environmental conditions. Larger groupings of these species fission and fuse, making intraunit relationships essential to maintain the integrity of the smallest social units. We examine these intraunit relationships in four primates with multilevel social systems: proboscis monkeys (*Nasalis larvatus*), snub-nosed monkeys (*Rhinopithecus roxellana*), hamadryas baboons (*Papio hamadryas*), and geladas (*Theropithecus gelada*), using social network analysis. The proboscis monkeys and hamadryas baboons were wild and unprovisioned, whereas the snub-nosed monkeys and geladas were partly provisioned. Comparison of eigenvector centrality coefficients revealed a phylogenetic difference in the key individuals maintaining social networks between the colobines and the cercopithecines: females were more central in proboscis and snub-

---

I. Matsuda (✉)

Long-term Field Study Project, Primate Research Institute, Kyoto University, Inuyama,  
Aichi 484-8506, Japan  
e-mail: ikki.matsuda@gmail.com

I. Matsuda

e-mail: matsuda@pri.kyoto-u.ac.jp

P. Zhang

Anthropology Department, Sun Yat-sen University, Guang Zhou 510275, China

L. Swedell

Department of Anthropology, Queens College, City University of New York, Flushing, NY 11367,  
USA

L. Swedell

New York Consortium in Evolutionary Primatology, New York, NY, USA

U. Mori

Nagoya Bunri University, Inazawa, Aichi, Japan

nosed monkeys, with males generally peripheral to social interaction, whereas males were more central than females in geladas and hamadryas. A comparison of sex differences in clustering coefficients, however, revealed a significant difference only in geladas, suggesting that one-male–multifemale units in this species become more unstable when females, but not males, are removed from social networks. Taken together, our results reveal the strongest differences between geladas, characterized by female philopatry and male dispersal, and the three species with bisexual dispersal. These results demonstrate the potential for social network analysis to reveal the social bonds most important for maintaining cohesion of the smallest units of primate multilevel societies. This, in turn, can serve as a proxy, in the absence of long-term data, for underlying patterns of sex-biased dispersal and philopatry.

**Keywords** Gelada · Hamadryas baboon · Proboscis monkey · Snub-nosed monkey  
Social network analysis · Social organization

## Introduction

Among primate social systems, the multilevel society, in which smaller levels of social organization aggregate into larger units, is one of the most complex. Several nonhuman primate species are characterized by multilevel societies, most notably geladas (*Theropithecus gelada*: Dunbar and Dunbar 1975; Kawai *et al.* 1983), hamadryas baboons (*Papio hamadryas*: Kummer 1984; Sigg *et al.* 1982; Swedell *et al.* 2011), snub-nosed monkeys (*Rhinopithecus avunculus*, *R. bieti*, *R. brelichi*, and *R. roxellana*: Kirkpatrick *et al.* 1998; Grüter and Zinner 2004; Zhang *et al.* 2012), and proboscis monkeys (*Nasalis larvatus*: Matsuda *et al.* 2010; Yeager 1991). Although the underlying social dynamics differ across these species (Grüter and Zinner 2004), they all share a common feature: their basic components of society, i.e., the minimum reproductive units, are one-male–multifemale units (OMUs) that aggregate with one another into larger social groups at sleeping sites and/or food resources. In an attempt to understand the evolution of these primate multilevel social systems, previous studies have focused on interunit relationships and how these relationships differ across species (Grueter and van Schaik 2010; Grüter and Zinner 2004). Equally important, however, is the comparative study of relationships *within* units, as intraunit relationships are the cohesive forces binding units together over space and time and

---

A. Tuuga  
Sabah Wildlife Department, Sabah, Malaysia

H. Bernard  
Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Sabah, Malaysia

C. Sueur  
Centre National de la Recherche Scientifique, Département Ecologie, Physiologie et Ethologie,  
Strasbourg, France

C. Sueur  
Institut Pluridisciplinaire Hubert Curien, Université de Strasbourg, Strasbourg, France

are responsible for maintaining integrity of units when they aggregate to form larger groupings. The social structure of a given species, whether simple or complex, is an emergent property of the social relationships that comprise it, and it is these underlying social relationships that maintain its integrity (Hinde 1982, 1983). To achieve a better understanding of both the proximate mechanisms maintaining and the selective factors underlying primate multilevel social systems, we must break down each social system into its constituent parts: the individual OMUs and the individual interactions within them.

Studies of social bonding in gelada and hamadryas baboon OMUs are based largely on detailed social behavioral data from identified individuals (Dunbar 1979, 1993; Le Roux *et al.* 2010; Sigg 1980; Swedell 2002, 2006). These studies have revealed that geladas are characterized by male dispersal and female philopatry, with strong and differentiated kin-based social relationships among females providing the cohesive force maintaining the OMU structure (Dunbar and Dunbar 1975; Le Roux *et al.* 2010; Mancini and Palagi 2009). Hamadryas baboons, by contrast, are characterized by bisexual dispersal skewed toward females owing to male-enforced transfer of females among OMUs, with cohesion of OMUs maintained instead by strong cross-sex bonds between each female and her leader male (Abegglen 1984; Kummer 1968; Sigg 1980; Swedell 2002; Swedell and Schreier 2009; Swedell *et al.* 2011).

Compared to that for geladas and hamadryas baboons, information on dispersal patterns and social relationships within the multilevel societies of colobine monkeys is relatively rare. Several studies of proboscis and snub-nosed monkey activity budgets have reported data on social interactions (Grueter *et al.* *in press*), but very few studies have provided detailed data on agonistic interactions or grooming networks among identified individuals. Only one study of proboscis monkeys has focused on inter-individual relationships of identified adult members within OMUs, revealing a bisexual dispersal pattern with fewer hierarchical relationships and only weakly differentiated grooming patterns among unit members (Matsuda *et al.* 2012). In addition, the male in proboscis monkey OMUs appears to be socially peripheral compared to the females (Matsuda *et al.* 2012). A pattern of bisexual dispersal has also been suggested for provisioned, free-ranging Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) (Qi *et al.* 2009; Zhang *et al.* 2012), which also appear to exhibit relatively undifferentiated affiliation patterns among individuals within OMUs (Zhang *et al.* 2012). Researchers have suggested similar affiliation patterns among identified individuals in a captive OMU of the same species (Ren *et al.* 2010). None of these studies, however, have systematically compared intraunit relationships across the primate species characterized by multilevel social systems.

Social network analysis (SNA) is a valuable tool to investigate such relationships systematically (Kasper and Voelkl 2009; Sueur *et al.* 2011a). One can also use SNA to compare the patterning of relationships across different primate species (or groups) by comparing corrected quantitative data or collecting the data using the same methods (Dufour *et al.* 2011; Sueur *et al.* 2011b), although such comparative studies are less common than those investigating a single species. SNA measures individual as well as group indices and takes into account all relationships among all group members (Sueur *et al.* 2011a). Classic methods, by contrast, focus only on dyadic or triadic interactions and may be unable to reveal the complexity of multiple social relationships within groups. SNA also allows one to quantitatively measure

differences between groups or species, whereas many traditional methods can do this only qualitatively (Kasper and Voelkl 2009; Sueur *et al.* 2011a).

We here examine and compare social interactions within OMUs, with a focus on affiliative behaviors, across four primate species (*Theropithecus gelada*, *Papio hamadryas*, *Nasalis larvatus*, and *Rhinopithecus roxellana*) using SNA. In particular, we focus on the centrality indices of individuals within OMUs in an attempt to elucidate the key individual(s) responsible for maintaining cohesion and stability of OMUs. At the outset of this study we predicted that in hamadryas baboons, in which dispersal is skewed toward females, which are generally unrelated to one another within OMUs, the leader male of an OMU should have the highest *eigenvector* and *betweenness centrality coefficients* (cf. Sueur *et al.* 2011a), whereas in geladas the centralities should be biased toward females. By contrast, proboscis monkeys and snub-nosed monkeys are both characterized by bisexual dispersal and social relationships in these species (especially among females) are less differentiated and hierarchical, with males being peripheral to social interaction. We thus expected our analysis to reveal no key individual(s) within OMUs in these two species.

We also compare OMU stability across species by assessing the mean *clustering coefficient*, a measure of the degree of cliquishness of the social network and the extent to which neighbors of a focal animal/group are clustered in space. The value of this measure reveals whether one individual retains the attention of all individuals, which are not very connected to one another (high value), or whether all individuals are connected to one another to the same degree (low value). We expected to find a high clustering coefficient in gelada OMUs owing to female philopatry, whereas this should not be the case in hamadryas baboons, proboscis monkeys, or snub-nosed monkeys owing to their bisexual dispersal patterns and lower relatedness among females within OMUs. As adult females in the bisexual dispersal species repeatedly migrate to other OMUs, it may be difficult to establish firm allogrooming relationships for particular individuals within OMUs, unlike in female philopatric species (Matsuda *et al.* 2012). Finally, we use hierarchical cluster analysis to examine the amount of subdivision or subgrouping among adult females within OMUs in each species. We expected to find more subgrouping in a female philopatric system such as geladas compared to a system in which both sexes disperse, as female philopatric species confine their grooming to kin and gelada OMUs typically consist of several closely related females (Furuichi 1984; Le Roux *et al.* 2010; Matsuda *et al.* 2012). In a species in which females are not philopatric, by contrast, adult females regularly migrate to other groups and it may thus be difficult for females to establish any strong and/or stable affiliative relationships with particular individuals within units (Matsuda *et al.* 2012); such a pattern would be less likely to lead to subgrouping within OMUs.

## Methods

### Study Sites and Data Collections

*Proboscis Monkeys* I. Matsuda and two trained assistants conducted observations from May 2005 to May 2006 in riverine forests along the Menanggul River, a tributary of the Kinabatangan River, Sabah, Malaysia (118°30'E, 5°30'N). The mean

minimum and maximum temperatures were *ca.* 24 °C and 32 °C, respectively, and total precipitation at the site was 2510 mm (June 2005–May 2006) (Matsuda *et al.* 2009a).

The observers habituated one OMU of proboscis monkeys (BE-group) and identified all the individuals. They collected observational data using focal animal sampling (Altmann 1974) and separated into two groups to follow one adult male and one arbitrarily selected female simultaneously (Matsuda *et al.* 2009b). While following focal individuals, the observers recorded the time (sec) spent in grooming behavior. They summed the values of grooming given and received to compare these data with data from other species. The total observation time was 3506 h (male, 1968 h; female, 1539 h; Table I). During the study period, there was no replacement of the BE-group adult male, although one adult female immigrated with a juvenile offspring and one subadult female emigrated (Matsuda *et al.* 2012). At the end of the study period, the group comprised 16 individuals: 1 adult male, 6 adult females, 5 juveniles, and 4 infants. Additional information on the social behavior of these individuals is available in a previous publication (Matsuda *et al.* 2012).

*Snub-Nosed Monkeys* P. Zhang made observations over 183 d from October 2001 to April 2002, and from November 2002 to April 2003 on the northern slope of the Qinling Mountains near Yuhuangmiao Village in Zhouzhi National Nature Reserve, Shaanxi, central China (108°14′–18′E, 33°45′–50′N, elevation: 1400 m–2900 m a.s.l.). The climate is considered to be semihumid and mountainous, with snowfall common in winter between November and February. The reported mean temperature at the site was 6.4 °C with a minimum of –8.3 °C in January and a maximum of 21.7 °C in July; annual rainfall is 980 mm.

**Table I** Compositions of analyzed units in each primate species

	Group code	α-male	Adult female	Second male	Total	Observation efforts
Proboscis monkey	P 1	1	6	0	7	♂: 1968 h ♀: 256 h/individ
Snub-nosed monkey	S 1	1	4	0	5	max 276 scans/ individ
	S 2	1	4	0	5	max 336 scans/ individ
	S 3	1	5	0	5	max 276 scans/ individ
	S 4	1	5	0	6	max 336 scans/ individ
	S 5	1	5	0	6	max 336 scans/ individ
Hamadryas baboon	H 1	1	4	0	5	max 86 scans/ individ
	H 2	1	4	0	5	max 57 scans/ individ
	H 3	1	4	0	5	max 162 scans/ individ
	H 4	1	5	0	6	max 83 scans/ individ
	H 5	1	5	0	6	max 122 scans/ individ
	H 6	1	4	0	5	max 42 scans/ individ
Gelada	G 1	1	4	1	6	12.5 h/ individ
	G 2	1	4	1	6	23.3 h/ individ
	G 3	1	5	1	7	31.1 h/ individ

Two bands of snub-nosed monkeys (*Rhinopithecus roxellana*), East Ridge (ER) band and West Ridge (WR) band, live in the study area and are separated by the Nancha River (Zhang *et al.* 2011). The observer (P. Zhang) habituated WR band, which contains 10 OMUs and identified all adult monkeys in the band (total: 10 adults males and 35 adult females) (Zhang *et al.* 2006). To achieve better observation conditions, provisioning commenced on October 24, 2001 (Zhang *et al.* 2003). WR band consistently visited the provisioning site during the study periods. A total of 3.5 kg of corn grains and 20 kg of sliced apples and radishes were scattered across the valley at a fixed location at 09:00 h, 12:00 h, and 15:00 h. The monkeys also foraged for natural food items in and around the provisioning site. We conducted the study mainly when provisioning took place, meaning that artificial provisioning may have influenced the monkeys' behavior and social activities. To reduce the influence of provisioning on their behavior, the observer also collected proximity data during nonfeeding times, which differs from a previous study in which the observer constructed a proximity matrix of individuals during feeding times (Zhang *et al.* 2006). The observer limited provisioning to only the observation periods and only for *ca.* 4 mo of the year and avoided hand feeding or other physical contact with monkeys. Monkeys lived without disturbance from human observers during the remaining months.

The observer collected data on spatial proximity and grooming among individuals in the study band using scan sampling (Altmann 1974). The observer scanned the study group twice daily: at 11:00 h and 13:00 h after the monkeys had been away from the provisioning ground for  $\geq 30$  min. In total, the observer conducted 366 scans and identified a total of 3952 proximity interactions among individuals in the focal band. The spatial proximity criterion was defined as individuals within 1 m of each other at the time of sampling. One or several individuals could satisfy this criterion at any given sampling time. We used a simple ratio association index (SRI) to define the weight, *i.e.*, strength, of dyadic relationships between individuals. We calculated the SRI using the number of scans in which two individuals were seen in proximity divided by the total number of scans during which each was observed in the focal band (Cairns and Schwager 1987).

*Hamadryas Baboons* The focal population inhabits the region surrounding the Filoha outpost of the Awash National Park, *ca.* 150 km east of Addis Ababa, Ethiopia, in the semiarid lowlands of the northern Rift Valley of East Africa. The annual rainfall is 500–600 mm, most of which falls during July and August, and the mean annual temperature is 34 °C (Swedell *et al.* 2008).

The focal group numbered *ca.* 150 individuals in November 1996 and 170 individuals in September 1998. Data collection took place between November 1996 and September 1998, with a 6-mo interruption between June and December 1997 because of a field accident in May 1997, totaling 262 observation days and 985 contact hours (for more details, see Swedell 2006). The data that contribute to this analysis consist of instantaneous scan samples of the behavior of all members of individually identified one-male units at 10-min intervals. L. Swedell conducted scan samples of all OMUs when they came into view, for as long as they were in view. If a second OMU came into view, scan samples were then begun on that OMU, with scans staggered so that those for two OMUs did not occur at the same time. For each scan, the observer recorded any grooming behavior, including the directionality of

grooming. We identified all subjects individually; additional information on the social behavior of these individuals is available in previous publications (Swedell 2002, 2006; Swedell and Schreier 2009; Schreier and Swedell 2009; Swedell and Tesfaye 2004).

*Geladas* U. Mori conducted observations from July 1973 to March 1974 at Gich in the Simien Mountain National Park, Ethiopia (elevation: 3900 m.a.s.l.). Monthly mean air temperature was fairly stable at 6–9 °C throughout the year. The mean annual precipitation was 1465 mm (Iwamoto and Dunbar 1983; Kawai 1979).

To assist with the habituation of the study population, U. Mori provisioned them with barley for one month. After this had succeeded, provisioning was terminated and behavioral observations began, i.e., barley was not used throughout the study period. U. Mori studied one of the three bands (previously termed “herds”), named E-herd (including 106 individuals and 8 OMUs). Starting at dawn, the observer followed the OMUs for as long as possible each day. While following focal OMUs, the observer recorded the time devoted to grooming behavior using a modified focal animal sampling method (Altmann 1974). Because the baboons were primarily terrestrial and spent most of their time foraging on a grassy plain with good visibility, it was possible to record the behaviors of all individuals within OMUs at once, i.e., the observation time for each OMU equaled the observation time for each adult individual within it.

### Social Network Analysis

We measured affiliative relationships using grooming behavior for our proboscis monkey, hamadryas, and gelada data sets, and proximity for our snub-nosed monkey data set. To standardize the data set for methodological differences across species, we calculated a grooming index (GI) for each species. For proboscis monkeys and geladas, the GI from individual A to individual B was defined as follows:  $GI_A(B) = [Gm_A(B) \times 100] / [F(A) + F(B)]$ , where  $Gm_A(B)$  was the time A spent grooming B and  $F(A)$  and  $F(B)$  were the observation times for A and B, respectively. For snub-nosed monkeys and hamadryas baboons, we calculated the GI in the same way but used the number of scans for each individual within units instead of observation time. We rendered the matrices based on the grooming and proximity data among individuals within OMUs unidirectional to homogenize data across species.

To analyze the social networks based on the GI, we used SOCPROG 2.4 and Ucinet 6.0 (Borgatti *et al.* 2002; Sueur *et al.* 2011a; Whitehead 2009). To detect relevant features of social networks for each species, we adopted three network variables, measured per individual: eigenvector centrality coefficient, betweenness centrality coefficient, and clustering coefficient. Eigenvector centrality coefficient, which indicates the connection degree of an individual within its group, is calculated using the number and strengths of connections, while also taking into account the identities of the partners to which it is connected (Hanneman and Riddle 2005). This coefficient is suggested to be more revealing than other centrality coefficients for groups of nonhuman primates (Kasper and Voelkl 2009). The betweenness centrality coefficient is another measure of individual centrality, defined as the number of shortest paths that pass through the considered individual, with the shortest path

being the shortest distance, i.e., number of edges, between two nodes (Hanneman and Riddle 2005). The clustering coefficient is a measure of how well the associates of an individual are themselves associated. It describes how cliquish the network is, and measures the extent to which neighbors of a focal animal/group are clustered in space. The higher the clustering coefficient and betweenness centrality coefficient of an individual, the higher the probability that the group will become unstable after this individual is removed (Sueur *et al.* 2011a).

In addition, we calculated the group density, which is the number of observed edges divided by the number of possible edges, to reveal the unit structure properties. We also performed hierarchical cluster analysis with Ward's linkage method to assess the amount of subdivision or subgrouping among adult females in each species. We used the option modularity 1 (following the definition of Newman 2004; for details see Whitehead 2009) to detect automatically subgroups of individuals with stronger grooming/proximity relationships using a modularity coefficient  $>0.3$  (Newman 2004; Whitehead 2009).

The OMU is the minimum reproductive unit in all four primate species studied. In geladas and hamadryas baboons, one or two additional adult males (usually designated follower males) are often members of OMUs, but these males usually do not copulate with adult females in the OMU (Kawai 1979; Kummer 1968). We did not include data for these additional males when we analyzed the network variables described in the preceding text, i.e., we analyzed only the data from the  $\alpha$ -male and the adult females of an OMU. Further, we selected only OMUs consisting of five to seven adults ( $\alpha$ -males plus adult females) for each species to homogenize data and to avoid any confounding effects of group size, as the relationship (grooming or proximity time) an individual has with conspecifics may vary depending on group size. Table 1 shows the composition of OMUs studied and the observation time.

## Statistical Analysis

Most statistical analyses were conducted for only three primate species (snub-nosed monkey, gelada, and hamadryas baboon) because data were available for only one proboscis monkey OMU. We examined the mean eigenvector centrality coefficient and the mean betweenness centrality coefficient between sexes for each primate species using a Mann–Whitney  $U$  test. We also compared the mean clustering coefficient between the sexes using a Welch's  $t$ -test. We set statistical significance for these tests at  $P < 0.05$ . We performed a Mann–Whitney  $U$  test to compare the mean eigenvector centrality coefficient and the mean clustering coefficient for females among all four primate species, i.e., including the proboscis monkey, with a Bonferroni correction ( $P = 0.05/N$ :  $N$  is the number of comparisons made, i.e., 0.008). We compared density values among species using a Mann–Whitney  $U$  test with a Bonferroni correction ( $P = 0.05/N$ , i.e., 0.017). After conducting hierarchical cluster analysis, we used a Welch's  $t$ -test to compare the mean number of subgroups corrected by the number of adult females within each unit among primate species, again with a Bonferroni correction ( $P = 0.05/N$ , i.e., 0.017). For all results we report means with standard deviation (SD). We used the R 2.8.1 statistical package [R Development Core Team 2008] for these analyses.



## Results

### Sex Differences in Centrality

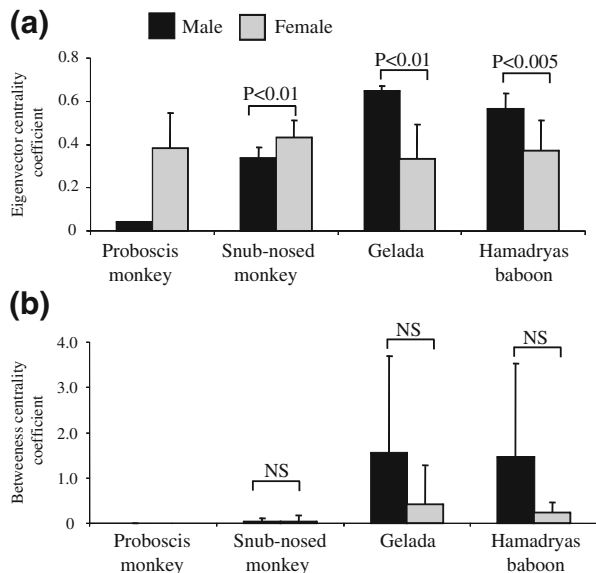
We found sex differences in the mean eigenvector centrality coefficients for all four species, and these differences were statistically significant in the three species for which we had sufficient data to conduct statistical analysis (Fig. 1a; snub-nosed monkeys:  $U$ -test:  $N^{\delta}=5$ ,  $N^{\varphi}=23$ ,  $Z=2.70$ ,  $P<0.01$ ; geladas:  $N^{\delta}=3$ ,  $N^{\varphi}=13$ ,  $Z=-2.62$ ,  $P<0.01$ ; hamadryas baboons:  $N^{\delta}=6$ ,  $N^{\varphi}=26$ ,  $Z=-3.09$ ,  $P<0.005$ ). The centrality of the females within the units was higher than that of  $\alpha$ -males in the social networks of the two colobine species (proboscis monkeys and snub-nosed monkeys). In other words, the  $\alpha$ -males in the colobines were peripheral, i.e., not central, to the social networks. However, the centrality of  $\alpha$ -males within the units was higher than that of females in both gelada and hamadryas baboons, indicating that the  $\alpha$ -males play a key role in maintaining social networks in these two species.

The betweenness centrality coefficient showed a similar pattern to the eigenvector centrality coefficient, but there were no significant sex differences in betweenness centrality coefficients (Fig. 1b, snub-nosed monkey:  $Z=0.27$ ,  $P=0.67$ ; gelada:  $Z=-1.01$ ,  $P=0.28$ ; hamadryas baboon:  $Z=-0.50$ ,  $P=0.60$ ).

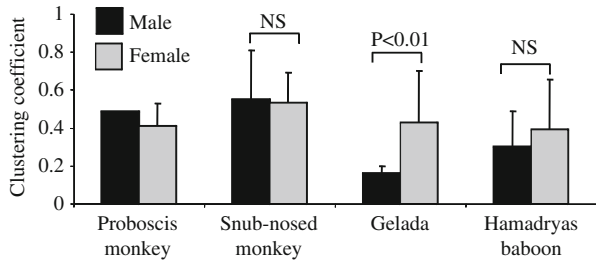
### Sex Differences in Clustering Coefficient

There was no sex difference in mean clustering coefficient in snub-nosed monkeys or hamadryas baboons (Fig. 2), indicating that the threat of the units becoming unstable was the same whether the male or females were removed for these species (snub-nosed monkey: Welch's  $t$ -test,  $t=0.97$ ,  $P=0.36$ ; hamadryas baboon:  $t=0.16$ ,  $P=0.88$ ). In geladas, however, the mean clustering coefficients of females was significantly

**Fig. 1** Mean  $\pm$  standard deviation (a) eigenvector centrality coefficient and (b) betweenness centrality coefficient of  $\alpha$ -males and adult females in four primate species. Proboscis monkey data represent only one OMU. See Results for details.



**Fig. 2** Mean  $\pm$  standard deviation for the clustering coefficient of  $\alpha$ -males and adult females in four primate species. Proboscis monkey data represent only one OMU. See Results for details.



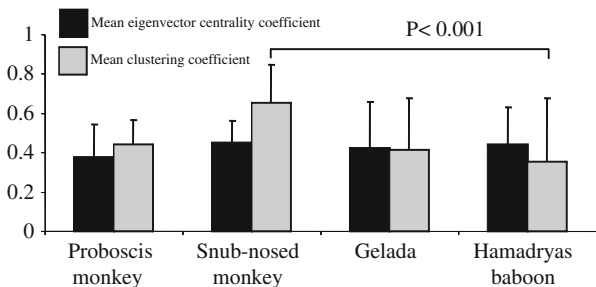
higher than that of  $\alpha$ -males ( $t=-3.24, P=0.007$ ), suggesting that a gelada OMU is more likely to become unstable after the removal of females from the social network compared to the removal of  $\alpha$ -males. This difference between males and females, however, may be an artifact of the way the clustering coefficient is calculated: as males have more connections (they have a higher eigenvector coefficient than females), females may have a higher clustering coefficient if they are linked to these males given that the clustering coefficient measures how well the associates of an individual are themselves associated.

Female Relationships

The mean eigenvector centrality coefficients of females were not significantly different across the four species (Fig. 3, Kruskal–Wallis test:  $H=1.40, P=0.71$ ). However, we did find a significant difference among the mean clustering coefficients of females across the four species as a whole (Fig. 3, K–W:  $H=14.92, P=0.002$ ), and the mean clustering coefficients of snub-nosed monkeys were significantly higher than those of hamadryas baboons (Fig. 3, proboscis monkeys vs. snub-nosed monkeys:  $Z=-2.21, P=0.03$ ; proboscis monkeys vs. geladas:  $Z=-0.65, P=0.52$ ; proboscis monkeys vs. hamadryas baboons:  $Z=-1.26, P=0.21$ ; snub-nosed monkeys vs. geladas:  $Z=-2.56, P=0.01$ ; snub-nosed monkeys vs. hamadryas baboons:  $Z=-3.32, P<0.001$ ; geladas vs. hamadryas baboons:  $Z=0.70, P=0.49$ ).

The density of OMUs was higher in the two colobines (proboscis monkey: 1.0; snub-nosed monkey:  $0.98\pm0.25$ ) compared to the two cercopithecines (gelada:  $0.77\pm0.25$ ; hamadryas baboon:  $0.80\pm0.16$ ), but we found no significant differences between individual pairs of species (snub-nosed monkeys vs. geladas:  $Z=-1.34, P=0.12$ ;

**Fig. 3** Comparison of mean eigenvector centrality coefficient and mean clustering coefficient among females in four primate species. See Results for details.



geladas vs. hamadryas baboons:  $Z=-0.26$ ,  $P=0.79$ ; snub-nosed monkey vs. hamadryas baboon:  $Z=-2.19$ ,  $P=0.021$ ).

Hierarchical cluster analysis revealed various levels of cliquishness among adult females in the OMUs of each species. The mean number of subgroups, corrected by the number of adult females within the units, was 0.33 ( $N=1$ ) in proboscis monkeys,  $0.35\pm 0.13$  ( $N=6$ ) in hamadryas baboons,  $0.39\pm 0.17$  ( $N=5$ ) in snub-nosed monkeys, and  $0.53\pm 0.06$  ( $N=3$ ) in geladas. More clustering (proboscis monkeys < hamadryas baboons < snub-nosed monkeys < geladas) indicates that the relationships among females were more differentiated. However, there were no significant differences among the three species (snub-nosed monkeys vs. geladas:  $t=1.75$ ,  $P=0.14$ ; geladas vs. hamadryas baboons:  $t=2.86$ ,  $P=0.02$ ; snub-nosed monkey vs. hamadryas baboon:  $t=0.43$ ,  $P=0.68$ ).

## Discussion

The results of this analysis should be interpreted with caution because of the differences in methods used to generate the data. Two of the four species were provisioned either during (snub-nosed monkeys) or before (geladas) data collection, whereas the other two were not provisioned. One data set is derived from proximity data (snub-nosed monkeys), and the other three from grooming data. Moreover, among the grooming data sets, one derives from individual focal sampling (proboscis monkeys), one from group focal sampling (geladas), and one from instantaneous scan sampling (hamadryas). Although comparisons across categories of behavior and differently derived data sets are not ideal, patterns of affiliation based on proximity data generally correlate with those based on grooming data (Clark 2011; King *et al.* 2011a, b; Silk *et al.* 2006a, b) and both focal and scan sampling are valid representations of overall patterns of affiliative interaction (Altmann 1974). Despite the disparities in data sets, therefore, these results are valuable in providing preliminary comparative data that may be useful in designing future analyses.

Overall, we found differences across species in interindividual relationships and mechanisms underlying cohesion of OMUs. Our analyses based on the eigenvector centrality coefficient revealed that the key individuals maintaining the social networks differed along phylogenetic lines. The colobines in our analysis (proboscis and snub-nosed monkeys) followed typical patterns reported for other Asian colobines: affiliative behaviors are primarily a female affair and males are generally peripheral to social interaction (Kirkpatrick 2007; Zhang *et al.* 2011; *cf.* Grueter *et al.* in press). In the cercopithecines (gelada and hamadryas), however, males were more central than females. One explanation for the higher centrality of females in the colobine taxa may be the frequency of allomothering behavior in colobines (Kirkpatrick and Grueter 2010; Newton and Dunbar 1994). Many female–female interactions in colobine monkeys are related to exchange of infants among adult females, which is not as common overall in cercopithecines compared to colobines, possibly because it is less permitted by mothers and more risky to infants (Maestripietri 1994). Because females within OMUs associate frequently with each other via infant handling, their centrality may be higher than that of the male. Indeed, in contrast to other colobine species, red colobus monkeys (*Procolobus badius*), which are characterized by a virtual absence

of allomothering, display a relative lack of cohesive grooming and affiliative behavior among females (Newton and Dunbar 1994; Struhsaker and Leland 1979). The difference in eigenvector centrality coefficient between the two subfamilies found here may thus not be reflective of a real difference in patterns of dyadic social bonding across these two subfamilies but rather an artifact of differences in infant-directed interactions.

Although the betweenness centrality coefficient showed a similar pattern to the eigenvector centrality coefficient, we found no significant sex differences for this measure. This result may be due to the way we calculated indices: whereas the eigenvector centrality takes into account the strength of relationships, the betweenness coefficient does not. Interindividual differences are thus more difficult to identify in small groups using the latter method. The low number of OMUs per species in our data set and the high variance among coefficients of individual OMUs within each species may also have contributed to the high variance in betweenness centrality, as may have differences in sociodemographic parameters in each OMU such as number of females, age of individuals, reproductive states and the possible presence of peripheral males.

A comparison of the clustering coefficients between the sexes across the four species revealed a significant difference between the sexes only in geladas. This is likely due to the fact that gelada OMUs are based on a matrilineal structure deriving from female philopatry and characterized by strong female bonds and stable, linear dominance hierarchies with matrilineal rank inheritance (Kawai 1979; Le Roux *et al.* 2010). In other words, because female relationships are strong and differentiated in geladas, OMUs will become more unstable with a higher probability of splitting into different subgroups when females are removed from their social networks, compared to when the male is removed. The lack of significant sex differences in clustering coefficients in the other three species may be related to their nonmatrilineal social organization deriving from bisexual dispersal (proboscis monkey: Matsuda *et al.* 2012; Murai 2004; Murai *et al.* 2007; snub-nosed monkey: Qi *et al.* 2009; hamadryas baboon: Swedell *et al.* 2011) and consequent weaker and less differentiated affiliative relationships among females (Matsuda *et al.* 2012; Swedell 2002). Clustering coefficients are thus useful as one potential indicator of sex-biased dispersal patterns in groups of nonhuman primates.

The mean eigenvector centrality coefficients of females did not differ among the four species. Contrary to our prediction, however, the mean clustering coefficients of females differed significantly across species and the female clustering coefficient in snub-nosed monkeys was particularly high (Fig. 3). It is difficult to interpret this result within the context of dispersal patterns alone. Unlike other Asian colobines, including proboscis monkeys (which devote only 0.47 % of total observation time to grooming: Matsuda *et al.* 2012), snub-nosed monkeys are comparatively social, with grooming occupying >7 % of their time (Grueter *et al.* in press). Thus, the fact that relationships among females within units are relatively rigid and less differentiated (Zhang *et al.* 2012) may be responsible for the high clustering coefficients found in this species. We may also need to consider methodological differences, i.e., that we assessed snub-nosed monkey affiliative behavior via proximity, but used grooming behavior to measure affiliation in the other three species. Provisioning may also further influence the quality and the quantity of social interactions (Zhang *et al.*

2003). Monkeys aggregated around the provisioning site, and may have had more opportunities for social interactions there. The relationships among females might thus be overestimated for snub-nosed monkeys, resulting in a higher clustering coefficient for one or several females and consequently a higher mean clustering coefficient, compared to other species, than might be found in a nonprovisioned population.

Our analysis of group density, which is an indicator of stability among females within units, revealed another phylogenetic difference: the values for this measure were higher in the two colobines (proboscis monkey and snub-nosed monkey) than in the two cercopithecines (gelada and hamadryas baboon). This likely relates to the lower differentiation of the colobine relationships compared to the cercopithecines: we observed grooming/proximity for all female–female dyads (increasing the group density) and OMU cohesion was higher overall for the colobines. Although this pattern may reflect phylogenetic constraints within subfamilies, we should also consider the effects of the small sizes of the OMUs in the data set, each consisting of four to six females, on the group density analysis. As the number of individuals in the OMU decreases, each individual has a higher probability of interacting with all group members, increasing the group density measure for that OMU.

Although the differences in the number of subgroups among the four species, measured with hierarchical cluster analysis, were not statistically significant, the result potentially supports a link between patterns of affiliation and dispersal; the number of sub-groups was the highest in the species characterized by female philopatry and male dispersal (gelada) and lowest in the species characterized by bisexual dispersal (proboscis monkey, snub-nosed monkey, and hamadryas baboon). Given that females in species characterized by female philopatry and male dispersal, e.g., Japanese macaques (*Macaca fuscata*) focus their grooming on kin and maintain strong and stable relationships between specific individuals (Oki and Maeda 1973; Silk *et al.* 2010; Yamada 1963), a higher degree of subgrouping in geladas may reflect kin groups within units. In the other species examined here, by contrast, adult females regularly migrate to other groups and it may thus be difficult for females to establish any strong and/or stable affiliative relationships with particular individuals within units.

In sum, we report the results of the first quantitative comparison of intraunit relationships among primate species living in multilevel social systems. Some of the patterns revealed in this study may be explained by the presence of allomothering behavior, which occurs frequently in colobines (Maestriperi 1994; Newton and Dunbar 1994). Most of the results, however, appear to result from variation in the patterns of dispersal characterizing each species. In geladas, females are philopatric, and these kin-based affiliative relationships play a primary role in maintaining the integrity of OMUs (Le Roux *et al.* 2010), a pattern that was revealed in this analysis. In hamadryas baboons, by contrast, OMU cohesion is maintained by bonds between males and females (Swedell and Schreier 2009; Swedell *et al.* 2011), though this pattern was not detected in these analyses, probably because the hamadryas male–female bond is maintained largely via herding whereas these analyses focused on grooming (which occurs among all age–sex classes in hamadryas). Overall, our analyses revealed a consistent difference between the social networks of geladas, which are female philopatric and female bonded, and the other three species, all of

which are characterized by bisexual dispersal. Future analyses with a larger and more comparable data set promise to generate additional insight into patterns of OMU cohesion in colobines and provide more detailed comparative data on patterns of social bonding across primate multilevel societies.

**Acknowledgments** I. Matsuda, A. Tuuga, and H. Bernard thank the Economic Planning Unit of the Malaysian Government, the Sabah Wildlife Department and the Sabah Forestry Department staff, the Kinabatangan Orangutan Conservation Project, and our research assistants for support. I. Matsuda truly appreciates Y. Matsuda for supporting his field work. I. Matsuda thanks a Grant-in-Aid for challenging Exploratory Research (24657170) and HOPE and Human Evolution Project of KUPRI for funding support in the field. P. Zhang thanks Zhouzhi Nature Reserve for giving him permission to conduct this research and to National Natural Science Foundation of China (31000175), the Scientific Research Foundation for the Returned Overseas Chinese Scholars and Resona-Asia-Oceania Foundation for funding support in the field. L. Swedell and U. Mori thank the Ethiopian Wildlife Conservation Authority for permission to conduct this research, and L. Swedell thanks the National Geographic Society, the Leakey Foundation, the Wenner-Gren Foundation, and the National Science Foundation for funding to support research at Filoha, Ethiopia. Finally, we thank C. Grüter, J. Setchell, and two anonymous reviewers for their helpful comments that improved this manuscript. Data collection for this study was carried in accordance with protocols approved by the Economic Planning Unit, Prime Minister's Department, Putrajaya, Malaysia and the Sabah Wildlife Department, Sabah, Malaysia (proboscis monkeys); the Zhouzhi National Reserve, China (snub-nosed monkeys); and the Wildlife Conservation Authority (formerly the Wildlife Conservation Organization) of Ethiopia (geladas and hamadryas baboons). All protocols adhere to the legal requirements of Malaysia, China, and Ethiopia, respectively.

## References

- Abegglen, J.-J. (1984). *On socialization in hamadryas baboons*. London: Associated University Presses.
- Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour*, *69*, 227–267.
- Borgatti, S., Everett, M., & Freeman, L. (2002). UCINET 6 for Windows: Software for social network analysis. Harvard, MA: Analytic Technologies.
- Cairns, S. J., & Schwager, S. J. (1987). A comparison of association indices. *Animal Behaviour*, *35*, 1454–1469.
- Clark, F. (2011). Space to choose: network analysis of social preferences in a captive chimpanzee community, and implications for management. *American Journal of Primatology*, *73*, 748–757.
- Dufour, V., Sueur, C., Whiten, A., & Buchanan-Smith, H. M. (2011). The impact of moving to a novel environment on social networks, activity and wellbeing in two New World primates. *American Journal of Primatology*, *73*, 802–811.
- Dunbar R. I. M (1993). Social organization of the Gelada. In N. G. Jablonski (Ed.), *Theropithecus: The Rise and Fall of a Primate Genus* (pp. 425–439). Cambridge: Cambridge University Press.
- Dunbar R. I. M (1979). Structure of gelada baboon reproductive units I. Stability of Social Relationships. *Behaviour* *69*, 72–87.
- Dunbar, R. I. M., & Dunbar, E. P. (1975). *Social dynamics of gelada baboons*. Basel: Karger.
- Furuichi, T. (1984). Symmetrical patterns in non-agonistic social interactions found in unprovisioned Japanese macaques. *Journal of Ethology*, *2*, 109–119.
- Grueter, C. C., & van Schaik, C. P. (2010). Evolutionary determinants of modular societies in colobines. *Behavioral Ecology*, *21*, 63–71.
- Grüter, C. C., & Zinner, D. (2004). Nested societies: convergent adaptations of baboons and snub-nosed monkeys? *Primate Report*, *70*, 1–98.
- Grueter, C. C., Li, D., Ren, B., & Wei, F. (in press) Insights into the social system of black-and-white Snub-nosed Monkeys. In C. L. Tan, C. C. Grueter, & B. W. Wright (Eds.), *Odd-nosed monkeys: Recent advances in the study of the forgotten colobines*. New York: Springer.
- Hanneman, R. A., & Riddle, M. (2005). *Introduction to social network methods*. Available at: <http://www.faculty.ucr.edu/~hanneman/nettext/>. Riverside: University of California.
- Hinde, R. A. (1982). *Ethology: Its nature and relations with other sciences*. New York: Oxford University Press.

- Hinde, R. A. (1983). A conceptual framework. In R. A. Hinde (Ed.), *Primate social relationships: An integrated approach* (pp. 1–7). Sunderland: Sinauer Associates.
- Iwamoto, T., & Dunbar, R. I. M. (1983). Thermoregulation, habitat quality and the behavioral ecology of gelada baboons. *Journal of Ecology*, *52*, 357–366.
- Kasper, C., & Voelkl, B. (2009). A social network analysis of primate groups. *Primates*, *50*, 343–356.
- Kawai, M. (1979). *Ecological and sociobiological studies of gelada baboons. Contributions to primatology*. Basel: Karger.
- Kawai, M., Dunbar, R. I. M., Ohsawa, H., & Mori, U. (1983). Social organization of gelada baboons: social units and definitions. *Primates*, *24*, 13–24.
- King, A. J., Clark, F. E., & Cowlshaw, G. (2011). The dining etiquette of desert baboons: the roles of social bonds, kinship, and dominance in co-feeding networks. *American Journal of Primatology*, *73*, 768–774.
- King, A. J., Sueur, C., Huchard, E., & Cowlshaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82*, 1337–1345.
- Kirkpatrick, R. C. (2007). The Asian colobines: Diversity among leaf-eating monkeys. In C. Campbell, A. Fuentes, K. MacKinnon, M. Panger, & S. Bearder (Eds.), *Primates in perspective* (pp. 186–200). Oxford: Oxford University Press.
- Kirkpatrick, R. C., & Grueter, C. C. (2010). Snub-nosed monkeys: multilevel societies across varied environments. *Evolutionary Anthropology*, *19*, 98–113.
- Kirkpatrick, R. C., Long, Y. C., Zhong, T., & Xiao, L. (1998). Social organization and range use in the Yunnan snub-nosed monkey *Rhinopithecus bieti*. *International Journal of Primatology*, *19*, 13–51.
- Kummer, H. (1968). *Social organization of hamadryas baboons: A field study*. Chicago: University of Chicago Press.
- Kummer, H. (1984). From laboratory to desert and back: a social system of hamadryas baboons. *Animal Behaviour*, *32*, 965–971.
- Le Roux, A., Beehner, J. C., & Bergman, T. J. (2010). Female philopatry and dominance patterns in wild geladas. *American Journal of Primatology*, *73*, 422–430.
- Maestripieri, D. (1994). Social structure, infant handling, and mothering styles in group-living Old World monkeys. *International Journal of Primatology*, *15*, 531–553.
- Mancini, G., & Palagi, E. (2009). Play and social dynamics in a captive herd of gelada baboons (*Theropithecus gelada*). *Behavioural Processes*, *82*, 286–292.
- Matsuda, I., Tuuga, A., & Higashi, S. (2009a). Ranging behaviour of proboscis monkeys in a riverine forest with special reference to ranging in inland forest. *International Journal of Primatology*, *30*, 313–325.
- Matsuda, I., Tuuga, A., & Higashi, S. (2009b). The feeding ecology and activity budget of proboscis monkeys. *American Journal of Primatology*, *71*, 478–492.
- Matsuda, I., Kubo, T., Tuuga, A., & Higashi, S. (2010). A Bayesian analysis of the temporal change of local density of proboscis monkeys: Implications for environmental effects on a multilevel society. *American Journal of Physical Anthropology*, *142*, 235–245.
- Matsuda, I., Tuuga, A., Bernard, H., & Furuichi, T. (2012). Inter-individual relationships in proboscis monkeys: a preliminary comparison with other non-human primates. *Primates*, *53*, 13–23.
- Murai, T. (2004). Social behaviors of all-male proboscis monkeys when joined by females. *Ecological Research*, *19*, 451–454.
- Murai, T., Mohamed, M., Bernard, H., Mahedi, P. A., Saburi, R., & Higashi, S. (2007). Female transfer between one-male groups of proboscis monkey (*Nsalis larvatus*). *Primates*, *48*, 117–121.
- Newman, M. E. J. (2004). Analysis of weighted networks. *Physical Review E: Statistical, Linear, and Soft Matter Physics*, *70*, 056131.
- Newton, P. N., & Dunbar, R. I. M. (1994). Colobine monkey society. In A. G. Davies & J. F. Oates (Eds.), *Colobine monkeys: Their ecology, behaviour and evolution* (pp. 311–346). Cambridge: Cambridge University Press.
- Oki, J., & Maeda, Y. (1973). Grooming as a regulator of behavior in Japanese macaques. In C. R. Carpenter (Ed.), *Behavioral regulator of behavior in primates* (pp. 149–163). Lewisburg: Bucknell University Press.
- Qi, X. G., Li, B. G., Garber, P. A., Ji, W., & Watanabe, K. (2009). Social dynamics of the golden snub-nosed monkey (*Rhinopithecus roxellana*): female transfer and one-male unit succession. *American Journal of Primatology*, *71*, 670–679.
- R Development Core Team. (2008). *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing.
- Ren, R. M., Yan, K. H., Xia, S. Z., Jin, H. Y., Qiu, J. J., & Romero, T. (2010). Social behavior of a captive group of golden snub-nosed langur *Rhinopithecus roxellana*. *Zoological Studies*, *49*, 1–8.
- Schreier, A., & Swedell, L. (2009). The fourth level of social structure in a multi-level society: ecological and social functions of clans in hamadryas baboons. *American Journal of Primatology*, *71*, 948–955.

- Sigg, H. (1980). Differentiation of female positions in hamadryas one-male-units. *Zeitschrift für Tierpsychologie*, *53*, 265–302.
- Sigg, H., Stolba, A., Abegglen, J. J., & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters, and family relationship. *Primates*, *23*, 473–487.
- Silk, J., Alberts, S., & Altmann, J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, *61*, 197–204.
- Silk, J., Altmann, J., & Alberts, S. (2006). Social relationships among adult female baboons (*Papio cynocephalus*) I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, *61*, 183–195.
- Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., et al. (2010). Female chacma baboons form strong, equitable, and enduring social bonds. *Behavioural Ecology and Sociobiology*, *64*, 1733–1747.
- Struhsaker, T. T., & Leland, L. (1979). Socioecology of five sympatric monkey species in the Kibale Forest, Uganda. In J. Rosenblatt, R. A. Hinde, C. Beer, & M. C. Busnel (Eds.), *Advances in the study of behavior*, vol. 9 (pp. 158–228). New York: Academic Press.
- Sueur, C., Jacobs, A., Amblard, F., Petit, O., & King, A. J. (2011a). How can social network analysis improve the study of primate behavior? *American Journal of Primatology*, *73*, 703–709.
- Sueur, C., Petit, O., De Marco, A., Jacobs, A., Watanabe, K., & Thierry, B. (2011b). A comparative network analysis of social style in macaques. *Animal Behaviour*, *82*, 845–852 doi: [10.1016/j.anbehav.2011.07.020](https://doi.org/10.1016/j.anbehav.2011.07.020).
- Swedell, L. (2002). Affiliation among females in wild hamadryas baboons (*Papio hamadryas hamadryas*). *International Journal of Primatology*, *23*, 1205–1226.
- Swedell, L. (2006). *Strategies of sex and survival in hamadryas baboons: Through a female lens*. Upper Saddle River: Pearson Prentice Hall.
- Swedell, L., & Schreier, A. (2009). Male aggression towards females in hamadryas baboons: Conditioning, coercion, and control. In M. Muller & R. Wrangham (Eds.), *Sexual coercion in primates: An evolutionary perspective on male aggression against females*. Cambridge: Harvard University Press.
- Swedell, L., Hailemeskel, G., & Schreier, A. (2008). Composition and seasonality of diet in wild hamadryas baboons: preliminary findings from Filoha. *Folia Primatologica*, *79*, 476–490.
- 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. *American Journal of Physical Anthropology*, *145*, 360–370.
- Whitehead, H. (2009). SOCPROG programs: analyzing animal social structure. *Behavioral Ecology and Sociobiology*, *63*, 765–778.
- Yamada, M. (1963). A study of blood-relationship in the natural society of Japanese macaque. *Primates*, *4*, 43–65.
- Yeager, C. P. (1991). Proboscis monkey (*Nasalis larvatus*) social organization: intergroup patterns of association. *American Journal of Primatology*, *23*, 73–86.
- Zhang P., Li B. G., Wada, K., Tan, C. L., & Watanabe K. (2003). Social structure of Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Acta Zoologica Sinica*, *49*, 727–735.
- Zhang, P., Watanabe, K., Li, B. G., & Tan, C. L. (2006). Social organization of the Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Primates*, *47*, 374–382.
- Zhang, P., Li, B. G., Watanabe, K., & Qi, X. G. (2011). Sleeping cluster patterns and retiring behavior during winter in a free-ranging band of the Sichuan snub-nosed monkey. *Primates* *52*, 221–228.
- Zhang, P., Li, B., MacIntosh, A. J. J., Watanabe, K., & Qi X (2012). A proximity-based social network of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*). *International Journal of Primatology*, *33*. doi: [10.1007/s10764-012-9608-1](https://doi.org/10.1007/s10764-012-9608-1).