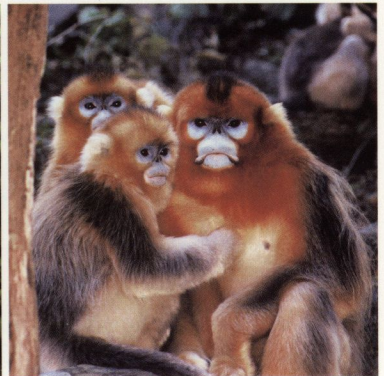
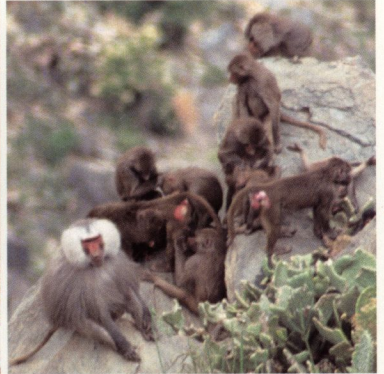
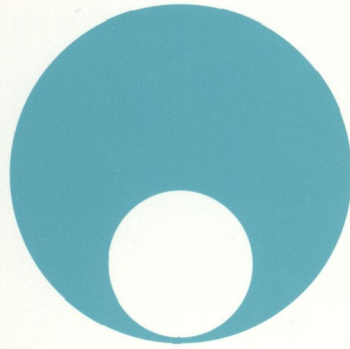


# 70 PRIMATE REPORT

Nov. 2004



## Nested Societies Convergent Adaptations of Baboons and Snub-nosed Monkeys?

**Cover picture:**

Upper left: Gelada (*Theropithecus gelada*), one-male unit, Duisburg Zoo, Germany (Photo: D. Zinner).

Upper right: Hamadryas baboon (*Papio hamadryas*), one-male unit, Durfo Valley, Eritrea (Photo: D. Zinner).

Lower left: Black-and white snub-nosed monkey (*Rhinopithecus bieti*), one-male unit, Baimaxueshan Nature Reserve, China (Photo: Xiao Lin).

Lower right: Golden monkey (*Rhinopithecus roxellana*), one-male unit, Zhouzhi Nature Reserve, China (Photo: C.C. Grüter).

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*Contents*

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**Contents**

Nested Societies. Convergent Adaptations of Baboons and Snub-nosed Monkeys?  
GRÜTER, C.C. and ZINNER, D.

Abstract . . . . .	1
Introduction . . . . .	2
Species . . . . .	3
Database . . . . .	6
Ecology . . . . .	7
Social System. . . . .	16
Social Organization. . . . .	16
Social Structure. . . . .	29
Mating System and Reproduction . . . . .	40
Evolution of Nested Systems . . . . .	54
Acknowledgements. . . . .	67
References . . . . .	68
Authors' Address . . . . .	98

NESTED SOCIETIES. CONVERGENT ADAPTATIONS OF BABOONS AND  
SNUB-NOSED MONKEYS? GRÜTER, C.C. AND ZINNER, D.

Key Words: *Rhinopithecus*, *Theropithecus*, *Papio*, hamadryas baboon, gelada, snub-nosed monkeys, ecology, social system, evolution of multi-level society

Abstract

The social systems of geladas (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*), black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) and golden monkeys (*Rhinopithecus roxellana*) show some superficial similarities, mainly in their social organization. All four species live in a nested or multi-level society with one-male units (OMUs) as basal social entities (modules). Several OMUs group together and constitute a second level of the social organization, the band. Aggregations of OMUs and bands can comprise several hundred individuals and are among the largest primate groupings. However, despite those similarities, one can also observe differences in the social organization, e.g. the existence of all-male units (AMUs) in geladas and snub-nosed monkeys, but not in hamadryas baboons, in the social structure, e.g. male-female relationships and the ontogeny of OMUs, and most likely also in the mating system. Furthermore, although the pattern of the social organization is superficially similar, the phylogenetic processes that led to a nested social system seem to be strikingly different. For geladas and hamadryas baboons, the origin of their system was most likely a multimale-multifemale group that split into OMUs, whereas in snub-nosed monkeys it seems more likely that the ancestral state were independent OMUs that grouped together.

According to socio-ecological models of the evolution of primate social systems, ecological factors such as food-distribution and predation risk have major impacts on the spatio-temporal organization of primate females (and secondarily also of males) and their social relationships, and hence on the social system of a particular taxon. On a functional level, various hypotheses have been proposed to explain the evolution of multi-level societies in primates, such as optimal habitat use, minimizing predation risk, male mate defense and infanticide avoidance.

In a comparative approach, based on a thorough review of the relevant literature, we contrasted the social systems of the four taxa and compared their ecology to extract common ecological factors that would possibly determine the social organization of the four species. However, the ecology of the four taxa is strikingly different, and it seems unlikely that their social systems are the result of similar environmental conditions. The only common character is that they all live in extreme or marginal habitats for a primate, such as semi-desert, temperate forests or in high mountains.

Taking a second noticeable trait of the social organization of the four species into account, we propose an alternative, 'demographic' hypothesis. The respective trait is that the four species also form large groups or aggregations (> 150 individuals) on a permanent or regular basis. These large groupings can be determined by various ecological needs, such as predation avoidance or optimal habitat use and foraging. Most important, these large groups may result in a possibly insecure social environ-

ment where females do best when they attach themselves to certain males. Thereby they can reduce harassment and coercion by unfamiliar group members, especially by males and reduce the risk of infanticide. Males would do best when they stick to certain females permanently (monopolize) instead of competing with a large number of males for every single mating.

However, the general conclusion of our review is that to date, none of the hypotheses can account for the evolution of nested systems in all four species. More comparable quantitative ecological and behavioral data are needed to test hypotheses about the ultimate causes for the convergent evolution of their nested social systems.

### Introduction

Compared to other mammalian orders, primates show a large diversity of social systems (e.g. FLEAGLE, 1999; ROWE, 1996). In general, it is believed that social systems are evolutionarily shaped by the ecology of the respective taxon, i.e. that they constitute adaptations to certain historical or present environmental conditions, but that they are influenced also by the taxon's life-history and by phylogenetic constraints (e.g. KUMMER, 1971; KAPPELER and van SCHAIK, 2002; KAPPELER et al., 2003). Among the different social systems, the most complex system seems to be the nested or multi-level social system, where two or more levels of organization (modules) are recognizable, at least large groups composed of stable one-male units (OMUs). It is only found in the genera *Rhinopithecus* and *Theropithecus* and in one (sub)species of the genus *Papio*. Although snub-nosed monkeys (genus *Rhinopithecus*, Colobinae) and baboons (genera *Theropithecus* and *Papio*, Cercopithecinae) represent two different evolutionary lineages within the Old World monkeys (Fig. 1), their social systems are superficially similar. Because of phylogenetic

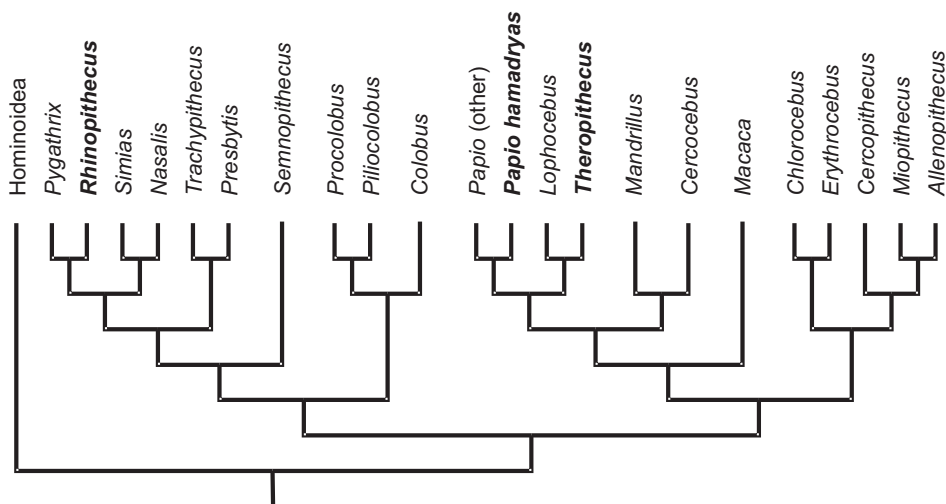


Fig. 1: Position of focal species (bold letters) in a phylogram of Old World monkeys. (Phylogeny based on PURVIS, 1995; DISOTELL, 1996; TOSI et al., 2003).

distance, it is assumed that this social system has evolved most likely two or three times independently. Therefore, these systems are thought to constitute a case of convergence.

Geladas, hamadryas baboons and snub-nosed monkeys do not only have a nested social system in common, but they also resemble one another in several other features. All of them have a rather restricted distribution and they are all large-bodied, sexually dimorphic and often travel and forage on the ground (ROWE, 1996). All of them have to deal with marginal environmental conditions such as severe climates that directly influence a number of aspects of their morphology, physiology and also of their behavioral ecology (e.g. IWAMOTO and DUNBAR, 1983). Both geladas and snub-nosed monkeys live in temperate montane habitats at elevations up to 4000 m, with temperatures regularly falling below 0° C and hamadryas baboons occupy arid mountains, steppes and semi-deserts. All these habitats seem to be suboptimal or marginal compared to the originally forest living arboreal primates.

In a comparative approach we will review information of the social systems and ecology of four species, representing the above three genera: black-and-white snub-nosed monkeys or Yunnan snub-nosed monkeys (*Rhinopithecus bieti*); golden monkeys or Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*), geladas (*Theropithecus gelada*) and hamadryas baboons (*Papio hamadryas*). Inter-specific comparisons are strong tools in testing the validity of socio-ecological models or the effect of phylogenetic inertia. A similar approach has been undertaken by CALDECOTT et al. (1996) to compare the ecological strategies of not closely related primate taxa (pigtailed macaques *Macaca nemestrina*, mandrills *Mandrillus sphinx*, drills *Mandrillus leucophaeus*) and by RUBENSTEIN and HACK (2004) to compare the multi-level societies of even more distantly related mammal taxa (zebras, baboons). Comparisons of closely related taxa are more frequent (e.g. for baboons: BARTON et al., 1996). Our aim here is to provide a descriptive heuristic synthesis based on an inter-generic comparison of the four species with respect to their social system and ecology and to discuss hypotheses about the evolution of the respective systems.

According to KAPPELER and van SCHAIK (2002), the social system consists of three distinct aspects, the social organization (e.g. group composition and spatio-temporal cohesion), the social structure (e.g. social interactions and relationships) and the mating system (e.g. who mates with whom and what are the genetical consequences). Our paper is organized according these components of the social system with some additional data on the species' ecology. However, data availability is very unequally distributed among the four species. Since geladas and hamadryas baboons are highly terrestrial primates living in an open environment, field observations are much easier to carry out and individual recognition is much easier to achieve than in the elusive snub-nosed monkeys. Snub-nosed monkeys live in montane forests, which is probably one of the main reasons why knowledge about their socio-ecology is still preliminary compared to geladas and hamadryas baboons.

### Species

**Geladas** (*Theropithecus gelada*) live in harsh mountain areas, being found in Ethiopia on the central plateau at elevations between 1400 and 4500 m (IWAMOTO,

1993a). Recently an additional population was detected in the Arsi region south of the Rift Valley east of Bale Mountains (Fig. 2a), possibly representing a distinct (sub)species (MORI and BELAY, 1990; BELAY and SHOTAKE, 1998). However, fossil *Theropithecus* had a much wider distribution during the Pleistocene (PICKFORD, 1993). Their present day habitat consists of montane grassland with no tall trees and it is characterized as wet and cool (DUNBAR and DUNBAR, 1975). When looking at different habitat types within the gelada range, there are marked distinctions in vegetation and climate (IWAMOTO and DUNBAR, 1983). In general, geladas of the northern population live in a habitat that is relatively rich in terms of food availability with abundant sleeping and drinking sites. The higher the altitude, the longer the vegetation stays green, due to high rainfall and low temperature (IWAMOTO, 1993a). Their main diet consists of grass, a unique dietary adaptation for primates. Gelada sleeping sites are located on rock cliff faces. Infant survival is high. DUNBAR (1980b) estimated that nearly 90 % of infants born survive to puberty. Although geladas have low reproductive rates, mortality rates are so low that population growth rates are among the highest recorded for any primate population (OHSAWA and DUNBAR, 1984). Concerning their activity budget, approximately 36-45 % of their time is spent feeding, with an additional 17-20 % spent moving from one feeding site to another, 19-21 % socializing and 14-26 % resting (DUNBAR, 1984a). Feeding time increases with altitude due to a combination of increasing temperature dependent energy requirements and declining habitat quality (IWAMOTO and DUNBAR, 1983). Their social system is based on OMUs and all-male units (AMUs) which temporarily form higher levels of social aggregations. This species is thought to be 'near threatened' (IUCN, 2002).

**Hamadryas baboons (sacred baboon, mantled baboon, *Papio hamadryas*)** are the only member of the genus *Papio* whose range extends beyond the African continent, being found both in the Horn of Africa (eastern parts of Eritrea and Ethiopia, Djibouti and parts of Somalia) and across the Red Sea in western Saudi Arabia and Yemen (Fig. 2a). Their habitat in Northeast Africa and Arabia resembles that of all other three focal species in its extreme climatic profile and its harsh living conditions. Although primarily living in arid savanna and semi-deserts, the baboons also range up to 3000 m into subalpine zones (KUMMER, 1968a; BIQUAND et al., 1992b; ZINNER et al., 2001a). Habitat quality, as determined by plant productivity, is relatively poor, and in particular water becomes a limiting resource (ZINNER et al., 2001a, 2001/2003). Hamadryas and gelada baboons are partially sympatric. In the overlap zone, the two genera sometimes interbreed (JOLLY et al., 1997). Hamadryas baboons choose vertical cliffs as sleeping sites, but also rocky outcrops in the coastal lowlands of Eritrea (KUMMER, 1968a; ZINNER et al., 2001a). Survival of juveniles appears also high in hamadryas baboons (SIGG et al., 1982). The superficial pattern of social organization is similar to geladas, but closer studies have revealed many differences in the finer social structure of the two species which are summarized in detail below. According to the IUCN (2002), hamadryas baboons are 'near threatened'.

The genus *Rhinopithecus* (snub-nosed monkeys) belongs to the subfamily Colobinae, and is comprised of four distinct allopatric species (GROVES, 2001; LI et al., 2004): *Rhinopithecus avunculus*, *R. brelichi*, *R. bieti* and *R. roxellana*, of which the latter two are included in our review.

**Black-and-white snub-nosed monkeys or Yunnan snub-nosed monkeys (*Rhinopithecus bieti*)** are enigmatic primates inhabiting remote montane areas in Northwestern Yunnan Province, China (Fig. 2b) and neighboring regions in Eastern Tibet (LONG et al., 1994). They are considered to be semi-terrestrial (WU, 1993; KIRKPATRICK and LONG, 1994; KIRKPATRICK et al., 1998). Their habitat is characterized as temperate deciduous/evergreen broadleaf and coniferous forests (e.g. KIRKPATRICK, 1998; YANG and ZHAO, 2001; DING and ZHAO, 2004). Snow is common in winter. The highest recorded altitude of *R. bieti* is 4700 m (LONG et al., 1994). There is, however, evidence that snub-nosed monkeys were distributed at lower altitude areas in China in historic times (LI et al., 2003). Within the distribution of *R. bieti*, temperature, precipitation and diversity of vegetation increase in accordance with a reduction of elevation from north to south (LONG et al., 1994). Black-and-white snub-nosed monkeys sleep preferentially in conifer trees in the middle part of hillsides (LIU and ZHAO, 2004). They are folivorous, with lichens being of paramount importance as food resource. Infant mortality during the first winter appears to reach 55 to 60 % (KIRKPATRICK, 1996a), which is high compared to other colobines and baboons. The daily activity budget of the Tacheng group is, on annual average, made up of 35 % feeding, 33 % resting, 15 % moving and 13 % socializing (DING and ZHAO, 2004). Black-and-white snub-nosed monkeys form large cohesive bands of up to 370 individuals comprising several one-male units (OMUs) and occasional all-male units (AMUs). Despite the attractive appearance and the endangered status of this species (IUCN, 2002; XIAO et al., 2003), in depth studies of its behavior and ecology under natural conditions have started only recently. Field work has been devoted primarily to the specialized dietary ecology and, to a lesser degree, to the overall social organization of *R. bieti*. Many questions concerning pat-

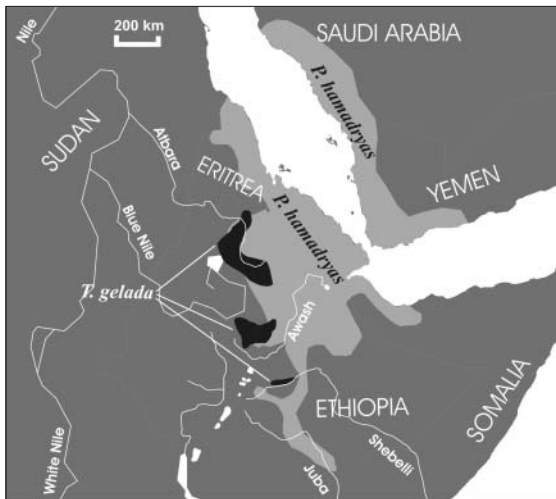


Fig. 2a: Distribution of *T. gelada* (black) and *P. hamadryas* (light gray). Some populations of *P. hamadryas* and *T. gelada* are sympatric. (Map based on YALDEN et al., 1977; MORI and BELAY, 1990.)



Fig. 2b: Distribution of snub-nosed monkeys. (Based on a map by R.C. KIRKPATRICK).



terns of behaviors that occur within OMUs remain unanswered. This is largely due to difficult observation conditions and due to the fact that it is almost impossible to individually recognize animals in such large bands.

**Golden monkeys or Sichuan snub-nosed monkeys (*Rhinopithecus roxellana*)** are endemic to China, dwelling in the temperate forests of Sichuan, Gansu, Shaanxi and Hubei (Fig. 2b). They are closely related to black-and-white snub-nosed monkeys, but are not sympatric with them. *R. roxellana* is the primate species that lives in the coldest environment inhabited by any nonhuman primate and is found at altitudes between 1400 and 3400 m (SU et al., 1998). Foraging and traveling takes place both on the ground and in trees (*ibid.*), but sleeping is confined to trees. The forests frequented by *R. roxellana* are a mix of evergreen conifer and deciduous broadleaf trees; snow is common in winter (e.g. LI et al., 2002). As in all other species discussed here, a multi-level social organization has been described for this species. This species is classified as ‘vulnerable’ (IUCN, 2002).

#### Database

No field data were collected specifically for this study. Instead, a thorough literature search was undertaken in order to find comparable data for all four species. The findings for each socio-ecological topic are quoted in the ‘results’ section of this paper and are followed by a discussion. A preliminary overview of ecology and behavior of snub-nosed monkeys can be found in KIRKPATRICK’s (1998) review (including the Chinese literature), a comparative analysis of social structure between gelada and hamadryas in DUNBAR (1983d) and STAMMBACH (1987) and an overview of social organization and ecology of geladas in IWAMOTO (1993a) and DUNBAR (1993).

In this review, we follow the nomenclature and taxonomy of GROVES (2001) and GEISSMANN (2003). Therefore, all taxa are considered as having full species status despite the fact that the species status of hamadryas baboons is still debated (JOLLY, 1993; GROVES, 2001). The database which we refer to stems mainly from field studies listed in Table 1.

Table 1: List of field studies of geladas, hamadryas baboons and snub-nosed monkeys on which our review is primarily based.

Site	Investigator	Period	Reference
<i>T. gelada</i>			
Sankaber and Bole Valley in Simien Mountains National Park (Ethiopia)	R.I.M. Dunbar and E.P. Dunbar	Jul 1971 – Mar 1972 May – Oct 1972 Nov 1974 – Jul 1975	DUNBAR and DUNBAR, 1975
Gich in Simien Mountains National Park (Ethiopia)	U. Mori, M. Kawai, H. Ohsawa and T. Iwamoto	Jun 1973 – Mar 1974 Nov 1975 – Mar 1976	KAWAI, 1979a
Arsi (Ethiopia)	A. Mori, T. Iwamoto, et al.	Dec 1994 – Feb 1995; Nov 1995 – May 1996	MORI et al., 1997, 1999, 2003
	G. Belay	Oct 1995 – Feb 1996	BELAY and SHOTAKE, 1998
<i>P. hamadryas</i>			
Erer-Gota (Ethiopia)	H. Kummer	Nov 1960 – Oct 1961	KUMMER, 1968a
	J. J. Abegglen and H.U. Müller	May 1971 – Jul 1972	ABEGGLEN, 1984; MÜLLER, 1980
	H. Sigg and A. Stolba	Feb 1974 – Jun 1975	SIGG and STOLBA, 1981

Site	Investigator	Period	Reference
<b><i>P. hamadryas</i></b>			
Erer-Gota (Ethiopia)	J.J. Abegglen and R. Wey	Jan 1976 – Feb 1977	SIGG et al., 1982
Filoha in Awash National Park (Ethiopia)	L. Swedell	Nov 1996 – Sep 1998	SWEDELL, 2000b
Eritrea	D. Zinner et al.	Oct – Nov 1997 Mar – Apr 1998 Oct – Nov 1998	ZINNER et al., 2001a,b
Saudi Arabia	S. Biquand, A. Boug et al.	Dec 1987 – Apr 1989	BIQUAND et al., 1992a
	H. Kummer et al.	Jan – Feb 1980	KUMMER et al., 1981
<b><i>R. bieti</i></b>			
Wuyapiya (Yeri district) in Baimaxueshan National Nature Reserve (Deqin, Yunnan, China)	R.C. Kirkpatrick, Y.C. Long et al.	1992 – 1994 (approx. 14 months)	KIRKPATRICK, 1996a
Yeri district	B.Q. Wu et al.	1986 – 1988 (approx. 9 months)	WU, 1993
Nanren / Sharong in Baimaxueshan National Nature Reserve (Deqin, Yunnan, China)	L.W. Cui	Nov 2000 – Nov 2001 (9 months)	e.g. CUI, 2003
	MacLennan et al.	Jul – Aug 1999	MacLENNAN, 1999
Tacheng in Baimaxueshan Nature Reserve (Weixi, Yunnan, China)	W. Ding	1999 – 2001 (approx. 10 months)	DING, 2003
	C.C. Grüter	Jan – Feb 2003	
Jinsichang (Lijang, Yunnan, China)	S.J. Yang	1997 – 1998 (5 months)	YANG, 2000
Laojunshan (Lijiang etc., Yunnan, China)	B.P. Ren et al.	2003 – ongoing	
Fuheshan (Lanping, Yunnan, China)	Z.H. Liu	Nov 2000 – Jan 2002	e.g. LIU et al., 2004
Longmashan (Yunlong, Yunnan, China)	Z.F. Xiang	2002 – 2004 (8 months)	
Xiaochangdu in Mangkang National Nature Reserve (Mangkang, Tibet)	S. Huo	2003 – ongoing	
<b><i>R. roxellana</i></b>			
Shennongjia Nature Reserve (Hubei, China)	R.M. Ren, K.H. Yan, Y.J. Su et al., Y.M. Li	1991 – ongoing	REN et al., 2000; e.g. LI et al., 2002b
Zhouzhi Nature Reserve (Yuhuangmiao, Qinlingshan, Shaanxi, China)	B.G. Li, C.L. Tan et al.	1989 – ongoing	e.g. LI et al., 2000
Baihe Nature Reserve (Sichuan, China)	R.C. Kirkpatrick and H.J. Gu	1996 – 1998 (15 months)	KIRKPATRICK et al., 1999

### Ecology

According to socio-ecological models of the evolution of primate social systems, ecological factors such as food distribution and predation pressure are among the most important determinants of the social organization. They have also an impact on social structure and mating system (van SCHAIK, 1996; STERCK et al., 1997;

LINDENFORS et al., 2004). Therefore, when comparing social systems and their adaptive value one has to include these determine factors in the analysis. However, problems at least at two levels may arise. (1) Contemporary predator densities and food distribution may not be the same as during most of the evolutionary history of the respective species, and (2) for most species, including the four species under discussion, quantitative data of predator abundance and predation pressure, as well as for the distribution of food are not available. Hence, any inferences from ecological factors on the evolution of the respective social system have to be preliminary.

As mentioned earlier, all four species under discussion live in extreme or marginal habitats compared to the majority of primate species. Their habitats include high mountains in the tropical and temperate zone but also arid environments such as the semi-deserts at the Horn of Africa. Some basic abiotic ecological characters of their habitats are given in Table 2.

Table 2: Abiotic habitat characteristics.

Altitude (m)	Precipitation (mm/a)	Temperature (°C)	Seasonality	Reference
<b><i>T. gelada</i></b>				
1400-4500	1500	5 - 9 (average)	less pronounced	IWAMOTO, 1993a; IWAMOTO and DUNBAR, 1983
<b><i>P. hamadryas</i></b>				
0-3000	100-1000	0 - >40	pronounced with short rains and long dry season	KUMMER, 1968a; ZINNER et al., 2001a
<b><i>R. bieti</i></b>				
up to 4700	1600	-13 - 16	pronounced with snowy winters	LONG et al., 1994; YANG, 2000; KIRKPATRICK et al., 1998
<b><i>R. roxellana</i></b>				
1400-3400		0 - 9 (average) (lowest -30)	pronounced with snowy winters	SU et al., 1998

Seasonality is one of the key climatic parameters that has profound influences on several aspects of the eco-ethology of the species discussed here such as foraging, ranging behavior and reproduction. The time budgets of *Rhinopithecus* and *Theropithecus* are also subjected to marked seasonal changes. Geladas for example tend to increase time spent feeding during the dry season (IWAMOTO, 1993a). Snub-nosed monkeys tend to stay in sleeping trees longer in winter than in other seasons (SU et al., 1998; LIU and ZHAO, 2004; C.C. GRÜTER (C.C.G.), pers. obs.). According to DUNBAR (1983a), the freedom of social interaction is restricted by time-budget constraints such as acquiring the daily nutritional requirements. This is of particular importance for species living in harsh environments such as geladas, hamadryas and snub-nosed monkeys.

#### Diet and Feeding Behavior

***T. gelada*** is highly graminivorous (DUNBAR, 1977, 1992a; IWAMOTO, 1979, 1993b; IWAMOTO and DUNBAR, 1983), with grasses forming more than 90 % of their diet in most habitats and seasons. Supplementary foods include fruits, tubers,

leaves and flowers (DUNBAR, 1977). Geladas show seasonal variation in food intake. They increase food intake in the dry season by prolonging the time spent feeding and changing their dietary habits from grasses to herbs. The greater energy intake in the dry season might be explained by the need for more food for body temperature regulation during the cold dry season (IWAMOTO, 1993a). Geladas at higher altitudes spend more time feeding, due to thermoregulatory needs (IWAMOTO and DUNBAR, 1983). Furthermore, gelada populations appear to differ in their feeding habits. The diet of the Arsi population in the southern part of their range contains considerable amounts of fruits which have rarely been used by geladas living in the northern part (IWAMOTO et al., 1996).

***P. hamadryas*** is omnivorous and opportunistic and feeds on grass seeds, roots, tubers, leaves, flowers, palm nuts, pods, blades, fruits and animal prey (e.g. STAMMBACH, 1987). They also make use of rubbish dumps and raid crops (KUMMER et al., 1985; BIQUAND et al., 1992a, 1994; ZINNER et al., 2001a). At certain sites, *Acacia* species and grass roots account for their main food. In general, food distribution is believed to be of the dispersed type (KUMMER, 1968a), although no quantitative estimations are available. Water is a crucial and limiting resource for hamadryas baboons (ZINNER et al., 2001a).

In Wuyapiya, ***R. bieti*** spent 60 % of the daytime feeding on lichens in spring, and 95 % in winter (KIRKPATRICK, 1996a). Additional foods at this site include dicot leaves and monocot leaves of grasses. In Jinsichang, *R. bieti* basically eats bamboo leaves (YANG and ZHAO, 2001). In Tacheng, the monkeys feed on bamboo leaves, broad leaves, lichens, fruits, buds, bark and seeds (DING and ZHAO, 2004). In total, 59 different plant species (of which 90 parts were consumed) were recorded (*ibid.*). At Bamei, the monkeys incorporate oak acorns into their diet (ZHONG et al., 1998). Prey on bird nestlings and egg eating has been observed (W. DING, pers. com.). Eating snow and geophagy is also common as well as active drinking at ponds (C.C.G., pers. obs.). As for hamadryas baboons, water is most likely also a limiting resource for *R. bieti* (GRÜTER, unpubl.).

***R. roxellana*** feed on mature leaves in summer and on lichens, bark and buds in winter (KIRKPATRICK et al., 1999). Additionally, they take insects (LI, 2001), possibly bird eggs and birds (POIRIER and HU, 1983; HAPPEL and CHEEK, 1986) and occasionally fruits in autumn (KIRKPATRICK and GU, 2002). Pine nuts are an essential part of their diet in autumn and winter (SU et al., 1998). The animals have never been observed to drink, but they have been seen to eat snow in winter (SU et al., 1998).

The main diet of *T. gelada* consists of grass. A similar restriction of the diet on only a few different food items is found in *R. bieti* in some high altitude regions, where they heavily rely on lichens. These dietary restrictions represent high specializations quite unique among primates. Although pendulous lichens are found in the Simien Mountains as well, we have no information that geladas feed on them. Grasses and lichens both occur in vast amounts, in which harvesting time, rather than direct competitive ability, is the constraining factor (KIRKPATRICK et al., 1998). Similar dietary adaptations are found in other temperate primates. Barbary macaques in high altitude fir forests at the Ghomoran Rif survive cold, snowy winters by utilizing one major food resource, conifer foliage (MEHLMAN, 1988). And in

Algerian oak forests they rely on lichens and grasses during winter (MÉNARD, 1985). Such a seasonal flexibility between an extremely restricted diet in winter and a high dietary diversity in spring and summer is also a characteristic of the Japanese macaque (*Macaca fuscata*) living in areas where severe winters with low temperatures and snow are common (e.g. MARUHASHI, 1980). Lichenivory is a rare phenomenon in nonhuman primates. Apart from the Chinese snub-nosed monkeys (*R. bieti*: WU, 1991; KIRKPATRICK, 1996a; *R. roxellana*: LI, 2001; *R. brelichi*: YANG et al., 2002), the only other taxa that incorporate certain amounts of lichens into their diet are Barbary macaques (*Macaca sylvanus*) and Angolan colobus (*Colobus angolensis*) at Nyungwe (FIMBEL et al., 2001; VEDDER and FASHING, 2002). Also, yellow-tailed woolly monkeys (*Oreonax flavicuada*) living in high-altitude habitats in Peru have been observed feeding on lichens (BUTCHART et al., 1995). Lichens are a valuable energy source (KIRKPATRICK et al., 2001) and generally available in large quantities. The non-structural carbohydrates in lichens provide digestible energy for thermoregulation, particularly important during the freezing winters. Acorn feeding is not only prevalent in *Rhinopithecus*, but also in Barbary macaques (MÉNARD, 1985).

At Tacheng, far less plant species were eaten by *R. bieti* in winter in comparison with other seasons (DING and ZHAO, 2004). There was also a significant seasonal variance in lichen intake at Tacheng, with more time devoted to lichen harvesting in winter than in summer. This roughly corresponds to findings from Wuyapiya (KIRKPATRICK, 1996a). In sum, differences across populations and seasonal dietary shifts are hallmarks of the feeding ecology of *R. bieti*. Shifts in diet composition on a seasonal basis are also typical for *R. roxellana* (KIRKPATRICK et al., 1999). The winter foods of *R. roxellana* appear similar to the bark and buds diet of snow-living Japanese macaques (WATANUKI et al., 1994).

#### Predation Pressure

Data on predation risk are mainly inferred from anecdotal observations and from indirect evidence of the presence of a particular predator in the range of the primate species.

*T. gelada* probably experienced great predation pressure by natural enemies in the past, but present predation pressure is minimal (IWAMOTO, 1993a). Humans and especially domestic dogs are the main predators at present (DUNBAR, 1993). Active anti-predator behavior against domestic dogs and leopards has been observed at Arsi (IWAMOTO et al., 1996).

KUMMER (1968a) mentioned lions, leopards and cheetahs as possible predators of *P. hamadryas* in Ethiopia. SIGG (1980) added hyenas, jackals and feral dogs. For Saudi Arabia, wolves, hyenas and leopards are regarded as potential predators by BIQUAND et al. (1992b). However, observers have seen only a few attacks by dogs (SIGG, 1980), one case of harassment of a sick female by two jackals, and one possible attack of a leopard (NAGEL, 1973). In the central Eritrean highlands, Verreaux's eagles interacted with hamadryas baboons. The behavior of the eagles and the reactions of the baboons towards them provide evidence that eagles attack the baboons and that there is predation by eagles, at least on immatures (ZINNER and PELÁEZ, 1999). The current main predators of hamadryas, though, seem to be people and their dogs (ZINNER et al., 2001a). Predation pressure is possibly higher

in Ethiopia (KUMMER, 1968a) than in Saudi Arabia (KUMMER et al., 1985). In Arabia, where hamadryas baboons are not subjected to high predation risk, their OMUs tend to forage alone instead of congregating within bands (*ibid.*). The lack of predation has also been suggested to explain observations of baboons sleeping in the open in Saudi Arabia (KUMMER et al., 1981; but see BIQUAND et al., 1992b). Males exhibit protective behavior defending their females and infants against predators such as eagles, dogs, jackals and humans (KUMMER, 1995; ZINNER and PELÁEZ, 1999; ZINNER et al., 1999/2000). Further, subadult and adult bachelor males have been observed to engage in predator defense of the group (ZINNER et al., 1999/2000).

Predation appears to be virtually nonexistent in *R. bieti* and there is no direct evidence to suggest that past predation was significantly greater (KIRKPATRICK et al., 1998). Birds of prey seem to be the main predators of young *R. bieti*. A predator-prey interaction between a buzzard and a group of *R. bieti* was described by CUI (2003). Potential terrestrial predators such as wolves still exist within the range of *R. bieti* (C.C.G., pers. obs.), and the existence of snow leopards in Northwest Yunnan was recently confirmed (MA et al., 2002). Hunting by humans used to be common in the last decades, and has probably not yet been fully stopped (LI et al., 2002a, 2003).

In general, predation by mammals appears to be rare in *R. roxellana*. Predation is chiefly by raptors, but it has also been suggested that leopards, jackals, lynxes and wolves may prey on the monkeys (HU et al., 1980; SHI et al., 1982). Predation of a juvenile monkey by a goshawk was observed in the Qinling Mountains by ZHANG et al. (1999a). There is a report of adult males having been killed while protecting other group members against a wolf attack (YAN et al., 1995).

Predator abundance in all habitats occupied by the species discussed here was most likely higher in the past than it is today. Therefore, it is important to stress that present predation risk and rate in any population does not necessarily reflect the former predation regime that selected the current anti-predation behavior and respective social organization (CHENEY and WRANGHAM, 1987).

The choice of sleeping site is believed to be influenced by their safety from predators. Geladas and hamadryas baboons are unusual among primates in occupying sleeping sites on cliff edges. Such cliffs are most likely the safest places for these primates in an environment where large trees are scarce. In contrast, snub-nosed monkeys sleep in trees, but also here avoiding detection by predators appears to be one of the driving forces behind sleeping site choice (LIU and ZHAO, 2004).

#### Ranging Behavior

In *T. gelada*, daily moving distance is between 1 and 2 km (IWAMOTO and DUNBAR, 1983). Differential use of the home range has been observed between dry and wet season due to the fact that green grass is more patchily distributed during the dry season (DUNBAR, 1977).

Home range size of *P. hamadryas* at Erer Gota was estimated to be approximately 28 km<sup>2</sup> and day range around 9 or 10 km (SIGG and STOLBA, 1981). SWEDELL (2002a) estimated a mean daily path length of 7.5 km and a home range size of 30 km<sup>2</sup>. Both BOUG et al. (1994) and SWEDELL (2002a) suggest a pattern of longer daily path lengths during periods of resource abundance and shorter path lengths during periods of resource scarcity.

Range size of *R. bieti* is 16-25 km<sup>2</sup>. The mean daily travel distance is about 1300 m (KIRKPATRICK et al., 1998). The daily travel distance is shorter in winter than in summer (*ibid.*; LIU et al., 2004). Partial home range overlap (less than 30%) exists between two bands of *R. bieti* at Tacheng (W. DING, pers. com.). A case of probably human induced home range shift was reported for a band of *R. bieti* in the Hengduan Mountains (MacLENNAN, 1999). Altitudinal ranging appears not to be stratified by season in Wuyapiya in the northern part of the range of *R. bieti* (ZHAO et al., 1988; KIRKPATRICK and LONG, 1994; KIRKPATRICK et al., 1998). In this area, the monkeys consistently prefer the upper forest sections, even in snowy winters (ZHAO et al., 1988; CUI and ZHAO, 2002). However, short-term descendance to lower altitudes due to heavy snowstorms has been observed (KIRKPATRICK and LONG, 1994; C.C.G., pers. obs.). At Jinsichang in the southern part, on the other hand, the monkey group confined its ranging to the lower half of the forest belt (YANG, 2003). At Fuheshan, the monkeys often stayed at lower altitudes in winter and spring compared to summer and fall (LIU et al., 2004).

The annual home range of a band of *R. roxellana* in the Qinling Mountains covers an area of 22.5 and 19.5 km<sup>2</sup>, respectively (LI et al., 2000; GUO et al., 2004). Seasonal changes of home range area have been noted in the Qinling Mountains, with the smallest range coverage recorded in summer (LI et al., 2000). Home range size of *R. roxellana* at Shennongjia is about 40 km<sup>2</sup> and mean daily ranging length is usually less than 1 km (SU et al., 1998). In summer and autumn, the mean daily travel distance is significantly longer than in winter and spring at Shennongjia (LI, 2002). Also, the range size is significantly larger in summer or autumn than in winter or spring (LI, 2004). In the Qinling Mountains, human disturbance is probably responsible for the observed change of the summer home range of a band of *R. roxellana* (LI et al., 1999). Home range overlap seems to exist at Shennongjia (REN et al., 2000), and at least seasonally, in the Qinling Mountains (GUO et al., 2004). At Shennongjia, no evidence was found that altitudinal ranging occurs on a seasonal basis (REN et al., 2000). Also at Baihe, *R. roxellana* favored high altitude conifer forests for the majority of the winter period, but short-term descendance to lower altitudes due to heavy snowstorms has been observed (SHI et al., 1982). On the other hand, HU et al. (1980) claim that altitudinal ranging is stratified by season at Wolong.

As food availability is much greater in the highlands than in the lowland, geladas move for only a short distance each day (DUNBAR and DUNBAR, 1975; KAWAI, 1979a). Hamadryas baboons have the largest day ranges recorded for any primate (mean 13.2 km, maximum 19 km, KUMMER, 1968a). At other sites in Ethiopia and Saudi Arabia the daily travel path length varied between 1 and 14 km (SWEDELL, 2002a). The long and variable travel path lengths of hamadryas baboons do not necessarily reflect low food availability, but can be a result of the scarcity of water places and safe sleeping sites. In parts of Eritrea, hamadryas baboons have to vanish each day an altitude of more than 1000 m. In the morning they come down from their sleeping site on top of the mountain to their drinking place in the valley more than 1000 m below. During the afternoon they climb again 1000 m to their sleeping cliff. On their way up and down they feed on the plenty food sources (*Opuntia* spp.) that are available in this particular region (ZINNER et al., 2001a).

Home ranges in snub-nosed monkeys are unusually large. The range size of *R. bieti* is above the largest estimate for any colobine species outside *Rhinopithecus*, and the daily travel distance is the longest documented for any species of the Colobinae (KIRKPATRICK et al., 1998).

A frequently used method to infer scramble competition, i.e., the effect of group size on foraging efficiency, involves showing a positive association between group size and daily travel path length. If food is limited, a larger group is expected to move farther to obtain sufficient food. Thus, daily path length should increase with increasing group size (ISBELL, 1991). However, in Asian colobines as a whole, there is neither a positive correlation between daily path length and group size nor between home range size and group size (YEAGER and KIRKPATRICK, 1998). Therefore, food competition seems to be of minor importance in these species. An exception to the above findings is a population of *R. roxellana* at Shennongjia where a positive association between home range size and group size was found. A large group had larger ranges than a small group in the same season (LI, 2004).

Daily path length in all species seems to be subjected to marked seasonal differences. Seasonality of food resources is probably a central factor in determining the range size and use of *R. roxellana* and *R. bieti* (KIRKPATRICK, 1998). Shorter day length in winter may reflect a trade-off between the energetic costs of travel and thermoregulation (KIRKPATRICK et al., 1998). According to KIRKPATRICK (1996a), the extraordinarily slow growth of lichen appears to be a central factor in the range size and use of *R. bieti* and also *R. roxellana*.

Seasonal shifts in altitudinal range use have been reported to occur in primates that live in more temperate regions (e.g. hanuman langur: DOLHINOW, 1972). In geladas, there are apparently no altitudinal migration patterns over the course of a year. Reports about seasonal differences in altitudinal ranging for *R. bieti* and *R. roxellana* are conflicting and might be location-specific. Furthermore, some results are based on indirect estimations using distribution of feces. Food resource distribution, e.g. greater density of lichens at higher altitudes (KIRKPATRICK, 1996a) seems to be the key factor determining altitudinal range use in *Rhinopithecus*.

#### Group Movement

The movements of *T. gelada* herds are determined more by a gravitational effect than by collective decision making. The more animals seem to move in a given direction, the more likely it is that units in the rear of the herd will go that way too. As a result, gelada herd movements often appear to be confused and aimless (DUNBAR and DUNBAR, 1975). Geladas appear to select routes more opportunistically, as they move from one feeding stop to the next. In addition, this process seems to involve only a single OMU. Initiation of movement, that is, proposing a certain direction, is done mainly by lactating females. The proposed directions of lactating females are generally accepted, especially by their subordinate grooming partners. Whether such an initiation by lactating females is followed by the rest of the group is largely a function of the behavior of the dominant female. If she followed the lead, then the male and the rest of the group would also. The gelada male leader has to pay attention mainly to the alpha female, who is responsible for maintaining group cohesion. Less frequently the male himself or even another individual of the OMU will be able to direct the group in a particular direction.



The most common configuration of the unit's members during foraging is a line formation (DUNBAR, 1983c). A characteristic pattern in many progressions was that, after it had been initiated (by a lactating female, for example), there was often a delay before the rest of the unit followed (*ibid*). AMUs act as flanks during group movement.

Through strong male-male relationships, *P. hamadryas* males coordinate band movement during the day's foraging, communicating decisions about direction and the timing of resting and watering stops and generally preventing the individual OMUs from becoming too dispersed and getting completely separated (STOLBA, 1979). The relationships are manifested by a unique set of behavior patterns, e.g. 'notifying' (KUMMER, 1968a; STOLBA, 1979; PELÁEZ, 1982). Males wanting to move in a particular direction approach a neighboring male look closely at him and then abruptly turn round and present their rears. STOLBA (1979) examined this process of 'decision making'. He found that the decision is apparently made mainly by the adult and subadult males of the band. A male leader, followed by the other members of his OMU, moves some steps in one direction. The other males may support this initiation by moving in the same direction, they may initiate movement in another direction, or they may not move at all. If an initial move is made by a male, another male of the same clan is more likely to agree. If the majority of the OMU leaders agree with an initial movement, the band will move on. Such processes have not been reported from any other study site of hamadryas baboons, maybe one has not looked at them.

Females often walk in an approximate line between their OMU leader and a second OMU leader (KUMMER, 1968a). While subadult males generally run along anywhere in the unit's neighborhood during a march, adult male followers usually bring up the unit's rear (KUMMER, 1990). When OMUs pass nomads, dogs or predators, SIGG (1980) observed that followers and unit males alike walk on the flank exposed to the potential source of danger. It has also been observed that the so-called 'peripheral female', the one that is less active socially, approached areas that might hide a predator significantly more often than the other OMU members. This 'peripheral female' has thus been assumed to take on the role of reconnoitering potential dangers (SIGG, 1980). In Eritrea, subadult and adult bachelor males were the first to enter into dangerous areas (ZINNER et al., 1999/2000).

OMUs of the *R. bieti* band at Wuyapiya traveled together over long distances and often used the same travel path, though how travel was coordinated is unclear (KIRKPATRICK et al., 1998). When they crossed the meadow, there were parallel columns of monkeys separated by about 100 m. The band at Tacheng was seen to move cohesively in an open area, often in a single line (DING et al., 2004, in press). AMUs seem to act as front and/or rear guards while crossing a meadow. Single males often are the first to enter a gully or go to the water hole (*ibid.*). L.W. CUI (unpubl.) observed that not the adult males and juveniles walking in the front of a progression of the whole band, but the central part of the band consisting of several OMUs made the final decision where to settle for the night. Group movement in *R. bieti* is accompanied by frequent, almost non-stop noisy vocalizing, especially when followed by observers. These vocalizations may serve the coordination of movements (C.C.G., pers. obs.). According to KIRKPATRICK (1996a), however, no vocalizations to organize the travel of the entire band were apparent. In addition, the white patches

found around the elbows and at the hindquarters may serve as optical signals for facilitating group progression in dense vegetation.

While moving, the *R. roxellana* group divides into two to four columns (REN et al., 2000). While moving, OMUs are located in the central part of the band (*ibid.*; SU et al., 2002). Bachelor males both lead the band and bring up the rear (REN et al., 2000). When moving in the forest, the band usually becomes more scattered than in an open area (*ibid.*). Males exhibit some sort of informing behavior among each other when the group is to move (*ibid.*).

Route decision processes such as proposing a certain walking direction differs between geladas and hamadryas baboons. Besides, gelada herds are more open and fluid than hamadryas bands, with members of OMUs intermingled, and there is no observable cooperative behavior among the units such as ‘notifying’ as among hamadryas baboon males (MORI, 1979f). So gelada herd movements lack the conspicuous decisiveness which can be observed in hamadryas baboons. The difference in herd movements between geladas and hamadryas baboons may be traced to habitat differences. Hamadryas baboons live in areas where important resources can be scarce and widely scattered. Reliable decision making is essential in order to prevent shortcomings (DUNBAR, 1983d). It is interesting that decisions on the direction of travel seem to be made by females in savanna baboon groups, whereas they are made by males in the hamadryas band (STOLBA, 1979). In geladas, initiation of movement is done mainly by lactating females. DUNBAR (1983c) suggests that this occurs because of their largely increased need for food intake. The only means of increasing the amount of food is to increase progression speed. Both in geladas and hamadryas, water sites are one of the most important factors in deciding the daily movement patterns. This might well be the case in *R. bieti* too, at least in the dry season.

Moving in a single line with recognizable distances between family units has been observed in both *R. bieti* and *R. roxellana* as well as in *R. brelichi* (YANG et al., 2002). In both *Rhinopithecus* species discussed here, AMUs usually form the front and/or rear units and in geladas, the flanking units. In *R. brelichi*, AMUs apparently also make up the rear unit and keep a distance from the moving band (*ibid.*). The individuals within the ‘vanguard’ may incur enhanced predation risk compared with subsequent group members (BOINSKI, 2000), but no data are available to test this assumption. The positioning of individuals of differential vulnerability might reflect the predation risk of different group positions. A group of males in the front is less vulnerable than a group with only one male. *R. roxellana* males show an ‘informing’ behavior before progression starts. This remotely resembles the ‘notifying’ of hamadryas baboons.

Vocal signals to initiate and lead group travel are much less commonly used among hamadryas baboons compared with many forest primates (for a review see BYRNE, 2000). Visual contact among group members is usually a sufficiently effective communication mode in the terrestrial baboons (KUMMER, 1995).

#### Population Densities

*T. gelada* density in the Gich area was 63 animals per km<sup>2</sup> (IWAMOTO, 1993a). In Ethiopia, *P. hamadryas* average only 1.8 to 3.4 animals per km<sup>2</sup> (KUMMER,

1968a), but at two sites in Eritrea density was considerably higher, 10.2 and 23.9 individuals per km<sup>2</sup> respectively (ZINNER et al., 2001/2003). In *R. bieti*, population densities range from 1.6 to 11.8 individuals per km<sup>2</sup> and in *R. roxellana*, population densities range from 1.1 to 17 individuals per km<sup>2</sup>, depending on the study site for both species (KIRKPATRICK, 1998).

The density of gelada baboons is high compared with hamadryas baboons and with primates in general (DUNBAR and DUNBAR, 1974; IWAMOTO, 1993a). Such high densities might be attributed to the gaminivorous feeding habits of geladas (IWAMOTO, 1993a), but it can also be a matter of methodological problems when calculating the densities. It is not always clear, on which criteria the selection of the area is based on. It may be just the home range of several groups or it can be the area encompassing the whole population within a certain region. Compared with other colobines, population densities in snub-nosed monkeys are low. KIRKPATRICK et al. (1998) conclude that low biomasses in *R. bieti* probably reflect low plant productivity and thus low food availability.

## Social System

### Social Organization

#### Group Size and Composition

It is most striking that in the four species often very large groups are found, among them the largest groups reported for free-ranging primates (Table 3). Groups comprise stable heterosexual subgroupings of which the basic subunit in all four focal species is the one-male unit (OMU). Several of these OMUs consistently stay together in a band, thereby forming a higher level of social organization. Some authors have suggested additional intermediate grouping levels between the one-male unit and the band (e.g. KAWAI et al., 1983; ABEGGLEN, 1984; REN et al., 2000), and even aggregations above the band level, albeit unstable, have been reported (e.g. KUMMER, 1968a; KAWAI et al., 1983). Another clearly distinguished unit within the social system of at least three of the four species is the all-male unit which is made up of excess males not belonging to OMUs.

Table 3: Demographic data for geladas, hamadryas baboons and snub-nosed monkeys (if not otherwise stated, averages and ranges are given).

Study Site	Troop Size (Herd*)	Band Size	Adult Sex Ratio M / F	OMUs / Band	Reference
<i>T. gelada</i>					
Arsi		54	1 / 1.87		MORI et al, 1999
Bole Valley		60.3 (48-78, n=3)	1 / 4.21	3.3	DUNBAR, 1984a
Sankaber		131.5 (30-262, n=11)	1 / 2.75	10.7	DUNBAR, 1984a; OHSAWA and DUNBAR, 1984
Gich		107.2 (27-170, n=6)	1 / 2.35	9.7	

Study Site	Troop Size (Herd*)	Band Size	Adult Sex Ratio M / F	OMUs / Band	Reference
Gich		16-170		2-18	OHSAWA, 1979
Simiens Mountains	up to 600			2-27	DUNBAR and DUNBAR, 1975; DUNBAR, 1984a, 1993
<b><i>P. hamadryas</i></b>					
Eritrea	up to 800	139.2 (25-327, n=6)	1 / 2.77		ZINNER et al., 2001a,b
Yemen		22-89			AL-SAFADI, 1994
Saudi Arabia		37.8 (9-102)	1 / 2.18 <sup>a</sup> ; 1 / 2.31 <sup>b</sup>	1-12	BOUG et al., 1994; BIQUAND et al., 1992a
		13-70	1 / 2.51		KUMMER et al., 1981
Awash, Ethiopia		51-57			NAGEL, 1973
Filoha, Ethiopia		50-220			SWEDDELL, 2002a
Erer-Gota, Ethiopia	up to 750	30-90	1 / 1.86		KUMMER, 1968a
	up to 236	61-69			SIGG et al., 1982
		62-95			SIGG and STOLBA, 1981
		52-90			ABEGGLEN, 1984
<b><i>R. bieti</i></b>					
Xiangguqin (Tacheng)		366	1 / 3.3	24	DING et al., 2004, in press
Wuyapiya <sup>c</sup>		175	1 / 3.1	15-18	KIRKPATRICK et al., 1998
Nanren <sup>c</sup>		151	1 / 4.9	15	CUI, 2002
		approx. 250-290			MacLENNAN, 1999
Yeri district <sup>c</sup>		269			WU, 1991, 1993
Baimaxueshan			1 / 3.2		BAI et al., 1987
Jinsichang <sup>d</sup>		51	1 / 3.6	5	YANG, 2000
Laojunshan <sup>d</sup>		164			BP REN, pers. com.
Fuheshan		80			LIU et al., 2004
Xiaochangdu		approx. 200			ZF XIANG, pers. com.
Longmashan		>80			S HUO, pers. com.
Bamei (Deqin, Yunnan)		approx. 60	1 / 3.0		ZHONG et al., 1998
<b><i>R. roxellana</i></b>					
Baihe		>200	1 / 2.5		KIRKPATRICK et al., 1999
Wolong (Sichuan)		mean 275 (n=6); up to 600	1 / 2.1		HU et al., 1980
Baishuijiang (Gansu)		mean 80 (n=9)			LI et al., 1995
Dalongtan (Shennongjia)		up to 340		11-21	REN et al., 1998
Qianjiaping (Shennongjia)		104-114 / approx. 129			LI, 2004, subm.
		40-50			LI, 2001; LI et al., 2002b
Jinghouling (Shennongjia)		205			LI, 2004
Xiaolongtan / Yazikou (Shennongjia)		7			LI, 2001; LI et al., 2002b

Study Site	Troop Size (Herd*)	Band Size	Adult Sex Ratio M / F	OMUs / Band	Reference
Zhouzhi: West Ridge Troop <sup>§</sup>		approx. 90 / 63 / 88		8	TAN et al., 2003; ZHANG et al., 2003; WANG et al., 2004a
Qinlingshan		100 (n=39)			LI et al., 2003

<sup>a</sup>wild group, <sup>b</sup>commensal group, <sup>c</sup>this might be the same band of *R. bieti*, <sup>d</sup>this is most likely the same band of *R. bieti*  
\*Note: KAWAI (1979a) uses the term 'herd' for clusters of reproductive units in geladas. Consistent with DUNBAR and DUNBAR (1975), we instead use the term 'band' for this level of society. Similarly, the term 'band' is also used to refer to the cluster of OMUs in hamadryas (KUMMER, 1968a).  
<sup>§</sup>Note: TAN et al. (2003) use the term 'troop' instead of 'band' for *R. roxellana*. In this report, the terms 'troop' and 'herd' are exclusively used for temporary higher-level aggregations of baboons and not for snub-nosed monkeys. REN et al (2000) use the term 'band' for another level of social organization in *R. roxellana* below our 'band'. They refer to our 'band' as a 'social group'. Moreover, we refer to the reproductive or breeding units as OMUs despite the occasional occurrence of additional males.

Socionomic sex ratios in all focal species are female-biased. Sex ratios in Eritrean bands of *P. hamadryas* are significantly more female-biased than in Ethiopian ones, possibly due to fluctuating rainfall patterns with corresponding fluctuating reproduction rates and differential maturation of the sexes (ZINNER et al., 2001b). Also in Arabia, the percentage of adult males was found to be lower than in Ethiopia (KUMMER et al., 1985). Also, the skewed sex ratio in *T. gelada* has been proposed to be due to earlier maturation of females (OHSAWA and DUNBAR, 1984).

#### Spatiotemporal Cohesion

*T. gelada* lives in a multi-level social system consisting of several increasingly inclusive groupings (DUNBAR and DUNBAR, 1975; KAWAI et al., 1983; DUNBAR, 1993). Reproductive units consist of a number of long-term alliances between two to three reproductive females and their dependent offspring. One or several of these female-female alliances and one adult male form an OMU. These OMUs constitute the lowest grouping level in the gelada society. Several OMUs that share a common ranging area are termed a band (Fig. 3a). The band is a relatively closed social unit, composed of 2-27 OMUs and one to three all-male units (AMUs). The membership of gelada OMUs in a certain band is not constant since OMUs may visit other bands or even pass their day alone. A third level of organization is the herd which, like the hamadryas baboon troop, is not reported to be a social group in the strict sense, but rather a temporary congregation of OMUs at sites where grazing conditions are favorable. Herds are largest during dry season when the availability of food is spatially restricted. Some units of a band associate together more closely than they do with other units of the band, suggesting that it may be possible to identify a social grouping (named a team) intermediate between OMUs and band (KAWAI et al., 1983). KAWAI et al. (1983) identified at least one further level of grouping (the community) which consists of those bands whose ranging areas overlap extensively and who therefore are found in mixed-band herds.

According to DUNBAR (1993) the existence of bands among geladas can be explained as a consequence of the fact that the OMUs prefer to forage in large aggregations, and therefore tend to remain near to those units with whom they can most eas-

ily form larger aggregations. Since OMUs undergo fission from time to time and kinship is an important factor enabling animals to live together, it follows that closely related units will tend to remain in the same area. This naturally creates a band-like structure with kinship (probably mediated by familiarity) being the main factor determining whether units remain in the same band.

The society of *P. hamadryas* is organized on three, possibly four nested levels (KUMMER 1968a, 1984, STOLBA, 1979; SIGG et al., 1982; ABEGGLEN, 1984). The basic social entity of the hamadryas baboon society is the OMU (Fig. 3b). These units consist of an adult leader male together with one to 10 females and their dependent offspring. Two male units occur. (1) A peripheral, normally younger 'follower' male may or may not be associated with such a unit, or (2) a formerly leader male which was replaced by another male may stay in close spatial and social proximity to his former females and offspring. According to ABEGGLEN (1984), two or three OMUs cluster into a clan. A clan may consist of a set of age-graded males, their females and dependent offspring. The oldest male is often a single who has lost his females. Next in age are one or two prime males. They possess all the clan's adult females, which they monopolize against all other males. It is believed that the males of a clan are genetically related. Clans group together to form a band, which is characterized by the long-term stable and exclusive association of individual members. A band numbers about 60 to 100 baboons and is believed to be the equivalent to the multi-male multi-female group of savanna baboons. Bands travel together and, sometimes, fight each other as units. They are the autonomous 'ecological' unit whereas the OMU is the 'reproductive' unit (KUMMER, 1968a). However, in certain populations of hamadryas baboons, e.g. in Saudi Arabia, small groups, usually OMUs have been reported to forage alone and to do not aggregate into large bands (KUMMER et al., 1985; but see also BIQUAND et al., 1992a). Bands may join other bands at sleeping cliffs. These sleeping site aggregations are called troops and constitute the highest level of the hamadryas baboon social organization, often comprising several hundred individuals (KUMMER, 1968a; ZINNER et al., 2001b). Troops are variable aggregations but they do not function as cohesive social groups.

OMUs as subunits within large and rather cohesive bands have been observed to be prevalent in *R. bieti* (KIRKPATRICK et al., 1998; DING et al., 2004). There is evidence for the existence of multi-male units (MMUs) within bands as well (DING et al., 2004, in press) (Fig. 3c). It is not known whether specific units associate preferentially, as in hamadryas baboons. The substructuring of bands can be most clearly seen when looking at a marching band of *R. bieti*. In this case, there are visible spatial gaps between OMUs (*ibid.*).

OMUs within large bands are also the norm in *R. roxellana* (REN et al., 1998a). The OMUs do not consistently assemble together (TAN et al., 2003). A possible MMU has been described by KIRKPATRICK et al. (1999), and MMUs have been found at Shennongjia (REN et al., 1998a, 2000). REN et al. (2000) propose the occurrence of even more social levels than just OMU and band (Fig. 3c).

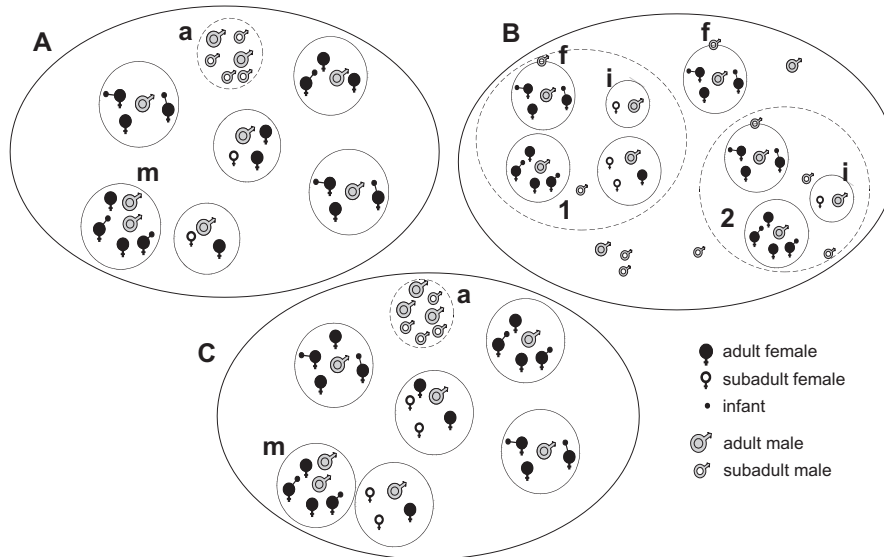


Fig. 3: Illustration of the social organization of (A) *Theropithecus gelada*, (B) *Papio hamadryas* and (C) *Rhinopithecus* spp. The hypothetical gelada band consists of five OMUs, one MMU (m) and one AMU (a), the hamadryas band consists of two "clans" (1 and 2) and one single OMU, several OMUs have a "follower" male (f) and two OMUs are initial units (i), consisting of an adult male and a subadult female. Non-OMU males do not form stable AMUs. The snub-nosed monkey band consists also of five OMUs, one MMU (m) and one AMU (a).

#### One-Male Units (OMUs)

Data on size and composition of OMUs of the four species are given in Table 4. Hamadryas baboons tend to have smaller OMUs than the three other species. Also the adult sex-ratio is on average less female biased in hamadryas baboons than in the other species.

Table 4: OMU size and composition (averages with ranges in parentheses, AF = adult females).

Study Site	OMU Size*	AF / OMU	Reference
<b><i>T. gelada</i></b>			
Gich	approx. 10 (2-25)	3.5 (1-8)	OHSAWA, 1979
	9.9 (2-17)	3.9	DUNBAR, 1984a
Bole Valley	17.1 (8-28)	5.9	
Sankaber	12.0 (3-26)	4.1	
Arsi	8.3 (2-15)	(1-6)	MORI et al., 1999
<b><i>P. hamadryas</i></b>			
Erer-Gota	7.3 (2-23)	(1-9)	SIGG et al., 1982
		1.8; 2.3	KUMMER, 1968a
Eritrea		3.61	ZINNER et al., 2001b
Saudi Arabia	6.46 (2-17) <sup>a</sup> 7.82 (2-19) <sup>b</sup>	2 <sup>a</sup> ; 3-4 <sup>b</sup>	BIQUAND et al., 1992a

Study Site	OMU Size*	AF / OMU	Reference
<b><i>R. bieti</i></b>			
Wuyapiya	up to 14-16	up to 5-6	KIRKPATRICK, 1996a; KIRKPATRICK et al., 1998
Nanren		5.3 (3-8)	CUI, 2002
Xiangguqin (Tacheng)	approx. 14 (2-39)	approx. 5	DING et al., in press
Jinsichang	10.2 (6-14)		YANG, 2000
<b><i>R. roxellana</i></b>			
Zhouzhi	7.9 (7-10)		TAN et al., 2003; ZHANG et al., 2003
Dalongtan (Shennongjia)	12 (2-45)		REN et al., 1998a
	18 (7-52)	7 (1-21)	REN et al., 2000; SU et al., 2002
(partially reprinted from STAMMBACH, 1987); <sup>a</sup> wild group, <sup>b</sup> commensal group			
*We do not distinguish here between OMUs and MMUs (multi-male units)			

CROOK (1966) noted that OMUs are the basic social unit in *T. gelada* societies and that they have a considerable degree of temporal stability. Although gelada units do not often appear to be spatially discrete (OMUs do not remain centered around their males), careful observations reveal that the members of different units rarely remain for long within the perimeter of another unit (DUNBAR and DUNBAR, 1975; MORI, 1979a). However, one case of unification of units was observed at Arsi (MORI et al., 2003). OMUs consist of a single breeding male and up to twelve adult females, plus their dependent young and some juveniles (DUNBAR and DUNBAR, 1975). Some units contain additional adult males (MORI, 1979f). Mean OMU size was found to be independent of any environmental factors tested so far (OHSAWA and DUNBAR, 1984). Almost all social interactions of adults are directed to individuals in their own OMUs (DUNBAR, 1979a). OMU size was smaller at Arsi (south of the Rift Valley) than in the northern populations, and band size was smaller than in the population of the Simien Mountains, but similar to the Bole population (MORI et al., 1999). Also OMUs at Arsi acted more independently from each other, thus reducing chances of leader males of several OMUs to cooperate in displaying and chasing out challenging males, which might explain the higher number of MMUs at Arsi (MORI et al., 1999). It was hypothesized that the smaller OMU size is a result of sub-division of the units by males who were originally accepted in the unit for defense against leopards (*ibid.*). OMU size in the north was reported to be least affected by environmental pressure, because it depends more on social factors (OHSAWA and DUNBAR, 1984).

According to KUMMER (1968a), small family groups such as OMUs in *P. hamadryas* have an increased capacity of exploiting the sparse and scattered food resources in their poor habitat. Additional males are not uncommon in hamadryas OMUs, either as 'follower' ("male in waiting position for acquisition of females", KUMMER, 1984) or as 'deposed old leader' (e.g. KUMMER, 1968a; BIQUAND et al., 1992a). OMUs in Arabia contain more females and are thus larger than in Ethiopia, probably because of increased food availability due to a commensal life (BIQUAND et al., 1992a). Also OMUs in Eritrea are larger than Ethiopian ones and comprise more females although they are not commensal and overall habitat quality is lower than in the Erer-Gota region of Ethiopia (ZINNER et al., 2001b).



OMUs as subunits are prevalent within a band of *R. bieti* (KIRKPATRICK et al., 1998, DING et al., 2004; DING et al., in press). These OMUs represent family units containing one adult male, several females with offspring and juveniles. KIRKPATRICK et al. (1998) also observed on several occasions that large individuals, potentially subadult males, were in OMUs. Additionally, some units appear to have more than one male attached to them (DING et al., 2004). OMUs of *R. bieti* were found to be distinct spatial entities when looking at the marching formation of a band (DING et al., in press). One might now argue that grouping patterns during traveling and during resting might not be the same, thus obtaining a misleading picture about socio-spatial relationships (*sensu* HARCOURT, 1978). However, scan observations of *R. bieti* revealed a high degree of OMU cohesion during inactivity periods, i.e., they tended to stay together in the same tree (GRÜTER, unpubl. data). In two other studies, only once was there more than one adult male seen in the same tree with females (KIRKPATRICK, 1996a; MacLENNAN, 1999). This is further support for the splitting of the group into discrete OMUs.

Subunits within a band of *R. roxellana* appeared to be OMUs of an adult male and several adult females and immatures (KIRKPATRICK et al., 1999). Members of each OMU huddle and sleep together separate from other units in the larger group to which they belong (CHEN et al., 1989; QI et al., 2004). Spatial distances among individuals from different social units are considerably larger than those among individuals from the same social unit (QI et al., 2004). More than 93 % of the OMUs have only one male, leaving only a few units that contain a second male (REN et al., 2000).

The additional males in these multi-male units (MMUs) might be analogous to follower males or deposed unit leaders in hamadryas baboons. It seems rather unlikely, though, that these putative second males form an 'age-graded male group' (*sensu* EISENBERG et al., 1972) in which the sons of a leader remain in the natal group after reaching full maturity. This reasoning is based on the assumption that subadult *Rhinopithecus* males are expelled from their natal unit and become members of an AMU. However, much further work is needed to clarify these topics.

#### All-Male Units (AMUs)

Since in all four species certain males seem to be able to, at least socially, monopolize more than one female, a number of males have to stay without a female. One possibility for such 'surplus' males is to form all-male units (AMU, Table 5). AMUs can be observed in three of the four species. In *P. hamadryas*, non-leader males do not form stable discrete AMUs. They live within the band but without being attached to any OMU. A second strategy for surplus males is to attach themselves as 'followers' to OMUs.

In *T. gelada*, those mature males that do not have their own OMUs of breeding females form stable AMUs that sometimes travel separately from bands (DUNBAR and DUNBAR, 1975; MORI et al., 1999). Bands typically contain one to three all-male bachelor groups (DUNBAR, 1993). AMUs are composed mostly of adolescent and younger adult males (DUNBAR and DUNBAR, 1975; MORI, 1979b). AMUs also seem to contain ousted former OMU leaders (DUNBAR, 1993). One case is reported where adult females joined an AMU temporarily (MORI et al., 2003). AMUs are closed social units: only few friendly interactions occur with non-members and aggressions within AMUs are rare (DUNBAR and DUNBAR, 1975). Relations between

males of reproductive units and those of AMUs are characteristically antagonistic (*ibid.*). According to MORI (1979c) and OHSAWA (1979), so called ‘freelancers’ which belong neither to OMUs nor to AMUs are found in geladas. ‘Junior freelancers’ appear to represent prospective future members of the AMU and sometimes move with an AMU. They walk around within the herd and are not antagonistic towards the units, unlike AMU members. ‘Senior freelancers’ are full-grown males whose age exceeds the average age of the AMU males (MORI, 1979c; OHSAWA, 1979). Senior freelancers have, in contrast to AMU males, close relationships with specific units, especially with their infants and juveniles (MORI, 1979c).

Table 5: AMU size and composition (averages and/or ranges).

Study Site	AMU Size	Reference
<b><i>T. gelada</i></b>		
Sankaber and Bole Valley	7.8 (3-13) males and juveniles	DUNBAR and DUNBAR, 1975
Gich	13-15 males and juveniles	OHSAWA, 1979
<b><i>P. hamadryas</i></b>		
Ethiopia, Eritrea, Saudi Arabia	bachelor males were present in bands and formed sleeping groups	KUMMER, 1968a; KUMMER et al., 1981; ZINNER et al., 2001b
<b><i>R. bieti</i></b>		
Wuyapiya	core of 2 males and several juveniles	KIRKPATRICK et al., 1998
Nanren	5	MacLENNAN, 1999
Xiangguqin (Tacheng)	14.5 (7-22) males and juveniles	DING et al., in press
<b><i>R. roxellana</i></b>		
Baihe	5-6	KIRKPATRICK et al., 1999
Dalongtan (Shennongjia)	3-5 (1-35)	REN et al., 2000
	4-7	REN et al., 1998a

In *P. hamadryas*, there exist no AMUs of any stability or spatial separation, but temporary bachelor sub-group formation does occur within a troop or band. Some males of all age classes lived outside OMUs, although still within the troop (KUMMER, 1968a). In Eritrea, some adult and subadult males were not attached to any parties of adult males and females. Together with juveniles, these bachelors formed parties without any adult or subadult females within a band (ZINNER et al., 2001b). BIQUAND et al. (1992a) also found parties composed of males and juveniles.

WU (1993) reported that *R. bieti* bands have "several large adult males" acting as "group leaders". This might well be an AMU. At Tacheng, AMUs with accompanying juveniles have been seen several times, moving at the periphery of the band, forming either the front or rear unit or both (DING et al., 2004, in press). Other authors also mentioned that AMUs are typically located at the front or rear of the whole monkey group (MacLENNAN, 1999). Further evidence for the peripheral positioning of AMUs in *R. bieti* comes from an observation at the water hole where the AMU was the last subunit to drink water after all OMUs had left (C.C.G., pers. obs.). AMUs were often the first units to be seen during field work, often staying at exposed positions such as in the tallest trees (*ibid.*). Almost all subadult males were associated with AMUs (KIRKPATRICK et al., 1998; DING et al., 2004, in press). The AMU observed by KIRKPATRICK et al. (1998) was variable in composition, with a

core of two males and several juveniles. AMU males have been seen playing together sometimes, indicating some degree of affiliative relationship among these males (C.C.G., pers. obs.). An encounter between an OMU and an AMU, on the other side, was characterized by threat gestures performed by the OMU leader directed towards the AMU (*ibid.*).

At Shennongjia, almost all subadult males and 60 % of adult males of *R. roxelana* were observed to be in 'guards' (i.e. AMUs) and hence do not belong to family units (REN et al., 2000). The largest band at Shennongjia comprised several of these AMUs (REN et al., 1998a). During a census at Baihe, AMUs were seen either on the periphery of the main band or 1.5 - 2 km away from it (KIRKPATRICK et al., 1999). REN et al. (2000) also note that some males depart from the group for long distances (more than 1500 m). AMUs are usually found in front and at rear of a walking band. AMUs in front seem to function as vanguards, and they also show a display before movement starts and they engage in cooperative aggression against enemies (*ibid.*). Both SHI et al. (1982) and CHEN et al. (1989) also hypothesized that AMU males are sentries along the band perimeter, that there is joint male leadership of travel routes and a linear dominance hierarchy among males. AMUs sometimes contain juveniles and adolescents, too (*ibid.*; SU et al., 2002).

The occurrence of stable AMUs is linked to an OMU-based social organization, but not necessarily to a nested system, e.g. hanuman langurs (SUGIYAMA, 1967). The formation of AMUs may be a response to mate competition; males may be able to form coalitions and alliances that improve their chances of success during a group takeover, as reported for hanuman langurs (HRDY, 1977). It has also been suggested that AMUs are more common amongst terrestrial species, and that this grouping pattern is an adaptation to increased predation pressures (STRUHSAKER, 1969; ISBELL, 1994). Moreover, a situation where feeding costs associated with group living are low, such as in snub-nosed monkeys, could favor extra-group males living in AMUs rather than alone (STOINSKI et al., 2004).

Extra OMU males may play a certain role in vigilance and group defense against predators. Observations on hamadryas baboons emphasize the role of males, particularly subadult and adult bachelor males, in defending the group against predators. They take more risks when entering potentially dangerous areas (ZINNER et al., 1999/2000), which may be one reason why bachelor males are tolerated in their native bands. It might be the case that *Rhinopithecus* AMU males act as band protectors or guards and benefit in turn from being accepted in the band and thus from being closer to the reproductive units. This closeness may enhance the AMU males' familiarity with the males and females of the reproductive units and may facilitate a possible later takeover attempt. This may be a similar situation as reported for zebras, where AMUs stay close to breeding units and can thereby learn how to behave toward females to later initiate and maintain bonds with them. These are social skills that can only be learned when consistently being within reach of the reproductive units, and these skills are needed for successful transition from non-breeder to breeder (RUBENSTEIN and HACK, 2004).

Whether or not AMUs in *Rhinopithecus* stay at the periphery of the band year-round or show seasonal changes in their spatial position in relation to the band is not known. Peripheral males of some macaque species have been reported to associate more with groups during the mating season (e.g. Japanese macaques: SPRA-

GUE, 1992), and influxes of normally extra group males during the mating period have been observed in cercopithecine species that form OMUs (e.g. *Cercopithecus* spp.: CORDS, 1988) and also mandrills (ABERNETHY et al., 2002).

Another hypothesis that has been proposed to explain the occurrence of all-male groups in mammals is that male groups may form to gain energetic benefits through enhanced thermoregulation (KOPROWSKI, 1991). This hypothesis would make sense in a severe habitat such as the one inhabited by snub-nosed monkeys. During warmer periods, however, when benefits of thermoregulation are absent, males are expected to act less cohesively. Though, no information is available whether or not the formation of cohesive all-male groups is a seasonal or year-round phenomenon in *Rhinopithecus*.

On occasion, juvenile *R. roxellana* males appeared to follow adult AMU males (REN et al., 1998), and also in *R. bieti*, many juveniles of unknown sex have been noticed in AMUs. The composition of *Rhinopithecus* AMUs bears some similarities to AMUs in hanuman langurs, which include three age classes: adults, subadults and juvenile males. Male juveniles provide the bulk of these AMUs, usually emigrating from their natal troop and joining an AMU with or without an ousted resident male (RAJPUROHIT, 1991). Also the AMUs of proboscis monkeys (*Nasalis larvatus*) consist of juvenile, adolescent and adult males (YEAGER, 1990).

The formation of AMUs is not restricted to the natural habitat. A group of *R. roxellana* in captivity separated itself into one OMU and one AMU with adult, subadult and juvenile males (REN et al., 2002). Similar to observations in the field, both male and female juveniles from the OMU went to the AMU to play, but females were sometimes chased away (*ibid.*).

#### Peer Groups

In *T. gelada*, yearlings and infants form temporary play groups between neighboring units (DUNBAR and DUNBAR, 1975). Play groups of intermingled males and females occur up to the junior stage, and mostly consist of members of the same or intimate units ('junior groups', MORI, 1979c). Male juveniles and puberties ('senior groups', *ibid.*), sometimes from different herds, temporarily assemble as an unstable voluntary group.

Play groups are also found in *P. hamadryas*, and infants and juveniles often spend their social time with baboons outside the maternal unit (KUMMER, 1968a). Play interactions were seen even among juvenile males of different bands (ABEGGLEN, 1984).

In *R. bieti*, several infants have been observed to be guarded by an adult male in a tree (crèche), sometimes while mothers were foraging elsewhere (W. DING, pers. com.). Not all of these infants probably belong to the same OMU. KIRKPATRICK et al. (1998) report of a playgroup of six animals (infants, yearlings, juveniles) and GRÜTER (pers. obs.) observed at maximum seven members in a juvenile play group, on several occasions accompanied by adult or subadult males.

REN et al. (2000) reported for *R. roxellana* the existence of 'crèches', i.e. gatherings of one or two males together with juveniles. They also observed gatherings of young monkeys without adults. The maximum number of individuals in these gatherings was 60. This high number indicates that the individuals involved in these gatherings must belong to different OMUs. Young golden monkeys assembled to

play and to explore their surroundings (*ibid.*). REN et al. (2000) also reported a case where five juvenile females and a young adult male formed a small unit that walked and rested together.

It is likely that the forming of 'crèches' are an adaptation to the strong seasonal breeding in snub-nosed monkeys, because here mothers experience simultaneous peak energy demands. Hence, crèches in which one individual (either male or female) cares for many infants at one time would be a possible solution to lower the energetic stress (CHISM, 2000).

#### Fission-Fusion

**T. gelada** bands are very fluid in their structure, with individual OMUs constantly leaving and joining (DUNBAR and DUNBAR, 1975; MORI, 1979f; KAWAI et al., 1983). There can also be periodic fission of bands into two daughter units (DUNBAR, 1993), and OMUs are occasionally solitary (DUNBAR and DUNBAR, 1975). Emigration by OMUs occurs as a consequence of the fission of a band and usually involves two to six OMUs moving away to establish a new ranging area elsewhere (DUNBAR, 1993). Due to low mortality rates, gelada bands undergo fission at intervals of eight to nine years, with a section of the band migrating out into a new, less densely used ranging area in a lower region on the escarpment face (OHSAWA and DUNBAR, 1984).

In **P. hamadryas**, bands consist of stable sub-divisions, called clans, which regularly split off from the band while foraging (ABEGGLEN, 1984; KUMMER, 1984). After leaving the sleeping rock, the band normally splits in clans or even single OMUs. These sub-units may search for feeding places on their own and so may move away from other band members, up to distances that exclude visual or auditory communication. Later, the whole band usually meets again at the water hole or sleeping cliff. On other occasions, parts of the band can also use different sleeping sites and can unite with the rest of the band only after several days. KUMMER (1990) comments that clans can split into OMUs for an hour or so but do not normally lose contact.

In **R. bieti**, fission is rare and lasts for an average of less than one day at Wuyapiya (KIRKPATRICK, 1996a). Splits appeared to be related to human disturbance and the logistics of travel. Water holes are small and patchily distributed within the forest at Tacheng and can probably not accommodate the whole band. Hence, short-term and reversible fission at the water hole (especially in the dry season) takes place in order to maximize drinking efficiency (C.C.G., pers. obs.). In addition, there may be less band cohesion in the breeding season; thus male reproductive strategies might be a driving force behind fission-fusion (KIRKPATRICK, 1996a). Long-term fission was only very rarely documented at Tacheng, but may occur as a response to human disturbance and/or to seasonal changes in food distribution (W. DING, pers. com.).

Reports about the extent of fission-fusion in **R. roxellana** are ambiguous. Seasonal fission-fusion, with larger bands in summer and smaller bands in winter, may occur (SCHALLER et al., 1985). Bands at Shennongjia were largest between October and December, the mating season (R.M. REN, cited in KIRKPATRICK, 1998). Nevertheless, REN et al. (2000) conclude that *R. roxellana* do not form fission-fusion

groups. Fission-fusion of another band at Baihe may occur over daily, not seasonal time (SHI et al., 1982). In the Qinling Mountains, the size of the band fluctuated throughout the study period (TAN et al., 2003). The independent units were semi-cohesive, suggesting a fission-fusion social system within the band. A large band at Baihe was observed to split into two factions of approximately equal size. The two factions were separated by about 1 km for at least a few days (KIRKPATRICK et al., 1999). This fission of the band in November may relate to a change in diet.

It was hypothesized that the possibility of splitting up into smaller groups in hamadryas baboons allows them to exploit the scarce and patchy food sources of their habitat in an optimal way. The smaller the food patch, the smaller will be the size of the social unit that can use it (KUMMER, 1971; STAMMBACH, 1987). The degree of fission seems further to depend on local predation pressure. Where hamadryas baboons are not subject to predation, the band structure tends to disintegrate, and OMUs more often forage alone, as in Saudi Arabia (KUMMER et al., 1985). Geladas can also adjust their grouping pattern to various degrees of predation pressure and resource competition. Geladas routinely form large groups on open grasslands where predation risk is high. However, this gathering has the side effect of increased food competition. When foraging in less risky habitats, such as on grassy slopes, bands break up into segregated OMUs, with feeding competition concomitantly being reduced (DUNBAR, 1986). Hamadryas bands are more cohesive than those of geladas. The constituent units normally maintain a coordinated route of daily travel even though they may become widely scattered in the process (SIGG and STOLBA, 1981). In *R. bieti*, which mainly feed on non-seasonal lichens, fission is rare. In the other snub-nosed monkey species (*R. roxellana*, *R. brelichi*, *R. avunculus*) which also depend on seasonal foods, fission is common and bands split for extended periods (KIRKPATRICK, 1998). Fission-fusion among stable OMUs has also been reported for another large-bodied odd-nosed colobine, the proboscis monkey (YEAGER, 1990).

#### Philopatry and Dispersal

In *T. geladas*, females generally remain in their natal units throughout their lives (DUNBAR and DUNBAR, 1975). Female transfers are extremely rare (DUNBAR, 1979a; MORI et al., 2003). Males, however, leave their natal units as sub-adults to join an AMU (DUNBAR and DUNBAR, 1975; MORI, 1979c). The evidence suggests that they tend to join a group in which they already have relatives (DUNBAR, 1984a). Some two to four years later, they return to the OMUs to acquire their own breeding females (DUNBAR, 1993). Adult males sometimes move between bands during the process of acquiring females (*ibid.*).

In *P. hamadryas*, most males stay in their natal band and even in their natal clan for life (SIGG et al., 1982). Male migration is rare (ABEGGLEN, 1984), but there have been observations of hamadryas males migrating into olive baboon groups at Awash (PHILLIPS-CONROY et al., 1992; PHILLIPS-CONROY and JOLLY, 2004), suggesting that male hamadryas baboons also migrate between bands. Maturing females typically transfer from their natal unit, and adult females may also transfer (STAMMBACH, 1987). Transfer of females between OMUs happens primarily within the band and more often within a clan than across clans (SIGG et

al., 1982), but females may also change from band to band when forced by their new leader. Females change OMUs two or three times in their life, but tend to transfer into units that already contain females with whom they formerly lived in an OMU (*ibid.*). ABEGGLEN (1984) reports that transferred females attempted to approach animals of their former OMU and tended to establish grooming relationships with unfamiliar females of the OMU rather slowly.

In an Arabian population, the intra- and inter-OMU genetic relatedness between males was found to be higher than between females (BIQUAND et al., 2000; HAMMOND et al., 2001). The results of a mitochondrial DNA study support the hypothesis of female transfer between neighboring local bands over a broad geographic range (HAPKE et al., 2001). Recent microsatellite data from Ethiopia, however, show a higher level of relatedness among females than typically exists for the dispersing sex in other taxa (WOOLLEY-BARKER, 1999; see also WOOLLEY-BARKER, 1998). The hamadryas baboon represents a rare exception from the pattern of female philopatry and thus male-biased dispersal predominant in Old World monkeys. It appears that, during hamadryas evolution, the ancestral 'savanna baboon' pattern of female philopatry and male dispersal evolved into a system in which neither males nor females regularly transfer between bands, but rather females are transferred on occasion by males (kidnapped) and males migrate on occasion to find females (SWEDELL and WOOLLEY-BARKER, 2001).

Data about dispersal patterns are so far not available for *R. bieti*, so this remains an unresolved issue.

REN et al. (2000) believe that *R. roxellana* males older than three years are expelled from the natal OMU. Female infants are not repelled by the father (*ibid.*). In the Qinling Mountains, an increase in OMU members was observed to take place in spring after immigration of immature individuals such as juveniles of unspecified sex and subadult females (ZHANG et al., 2003).

A tentative summary of colobine social systems by NEWTON and DUNBAR (1994) revealed that the following traits are typical for matrilineal societies of colobines: no sexual swellings, no dark natal coats, infant handling, female solicitation of mating and female-female grooming is common. All these features are existent in *R. bieti* which points towards a matrilineal social structure and thus female philopatry. The social system of *R. bieti* may be gelada-like, rather than hamadryas-like because females devoted more of their grooming to each other than to the male (KIRKPATRICK et al., 1998; see also BARTON, 2000). Juvenile males in several colobine taxa disperse and typically join all-male or non-reproductive groups, in which juvenile females are also occasionally observed. The occurrence of such AMUs in *R. bieti*, which contain almost all subadult males of the band, makes male natal dispersal very likely (DING et al., 2004, in press). This is supported by observations in captivity where males older than three years need to be separated from the adult male due to high rates of aggression received from the adult male (GRÜTER, 2003). Female transfer in colobines is rare. The only colobine species in which females are known to emigrate more frequently than males are red colobus (*Piliocolobus* spp.) and olive colobus (*Procolobus verus*) (STRUHSAKER and LELAND, 1987). Based on the above descriptions, female philopatry and male dispersal seem to be more likely in *Rhinopithecus*, but no final conclusion can be drawn at this time.

When population densities are low, however, as in the case of *R. bieti*, opportunities for male dispersal across bands will be restricted, and as result, a higher proportion of males may remain in their natal bands as peripherals. It is important to note that habitat modification and fragmentation led to unbalanced ecological communities of snub-nosed monkeys, e.g., if small population densities combined with lack of habitat corridors are recent human-made phenomena, then this has profound influences on dispersal patterns such as lack of dispersal opportunities. A study of two bands of *R. roxellana* in the Qinling Mountains revealed that no animals had migrated between the bands. This was most likely attributed to the fact that the bands are isolated by human-made barriers (LI et al., 2003).

### Social Structure

#### Interband Relationships

A *T. gelada* band may accept other bands or unfamiliar OMUs and merge into large mixed bands (OHSAWA, 1979). Geladas probably can form congregations without recognition among individuals (*ibid.*). Affiliative interactions, such as grooming between adults, are observed only between members of the same unit, and never between members of different units (MORI, 1979b). Since most social interactions are restricted to members of an OMU, dominance relationships across OMUs are difficult to assess.

ABEGGLEN (1984) observed only brief interactions among members of different *P. hamadryas* bands. Attempts of infants to interact across band units were suppressed, in contrast to the few encounters among juveniles. Adults seemed to avoid interband encounters completely. Very rarely intense physical aggression may occur, with the OMU leaders as the main fighters. Females remain in the 'attack shadow' of their males. Males of the same band defend their females cooperatively against other bands (KUMMER, 1984). KUMMER (1968a) induced such 'battles' experimentally when he offered corn in a pile near the sleeping rock.

In general, band contacts in *R. bieti* are rare due to low population densities (KIRKPATRICK et al., 1998). Two bands at Tacheng have been observed to meet (W. DING, pers. com.).

In the case of *R. roxellana*, encounters between bands have not been detected in the Qinling Mountains (LI et al., 1999; GUO et al., 2004; but see CHEN et al., 1989).

Interband relationships in geladas differ from those in hamadryas baboons. Band membership in geladas is not as consistent as in hamadryas baboons. Social interactions in hamadryas baboons are almost completely restricted to members of the same band. Low population densities as an evolutionary or recent phenomenon make interband encounters in snub-nosed monkeys a somewhat rare event.

#### Intraband Relationships

In *T. gelada*, physical contacts between males of different OMUs are extremely rare (DUNBAR and DUNBAR, 1975), and no overt dominance rank order exists among male unit leaders (MORI, 1979a). The male and, to a lesser extent, the dominant female played a critical role in maintaining the unit's spatial integrity both by threatening members of other units who encroached onto their unit's space and by



going to the aid of any members of their unit who are threatened by members of other units (DUNBAR, 1983c). Affinitive interactions do not usually occur among members of different units. The only exceptions are adult females and juveniles of some units who occasionally enter into affinitive interactions (MORI, 1979a; DUNBAR and DUNBAR, 1975). Furthermore, there are hardly any vocal exchanges between OMUs (DUNBAR and DUNBAR, 1975).

There are few interactions between adult unit members and non-members in *P. hamadryas*, but sporadic exchanges of threats between adult animals of different units occur (KUMMER, 1968a). Agonistic interactions between OMUs over food sources are rare (KUMMER, 1990). Grooming between members of different OMUs may occur but is limited to members of the same clan. In particular, the single adult males of the same clan will groom each other quite frequently (ABEGGLEN, 1984). Severe battles among adult males of the band are rare (STAMMBACH, 1987), but unit males fight any other male attempting to approach and interact with their females (KUMMER, 1990; see also SWEDELL and TESFAYE, 2003). Dominance relationships across OMUs are present in males of a hamadryas band (STOLBA, 1979). No aggression between females of different units was observed in the wild (KUMMER, 1968a). Interactions between adult females of different OMUs are prevented by male herding behavior (KUMMER, 1990).

In *R. bieti*, threatening gestures, aggressive vocal exchange and fighting between OMU leaders at the waterhole are not rare when they are forced to come too close together (C.C.G., pers. obs.). Inter-unit aggression was seen most often while OMUs were traveling along the same travel paths, and aggressive glares and chases, primarily between males, occurred when members of different OMUs came within 2 to 5 m of each other (KIRKPATRICK, 1996). OMUs allegedly also try to defend valuable feeding or sleeping trees from access by other OMUs (W. DING, pers. com.).

Fights between OMUs occurred frequently in *R. roxellana*, averaging 11 times a day (TAN et al., 2003). There was no observable cooperative behavior among the units constituting the band (*ibid.*). However, a case where several units cooperatively attacked a male was witnessed in the Qinling Mountains (C.C.G., pers. obs.). REN et al. (2000) report that strange males staying near an OMU were repelled by the adult male of the OMU. A linear dominance ranking order was found among unit males in a provisioned group (TAN et al., 2003). Higher-ranking social units always stayed in the center of the group, whereas lower-ranking units were found mostly at the edge of the group (QI et al., 2004; see also LI et al., 2004b).

In comparison to geladas, fights between OMU leaders seem to be more common in *R. bieti*. In geladas, interactions between males of different OMUs are in most cases settled by the two units moving apart after an exchange of sometimes intense threats (DUNBAR, 1983c). In geladas, OMUs are spread over a small area and thus become involved in many more agonistic interactions with neighboring units than when they are on their own or in small herds of only three or four units.

#### Interindividual Relationships

In a *T. gelada* OMU, agonistic interactions are rare (DUNBAR and DUNBAR, 1975). It is the females that form close affiliations and grooming relationships

(DUNBAR, 1979a). Linear dominance-rank orders are established among females within each OMU (MORI, 1979b; DUNBAR, 1983a). The results of a captive study by SWEDELL (1997) support the hypothesis that gelada baboons reconcile after aggression. The reconciliation level was found to be relatively high. REICHLER et al. (1998) argue that, although the dominance style of geladas should be classified as rather strict, they actually tend more towards the egalitarian end of the dominance style continuum.

In *P. hamadryas* OMUs, agonistic interactions are a rare event and agonistic interactions among females are usually prevented by the OMU male (STAMMBACH, 1987). It is the male leader of the OMU that is the focus of grooming by females (KUMMER, 1968a). There is no evidence of dominance relationships among free-living hamadryas females (SWEDELL, 2002b). Postconflict affiliation has also been demonstrated in hamadryas (e.g. ZARAGOZA and COLMENARES, 1997), and relationship strength seems to have a profound influence on reconciliation in this species (DeBOLT and JUDGE, 2003).

Data about interindividual relationships are largely lacking for *R. bieti*, but it is known from a field study that females spent more time grooming than males did (KIRKPATRICK et al., 1998). Postconflict affiliation occurs in captive *R. bieti* (GRÜTER, 2004). The conciliatory tendency is high, and explicit postconflict behavioral patterns have been noted. Overall, the patterns of aggression and reconciliation observed in captive *R. bieti* bear many of the traits that characterize tolerant primate species (*ibid.*).

Not much is known about interindividual relationships in *R. roxellana*. In the field, no aggressive or submissive behaviors between adult male and females in OMUs have been observed (REN et al., 2000). Most of the grooming that took place in a captive group was between females (*ibid.*). The study of REN et al. (1991) reveals that captive *R. roxellana* have a high conciliatory tendency and show behavioral specificity in their conciliatory behavior. TAN et al. (2004) hypothesize that wild *R. roxellana* engage in sexual behavior as a means of reinforcing bonds and alleviating tensions.

The amount of grooming is usually considered a good predictor of the strength of affiliative bonds in primates (DUNBAR, 1991), so we usually infer from high frequencies of female-female grooming that there is female bonding. The cohesion produced by the high level of grooming may help to maintain OMU integrity in the midst of a crowded neighborhood (DUNBAR, 1991). However, it is worth considering that the *fact* of an (grooming) interaction is sometimes more important than the actual *amount* of interaction in, e.g., eliciting coalitionary support among females (DUNBAR, 1980a).

Also reconciliation aims at preserving social relationships and reinforcing unit cohesion, all of which could be jeopardized by conflicts (DE WAAL, 1993; KUMMER, 1978). In fact, high reconciliation rates have been found in all our focus species (gelada: SWEDELL, 1997; hamadryas: e.g. BUTOVSKAYA et al., 1998, SILVEIRA et al., 2001; *R. bieti*: GRÜTER, 2004; *R. roxellana*: REN et al., 1991). Another means by which unit cohesion can be maintained is uttering contact calls. Such vocalizing has been heard in wild groups of all species discussed here (gelada: KAWAI, 1979b; hamadryas: KUMMER, 1968a; *R. bieti*: GRÜTER, unpubl.; KIRKPATRICK, 1996;

see also LI et al., 1982; *R. roxellana*: REN et al., 2000) and may be of particular importance when traveling in such crowded neighborhoods that multi-level societies entail.

In general, colobines exhibit a more egalitarian 'dominance style' and have less pronounced dominance hierarchies than cercopithecines (STRUHSAKER and LELAND, 1987). The nature of the dominance style is also reflected in a species's propensity to reconcile after aggression (DE WAAL, 1989).

#### Female-Female Relationships

**T. gelada** females form close affiliations and grooming relationships (DUNBAR, 1979a). The reproductive units are held together over time by the strength of the social bonds among the females, these bonds themselves being largely based on kinship (DUNBAR, 1979b, 1982, 1983a). Gelada females tend to stay together with their matrilineal relatives for life (DUNBAR, 1979a, 1984a). Females usually form strong social relationships with only one other female in the group (DUNBAR, 1979a, 1982). Most interventions in conflicts between females are by female allies of one or both opponents (DUNBAR, 1983b). The importance of female relationships is underlined by the fact that even after loss of the leader male, the females of a gelada OMU remain together (DUNBAR, 1983a; MORI, 1979d). No female was ever observed to actively interfere with the solicitations or copulations of other females (DUNBAR and DUNBAR, 1977).

Linear dominance-rank orders are established among females within each OMU (MORI, 1979b; DUNBAR, 1983a). Young adult females are most likely to be dominant (DUNBAR, 1980a). The dominance rank of a female is matrilineally determined (*ibid.*). The most dominant females of each matriline determine the relative ranks of the matrilines. The more aggressive the female, the higher will be the rank of her matriline and thus the ranks of her relatives. An individual female's dominance rank within her unit depends on two factors, her intrinsic power due to her own physical capacities and the extrinsic power that she gains through support from other more powerful individuals (DUNBAR, 1993). Females that are low in the hierarchy suffer an accumulation of low-level aggression and harassment from the females that rank above them. Coalitions between females function to reduce the stress on females by minimizing the frequency with which they are harassed by other members of their unit (*ibid.*). Females who are members of a coalition occupy significantly higher dominance ranks within the unit than those that are not (*ibid.*). The male, however, has little or no effect on the female dominance hierarchy so that, unlike a female ally, he cannot raise his partner's rank in the hierarchy by supporting her against her rivals (*ibid.*). No differences could be found between dominant and subordinate females in either the rates of mounting or the frequencies of ejaculation received from their males (DUNBAR and DUNBAR, 1977).

**P. hamadryas** females rather rarely interact with each other (KUMMER, 1968a; SIGG, 1980; ABEGGLEN, 1984). They do not form coalitions with one another in competition with other females and it is assumed that they are not close relatives (KUMMER, 1990). Grooming between the females of an OMU is roughly symmetrical, with each female grooming and being groomed approximately equally often (SIGG, 1980). There is no evidence of clear within-OMU dominance relationships among free-living hamadryas females when determined by winner-looser interac-

tions, because the leader male normally intervenes in such female-female interactions (KUMMER, 1968a; SWEDELL, 2002b). However, there is direct competition among the females for access to the male, with dominance probably being a key factor determining priority of access (KUMMER, 1968a). In a captive group at Antwerp Zoo, a linear and stable hierarchy was found among the females (DELEU et al., 1999). Despite the existence of a linear dominance hierarchy, grooming among females was not affected by rank (LEINFELDER et al., 2001). SIGG (1980) distinguished a central female within an OMU consisting of two females that is more active socially and that is higher ranking than the other female. The central female is, however less experienced in ecological tasks than the peripheral female. About half of the feeding places exploited by OMUs were first utilized by the peripheral female and thereby denoted to the other members of the OMU (*ibid.*).

A population of hamadryas observed Filoha, Ethiopia differs from the populations studied by H. KUMMER and colleagues. In showing variation among female social relationships from simple tolerance to frequent association and grooming. Most females spent about as much social time with other females as they did with the leader male. Affiliative relationships between females even occasionally extend across unit boundaries. Thus, female hamadryas may be, to some extent, female-bonded as well as cross-sex-bonded (SWEDELL, 2002b).

In *R. bieti*, females spend much time grooming socially, which suggests relative strength in their social relationships (KIRKPATRICK et al., 1998). The same was found in captivity (JIANG et al., 1995). Two females simultaneously grooming the leader male was a common sight in a captive group, with no evident direct competition among the females for access to the male (C.C.G., pers. obs.).

In *R. roxellana*, a dominance hierarchy among females within OMUs exists (REN et al., 2000). Even fights between adult females and between adult and subadult females have been observed (*ibid.*). 17 % of the females' sexual solicitations were interrupted by another female, which suggests that there is female-female competition (REN R. et al., 1995). In contrast, REN B.P. et al. (2003), never observed successful sexual harassment between females, and female social rank did not affect their sexual activities conspicuously in captivity. Female social rank, however, did affect their spatial positioning and feeding priorities (REN, 2002). Captive females have special dyadic affiliative relationships (REN et al., 2000). Of all age-sex classes observed in a captive group, grooming was most common between adult females (*ibid.*). This suggests that close bonds exist among them. Females have also been observed counter-attacking their leader male (C.C.G., pers. obs.), which also is an indication for cohesion among them.

Strong social relationships in gelada females seem to provide the basis for coalitionary support during agonistic encounters (DUNBAR, 1980a). In contrast to the OMUs of hamadryas baboons, the death or experimental removal of the male does not lead to the immediate dissolution of the female unit (KUMMER, 1968a; MORI, 1979d). BARTON (2000) argues that female bonds within gelada units are the result of contest between females to get access to small feeding sites that cannot accommodate many individuals. This would create a pressure for the establishment of dominance hierarchies, but limit the size of coalitions contesting access. A candidate for a small but valuable resource is rhizomes for which individuals dig with con-

siderable effort. In sum, female-female competition is intensified when gelada OMUs coalesce into larger aggregations on open grasslands.

Within-group contest competition among female hamadryas baboons for food is low (KUMMER, 1968a; SIGG, 1980; SWEDELL, 2002b). Thus, the weak affiliative and agonistic relationships among female hamadryas can be explained by the scarcity and wide dispersion of food resources that seems to be typical for hamadryas habitats (BARTON et al., 1996; BARTON, 2000) although quantitative data on food distribution is missing. But KUMMER (1990) argues that alliances among hamadryas females should be profitable to females in preventing non-kin females from joining the unit when it is at or above its optimal size for them. However, it is not clear what degree of relatedness OMU females have. Female-female relationships can look different under captive conditions. When contest competition occurs in captivity, stable linear dominance hierarchies and highly differentiated affiliative networks can be developed as predicted by the socio-ecological model (ZINNER, 1993; LEINFELDER, 2001). However, female coalitions are rarely or never observed, which has been attributed to the policing behavior of males that regularly intervene in female conflicts (but see DELEU et al., 2003). In general, the lack of more pronounced female bonding in hamadryas is probably due to the male herding behavior and the rigid, male-driven hamadryas social structure rather than to ecological factors (SWEDELL, 2002b).

According to the socio-ecological models (WRANGHAM, 1980; van SCHAIK, 1989; ISBELL, 1991; STERCK et al., 1997), many aspects of female social behavior depend on the distribution and defendability of food resources. Contest (aggressive or direct) competition for food between females of different groups is closely linked to female philopatry and strong affiliative relationships among females. However, in reality the connection between dispersal system and inter-group food competition may not be as strong as suggested by the theoretical formulations of the model (KORSTJENS et al., 2002). Affiliative bonds in *R. bieti* females seem to be strong whereas inter-unit competition for food is thought to be low. This finding would not be in accordance with the predictions of the socio-ecological models outlined above.

Within a unit, colobine females are generally more egalitarian and have less pronounced dominance hierarchies than cercopithecine females (STRUHSAKER and LELAND, 1987; NEWTON and DUNBAR, 1994). This egalitarianism of colobines is best explained by weak within-group feeding competition due to their mostly folivorous diet (YEAGER and KIRKPATRICK, 1998). Observations of the overall patterns of aggression and reconciliation in captive *R. bieti* and *R. roxellana* also revealed several of the traits that characterize tolerant species (REN et al., 1991; GRÜTER, 2004). If the model by ISBELL (1991) is applied, then strong linear dominance hierarchies among females are considered indicative of intragroup contest competition, both of which appear to be low in *R. bieti* (KIRKPATRICK et al., 1998).

#### Male-Female Relationships

A *T. gelada* male does not necessarily interact with all his females (besides mating), but rather tends to have a single predominant social partner (Fig. 4). Analysis of the characteristics of the male's main grooming partner reveals that these females tend to be those who lack female relatives within the OMU. The dominant female is able to monopolize access to the male, but in wild groups the female usually does it only when no alternative related female partner is available. The male's interac-

tions with his main partner are similar to those that characterize close female-female relationships. In social terms, the male seems to function as an alternative (though less preferred) source of coalitionary support for females which lack female relatives with whom to form long-term alliances (DUNBAR, 1983b). Moreover, the male's partner continues to remain his grooming partner even after he has been displaced as OMU-holder, despite the fact that she now mates with the new OMU male (DUNBAR, 1993). Male interventions in female disputes are mostly restricted to support for any females who lack female allies (DUNBAR, 1983b). According to MORI (1979b), the leader male of the OMU shows his closest social bond with the  $\alpha$ -female or the estrous females, and the second male usually has an intimate grooming bond with the  $\beta$ -female.

The frequency of herding by adult males is low, and it is relatively ineffective (DUNBAR, 1978; MORI, 1979b). The male may even be chased by two or more females after an attempt of herding (DUNBAR, 1983b). If a male tries to take a female back to the OMU, he will behave rather defensively by emitting appeasement vocalizations. Though in the early stage, a new OMU is characterized by strong male control of females. Evidence for female choice of specific males exists in geladas (DUNBAR, 1984a). Females in units play a key role in determining whether a new male will be accepted. Intruders must not only fight the resident male, but must solicit grooming and proximity with the females in the unit.

**P. hamadryas** females interact mainly with their OMU males (KUMMER, 1968a). Females rely heavily on their leader male for protection and cooperation against aggressors, and are thus more bonded to him than to other females in their unit (KUMMER, 1968a; STAMMBACH, 1978; SIGG, 1980; ABEGGLEN, 1984). Hamadryas OMUs are thus characterized by a 'star-shaped sociogram' (Fig. 4), whereby most affiliative interactions occur between the leader male and each female. Very little interaction occurs amongst the females themselves. It is the male leader of the OMU that is the focus of grooming by females, and centripetal females compete for access to him (KUMMER, 1968a). Females groom the male more often than they are groomed by him. In a captive study, the male was found to groom the lowest ranking females in particular (FRITZ, 1979; but see COLMENARES et al., 1994). Hamadryas males are active in policing the conflicts between their females (KUMMER, 1968a; COLMENARES and LÁZARO-PEREA, 1994; COLMENARES et al., 2000; COLMENARES and BARAJAS-ABAD, 2003; DELEU et al., 2003). Reconciliation rates are higher between OMU males and their females than among females, which strongly suggest that male-female relationships are highly valuable for both sexes (ZARAGOZA and COLMENARES, 2002).

The hamadryas OMU leaders may actively keep their females in their OMU by herding them. If a female moves away too far, the male will often threaten, chase and subsequently punish her with a neck bite (KUMMER and KURT, 1963; KUMMER, 1968a). The propensity of male hamadryas baboons to herd and control females is partially under genetic control (KUMMER, 1990). In late prime and old age, the male's restrictive behavior towards females becomes less intensive. The results of a captive study indicate that females change OMUs only when their males fail to herd them (HRUBESCH et al., 2003). HRUBESCH et al. (2003) also conclude that female choice of male mates can be expressed when OMUs dissolve. SWEDELL (2000a) also argues that female choice may play a role in takeovers in hamadryas baboons.

BACHMANN and KUMMER (1980) found experimental evidence in Ethiopian hamadryas that males' decisions to fight over a female depend upon the strength of the female's preference for her current male. Compared to African hamadryas, mate choice by females seems to be of greater importance in an Arabian population of hamadryas where young females were conspicuously floating between males (KUMMER et al., 1985).

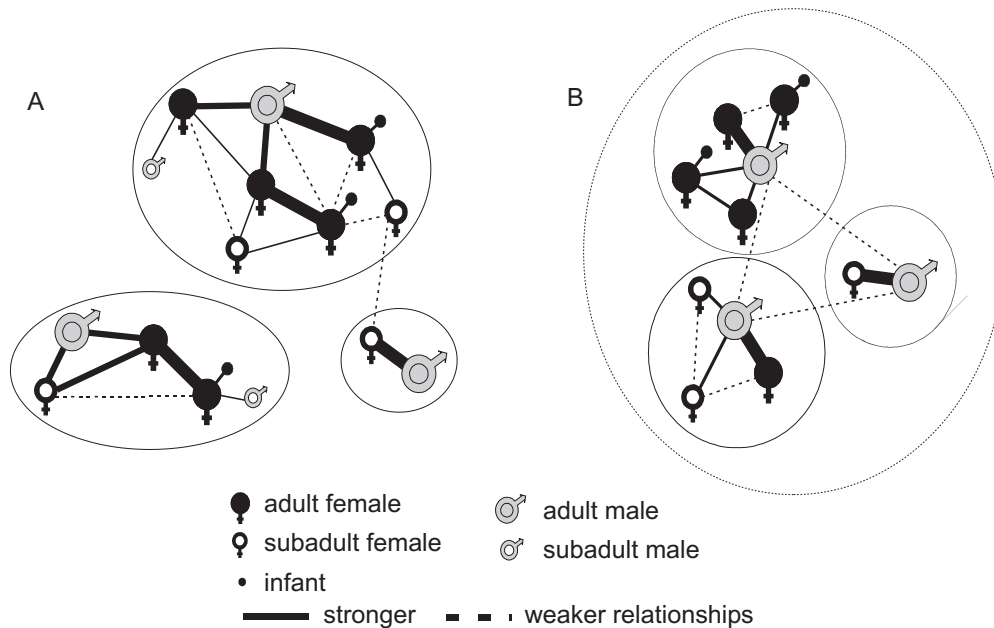


Fig. 4: Social relationships within *T. gelada* OMUs (A) and clan of *P. hamadryas* (B) indicating the star-shaped pattern of social relationships within *P. hamadryas* OMUs.

The amount of grooming activity suggests that, *R. bieti* males are relatively affiliative with females when compared with males of other colobines (KIRKPATRICK et al., 1998; C.C.G., pers. obs.). Males of captive *R. bieti* are dominant above females ((JIANG et al., 1995; GRÜTER, 2003). During more than 200 hours of observations of a captive group, the adult male was attacked only once by an adult female (GRÜTER, 2003). Females sometimes aided the OMU male during aggressive interactions with other males in captivity (*ibid.*). Male policing of female conflicts, without the use of overt aggression, has been also observed in captivity (GRÜTER, 2004).

REN et al. (2000) note that females of captive *R. roxellana* are dominant over the adult male. Females often cooperatively attack the adult male. Generally, the adult male treats his females in a "very friendly manner" (*ibid.*). The adult male was the main receiver of grooming (*ibid.*). Peaceful male interventions in conflicts between females are frequent in captivity (REN et al., 1991). In the field, no aggressive or submissive interactions between adult male and females in OMUs have been observed (REN et al., 2000). Adult females often aided their unit male during aggres-

sive interactions in the wild (TAN et al., 2003). A male virtually never forced a female to consort with him in captivity unless she presented to him (REN et al., 2003).

The significance of male-female relationships in geladas seems to lie in the basis they provide for coalitionary support during agonistic encounters (DUNBAR, 1980a). DUNBAR (1993) believes that the main reason why the male is less preferred as a social partner is that he is rarely around for more than a few years. As a result, a female who establishes an alliance with her OMU male early on in her reproductive career is likely to find herself without an ally at the crucial point later on in her life when her own physical powers start to wane. Hence it is mostly older females who tend to show interest in the OMU male. In contrast, it is the younger low-ranking females who show most interest both in a new OMU male after a take-over has occurred and in any young follower males that happen to join the unit. However, this argumentation should also hold for hamadryas baboons where male tenure is also not longer than a few years (SIGG et al., 1982). Alternatively, one could hypothesize (1) that, compared to hamadryas baboons, in geladas there are more females per male in an OMU and hence not all females might get access to the male, (2) that females in gelada OMUs might be closer related to each other than females in hamadryas OMUs or (3) that hamadryas males might constitute a more valuable coalition partner for females than gelada males for their females, and hence hamadryas females invest more in a relationship with the unit male. Under captive conditions, female feeding success was significantly related to the dominance rank of their OMU male in the male dominance hierarchy (ZINNER, 1993) and, when food was offered in a highly competitive distribution (clumped), females spent more time grooming their male than under a more relaxed, dispersed food distribution (ZINNER and TIMMANN, 2003).

The gelada male is socially rather peripheral, compared to the hamadryas leader (DUNBAR, 1983b). Grooming sociograms of geladas appear less centripetal than in hamadryas baboons (Fig. 4). The interactions of the gelada male are limited primarily to only one or two of his females (DUNBAR, 1983a). Another interesting fact confirms that a gelada male is not the social center of the unit. An estrous hamadryas female will increase her time spent interacting with her leader, whereas among geladas, female estrus has minimal disruptive effects (DUNBAR, 1983d). BYRNE et al. (1990) proposed the term 'cross-sex bonding' to describe a hamadryas-like social organization in which intersexual affiliative bonds are stronger than intrasexual bonds. If the hamadryas social system evolved from a savanna baboon system, the male-female bond has two possible antecedents: the temporary sexual consort pair and the more lasting 'special friendship' between a female and one or two males (SMUTS, 1985; KUMMER, 1990). In *R. bieti*, males are more integrated into OMUs than males of other colobine species (KIRKPATRICK, 1996a). Male-female relations seem to be less patriarchal in snub-nosed monkeys than in hamadryas baboons and thus resemble gelada baboons.

Female 'neighborhood-to-male rank' was found to be a function of dominance rank in both gelada and hamadryas baboons (SIGG, 1980; DUNBAR, 1983c). In hamadryas baboons, this is largely a consequence of competition to monopolize access to the male, whereas in geladas, it is probably more closely linked to the pivotal role occupied by the dominant female (DUNBAR, 1983b).



In OMUs, the dominant male is expected to have a strong interest in the compatibility of the females with whom he is associated, since monopolizability of an OMU depends on its cohesiveness. Thus, the tendency for males to make impartial interventions in within-group conflicts among females seems to be more prevalent in species with single male groups. The reason for the higher frequency of policing in OMUs may be because males in multi-male groups face a collective action problem in trying to police female conflicts (STERCK et al., 1997).

Gelada males do not herd their females in a comparable way as hamadryas males do. However, there is also an intraspecific difference in males' capability to monitor and control their females due to different ecological conditions. Geladas at Arsi frequently use cliff faces, where monitoring females is more difficult due to poor visibility than in the Simien Mountains where they mainly forage on the plains (MORI et al., 1999). This may be one reason why OMUs in Arsi are significantly smaller than in the Simien Mountains. Herding of hamadryas males ultimately serves to prevent female contacts with other males (KUMMER, 1990). Savanna baboon males compete for a female only at times when she is sexually receptive, whereas hamadryas baboon males defend their females against other males regardless of the females' momentary sexual conditions. In the dense habitat of *R. bieti* with poor visibility, male monopolization of females might be more difficult than in open areas with good visibility where hamadryas and geladas live (*sensu* ROWELL, 1988).

#### Male-Male Relationships

*T. gelada* OMU leaders seldom interact with each other (DUNBAR, 1983d). No overt dominance rank order exists among male unit leaders (MORI, 1979a). There is a distinctive dominance-subordination relationship between the leader and the second male in a unit (MORI, 1979b). The two maintain a friendly relationship with little overt aggression. The second male also cooperates with his leader when the latter fights with males from an AMU and tries to chase them away.

Male OMU-leaders of a *P. hamadryas* clan interact quite extensively with each other, and these relationships depend possibly on male kinship (STOLBA, 1979; ABEGGLEN, 1984). Strong male-male associations also occurred in a large captive group, but only between related males (COLMENARES, 1992). Severe battles among adult males of a band are rare (STAMMBACH, 1987), but unit males fight any other male attempting to approach and interact with their females (KUMMER, 1990). Clan males normally respect the close male-female bonds in an OMU belonging to their own clan, as KUMMER et al. (1974) were able to prove experimentally (see also SIGG and FALETT, 1985). This respect is expressed in a restraint to interfere in the male-female bond. Such a restraint does not exist with regard to the sexual bonds of non-clan males (KUMMER et al., 1974; GÖTZ et al., 1978). The males express their affiliation by ritualized sexual presentations and mountings that serve as 'greetings'. In another field investigation, hamadryas leader males frequently engaged in aggressive interactions involving chases, threats, and physical fights with other males (SWEDELL and TESFAYE, 2003). Dominance relationships in males of free-ranging and captive hamadryas bands are present across OMUs (STOLBA, 1979; ZINNER, 1993). Young followers and unit leaders interact for instance in directing their route of travel (KUMMER, 1968a). OMU-leaders were observed only a few times to chase away their followers (ABEGGLEN, 1984).

***R. bieti*** males not belonging to AMUs do not associate with one another in the wild (KIRKPATRICK, 1996a). No grooming between adult males was observed (KIRKPATRICK et al., 1998). Virtually all inter-OMU aggression was between males (*ibid.*). There is a positive correlation between number of copulations by month and the rate of male-male aggression (KIRKPATRICK, 1996a).

***R. roxellana*** males are intolerant of one another when in the presence of females. In captivity, this leads to regularly hurting and maiming each other in fights (e.g. SHI et al., 1982). Aggression between males is common in the wild, too (R.M. REN, pers. com.). A linear dominance order was found among unit males in a provisioned group (TAN et al., 2003). Exchange of affiliative behavior occurs between members of an AMU (REN et al., 1998a). Under semifree-ranging conditions, members of an AMU were subordinate to an OMU, and they were not allowed to copulate with females of the OMU (REN et al., 2002). There was also no reconciliation between members of the OMU and the AMU (*ibid.*), and the OMU and AMU usually stayed in different parts of the enclosure, thereby avoiding each other's proximity (C.C.G., pers. obs.).

Male-male interactions are infrequent in the above species, with hamadryas baboons partially being an exception. Permanent cooperative relationships with other males seem to be a prerequisite in hamadryas baboons for effective cooperative defense of females. Multiple bonds among males also seem to be the framework that holds a band together (KUMMER, 1968a, 1984). In snub-nosed monkeys, unit leaders seem to be largely intolerant of one another, and male-male competition appears to be high. The fact that dominance relationships across OMUs are present in males of a hamadryas band and absent in gelada males is consistent with the view that hamadryas males are part of a stable social unit, the band, whereas gelada males do not have regular and similarly intense social contacts.

#### Ontogeny of OMUs

A striking fact concerning the behavior of our four focal species is that a similar but among primates unique form of social system is established and maintained by different processes (at least in geladas and hamadryas baboons). The spatio-temporal stability and cohesiveness of OMUs differ quite markedly between the two species. Hamadryas baboon OMUs are held together, at least partly, by leader males whose aggressive behavior forces their females to stay within the OMU. Geladas, on the other hand, appear to have followed a different mechanism. The stability of gelada OMUs is due to strong female-female bonds (DUNBAR, 1983a).

The processes involved in the ontogeny of the OMUs are at least partly comparable. In principle there are a variety of ways in which males could acquire females and form OMUs of their own. The most usual way in geladas and hamadryas baboons is for a young male to acquire females by joining an OMU as a follower (KUMMER, 1968a; DUNBAR and DUNBAR, 1975), trying to establish relationships with the OMU females, in particular with young pre-reproductive females. OMU leaders are normally not sexually interested in these young females, most likely because they are their offspring. After the young females have reached maturity, in geladas the follower male tries to separate his females from the parent OMU. This is usually a gradual process, and the two OMUs may remain in social contact for a considerable

time (DUNBAR and DUNBAR, 1975). However, a group takeover can also be a fast (within several days) and aggressive process, when a younger male attacks and defeats an older OMU leader and takes over the leadership of the entire unit at once. In hamadryas baboons, another process of acquiring females is reported as typical by KUMMER (1968). A young male kidnaps a pre-reproductive female, sometimes not older than one year, and forms an initial unit. The male at this stage directs mostly a kind of 'maternal' behavior towards the young female. He 'adopts' the female (KUMMER, 1968a). After the females have reached maturity, they become the first reproductive females of the male. Males can also acquire adult females through a gradual process, similar to the initial process, but also by taking over females from a defeated OMU leader. In contrast to geladas, the integrity of the female group is not warranted. In hamadryas baboons, a group of females whose leader was defeated often disintegrates and several other males take over single females or groups of females (SIGG et al., 1982).

Until now, the processes and mechanisms of acquiring and maintaining females remain largely unexplored in the genus *Rhinopithecus*.

#### Mating System and Reproduction

Based on the OMU type social organization and the particular social relationships between males and females, one can expect to find a polygyn-monandrous mating system. Males have the potential and ability to monopolize females and to establish and maintain OMUs even through the females' periovulatory period. Hence, the overall operational sex-ratio is strongly male biased, due to the large number of surplus males. Pre-copulatory male-male competition is expected to be intense. Consistent with male-male competition, sexual dimorphism in body and canine size is found in all four species, and possibly as an attractant to females and/or a signal of male quality, secondary sexual traits such as skin and coat color or the lengths of hair of certain body parts are exaggerated. Furthermore, the mating system of a species has not only profound impacts on the morphology of males and females (e.g. female sexual swellings), but also on the reproductive physiology of both sexes. In species with a multi-male mating system, males usually have larger testes relative to their body size than do males of taxa where usually only one male mates (single-male mating system). In multi-male systems, sperm competition may play an important role and hence larger amounts of sperm produced by larger testes may be advantageous. In single-male systems, sperm competition is reduced and therefore, one normally finds smaller testes (HARCOURT et al., 1981).

Due to pre-copulatory competition and monopolization of females in our four species, the impact of sperm competition should be low compared to related taxa that live in multi-male multi-female groups with a more promiscuous mating system (SMITH, 1984). Hence, small relative testes size is expected. However, the close spatial relationship of several OMUs within a band and the existence of single extra OMU males or AMUs make extra OMU copulations and hence sperm competition more likely as in species with spatially and socially isolated OMUs such as *Cercopithecus* or *Colobus* species.

For the moment analyses of the mating system of the four species are restricted to the social aspects of the mating system, i.e. who mates with whom. These analyses are based on observations of copulations in the field and in captivity. The genetical aspects of the mating system, i.e. who eventually contributes to the gene pool of the

next generation has to remain unanswered for the moment, because no genetical data are available for paternity testing.

#### General Reproductive Parameters

Reproductive parameters are listed in Table 6. Values are generally similar among the four species, though there is a tendency towards longer gestation duration in *Rhinopithecus* (6.5-7 months compared to 5.5-6 months in gelada and hamadryas baboon) and shorter cycle duration (24-28 days compared to 30-44 days in gelada and hamadryas baboon). Interbirth intervals in all four species are about two years.

Table 6: Reproductive parameters of geladas, hamadryas baboons and snub-nosed monkeys (mean values and/or ranges are given).

Study Site	Age at Sexual Maturity	Gestation Length	Cycle Length	Interbirth Interval	Reference
<b><i>T. gelada</i></b>					
captivity		(5-6) mo			MORI, 1979e
		(147-192) d			MALLINSON, 1974
		(5-6) mo (captivity)			DUNBAR, 1984a
Sankaber			approx. 35 d		DUNBAR, 1980b
				approx. 24 (12-30) mo	DUNBAR, 1984a
			(30-39) d		HAYSSEN et al., 1993
			35.7 d		NAPIER, 1981
	♀: 49.5 mo	170 d	34 d	525 d	HARVEY et al., 1987
<b><i>P. hamadryas</i></b>					
captivity		(5.5-5.8) mo			KUMMER, 1968a
	♀: 35.3 (30-42) mo ♂: 48 mo	181.3 (171-191) d	44.2 d	419.0 d (n=18)	KAUMANNNS et al., 1989; ZINNER et al., subm.; ZINNER and Stahl, in prep.
Erer-Gota	♀: 51.5 (48-60) mo; ♂: (57.5-81.5) mo			24 (12-36) mo	SIGG et al., 1982
			30 d		LOY, 1987
		172 d			HARVEY et al., 1987
<b><i>R. bieti</i></b>					
captivity				2 y	L.W. CUI, unpubl.
		203.7 d	23.6 d		HE et al., 2001
	♀: 4-5 y; ♂: 5-6 y	195 d	26 d		JI et al., 1998; ZOU et al., 1995
Wuyapiya		6.5-7 mo			KIRKPATRICK, 1996a
Tacheng				2 y	W. DING, unpubl.
<b><i>R. roxellana</i></b>					
captivity		174 d			RAPAPORT and MELLEN, 1990
	♀: 3-4 y; ♂: 4 y				DAVISON, 1982
		208 d	29 d		HAMA et al., 1995, 1997

Study Site	Age at Sexual Maturity	Gestation Length	Cycle Length	Interbirth Interval	Reference
captivity	♀: 3-4 y; ♂: approx. 6-7 y				LIANG et al., 2000
	6 y	(193.5-203) d			QI, 1986
				18-20 mo	REN et al., 2003
					ZHANG et al., 2000
		approx. 200 d	approx. 28 d		YAN et al., 2003
Shennon-gjia				an adult female can give birth twice in two successive years	REN et al., 2000
(partially reprinted from STAMMBACH, 1987)					

### Timing of Reproduction

Data on the timing of matings and births are given in Table 7. Due to the very seasonal environment, in particular in snub-nosed monkeys, a tendency for seasonal breeding can be expected as it is also found e.g. in Barbary macaques (KUESTER and PAUL, 1984).

DUNBAR (1980b) reports two fairly distinct birth peaks in *T. gelada* that are correlated with seasonal rainfall. Births occur most frequently during the dry season. According to MORI (1979e), however, there is no clear birth seasonality.

There seems to be no clear birth seasonality in wild *P. hamadryas* and neither in captivity a tendency for a birth peak was observed (ZINNER et al., 1993).

With August and September as the height of the mating season in *R. bieti* and with a gestation of 6.5-7 months, there should be a birth season centering on March and April (KIRKPATRICK, 1996a). There is also some indication that *R. bieti* in captivity is a seasonal breeder (JI et al., 1998).

In captivity, *R. roxellana* displayed a marked seasonality of mating and births. The peak of matings occurred around October, and births occurred in March-June (ZHANG et al., 2000; REN et al., 2003). This seasonality of matings and births was similar to observations made in the wild (REN et al., 2000).

Table 7: Mating and birth seasons in geladas, hamadryas baboons and snub-nosed monkeys.

Study Site	Mating Season	Birth Season	Reference
<b><i>T. gelada</i></b>			
Gich	(None)	(None)	MORI, 1979e
Sankaber		Peaks in Jun/Jul, Nov/Dec	DUNBAR, 1980b, 1984a
<b><i>P. hamadryas</i></b>			
Erer-Gota		None	SIGG et al., 1982
		Peaks in May/June, Nov/Dec	KUMMER, 1968a
<b><i>R. bieti</i></b>			
captivity	June-Dec		JI et al., 1998; ZOU et al., 1995
Wuyapiya		(Mar-Apr)	KIRKPATRICK, 1996a
Baimaxueshan		Apr	BAI et al., 1987
Tacheng		Jan-Apr	W. DING, unpubl.

Study Site	Mating Season	Birth Season	Reference
<i>R. roxellana</i>			
captivity		Apr-May	REN et al., 1995
	Sept-Nov		YAN and JIANG, 2002
	Oct-Dec	Mar-Jun	REN et al., 2003
	Oct	Mar-Jun	ZHANG et al., 2000
	Aug-Nov		QI, 1986
Qinlingshan		Mar-Jun	GAO and LIU, 1995
	Aug-Oct	Mar-Apr	CHEN et al., 1983
		Mar-Apr	TAN et al., 2004
Baihe	Jul-Aug	Mar-Apr	SHI et al., 1982
Shennongjia	Sept-Dec		REN et al., 2000
	Oct-Dec	Apr-Jun	ZHU et al., 1994

To avoid nutritional stress, females should give birth in the season in which resources are most abundant. In *R. bieti*, however, females give birth to newborns in the coldest season when valuable food items are scarce. One possible explanation for this fact is that the corresponding weaning time of the infants falls into the food-rich season which would clearly be a benefit (KOENIG et al., 1997; W. DING, pers. com.). Foods are plentiful in summer when matings take place; food abundance is thought to be fundamental for providing enough energy for males to engage in sexual displays and agonistic encounters for effective male-male competition. *R. roxellana* females give birth when food becomes more abundant in spring. Reproductive seasonality is common in other temperate primate taxa as well. All populations of Himalayan langurs (*Semnopithecus entellus*) studied so far also have a pronounced birth season from December to May (NEWTON and DUNBAR, 1994).

Also the tendency in snub-nosed monkey females for shorter cycles may be an adaptation to a short mating season. There are no information available on how many cycles a female sub-nosed monkey needs to conceive. However, in another strictly seasonal breeder, Barbary macaques, females usually exhibit not more than three cycles in the short mating season (KUESTER and PAUL, 1984). Females that do not conceive during their first or second cycle will not become pregnant in that particular mating season and thus have to wait one year. If things are similar in sub-nosed monkeys, relatively short cycles would possibly be beneficial for a female, because she may squeeze in a second or third cycle in the mating season if necessary.

#### Mating System

*T. gelada* males are characterized by small testes in relation to body mass (Table 8), as expected for a species living in a single-male mating system (HARCOURT et al., 1995; BARTON, 2000). Females are responsible for initiating most sexual interactions (DUNBAR, 1978). Follower males also engage in mating, although the OMU male may sometimes try to prevent copulations by the follower (DUNBAR, 1984a). MORI (1979b), however, notes that a second male in a unit is completely restrained by the leader male from having sexual relations with the females of the unit. Males do not attempt to interact (sexually) with females of units other than their own (DUNBAR and DUNBAR, 1975).

*P. hamadryas* males have smaller testes in relation to their body mass than other *Papio* species living in multi-male systems (HARCOURT et al., 1995; BARTON, 2000; JOLLY and PHILLIPS-CONROY, 2003). Mountings can be initiated by either sex (KUMMER, 1968a). Estrous females are mated almost exclusively by their OMU leaders. A recent genetical study of Saudi Arabian hamadryas baboons provided some evidence that at least extra-unit paternities exist (YAMANE et al., 2003). Whether the unidentified fathers in this study were other OMU leaders or adult or subadult bachelor males could not be determined. Sometimes, younger males are able to ‘sneak’ a copulation behind the back of the leader (STAMMBACH, 1987). Copulations with older juveniles or young subadult males have been believed not to result in conceptions (KUMMER, 1968a). However, under captive conditions where all adult males have been vasectomized, adolescent males (younger than 5 years) have been responsible for several successful conceptions (ZINNER et al., subm.). On the other hand, adult hamadryas males have never been observed successfully copulating with extra-unit females, even when actively solicited by fully-swollen females from other units (KUMMER, 1968a).

In *R. bieti*, testes are most likely larger in relation to body size compared to other colobine single male species (Fig. 5a; Table 8) (C.C.G., pers. obs., although no quantitative data re available). About half of the sexual mounts observed in a captive group were initiated by the OMU male (L.W. CUI, unpubl.). It is not known whether males engage in copulations with females belonging to other OMUs than their own or whether females try to solicit extra-OMU males.

Table 8: Mating system and relative testes mass (MM multi-male; SM single-male).

Species	Mating System	Rel. Testes Size (% of Body Mass)	Source
<i>Macaca mulatta</i>	MM	0.50	HARCOURT et al., 1981
<i>Papio anubis</i>	MM	0.35	
<i>Mandrillus sphinx</i>	MM?	0.19	
<i>Papio hamadryas</i>	SM	0.13	
<i>Theropithecus gelada</i>	SM	0.08	
<i>Nasalis larvatus</i>	SM	0.06	
<i>Semnopithecus entellus</i>	SM	0.06	PENG et al., 1993
<i>Rhinopithecus brelichi</i>	SM?	0.18	
<i>Rhinopithecus bieti</i>	SM?	0.18?	
<i>Rhinopithecus roxellana</i>	SM?	0.18?	estimate

Also in *R. roxellana*, testes are most likely larger than in related colobine species with a single male mating system (Fig. 5a; Table 8). Females are responsible for 95 % of all proceptive behavior (REN et al., 1995; see also REN et al., 2003). In the Qinling Mountains, less than 60 % of the observed sexual activities were initiated by the male (TAN et al., 2004). Female solicitations for copulations were also found during lactation and pregnancy (REN et al., 2003; YAN and JIANG, 2002, 2004), and sexual activities are not restricted to the mating season (TAN et al., 2004). There are recent observations of extra-unit sexual behavior among provisioned *R. roxellana* in the Qinling Mountains (ZHAO et al., 2004).

Since for the genus *Rhinopithecus* data on relative testes size is only available for *R. brelichi* (PENG et al., 1993), we used a rather indirect measure for testes size of *R. bieti* and *R. roxellana*. Based on the obvious similarity of the testes size within the genus (Fig. 5a and b), we assume that relative testes size in *R. bieti* and *R. roxellana* is similar to *R. brelichi*.



Fig. 5a: Male *R. bieti* and male *R. roxellana*. Note that the size of the testes in both species is similar to *R. brelichi* (Fig. 5b).



Fig. 5b: Male *R. brelichi*. Note the conspicuous size and color of the testes. In this species mean relative testes mass is about 0.18 % of body mass (PENG et al., 1993).

Comparisons have to be preliminary, but the most striking point is that *Rhinopithecus* seems to have much larger testes than other species that show a single-male mating system (Table 8). If our estimation is correct, *R. bieti* and *R. roxellana*



have larger testes than phylogenetically related species such as *Nasalis larvatus* or *Semnopithecus entellus*, and their relative testes size is most likely also bigger than in geladas (and hamadryas baboons). On the other hand, they do not have as large testes as obligatory promiscuous species such as rhesus macaques or olive baboons. The sperm competition hypothesis correlates relative testes size with the mating systems of primates in general (HARCOURT et al., 1981). According to this hypothesis, intrasexual competition occurs mainly on the level of male-male competition that has resulted in extreme sexual dimorphism, the long-term monopolization of several females by one male, and no selection for increased testes size which is in accordance with the findings in geladas and probably hamadryas. The small testis of geladas indicates that the gelada one-male mating system may be stricter than in hamadryas or has a longer evolutionary history or both (BARTON, 2000).

However, why do male *Rhinopithecus*, living year round in OMUs, have such large testes? One possible explanation would be that testes size in *Rhinopithecus* is a non-adaptive trait disassociated from other sexually selected traits including their extreme sexual dimorphism and that sexually selected behavior has not evolved in tandem with morphological traits (cf. ROBBINS, 2001). Though, the most parsimonious explanation for this dichotomy would be that the breeding system in *R. bieti* and *R. roxellana* has at least multi-male multi-female (polygynandrous) components, whereas the social organization is one-male (cf. PENG et al., 1993; see also ZHAO et al., 2004). Besides, seasonal breeding primate species are more prone to have a multi-male mating system. The reason behind this presumption is that a single male will have more difficulties defending several simultaneously fertile females (EMLEN and ORING, 1977; RIDLEY, 1986). KIRKPATRICK (1998) argues that female proceptive behaviors and female-female competition, both found in *R. roxellana*, could mean that mating is more promiscuous than one-male social groups would suggest. Furthermore, the unusual social organization of *Rhinopithecus* where a large number of units are mostly in close proximity to each other creates an easier opportunity for extra-group mating than if units were separated and far apart.

Moreover, seasonally breeding species such as *R. bieti* and *R. roxellana* might have to produce more sperm in a shorter time period than would a non-seasonal breeder. These species would also have larger testes because of the concentration of fertile females in a brief period and the consequently high frequency of copulation (*sensu* HARCOURT et al. 1981; but see HARCOURT et al., 1995) as it is found in several highly seasonal prosimians (SCHMID and KAPPELER, 1998; HILGARTNER et al., in prep.). DUNBAR and COWLISHAW (1992) suggested that seasonal breeding would intensify sperm competition, hence resulting in relatively larger testes in seasonally breeding species like snub-nosed monkeys compared to non-seasonal breeders like baboons. However, it is notable that seasonality of reproduction is only a crude predictor of whether estrous periods are likely to overlap (PEREIRA, 1991; DUNBAR, 2000; EBERLE and KAPPELER, 2004), and seasonal breeding may actually facilitate male monopolization of reproduction within groups because males are best able to sustain the necessary agonistic power over relatively short periods of time (e.g. CLUTTON-BROCK et al., 1982).

It is notable that in geladas and snub-nosed monkeys, there is a tendency for females to initiate a high proportion of copulations. That is probably because the male is likely a limited resource for the females of his unit (*sensu* DUNBAR, 1978).

#### Male Life History

**T. gelada** males can pursue different options for acquiring breeding females. (1) They can join a unit as a submissive follower in order to build up a nuclear unit within an OMU with one or two of the socially more peripheral females. Such a nuclear unit could split off to pursue an independent existence (DUNBAR and DUNBAR, 1975; MORI, 1979c; DUNBAR, 1984a). In the early stage, such a new OMU is characterized by strong control of females by the male. (2) A second male strategy for becoming an OMU leader is as follows: A male member of an AMU may attack an OMU leader who is presumed to be weak. If he wins, he will take over the OMU and will become its new leader. The former leader will usually stay within the OMU as a second male (DUNBAR and DUNBAR, 1975; MORI, 1979d; DUNBAR, 1984a; MORI and DUNBAR, 1985). Whether the incumbent male succeeds in driving the intruder away or loses his unit to the intruder depends wholly on the reactions of the females. (3) MORI (1979d) also suggests that OMUs, having lost their leader, remain intact and are taken over as a group by an AMU male or merge entirely with another OMU. In contrast to the hamadryas baboons, therefore, bonds among the females of each OMU are so strong that a splitting up of the females among different OMUs does not occur. (4) The simplest strategy for acquiring females would be to 'kidnap' a loose female and form a small unit with her. These latter two male strategies are probably rather rare in practice (DUNBAR, 1984a). DUNBAR (1984a) estimated that gelada males hold the breeding position within the OMU for 3.5 to 7 years and that male life expectancy is 12.3 years. Once an OMU-holder has been defeated, he remains in the unit as an old follower and maintains his relationships with his former females, though he does not normally mate with them. Old followers remain in their units for about two years and then seem to drift off to rejoin an AMU (DUNBAR, 1993). Old leaders may stay within the unit because they can possibly protect their infants against infanticide (DUNBAR and DUNBAR, 1975). A more detailed scheme of the life history of geladas males with several more distinctive stages is given by MORI (1979c).

According to STAMMBACH (1987), male life history in **P. hamadryas** can be outlined as follows. Juvenile and subadult males frequently travel around with other clans or even other bands for a certain time, but most will return to their natal band/clan at adulthood (SIGG et al., 1982). Here they most often form the first stage of an OMU, an initial unit by establishing a relationship with a pre-reproductive juvenile or subadult female of one of the OMUs of their own clan (KUMMER, 1968a). Alternatively, they may attach themselves to an OMU as a follower. Later, they will attempt to take adult females away from old OMU leaders, usually during one of the rare but severe fights among adult males of bands. In the course of these fights, the females of one or more OMUs may be dispersed to new OMUs (ABEGGLEN, 1984; KUMMER, 1984). KUMMER (1984) estimated the leading (reproductive) period of a male to be only three to six years out of the approximately 20-year life of a hamadryas male. Defeated OMU leaders may live without females, but remain associated with their clan and continue to interact with their offspring (ABEGGLEN,

1984). SWEDELL (2000a) describes a re-acquisition of a female by a deposed leader male. JOLLY and PHILLIPS-CONROY (2003) have found some evidence that free-ranging male hamadryas baboons in Ethiopia become pubertal at a relative early age compared to parapatric olive baboon males. Their testes get larger long before they develop the characteristic attributes of an adult male hamadryas baboon, such as the silvery grey hair and long mantle. In a captive colony, adolescent males of four years produced viable sperm and were most likely responsible for several successful conceptions subsequent to the vasectomy of all males older than six years, including the OMU leaders (ZINNER et al., *subm.*). It is therefore possible that male hamadryas baboons are reproductively active and successful in two periods, first at adolescents and second as fully grown OMU leaders.

Data about individual male life histories are so far not available for *R. bieti* and almost nothing is known about male life history in *R. roxellana*. However, there is a recently witnessed case of a replacement of an OMU leader through take-over by a solitary male in a provisioned group of *R. roxellana* in the Qinling Mountains (WANG et al., 2004a,b). The ousted leader had been the resident male in his unit for at least 1.5 years. During the takeover process, no escalated fights between the resident and the challenging male were witnessed, but the new resident was found with a small injury. The former resident did not remain in the band. All former unit members stayed, suggesting that female preference might have played a role in the outcome of resident male replacement. It is not known whether or not OMU leader replacements are seasonal phenomena in *Rhinopithecus*, as for example in patas monkeys (*Erythrocebus patas*; OHSAWA et al., 1993). However, two observations of resident-male replacements in the Qinling Mountains (WANG et al., 2004a,b) are in line with the prediction that takeovers should take place between the birth and the mating season (NEWTON and DUNBAR, 1994).

The forming of an initial unit in hamadryas baboons appears to be a career strategy of young males by which they bypass the competition of prime males, who respect the bond even after the female has reached sexual maturity (KUMMER, 1968a). Takeovers of an entire unit after challenging an OMU-holder have been found in geladas, which is in contrast to hamadryas baboons, where such incidents are not common (BACHMANN and KUMMER, 1980). However, SWEDELL (2000a) observed two takeovers from established OMUs. In each case, three females were taken over by other leaders and two females were taken over by solitary or unknown males. This contrasts with previous reports of takeovers in wild hamadryas, which have indicated that most females are taken over by solitary or follower males (ABEGGLEN, 1984; KUMMER, 1968a; SIGG et al., 1982).

The risk of takeovers may be reduced in OMUs containing an additional male, the follower. The follower strategy is adopted by both geladas and hamadryas baboons. In hamadryas, followers form age-graded queues, and the oldest followers of leader males are most likely to challenge the leader male and to acquire females in this way (ABEGGLEN, 1984; KUMMER, 1984). Furthermore, larger OMUs (four to ten females) of geladas experienced male takeover at a much higher rate than smaller OMUs (DUNBAR, 1984a). Gelada followers have higher chances of success compared with males trying to take over a unit. However, males who attempt takeovers gain more females when they are successful (*ibid.*). Thus, the two strategies

are suggested to be equally profitable over the lifetime because the initial advantage incurred by takeover strategists in terms of a larger initial OMU size is offset by the fact that they cannot survive as OMU males for as long as a follower can (*ibid.*). The relative contribution of following and takeover attempts to variation in male reproductive success of hamadryas baboons have not been analyzed in detail.

Also mountain gorilla (*Gorilla beringei beringei*) males growing up in OMUs show variation in life history tactics, i.e., they have the option of either becoming a 'follower' or a 'bachelor' (reviewed in WATTS, 2000). In hanuman langurs males exhibit either gradual male replacement or rapid male replacement (takeover) (reviewed in NEWTON, 1987).

### Sexual Dimorphism

All four species are characterized by a large sexual dimorphism in both body mass (Table 9) and canine size (PLAVCAN and van SCHAIK, 1992; JABLONSKI and PAN, 1995). In hamadryas baboons, males and females are also sexually dichromatic. Pronounced sexual dimorphism suggests strong male-male competition (PLAVCAN and van SCHAIK, 1992; 1997) and is a prerequisite for a social system that is based on OMUs. Since comparable data on canine size are not available for the four species due to methodological differences in determining canine size dimorphism, we are not able to use this morphological trait for an interspecific estimate of the level of male-male competition. In case of *R. bieti*, JABLONSKI and PAN (1995) assume that the very high degree of canine dimorphism is due to the intensity of intermale competition for mates during a temporally restricted breeding season.

Table 9: Body mass and magnitude of sexual body mass dimorphism in geladas, hamadryas baboons and snub-nosed monkeys.

Species	Male	Female	Dimorphism	Reference
<i>T. gelada</i>	20.5 kg	13.6 kg	1.51	HARVEY et al., 1987
<i>P. hamadryas</i>	21.5 kg	9.4 kg	2.29	
<i>R. bieti</i> *	approx. 15 kg	approx. 9 kg	approx. 1.67	KIRKPATRICK, 1998
<i>R. roxellana</i>	approx. 16 kg	approx. 9 kg	approx. 1.78	

\*There are unverified reports of wild adult males weighing more than 30 kg

### Morphological Features / Sexual Adornments of Males

Adult male *T. gelada* have long, heavy, dark capes or mantles. A patch of sexual skin occurs on the male's chest and is brightest in those males that succeed in associating with females to form OMUs. When a resident male is deposed during a takeover by extra-group males, the brightness of his chest patch fades rapidly, whereas those of newly dominant individuals increase in coloration (DUNBAR, 1984a).

In *P. hamadryas*, the adult male's prominent cape of white and silvery-grey hair is androgen-dependent (ZUCKERMAN and PARKES, 1939). Loss of the cape has been observed to occur in some males after receipt of aggression and reduction in social rank (KUMMER, 1990). The rump of male hamadryas is brightly red colored and reminiscent of the female's swelling. These structures might be of value during socio-sexual communication while presenting, such as during the males' greeting be-

havior ('notifying', WICKLER, 1967; KUMMER, 1968a; PELÁEZ, 1982; DIXSON, 1998).

*R. bieti* males also possess capes (JABLONSKI and PAN, 1995). The face is quite colorful and the scrotum is conspicuously white. Snub-nosed monkeys are similar with terrestrial cercopithecines in bright facial and genital coloring (DAVISON, 1982).

As *R. roxellana* males develop, they display several secondary sexual characters such as two warts located on each corner of their upper-lip and long, golden-colored hairs on their shoulder, back and waist (LIANG et al., 2000). The scrotum is as in *R. bieti* and *R. brelichi* conspicuously white.

Adult male geladas, hamadryas baboons and *R. bieti* have long capes of hair. It was hypothesized that the striking capes probably function, on a proximate level, as an organ of attraction to females (JOLLY, 1963; KUMMER, 1968a,b). On an ultimate level, they could also be an honest signal of the male's condition to both mates and potential rivals in the sense of ZAHAVI (1975) or HAMILTON and ZUK (1982). The exaggerated secondary characters of the males may than be an equivalent to long tails in some bird species (e.g. MØLLER, 1988, 1989) and hence a trait preferred by females. Additionally, the capes might fulfill a thermoregulatory function in cold environments. However, if insulation is the main reason for the existence of this morphological feature, females are expected to have developed it too.

Moreover, by these conspicuous traits long-distance visibility of males by conspecifics may be enhanced (CHAPLIN and JABLONSKI, 1998). The cape can probably be shown to its fullest advantage in the open habitat of hamadryas and gelada and especially when using exposed rocky outcrops in *R. bieti* (cf. *ibid.*). Anecdotal accounts of changes in secondary sexual traits, as a result of rank reversals (similar to mandrill, SETCHELL and DIXSON, 2001), are available for geladas and hamadryas baboons (DUNBAR, 1984a).

The upper-lip wart in adult male golden monkeys is unique amongst primates. This special tissue is not only absent in conspecific adult females, but also in adult males of the three other species in this genus. The function of the structure has never been studied, but it is argued that it may secrete certain materials which serve as chemical signals (LIANG et al., 2000; see also LIANG et al., 2002). DIXSON (1998, Table 7.6) lists the 'fleshy flaps at corners of mouth' of male *R. roxellana* as secondary sexual adornments. *R. brelichi* males also possess a highly conspicuous morphological feature: the white nipples (Fig. 5b). In female *R. brelichi*, the nipples are dark.

#### Infanticide

Infanticide has been frequently noticed in captive *T. geladas* after replacement of OMU leaders in the absence of old followers (ANGST and THOMMEN, 1977; MOOS et al., 1985). Cases of infanticide subsequent to a change of the OMU leader male were also observed in the field in Arsi (MORI et al., 1997, 2003).

Infanticide following unit takeovers also occurs in captive *P. hamadryas* (e.g. GOMENDIO and COLMENARES, 1989; ZINNER et al., 1993). Recently, the first observational evidence of infanticide in wild hamadryas was reported by SWEDELL and TESFAYE (2003).

No reports about infanticide in *R. bieti* are available. However, severe injuries of an infant after a male's attack have been observed (W. DING, pers. com.).

There is one report of infanticide that took place in captive *R. roxellana* (ZHANG et al., 1999b). During a takeover in a free-ranging band, no infanticide occurred even though infants were present (WANG et al., 2004a,b). Similarly, when a new male became leader of an OMU after a takeover at Shanghai Wildlife Park, no infant killing happened (REN, 2002).

There is evidence that infanticide rates by males decline as the number the number of males per group increases (JANSON and van SCHAIK, 2000) and possibly more common in single male groups than in others (LELAND et al., 1984). The presence of a young or old follower in the gelada unit as a second male reduces the probability of infanticide (DUNBAR, 1984a; van SCHAIK, 2000). An alternate route for a female to ensure protection against infanticide is association, and exclusive copulation, with a single protective male. There is evidence suggesting that the latter strategy, one of paternity concentration rather than paternity confusion, is used by female hamadryas baboons (SWEDELL and SAUNDERS, 2003). It has been observed that female hamadryas, even when they are not receptive, resume sexual swelling in the wake of male takeovers (COLMENARES and GOMENDIO, 1988). ZINNER and DESCHNER (2000) suggest that such sexual swellings after male takeovers are used by female hamadryas baboons as a counter-strategy to reduce the risk of infanticide.

According to GOMENDIO and COLMENARES (1989), a hamadryas takeover is a gradual process, and the new leader male, having previously been a follower male to the unit, is typically already familiar with the unit's females. Such a gradual process would possibly remove or reduce the proximate mechanism for infanticide if, on a proximate level, infanticide is stimulated by a short period of social upheaval and by the unfamiliarity of the females with the new male (e.g. langurs, SOMMER, 1985). Furthermore in hamadryas baboons, leader males and the males who take over their units may be related (ABEGGLEN, 1984), and this may reduce the benefits for an infanticidal male. However, takeovers in hamadryas baboons are not always a gradual process and often do not appear to involve males with close kin or social relationships prior to the takeover (SWEDELL, 2000b). In such cases, the sexual selection hypothesis would predict that a female's new leader male would benefit from killing her infant. SIGG et al. (1982) pointed out that infant survival is higher in hamadryas baboons than in other baboons and suggested that the hamadryas baboon society provides a safer environment for infants and juveniles than the multi-male multi-female social system of other baboons. This suggests that a leader male plays an important role in protecting the infants in his unit, and that his presence alone may largely account for the higher rates of infant survival and the rarity of observations of infanticide in hamadryas baboons compared to other baboons.

In principle, similar hypothetical scenarios can be applied to the other three species. One possible explanation for the occurrence of infanticide in the gelada population at Arsi is given by MORI et al. (1997). Gelada males in this area may be able to join units more easily to form multi-male units but then have shorter tenure in the units. Facing the unstable condition of units, the males may sometimes engage in infanticide to increase their breeding opportunities, even before becoming a leader.

#### Female Estrus Signs

***T. gelada*** females develop beadings at the border of their sexual skin, a naked reddish area on their chests (ALVAREZ, 1973) and, additionally, a swollen, protruding vulva. The size and color of the naked, triangular chest patch is affected by cyclical hormonal changes in females. Sexual signals are thought to be located on the chest because of better visibility due to frequent sitting (WICKLER, 1967). Female ***P. hamadryas*** show the typical genital swellings of many catarrhine species, including red colobus, several macaque species, bonobos and chimpanzees (DIXSON, 1998). There are no sex skins in female ***R. bieti*** (C.C.G., pers. obs.) and female ***R. roxellana*** (QI, 1986).

A strong association was found between the mating systems of catarrhine primates and the occurrence of exaggerated sexual swellings in females. Females living in multi-male mating systems tend more to show swellings than females living in single-male systems (CLUTTON-BROCK and HARVEY, 1976). Exceptions to this rule seem to be geladas and hamadryas baboons, which live apparently in single-male mating systems. However, these exceptions are explicable by arguing that the ancestors of hamadryas baboons and geladas lived in multi-male social groups. Sexual skins might have arisen in such ancestral species and have been retained to the present day (DIXSON, 1983). The closest phylogenetic relatives of *Rhinopithecus* all live in single-male mating systems and they all lack sexual swellings. The discussion about the functional significance of sexual swellings and their evolutionary pathways is still a controversial issue (NUNN et al., 2001; DOMB and PAGEL, 2001; ZINNER et al., 2002, 2004).

#### Alloparental Care and Male Infant Care

Allocare is rare in ***T. geladas***; and so far, only juvenile females are known to engage in allocare (DUNBAR, cited in ROSS and MacLARNON, 2000). Infants are used by male geladas in agonistic contexts (DUNBAR, 1984b). This is explained with agonistic buffering, progeny protection and/or soliciting support. When two males are present in social units of geladas, the young follower, but not the dominant OMU leader, frequently affiliates with infants. MORI (1979b) suggested that gelada followers use infants to establish sexual relationships with the infant's mothers. A deposed OMU leader often remains in the OMU and actively defends the group's infants when threatened by the new leader or by other males (DUNBAR and DUNBAR, 1975; DUNBAR, 1984b).

In ***P. hamadryas***, female care of an infant other than her own is rare (KUMMER, 1968a), but long-term adoptions of infants by allo-mothers occur in captivity (D. ZINNER, pers. obs.). Subadult males have a peculiar interest in carrying or handling infants for short periods and do so even more often than pre-reproductive females (KUMMER, 1968a). Young adult hamadryas baboon males develop close associations with weanlings as a first step in the establishment of a breeding unit (*ibid.*). In this case, the males adopt the role of a 'surrogate mother' for the young female, carrying her on his back and offering her comfort, but also aggressively herding her. Subadult males also show a kind of agonistic buffering and use infants to protect themselves when under threat from an adult male, assigned by KUMMER (1967) under the term 'tripartite' relationships. Furthermore, defeated males groom and interact with their own offspring, but OMU leaders do not (ABEGGLEN, 1984).

At Wuyapiya juvenile *R. bieti* were observed to provide alloparental care. Contributions to alloparental care by adult females could not be determined because individual females were not identified (KIRKPATRICK et al., 1998). Adult males were never seen grooming or carrying infants (*ibid.*), but they might be involved in the formation of 'crèches'. MacLENNAN (1999) saw at least one adult male accompanied by a yearling. 'Real' male infant caretaking has been reported to happen at the Tacheng field site, especially during winter (W. DING, pers. com.; C.C.G., pers. obs.). Here a young juvenile was seen grooming an adult male, and two adult males (probably members of an AMU) were seen traveling together of which the younger one of them was carrying a yearling or young juvenile of unknown sex. Males are apparently also protective towards infants in the sense that they defend them against attacks of avian predators (W. DING, pers. com.). In a captive group, the adult OMU male was also very protective towards infants/young juveniles by intervening aggressively in conflicts between them and older juveniles. The male threatened the older juveniles. Male tolerance towards juveniles decreased with age of the juveniles. In the same captive group, a two year old juvenile experienced regular displacements/threats, but nevertheless, in two cases, the adult male was observed to play with it (GRÜTER, 2003).

In *R. roxellana*, allo-mothering has been observed both in the field and in captivity (ZHU et al., 1994; C.C.G., pers. obs.). There are observations from wild groups that juveniles groom and carry infants (HU et al., 1980). REN et al. (2000) found an adult male with a juvenile female sleeping in embrace, some distance apart from the OMU. Such kind of observation as well as reports of 'crèches' of males with young females may be interpreted as a parallel to a hamadryas-like strategy of OMU formation (initial unit), where adult males bond with pre-reproductive females. There is also a report of a male grooming an infant (SCHALLER, 1985), and postconflict affiliative exchanges between adult males and juveniles do occur in the wild as well (C.C.G., pers. obs.). Carrying of infants by adult males, however, does not appear to be common in golden monkeys (R.M. REN, pers. com.).

Protective behavior of defeated males towards offspring in the presence of newcomers or newly dominant males is apparently a common feature in hamadryas baboons and geladas. Paternity certainty is probably quite high for hamadryas leader males (but see YAMANE et al., 2003), and protective behavior towards infants has probably been selected for (SWEDELL and SAUNDERS, 2003). Confidence of paternity might also trigger a similar behavior in geladas. Tripartite male-infant-male interactions, where young followers threatened by an OMU leader often grasp an infant and carry it in front of the adult male, are known from geladas and hamadryas baboons. PAUL et al. (2000) argue that infanticide risk might provide an indirect explanation for why infants function as 'buffers' in such 'tripartite' interactions. Namely, by carrying unrelated infants to more dominant males who are likely sires of the infants, males would reduce the likelihood of an escalated fight because any severe aggression performed by the dominant male would put his own offspring at a serious risk.

There is circumstantial evidence for male infant care in *R. bieti*. Only the males of two other socially non-monogamous primate species practice male infant care intensively: Barbary macaques (TAUB, 1984) and Tibetan macaques (*Macaca thibetana*;



DENG and ZHAO, 1996), both of which inhabit temperate environments. Male care in Tibetan macaques may enhance offspring viability in stressful environments. However, male-infant interactions in Barbary macaques are often explained with the 'agonistic buffering hypothesis' (PAUL et al., 1996), which states that males use infants to regulate their relationships with other males. Tibetan macaques also engage in triadic male-infant-male interactions similar to the ones described for Barbary macaques (ZHAO, 1996). Male care of infants in *R. bieti* may have evolved in order to increase the mother's freedom to forage ('baby-sitting hypothesis', POIRIER, 1968) and to reduce energetic costs of lactating females in harsh environments.

In contrast to baboons, most colobines are equipped with flamboyant natal coats, which are thought to have evolved to facilitate infant-handling (HRDY, 1976). Infants of both *R. bieti* and *R. roxellana* possess a light pelage that differs from the adult black-and-white or golden fur, respectively, and this may have something to do with allocare in these species. Baboon infants also have a different color than older individuals. In most baboon taxa they have a black fur for the first three to five months with the exception of the Kinda baboon of western Zambia and Angola. Here the infants have a whitish neonatal coat. According to NEWTON and DUNBAR (1994), natal coats are considered flamboyant only if they are striking, highly visible and not dark. Baboon babies with their normally dark coats thus would not fit into this category. Nevertheless, the black color of infant baboons is also explained as a signal to the adults to take special care (TREVES, 1997; ROSS and REGAN, 2000).

#### Evolution of Nested Social Systems

When we speak about the evolution of social systems, we are aware by all means that selection does not work on something such as a 'social system'. The targets of selection are behavioral strategies of individuals, e.g. their spatio-temporal distribution, grouping patterns and their social and sexual interactions (KAPPELER and van SCHAIK, 2002). According to socio-ecological models (CROOK, 1970; EMLEN and ORING, 1977; van SCHAIK and van HOOFF, 1983; TERBORGH and JANSON, 1986), individual strategies are probably largely shaped by ecological factors such as distribution of resources and risks. Additionally, the demographic conditions created by individual behavioral strategies may impose constraints on the behavioral options of the same individuals, leading to complex feedback loops (JANSON, 1986; van SCHAIK, 1996). This becomes especially obvious when considering food competition within groups and the impact of sexual conflict on male-female relationships. As a result of the interplay between individual strategies, we may observe a certain social organization, social structure and mating system, the three elements that constitute the social system. However, these elements are not necessarily congruent, and depending on the reaction norm of the species, under particular conditions we will find more or less plasticity in one or more of the elements.

The social systems of geladas, hamadryas baboons and snub-nosed monkeys are complex arrangements of hierarchically organized or nested social groupings. The similarity among their systems is mainly based on the similarity of their social organization, which comprises two main levels or modules, OMUs and bands. Further additional modules such as teams, clans and troops have been proposed, too, but can not be found in all species. In general, OMUs provide the context in which most social behavior and most or all reproductive activities take place, whereas the band is

regarded as the basic ecological unit serving purposes such as reducing predation risk. Although there are obvious similarities in the social organization of the species, other components of the social system show some variation, such as the social structure and possibly also the mating system (given that the assumed differences in relative testis size apply). The inter-individual relationships within OMUs, in particular the male-female relationships and the ontogeny of these relationships differ at least between hamadryas baboons and geladas, but most likely also between baboons and snub-nosed monkeys. Another striking similarity is that all species seem to form large aggregations of more than 150 animals on a permanent or regular basis, which is not a common phenomenon among primates. Whether these two traits of the social organization are linked will be discussed below.

Although in all four species, OMUs constitute the basic social entities (modules) which are nested into a larger group (band), the species show some marked differences in their social organization, social structure and mating system. Furthermore, they also differ dramatically in their ecology, in particular their feeding ecology. Average OMU size is biggest in snub-nosed monkeys and smallest in hamadryas baboons. Stable all male units (AMUs) are not known from hamadryas baboons, but are a regular component of gelada and snub-nosed monkey social organization. Females in hamadryas OMUs are believed not to be close kin, and the social relationships among them are relatively weak. The most important adult social partner of a hamadryas female is the OMU male. Females normally do not stay in their natal OMU and a certain degree of female and male migration even between bands occurs. In geladas, females normally stay in their natal OMU and therefore, OMU females may represent close kin. The social relationships among them are normally stronger than those with the OMU male. However, neither for hamadryas nor for geladas genetical data are available to analyze female-female relationships within and among OMUs. Many questions about the social organization and social structure of snub-nosed monkeys have to remain unresolved due to a lack of data. Anyhow, it seems that males leave or have to leave their natal OMUs when they reach puberty and that the social relationships among OMU females are closer than between male and females.

#### Evolutionary Hypotheses

The peculiarities of the nested social system have stimulated many primatologists to think about its adaptive value and its evolutionary origins. This is of particular interest when considering that closely related species do not show such a system, e.g. hamadryas baboons and 'savanna baboons' (CROOK and GARTLAN, 1966; KUMMER, 1968b, 1990; DUNBAR, 1986, 1988; STAMMBACH, 1987; BARTON, 2000; HENZI and BARRETT, 2003, in press). Several hypotheses have been proposed to explain the function and evolution of nested systems, most of them within the socio-ecological framework (Table 10). Within this framework food resource availability and predation risk are the most important ecological factors influencing group size and composition and social relationships (WRANGHAM, 1980; van SCHAIK 1983; JANSON and GOLDSMITH, 1995). Beside these ecological factors, sexual conflict, in particular female coercion and infanticide by males, are believed to be critical factors that shape the social system (SMUTS and SMUTS, 1993; van SCHAIK and JANSON, 2000). Additionally, cognitive aspects may also play a role (DUNBAR, 1992c, 1998).

Table 10: Evolutionary hypotheses.

Hypothesis	Author
Ecological hypotheses	
Resource distribution and predation pressure	KUMMER, 1968b, 1990; DUNBAR, 1986, 1988; BARTON, 2000; HENZI and BARRETT, 2003
Time constraint	DUNBAR, 1992b
Sexual conflict, infanticide avoidance	ZINNER et al., 2001c; HENZI and BARRETT, 2003
Social brain	DUNBAR, 1992c

These hypotheses refer to either *Papio* baboons or geladas and not to snub-nosed monkeys. This bias is certainly caused by the long history of baboon research and by the interest of researchers in the strikingly different social systems of hamadryas baboons and the closely related ‘savanna’ baboons. Generally, savanna baboons show a high degree of ecological plasticity. They occupy various habitats such as semi-deserts, high mountains and different forms of savannas and forests. They also show some degree of social flexibility. Usually they live in multi-male multi-female groups, but they also form single one-male units under certain local environmental conditions such as in the mountains of South Africa (BYRNE et al., 1987; ANDERSON, 1990; HAMILTON and BULGER, 1992). In contrast, such a degree of social flexibility was not found in hamadryas baboons. All studied populations so far in Ethiopia, Eritrea and Arabia show the same, typical hamadryas system, OMUs nested in bands. Even under captive conditions they keep their system for generations, and interestingly, in captive groups composed only of females, these females tend to organize themselves around the dominant female just as an OMU (STAMMBACH, 1978). The tendency to form OMUs appears also in groups of hybrids between olive and hamadryas baboons in the Awash National Park in Ethiopia (NAGEL, 1973; SUGAWARA, 1979) providing some evidence for a clear genetic component (STAMMBACH, 1987).

When discussing possible evolutionary scenarios, phylogenetic constraints are another crucial point one has to take into account. All of the four species discussed here form one-male units within larger groups. However, according to phylogenetic reconstructions (Fig. 6), these one-male units may derive from ancestral species living in single OMUs, which united to form larger groups, as in the case of the snub-nosed monkeys, or from ancestral species living in multi-male multi-female groups which split into distinct OMUs, as in geladas or hamadryas baboons. NEWMAN and ROGERS (1999) on the other hand, see no reason to conclude that OMUs are a derived characteristic relative to multi-male multi-female groups because geladas, hamadryas, guinea and (to a lesser extent) chacma baboons all exhibit OMUs. They argue that it is equally possible, and more parsimonious, to infer that OMUs are plesiomorphic for the *Papio-Theropithecus* clade, and that savanna baboons exhibit a derived form of social organization. NEWMAN et al. (2004) argue that the tendency to form permanent male-female bonds within a multi-male multi-female social system merits at least attention as a possible plesiomorphy retained from an early, though not necessarily basal, ancestor.

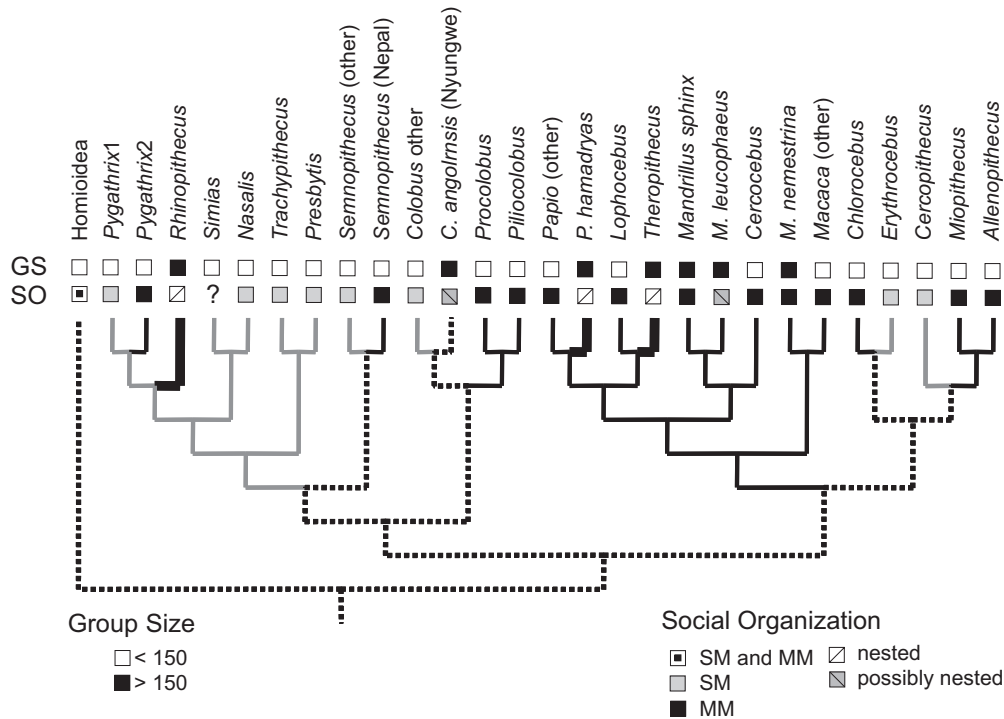


Fig. 6: Phylogenetic reconstruction of social organization (SO) in Old World monkeys. Group sizes (GS) regularly above or below 150 individuals are indicated in the top row of boxes (SM = single male, MM = multimale). (Phylogeny based on PURVIS, 1995; DISOTELL, 1996; TOSI et al., 2003).

#### Nested Systems vs. Fission-Fusion Systems

One function of the nested system of hamadryas baboons and geladas is that it allows fission-fusion (DUNBAR, 1988; KUMMER, 1990). Single OMUs or groups of OMUs can forage independently from each other, but they will gather again at certain sites in their home range, such as water places or sleeping cliffs. However, there are some peculiar differences between the hamadryas and gelada system on the one side and the 'classical' fission-fusion systems, such as in chimpanzees, on the other.

Based on the available data, hamadryas baboons and probably black-and-white snub-nosed monkeys appear to have a strict nested system because both apparently live in social systems with at least two stable and rather closed modules, i.e. the subgroup (OMU) and the larger social group (band). On the other hand, in geladas bands are more flexible and not as consistent as in hamadryas baboons, with OMUs regularly visiting other bands. Taking this into account, the gelada system can be seen as a flexible nested system with stable subunits, but unstable higher groupings. It is premature to conclude to which type of system the golden monkey social system belongs. Both types of nested systems, the strict and the flexible, contrast with classical fission-fusion societies which are characterized by only one stable higher level social unit whereas subunits are flexible and unpredictable in terms of size and composition (SYMINGTON, 1990; CHAPMAN et al., 1993). A fission-fusion

system with unstable subgroups of varying size and composition has been detected in spider monkeys (*Ateles* spp.), muriquis (*Brachyteles arachnoides*), chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) (CHAPMAN, 1990; KANO, 1982; NISHIDA, 1968; STRIER, 1992) and other mammals (e.g. lions, *Panthera leo*: SCHALLER, 1972; Bechstein's bats, *Myotis bechsteinii*: KERTH and KÖNIG, 1999).

We propose the following distinctions between fission-fusion and nested systems:

- Type I: classical fission-fusion society: level 1 (lower level) flexible, level 2 (higher level) stable (e.g. chimpanzees, spider monkeys, Bechstein's bats)
- Type II: flexible nested society: level 1 stable, level 2 unstable (e.g. geladas, proboscis monkeys (*Nasalis larvatus*), plains zebras (*Equus burchelli*), African elephants (*Loxodonta africana*))
- Type III: strict nested society: levels 1 and 2 stable (additional levels are possibly not stable) (e.g. hamadryas, possibly black-and-white snub-nosed monkeys)

The distinction between 'stable' and 'unstable' refers both to the temporal stability of group composition and to the spatio-temporal cohesiveness of the group.

#### Baboons and Evolutionary Hypotheses

The similarity between the hamadryas and gelada social organizations has often led commentators to assume that they are the products of similar selection pressures (e.g. CROOK and GARTLAN, 1966), and various authors have suggested that the ancestral forms of geladas and hamadryas baboons lived in multi-male multi-female groups such as occur in present-day savanna baboons (DUNBAR, 1988; KUMMER, 1990; BARTON, 2000). The 'band' of hamadryas baboon is regarded as the social unit analogous to the gelada 'band' and to the 'troop' or 'group' of other papionin monkeys (KUMMER, 1968a,b). There appears to be no clear equivalent in the gelada social system to the hamadryas clan. According to DUNBAR (1988), it is suggested that the following social groupings in savanna baboons and hamadryas baboons, respectively, are homologous: multi-male groups and hamadryas bands, male-female special relationships ('friendships') and OMUs, male-male coalitions and 'clans'.

#### Ecology

Ecological hypotheses assume that the multi-level organization of hamadryas was selected in response to the arid, semi-desert climate and scarcity of food resources in the habitats in which hamadryas probably evolved (JOLLY, 1963; DUNBAR, 1988; KUMMER, 1995). The hamadryas band itself seems to serve an anti-predator function since in areas with low predation bands tend to disintegrate (KUMMER et al., 1985). KUMMER (1990) further argues that, in the case of hamadryas baboons, ancestral multi-male multi-female troops began to split into smaller foraging units in response to ecological conditions (i.e. sparse dispersed food resources occurring in small patches demanding small group size and moderate predator pressure allowing small group size). At the same time there is a need for the small units to congregate regularly at certain resources, such as safe sleeping sites and water places. The distribution of food and sleeping sites then explains the fission-fusion aspect of the hamadryas system.

Female relatives tended to band together in small foraging units. A male was then able to monopolize such a small female group and a mating system based on female defense polygyny developed. KUMMER (1990) suggested that this stage is comparable with gelada OMUs. However, in the case of ancestral hamadryas baboons, the further development of herding techniques enabled males to assemble units of unrelated females which is in contrast to the gelada. Therefore, the units of hamadryas baboons are not female-bonded, but they are probably secondarily derived from a female-bonded society. BARTON (2000) argues that there is some reason to believe that hamadryas bands are effectively multi-male groups, with less cohesion among females, and perhaps more cohesion between females and males than is the case for savanna baboons (cross-bonding, BYRNE et al., 1989). Assuming the ancestral condition to have been multi-male groups, the shift to a hamadryas-type system could occur simply by weakening of female-female bonds. Males can then form autonomous units with these weakly bonded females.

Food distribution (i.e. large patches of suitable grass) allows and forces geladas to congregate into large numbers, and DUNBAR (1986, 1988, 1989) argues that, having begun with a *Papio*-like multi-male multi-female social group, the increased aggression and also reduced reproductive output associated with growing group size resulted in the females tending to bond together into small matrilineal groups for mutual protection in order to buffer themselves against the stresses imposed on them by living in large groups. The security from predators when staying on cliffs caused the small female kinship cliques to drift apart from one another, thereby making it possible for individual males to establish hegemony over them (DUNBAR, 1986). A second argument in favor of large groups is predation risk. Herd sizes are largest in areas where predation risk is high (DUNBAR, 1986). At steep safe cliffs, herds are smaller than on the plateau (*ibid.*). In order to be able to exploit the rich food sources offered by the plateau, geladas need to be able to form large herds for mutual protection against predators.

Aggregations of more than 150 individuals, sometimes more than 600, have been found in hamadryas baboons at most sleeping cliffs (KUMMER, 1968a; ZINNER et al., 2001a,b) as well as in geladas (DUNBAR and DUNBAR, 1975). In case of hamadryas baboons, these aggregations comprise normally more than one band and are not necessarily stable over time. They may change in size and composition from day to day. However, in contrast to other species that might also form large aggregations occasionally, e.g. sometimes more than one band of savanna baboons sleep at the same site (ALTMANN and ALTMANN, 1970) or under special circumstances, e.g. artificial feeding in Japanese macaques, YAMAGIWA and HILL, 1998), large aggregations in hamadryas baboons, geladas and snub-nosed monkeys seem to be more the rule than the exception.

According to DUNBAR's (1992b) 'time constraint model', maximum tolerable group size of savanna baboons in different habitats depends on environmental factors, e.g. rainfall pattern. If group size becomes too large for a certain habitat, the groups exhibit signs of ecological stress, e.g. individuals have to spend more time foraging and less time resting and in social activity. Within group competition and the concomitant need for coalitionary support among females increases, while the same time a female can allocate to service the relationships on which this support is based is reduced. When a female cohort grows too large, it is not possible anymore for fe-

males to sustain alliances, thus causing fission of the group, resulting in two stable, independent multi-male multi-female groups. A similar reasoning may account for the formation of a nested social system in geladas and hamadryas baboons. For what ever ecological reason these two species form large aggregations (e.g. predation risk, food distribution), such large groups can be assumed to be also beyond the limits within females can manage their social relationships in an adaptive way. However, in geladas and hamadryas baboons there seems to be a need to form large groups on a daily or permanent basis, and these large groups are not a result of an increase in population size as in savanna baboons. Thus permanent fission seems not an option for hamadryas baboons and geladas. Alternatively, 'internal' fission may solve the problems of females by forming small subunits. In such small units females can maintain strong social relationships to ensure coalitionary support in case it is needed.

An extended time constraint model may be sufficient to explain the internal fission of the gelada system, however, it would not fit to the hamadryas baboon system. Gelada females are believed to compete to get access to small feeding sites that cannot accommodate many individuals, and female-female competition is intensified when gelada OMUs coalesce into larger aggregations on open grasslands (BARTON, 2000). Therefore, gelada females maintain strong social bonds within small units and exhibit coalitionary support (MORI, 1979d; DUNBAR, 1979b, 1980a, 1982, 1983a). In hamadryas baboons, contest competition for food seems to play a minor role and hence, there is no need for coalitionary support among females, and female-female bonds are weak (KUMMER, 1968a; SIGG, 1980; SWEDELL, 2002b). Considering the large aggregations, an increase in the potential of sexual conflict may constitute an additional factor that shapes social structure and organization.

#### Sexual Conflict

Large groupings can be determined by various ecological needs, such as predation avoidance or optimal habitat use and foraging. Most important, these large groups may provide a possibly insecure social environment. The danger of being harassed or attacked by an unfamiliar individual might be greater than in a normal sized multi-male multi-female group of savanna baboons. In particular, the presence of a large number of unfamiliar males may pose a threat of sexual coercion and infanticide on females. In such a situation, other females may not be effective coalition partners and a female-female social network would not represent the best solution to this problem. Under such conditions, it would be in the females' interest to form stable relationships to a more powerful coalition partner, a male. Female-female relationships are loosened or given up in favor of female-male relationships (ZINNER et al., 2001c). Males in such a situation would do best when they stick to certain females permanently (monopolize) instead of competing with a large number of males for every single estrous female or mating. If additionally power differences exist among males, or if the sex ratio is female biased, OMUs with reproductive 'monopoly' for the male evolve as a result of individual female and male strategies. Ultimately, it is the demographic change, i.e. an increase in aggregation size due to ecological needs with increasing risk of harassment and infanticide, which forces females into small stable OMUs.

Also HENZI and BARRETT (2003) consider the risk of infanticide as having played a major role in shaping the hamadryas social system. However, they argue

that males cannot switch between widely dispersing temporary foraging parties of females without placing their own offspring at risk. Therefore, they adopt a herding strategy. It is both in the males' interest to bond with a few OMU females (*ibid.*) and in the females' interest to bond with one single protector male to counteract the danger of infanticidal attacks (*ibid.*; SWEDDELL and SAUNDERS, 2003). A male's herding of a few females can be seen as an energetically inexpensive alternative strategy to the intense male-male competition that characterizes the other *Papio* species (POPP, 1983). When all other males adopt this strategy, a nested system with bands composed of such OMUs emerges together with pre- or post-reproductive surplus males.

#### 'Social Brain' Hypothesis

Similar to the time-constraint model, it has also been proposed that neocortical size may constrain group size in primates because it determines the ability to process complex information about social relationships (DUNBAR, 1992c, 1998; but see van SCHAIK and DEANER, 2003). Large groups of several hundred members may therefore only persist on the condition that smaller closed subunits are formed (in the case of hamadryas baboons and geladas OMUs) in which information transfer is still feasible.

#### Snub-Nosed Monkeys and Evolutionary Hypotheses

Groups with a single male (OMUs) are the norm social units in many African (e.g. black-and-white colobus, *Colobus* spp.) and Asian colobines (DAVIES and OATES, 1994). However, within the odd-nosed monkey clade one can observe certain tendencies to form multi-male groups (douc langur, *Pygathrix* spp., LIPPOLD, 1998), monogamous groups (simakobu, *Simias concolor* TENAZA and FUENTES, 1995) and multi-level societies (*Rhinopithecus*, *Nasalis*, KIRKPATRICK, 1996b). These multi-level societies range from loose 'neighborhoods' of OMUs in proboscis monkeys, where stable one-male units regularly associate with specific other OMUs at their sleeping sites (BENNETT and SEBASTIAN, 1988; YEAGER, 1990) to tight bands of OMUs in *R. bieti* (KIRKPATRICK et al., 1998). Also in some other colobine species, OMUs have complete range overlap and at times travel together (e.g. capped langur, *Trachypithecus pileatus*, STANFORD, 1991). Nevertheless, it is most parsimonious to assume that single OMUs are the ancestral social organization of the Asian colobines (Fig. 6).

#### Ecology

In principle, similar basic hypotheses as for baboons have been proposed to explain the functional significance of the multi-level social organization in snub-nosed monkeys, although the origin of the multi-level organization is different for baboons (multi-male multi-female group) and snub-nosed monkeys (single OMU). In contrast to baboons, in snub-nosed monkeys one has to explain why several independent OMUs join together to form stable bands and not why stable multi-male multi-female groups split up into OMUs. Large group sizes seem to be a common feature in wild snub-nosed monkeys (Tab. 3). Therefore, one has possibly to focus more on benefits of large groups instead of the fission-fusion potential as in the gelada or hamadryas baboon systems.



KIRKPATRICK et al. (1998) and KIRKPATRICK (1998) provide a discussion of selection pressures favoring large group sizes in *R. bieti* at Wuyapiya and conclude that intergroup resource competition is not operant in the formation of bands and there is no obvious predation risk to produce bands of such size. However, past predation pressure (e.g. by large felids) may have formed the particular grouping patterns (KIRKPATRICK, cited in YEAGER and KOOL, 2000). It is noteworthy that snub-nosed monkeys always seem to cross open areas on the ground cohesively with all units joining in. This behavior may have been shaped by either past or recent predation or human disturbance. In any case it seems that the spatial and temporal dynamics of their primary food (lichens; KIRKPATRICK et al., 1998) does not promote strong intraband competition for food resources and thus allowing the formation of large bands (*sensu* TERBORGH and JANSON, 1986). Small band sizes of *R. bieti* in their southern range appear to reflect effects of strong environmental and human disturbances (DING et al., 2003; LONG et al., 1994). Here again, just as in geladas and hamadryas baboons, one has to take the historical socio-ecology of the species into account (HENZI and BARRETT, in press).

Large bands might also form for purposes of information sharing, perhaps as family groups follow each other to poorly known resource patches, or use each other's knowledge to avoid patches already visited (BLEISCH and XIE, 1998; KIRKPATRICK et al., 1998). This may be of particular significance in habitats where food-resources are plenty but regeneration time is low. An area that has been picked clean of lichens by snub-nosed monkeys requires at least two decades to recover. By forming large bands where all individuals visit the same feeding area, individual snub-nosed monkeys minimize the chances of foraging in an area recently picked clean of lichens. Furthermore, this may explain why these monkeys need a large home range.

Moreover, a thermoregulatory function of large bands has also been proposed. Living in large bands may provide more partners for thermal huddling (van SCHAIK, cited in BLEISCH and XIE, 1998). However, since OMUs are discrete social entities no huddling involving more than one unit is expected to occur. Furthermore, associating in bands may be an adaptation to encourage outbreeding by facilitating transfer between subgroups. However, these two latter hypotheses seem rather unlikely explanations for the evolution of large multi-level societies in *Rhinopithecus*.

#### Sexual Conflict

As in baboons, some hypotheses are related to male and female reproductive strategies. Large bands might form as OMUs aggregate to decrease the amount of harassment and possibly the risk of infanticide by non-reproductive bachelor groups, which is in the interest of females and OMU males (BLEISCH and XIE, 1998). TREVES and CHAPMAN (1996) argue for hanuman langurs that conspecific threat is the most important selective pressure influencing group size and composition. Conspecific threat was measured by using the number of non-group males divided by the number of bisexual groups. Also RUBENSTEIN (1986) argues that the most plausible scenario for the evolution of multi-level societies in zebras is that harems (OMUs) associate together in order to effectively keep their females away from the advances of bachelor males. Time allocation of vigilance is reduced

and more time can be devoted to food intake when harems are in herds compared to solitary harems (RUBENSTEIN and HACK, 2004). Protection from bachelor pressure may have some power to explain multi-level societies in snub-nosed monkeys and also geladas, but it is weakened by the fact that cooperative behavior among unit leaders does not seem to be the norm in these latter species.

In general, the perpetuation of sub-structuring of bands into OMUs is thought to be due to intense intermale competition for mates. Provided that males are able to monopolize matings, reproductive benefits to OMU males are high and predictable in a highly seasonal environment (KIRKPATRICK et al., 1998). Thus, mate defense appears to be the driving force behind the retention of OMU social organization in *R. bieti*. Based on the model of BARTON et al. (1996), it has been further argued that *R. bieti* females do not oppose male efforts to keep the band divided into OMUs because low intragroup food competition makes extended networks of females irrelevant to feeding success (KIRKPATRICK et al., 1998). If the monopolization argument is correct, the question remains why snub-nosed monkey males have large testes compared to males in single-male mating systems. This however points to a certain degree of sperm competition. Larger testes would make sense as a secondary adaptation to a decreased monopolization potential of OMU males due to the highly seasonal reproduction and the spatial closeness of possible male competitors in large bands.

#### Testing the Hypotheses

At the moment it appears impossible to test the different and not always mutual exclusive hypotheses for various reasons. Quantitative and comparable data on important variables such as food distribution and predation risk are only rarely available. In particular for hamadryas baboons a certain amount of speculation about their 'semi-arid' habitat has influenced the development of ecological hypotheses. Similarly, the impact of aggregation size on infanticide risk and therefore on female counter strategies has to remain speculative for the moment. Furthermore, it is not clear how far the contemporary 'ecological setting' of the species resembles the situation under which the individual behavioral strategies have been selected. It is important to know to what extent evolutionary environments have constrained group size and influenced adult sex ratios and, thereby, structured responses to the threat of infanticide (HENZI and BARRETT, in press). The problem of evolutionary environment becomes even worse, when one takes the variety of habitats into account that contemporary baboons in general, but also hamadryas baboons occupy (ZINNER et al., 2001a). Contemporary hamadryas baboons are by no means 'the' desert baboons, and it seems difficult to identify ecological parameters that may explain the exceptional hamadryas baboon system.

The social organization of *R. bieti* may partly be explained by constraining phylogenetic inertia and thus, low social plasticity. All four *Rhinopithecus* species are typified by OMUs in bands even though they live in strikingly different habitats, ranging from temperate to tropical (BLEISCH and XIE, 1998; BOONRATANA and LE, 1998; KIRKPATRICK, 1998). Also on the intraspecific level, the overall social organization of two *R. bieti* populations at Tacheng and Wuyapiya appears to be similar in spite of differing habitat characteristics and food preferences.

The low social plasticity or reaction norm (*sensu* KAPPELER and van SCHAIK, 2002) of geladas, hamadryas baboons and sub-nosed monkeys compared to their eco-

logical plasticity may arise from an evolved genetic substrate that is a response to historic environmental features, rather than to the precise conditions of present day habitats and may be what DUNBAR (1988) has called ‘deep’ social structure.

#### One-Male Units as a Base for Large Primate Groups?

It is noticeable that species living in a nested social organization are also species that are regularly found in large aggregations, for whatever reason, of more than 150 individuals. Based on this relation, ZINNER et al. (2001c) assumed that large aggregations are possibly incompatible with a female-female network found in a typical female bonded multi-male multi-female group. In sum, the ‘demographic’ hypothesis (*ibid.*) outlined above states that females in large aggregations tend to bond with a powerful male alliance partner rather than with other females in order to lower the risk of male harassment and infanticide. However, in gelada OMUs, a female-female social network is still existent to some degree, but reduced and mostly restricted to members of the same unit (DUNBAR and DUNBAR, 1975). Furthermore, genetical data to test female kin alliances are not available for either of the discussed species.

Cohesive primate groups of the size found in baboons and snub-nosed monkeys are rare, especially among arboreal primate species. However, geladas, hamadryas baboons and snub-nosed monkeys are not the only species that regularly form large aggregations or bands. If the ‘demographic’ hypothesis would be applicable, these other species should also show a tendency to form OMUs or special female-male relationships. In Table 11, a few species are listed that form large aggregations on a more or less regular or permanent basis. For several of the species it is not clear whether these large aggregations consist of OMUs and resemble a nested social organization. These species could be used as possible test cases of the ‘demographic’ hypothesis.

Table 11: Large group sizes and evidence for OMUs in other primates.

Taxa	Group size	OMUs	Reference
<b>Catarrhini</b>			
Mandrill <i>Mandrillus sphinx</i>	up to 845	-	ABERNETHY et al., 2002
Drill <i>Mandrillus leucophaeus</i>	up to 200; (possibly up to 400)	+ / -	GARTLAN, 1970;MORGAN et al., 2004
Guinea baboon <i>Papio papio</i>	up to 250	+?	SHARMAN, 1981
Angolan colobus <i>Colobus angolensis</i> (Nyungwe Forest, Rwanda)	>300	?	FASHING et al., 2004
Pig-tailed macaque <i>Macaca nemestrina</i>	up to 100	(+) / -	CALDECOTT, 1986; ROBERTSON, 1986
<b>Platyrrhini</b>			
Bald uacari <i>Cacajao calvus (ucayalii)</i>	>100	?	FONTAINE, 1981;AQUINO, 1988, 1995
Black-headed uacari <i>Cacajao melanocephalus</i>	>100	(-)	BOUBLI, 1994; DEFLER, 1999; BARNETT and CASTILHO, 2000; BARNETT and BRANDON-JONES, 1996

**Mandrills (*Mandrillus shinx*)** were thought to be similar to hamadryas baboons and geladas in exhibiting a multi-level society (STAMMBACH, 1987). JOUVENTIN (1975) and HOSHINO et al. (1984) suggested that the large group in mandrills is a temporary aggregation of subgroups such as OMUs. However, recent investigations led to a slightly different picture. ROGERS et al. (1996) found that group composition is multi-male, leaving the possibility of subgroups. ABERNETHY et al. (2002) came to the conclusion that mandrill hordes are based on females, with mature males only entering the horde at the onset of seasonal cycles in females. However, recently molecular evidence was found that mandrills constitute two distinct clades, possibly on subspecies level (TELFER et al., 2003, 2004). Whether these two forms exhibit the same social organization is not known.

Even less is known about another forest-dwelling papionin primate, the **drill (*Mandrillus leucophaeus*)**. Here also exist at least two subspecies, a mainland form and the form from Bioko Island (GRUBB et al., 2003). It is not known whether the social organization of drills is based on OMUs. However, GARTLAN (1970) reported that during the dry season several OMUs may form a group as large as 200. These forest baboons are certainly intriguing in many respects, and especially their social structure warrants further investigation. They are, however, extremely difficult to observe in their low-visibility tropical lowland forests, and drills in particular are unfortunately at serious risk of becoming extinct (MORGAN et al., 2004).

Another papionin monkey, albeit a savanna-dwelling, the **Guinea baboon (*Papio papio*)** may have a nested social system in which one male and 3-4 females in a subgroup forage separately and several of these subgroups coalesce at night at the sleeping site (BOESE, 1975). Very large groups have been observed (up to 250; SHARMAN, 1981), apparently containing small units led by a single adult male (BARTON, 2000). However, the subdivision into stable OMUs seems not as strict and persistent as in hamadryas baboons (DUNBAR and NATHAN, 1972; ANDERSON and MCGREW, 1984). This is also an understudied taxon.

Among the African colobines, there is only a single population of **Angolan black and white colobus (*Colobus angolensis*)** that exhibits huge social groupings. In Rwanda's Nyungwe Forest, several large groups, each containing more than 300 individuals, have been observed (FIMBEL et al., 2001; FASHING et al., 2004). Interestingly, these colobus monkeys also eat a substantial amount of lichens, similar to the snub-nosed monkeys and, in contrast to most other African colobines, they exhibit a semi-nomadic ranging behavior. So far, it has not been evaluated whether these large groups comprise OMUs. This taxon would probably constitute a test case for the 'demographic' hypothesis.

**Pig-tailed macaques (*Macaca nemestrina*)** form multi-leveled societies, and one-male groups may be one grouping level (ROBERTSON, 1986). They occasionally also form super-groups counting up to 100 individuals (CALDECOTT 1986; CALDECOTT et al. 1996).

Super large groups or aggregations appear to be primarily an Old World monkey phenomenon, with one possible Neotropical exception. Largest troops of **uacaris (*Cacajao calvus (ucayalii)*, *Cacajao melanocephalus*)** consist of 100-200 animals and they, like the Nyungwe Forest colobus, seem to be semi-nomadic (AQUINO, 1988; DEFLEER, 1999). However, for uacaris no information are available about the existence of OMUs as subgroups, but BARNETT and BRANDON-JONES (1996) con-

clude that social organization in *Cacajao* appears to be multi-male, with possible fission-fusion. However, this taxon would also constitute a suitable test case for the 'demographic' hypothesis.

Large groups consisting of stable subunits such as OMUs are also found in plains zebras (*Equus burchelli*). They live in harems which regularly associate in large, spatially cohesive herds (RUBENSTEIN and HACK, 2004), possibly more similar to the gelada organization (type II, flexible nested) than to the hamadryas baboon organization (type III, strict nested). Among taxa that regularly form large aggregations of stable subunits are African elephants (*Loxodonta africana*: MOSS and POOLE, 1983; LEE and MOSS, 2004), sperm whales (*Physeter macrocephalus*: WHITEHEAD et al., 1991) and killer whales (*Orcinus orca*: BAIRD, 2000). However, in these species, the subunits consist of female bonded family groups and males are more or less peripheral or join these groups only temporarily. According to the rather meager data available for some of the above primate taxa, the evidence for the 'demographic' hypothesis is not overwhelming. However, there are at least species (drills, Nyungwe colobus, uacaris) which can be used to test the prediction that they should show an OMU based nested organization.

#### Conclusion and Future Research

There are clearly similarities in the surface social organization (OMUs in bands) among geladas, hamadryas baboons and snub-nosed monkeys, but there are differences in the social structure, i.e. inter-individual relationships within OMUs as well as the ontogeny of OMUs. Furthermore, there are differences in the phylogenetic origins of the OMU-based multi-level social organization. In snub-nosed monkeys, it is most likely that originally solitary OMUs grouped together to form bands; in baboons, originally multi-male multi-female bands broke into OMUs which formed the band. Regarding the mating system, based on differences in relative testes sizes, it is questionable whether reproductive monopolization of OMU females is comparably strong in all species.

From an ecological perspective, there is no general and uniform rule explaining the nested societies in the two clades. Generally, large groupings may be forced by predation risk (e.g. gelada herds), but food availability and distribution must allow it, or, food-distribution itself promotes large groupings. If there is any ecological need and adaptive advantage to form 'super' large groups, than social and reproductive problems may arise. In large groups with a large number of unfamiliar individuals around, social stress may reduce fecundity in females. Females may also experience more harassment and coercion by unfamiliar, potentially infanticidal males. Males have to face intense male-male competition, due to the larger number of males in the group. Under such circumstances, the formation of small, stable units of several females and one attached male seems to be an option. The anti-infanticide argument may not fit well for snub-nosed monkeys because infanticide seems not to be a good strategy in seasonal breeders. However, we do not know where snub-nosed monkeys originally evolved. If they evolved under more tropical, non-seasonal conditions, the risk of infanticide might have been a serious problem. Seasonality of reproduction can then be regarded as a secondary adaptation after snub-nosed monkeys have moved into more temperate, seasonal regions. And second, if interbirths inter-

vals are on average two years, infanticide could pay for a new male in the first year when the female then comes into estrus in the subsequent mating season.

The nested systems are intriguing, but currently several aspects of them are not entirely understood. We are not able to identify a common functional significance of the nested system in geladas, hamadryas baboons and snub-nosed monkeys and therefore, the discussion about their adaptive value and possible selection pressures has still to remain rather speculative. Yet there is a big potential to launch more research.

In hamadryas, further work is needed on male-male relationships, especially regarding clans. Genetical aspects of the mating system, e.g. reproductive success of males, as well as the genetical relationships of males and females within and between OMUs are crucial to understand the costs and benefits of the hamadryas system. Genetical data on reproductive success and population structure would also broaden our understanding of the gelada system. Quantitative data about resource abundance and distribution would allow testing some of the socio-ecological hypotheses outlined in this review. In particular the relationship between food distribution and deme size, demography and social organization is of interest, similar to the research in chacma baboons (e.g. WHITEN et al., 1987). What degree of flexibility can we expect from the hamadryas baboon or gelada systems in relation to different habitat conditions?

Snub-nosed monkeys are a rather neglected taxonomic group. We do not have enough data about social structure (interactions) and mating system for *Rhinopithecus*. Much more data are also needed about individual life histories in snub-nosed monkey, though such data are difficult to obtain in the wild given their huge group sizes. Further comparative approaches dealing with all *Rhinopithecus* species may help to elucidate the factors governing these systems. It is of particular interest to learn more about the behavior and ecology of *R. brelichi* and *R. avunculus* which live in different environments. However, it may be too late to obtain the necessary information on *R. avunculus* since this species is critically endangered of becoming extinct in the near future.

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