



The Proboscis Monkey (*Nasalis larvatus*)
Social Group Structures

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Abstract

The proboscis monkey (*Nasalis larvatus*) is a large old world monkey, indigenous to Borneo. In the coastal areas of this island, groups of proboscis monkeys live together without a lot of territorial aggression. Studies conducted on the social organization of this monkey do not unanimously agree on its group composition. Phylogenetically it differs a lot from the other Colobines and might therefore show more resemblance to the *Papio* genus. Comparing the proboscis monkey to other Colobines shows that snub-nosed monkeys have a similar social structure. The multilevel society and fission-fusion behaviour of these monkeys make it a good example for the possible social structures of the proboscis monkey. While the baboons also exhibit these behaviours, the levels of its multilevel society are more extensive than observed for the proboscis monkey. Because of this a lot of influences on the social organization are added. This draws the conclusion that snub-nosed monkeys have the most similar social organization to the proboscis monkey. The combined literature in this thesis gives an overview of the monkey's social behaviour in the wild and mentions new insights on how to successfully keep them in an artificial environment. With the knowledge on maintaining groups of proboscis monkeys in captivity, zoos can cooperate and work against the extinction of this species in the wild.

Background of This Thesis

Presently, several primate species are threatened with extinction, among them the proboscis monkey (*Nasalis larvatus*). Threats for this monkey include loss of habitat, hunting and tourism (Sha *et al.* 2008). To protect these animals and ensure their survival in the future, two ways of intervention are available. First and foremost protecting them in their natural habitat and second, maintaining populations in captivity. However, maintenance in captivity may be difficult for species when their natural history is not known. Challenges may include their diet, but also an optimal social organization is crucial to maintain welfare and species specific behaviour in captivity.

Proboscis monkeys are highly threatened (IUCN 2008); unfortunately maintenance in an artificial environment remains difficult as well. Part of this problem is due to their dietary requirements, yet stress is also often considered to highly affect their welfare. Improving social circumstances may reduce stress in these animals in captivity. Studies on the social organization of this monkey suggest that they live in a multilevel society, but this is not well known for this species. This thesis describes the available knowledge on the social organization of the proboscis monkey. Since several aspects are unclear, in particular for males, the two sources that may provide more insight will be discussed. These are the closest relatives, i.e. Colobines, and the species with similar social organization, i.e. multilevel baboons. On the basis of this information, any similarities, differences and gaps in our knowledge will be described. As a result of this research, recommendations will be given on how the proboscis monkey can be best housed.

Introduction: The Proboscis Monkey

Colobus monkeys are part of a group named the old world monkeys, also known as the Cercopithecoidea. This group can be divided into two subfamilies, the Colobinae and the Cercopithecoinae (Oates & Davies 1994). The Colobinae, in which the proboscis monkey is categorized, contains over 30 species distributed over Africa and Asia (Oates & Davies 1994). A phylogenetic tree based on DNA polymorphisms can give more insight on the taxonomy of the monkey (Figure 1). After the distinction between the Colobinae and the Cercopithecoinae, the Colobinae are further separated into an African clade (Colobus monkeys) and an Asian clade (Langurs) (Xing *et al.* 2005).

Colobinae are often discussed for their complex gastrointestinal tract. This gives the animals the ability to neutralize the chemical effects of digesting leaves and reduces the problems that come with the digestion of inhibitors and toxins. For this reason it allows them to have their folivorous/frugivorous diet (Chivers 1994).

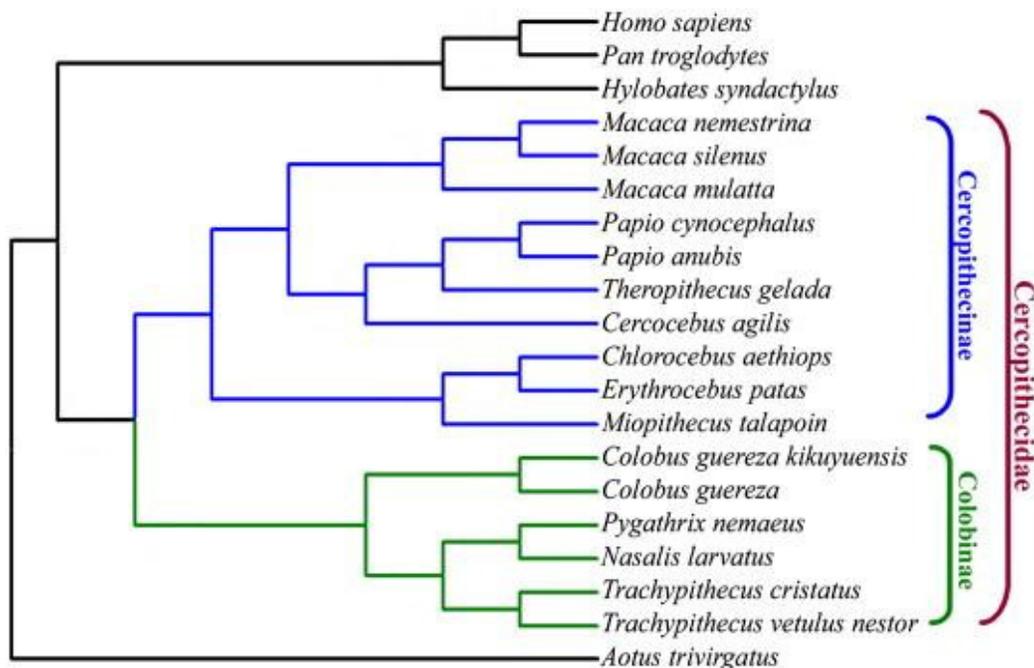


Figure 1 – A cladogram of the Cercopithecoidea phylogenetic tree, based on analysis of specific DNA polymorphisms. The proboscis monkey (*Nasalis larvatus*) is located in the centre of the Colobinae subcategory (Xing *et al.* 2005).

Like many Colobus monkeys, proboscis monkeys are arboreal, spending their nights in taller padada trees (Kawabe & Mano 1972). During night time, the proboscis monkey always tries to find a tree close to a river (Bennett & Davies 1994). During the day, groups of proboscis monkeys travel further inland, however the distance they travel is limited by the monkey's need to return to a river in the evening (Bennett & Sebastian 1988; Bennett & Davies 1994). As a result, depending on the location of rivers around the group, they can be restricted to a small part of the forest or range widely (Bennett & Davies 1994). As reviewed by (Sha *et al.* 2008), the monkeys can be found up to 750 km inland, but are often closer to the coastal area, on average 55 km away from the coast. The proboscis monkey is known to be mostly confined to riverine, mangrove, peat swamp and fresh water swamp forests (Bennett & Sebastian 1988; Meijaard & Nijman 2000). Populations of this monkey have been spotted in Kalimantan, Sabah, Sarawak and Brunei, all regions of the island of Borneo (Kawabe & Mano 1972; Meijaard & Nijman 2000).

As mentioned before, the social organization of the proboscis monkey remains rather unclear. In the early days of studies on this monkey, there has been a lot of discussion on whether or not the proboscis monkey lives in multi-male units (MMUs) or one-male units (OMUs). Mostly older studies mentioned observations of MMUs, describing the proboscis monkey as living in multi-male groups with a social organization comparable to the silver-leaf monkey (Kern 1964; Kawabe & Mano 1972; Macdonald 1982; Salter *et al.* 1985). Later on, the idea of the proboscis monkey in an OMU-based society was considered (Bennett & Sebastian 1988; Yeager 1990; Yeager 1991; Boonratana 2000).

Explanations for this large discrepancy between observations can be intraspecific variation or a discrepancy in methodology between the different studies could be the case (Yeager 1990). The definition of the term group seems to be one of the most important aspects. While early studies include individuals in a group when they are located within 100 meters of each other, more recent research has added further requirements (Kern 1964; Macdonald 1982). For instance, spatial distribution of the animals while in a 100 meter radius can help dividing the large multi-male group into smaller OMUs (Yeager 1990). In addition, observing the group movements can help deciding on its members. As described earlier, groups of proboscis monkeys join together during night times, which may have been a cause for the less apparent group formations. On the other hand, when evaluating the possibility of intraspecific variation for the proboscis monkey, this would mean that the habitat in which the observations were done may have an influence on the existence of multi-male groups (Yeager 1995). The first studies noticing loosely organized MMUs observed the proboscis monkey in nipa swamp forests (Kern 1964), while the stable MMUs are described during a study mostly in mangrove swamps and tropical rain forest (Kawabe & Mano 1972). Studies done in riverine forests mention observations of all-male units (AMUs) as well as OMUs (Bennett & Sebastian 1988; Boonratana 2000; Matsuda *et al.* 2009). This is equal to what is found in freshwater peat swamp

forest by (Yeager 1990). Looking at this, it might be concluded that nipa and mangrove swamp forests are a habitat preferred by MMUs, while riverine and freshwater peat swamp forests are inhabited by AMUs and OMUs. However, this option is severely disputed by studies that performed observations in the same area in which only MMUs were described earlier (Kern 1964; Macdonald 1982; Yeager 1995). With the use of the broadened methodology, described before, they conclude no MMUs exist in this area, thereby rejecting the possibility of intraspecific variation (Yeager 1995). The existence of MMUs was discarded and OMU is now accepted as the basic unit of the proboscis monkey.

Apart from the OMU, AMUs have been reported for the proboscis monkey as well. All-male groups for this species consist of around nine individuals, with members varying frequently and females occasionally joining the group too (Bennett & Sebastian 1988; Murai 2004). More recently however, larger groups of 29 individuals have been observed (Murai 2004), this suggests that the number of members within an AMU can vary widely. An interesting feature of AMUs is that they have a larger range than OMUs. It might be that AMUs come across OMUs more often this way, creating possibilities for the bachelor males to take over a harem group (Murai 2004). The AMUs seem to be a temporary option for most of its members. The group is joined by mostly juvenile or sub-adult males and left by young adults forming their own OMU (Murai 2004). While AMUs are a rather common sight, according to some reports the proboscis males are rarely observed solitary (Yeager 1990). This in contrast to what was thought in other studies on this monkey, in which males were suggested to be solitary frequently (Bennett & Sebastian 1988) or occasionally (Yeager 1991). More recent studies claim that young males can become solitary for a while, until reaching adulthood and joining a bisexual group to reproduce (Murai 2004).

Not only males can migrate between groups, females have also been reported to leave their group regularly (Murai *et al.* 2007). Sub-adult females switch more between groups than adult females and they spend time in AMUs as well (Murai 2004). One of the main causes for the females to leave their natal group is to avoid inbreeding (Clutton-Brock 1989). This is possibly the foremost reason why the transferring females are generally in a sub-adult status, since they leave their natal group when reaching sexual maturity (Murai *et al.* 2007). When an adult female decides to leave a group the dominant male of the old group might try to call the transferring female back to their original group. When it is a sub-adult female however, males might not even show interest in the female leaving (Murai 2004). When the females depart from their natal group, they often leave their sons to AMUs. This type of switching between groups is also known as fission-fusion. Fission-fusion dynamics refer to groups with a highly variable composition as a result of merging and splitting into subgroups, a social organization used by for instance chimpanzees or orang-utans (Amici *et al.* 2008). Fission-fusion activities go hand in hand with multilevel societies. A multilevel society can be recognized by its stable units, which

often or permanently associate with other units, creating another level of social grouping (Grueter & Van Schaik 2010). Thus, the proboscis monkey lives in a multilevel society with fission-fusion dynamics. In this society, the OMU is the basic unit, but AMUs are observed as well.

The proboscis monkeys currently have an endangered status on the IUCN Red List of Threatened Species (IUCN 2008) and there are signs that their numbers are further declining (Sha *et al.* 2008). Besides protecting the animals in their natural environment, zoos are able to help the survival of this animal as well. However, partly due to the uncertainties of the social organization of the proboscis monkey, they are not often successfully kept in an artificial environment. Only a small number of studies has been done regarding their social organization in captivity. The few studies mentioning the proboscis monkey in captive social units are describing OMUs, therefore this is most likely the most used social composition in captivity (Dierenfeld *et al.* 1992; Yeager *et al.* 1997; Agoramoorthy *et al.* 2004; Cui & Xiao 2004). A recent study however, has focussed on the maintenance of an AMU in captivity at Singapore Zoo (Sha *et al.* 2012). This idea was created due to the presence of surplus males, which can be a problem to maintain in captivity. They cannot remain in the same group as they grew up, since adding adult males to an OMU causes stress and fights within the group (Sha *et al.* 2012). For this reason the surplus males require extra maintenance and space; however it now seems that AMUs can be formed to solve this.

In sum, the multilevel society with fission-fusion structures is of great influence on the overall social organization of the proboscis monkey. It can be concluded that the monkeys may switch between groups during the different phases of their lives. Solely stating that they live in OMUs and AMUs does not explain the complete social situation of this monkey in the wild. This should be taken into consideration when reaching a conclusion after evaluating the resemblances between the different animal species.

Social Organization

To find out more about the social organization of Colobine and baboon species, it is important to be aware of the types of social living, primates exhibit. Depending on many factors, for instance nocturnal versus diurnal animals, primates have all developed their own social organization. The external influences on social organization can be summarized in a scheme (Figure 2). The three main ecological influences that can cause changes in social behaviour are also three aspects that are affected by the group formation, namely feeding, predation and reproduction (Van Schaik & Van Hooff 1983). Competition for food is higher in large groups and lower in smaller groups. Naturally the availability of food within the group's range is important as well (Van Schaik & Van Hooff 1983). On the other hand, predation pressure triggers an anti-predation response. These two behavioural responses affect group size, where both large groups and small groups can each have their advantages. Large groups are easily spotted by a possible predator; however the members of the group have a larger chance of spotting the predator as well and fleeing away in time. Small groups however, may not be spotted as easily, but they are more likely to be caught since they might not notice the predator in time (Alexander 1974). Group size and the group cohesion influence a male's ability to monopolize females and thereby affect mating strategies and the resulting group composition. At this point, the influencing factors start to have an effect on the social organization of the group. The scheme concludes with patterns in social behaviour, which is affected by the group composition and relatedness. Migration and emigration within a group influence the relatedness between members, which has an effect on animals coming to the aid of one another (Massey 1977).

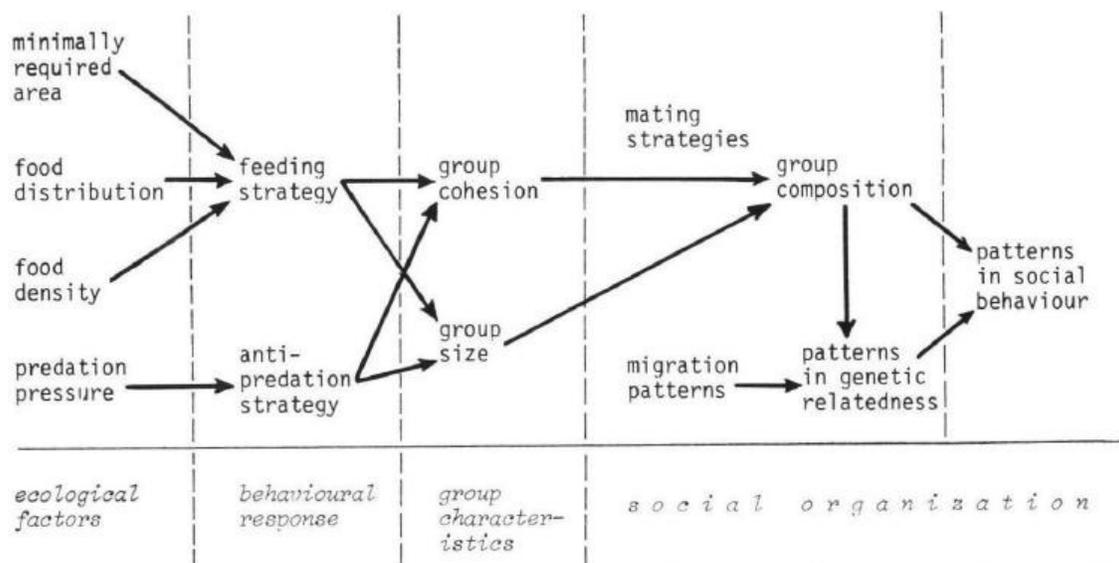


Figure 2 – Schematic view of the ecological effects on the social organization of primates, adjusted from (Van Schaik & Van Hooff 1983)

Animal species early in the evolution are generally thought to be solitary and nocturnal (Eisenberg *et al.* 1972). With this as a starting point, those species were affected by external influences to eventually change their social organization and evolve. Looking at social organization alone, three types of organization can be described, namely solitary animals or animals with one or multiple group members.

The social structure of solitary primates can be described as a neighbourhood, in which animals are familiar with other animals in their range, yet they all are separate social units (Richard 1985; Kappeler & Van Schaik 2002). A second form of social organization is living in pairs, which is one of the rarest forms of social organization in primates (Kappeler & Van Schaik 2002; van Schaik & Kappeler 2003). Living in pairs compared to in a group, does not seem beneficial most importantly for the reason that it declines reproduction options (Kappeler & Van Schaik 2002). The third type of social organization, exhibited by the majority of primates, is group-living.

Group living primates is a very broad type of social organization, in which many more distinctions are made that are all affecting the social behaviour of the animals. The ratio of male and female individuals within the group can give rise to further divisions within this large group, leading to multi-male, multi-female or multi-male multi-female units (Eisenberg *et al.* 1972; Kappeler & Van Schaik 2002). A second important distinction in group living animals is often made, namely between one-male and multi-male groups. This distinction can highly affect the social behaviour of the animals in terms of resource and group defence or aggression (Van Schaik & Van Hooft 1983; Terborgh & Janson 1986; van Schaik & Kappeler 2003). In groups with multiple males, the males will join together to form a cooperative defence against possible predators, while in one-male units defending multiple females might become a problem (Terborgh & Janson 1986). The social organization of group living primates could become even more complex when units join together and form multilevel societies and fission-fusion activities occur. A good example of a primate species living in a extensive multilevel society is the hamadryas baboon, which will be discussed in further detail later on (Stammbach 1987). In sum, group living primates can vary widely in social organization, from rather simple multi-male units to one-male units within multilevel societies.

After considering the types of social organization, it has become clear that all three types have their advantages as well as their disadvantages (Kappeler & Van Schaik 2002). Thus, there is no single optimal group structure; depending on environmental influences a group can find its own balance.

Colobines: Assessing Phylogenetic Species for Similarity in Social Organization

To find out whether the social organization of the proboscis monkey and the role of the males within these groups are comparable to what occurs in other Colobine species, this section will revolve around the social organization of the Asian Colobines. When only looking at group sizes of Asian Colobines, large differences can be found between species, for example the troop size ranges from around four animals (Mentawai leaf-monkeys) to troops of over 400 animals (snub-nosed monkeys) (Newton & Dunbar 1994). This and many other aspects affect the type of social organization per species.

Three types of social organization have been observed in Asian Colobines, namely separate OMUs also known as non-multilevel societies, multilevel societies and large multi-male multi-female groups (Grueter & Van Schaik 2009; Grueter & Van Schaik 2010). A couple of studies mention a monogamous lifestyle for some Colobine species as well (Bennett & Davies 1994; Newton & Dunbar 1994). In Table 1 an overview of the social organization of frequently studied Asian Colobines is given, including unit size, unit composition, the presence of AMUs and social organization. The first column represents unit size, which is for the proboscis monkey around 13.4 according to this study, however looking at other studies the number of members in one group often varies (Bennett & Sebastian 1988; Newton & Dunbar 1994; Grueter & Van Schaik 2009). Including the relatively larger AMUs, in which males can spend several years, the number is a little higher than suggested by earlier studies (Bennett & Sebastian 1988; Oates & Davies 1994). Secondly, unit composition is mentioned, described as either a one-male or a multi-male unit. The standard composition for the Asian Colobines seems to be the OMU, apart from several species of the genus *Semnopithecus* who have a clear multi-male multi-female organization (Grueter & Van Schaik 2010). The third column shows whether or not the species include AMUs, suggesting that in almost all species AMUs are present. Finally, the type of social organization is divided into two groups, namely multilevel or non-multilevel. As mentioned before, multilevel societies can be explained as stable units often or permanently associating with other units, creating another level of social grouping (Grueter & Van Schaik 2010). While most Asian Colobines are non-multilevel, the proboscis monkey and all species of the *Rhinopithecus* genus show a multilevel social organization. Table 1 shows that on all four aspects the Colobine species differ significantly from each other and it is not possible to form one conclusion about their social systems.

Species	Unit size	Unit composition	AMU	Social organization
<i>Presbytis comata</i>	6.7	OM	No	Non-multilevel
<i>Presbytis siamensis</i>	15.1	MM	UK	Multilevel
<i>Presbytis thomasi</i>	8.9	OM	Yes	Non-multilevel
<i>Presbytis potenziani</i>	3.8	OM	No	Non-multilevel
<i>Presbytis rubicunda</i>	6.4	OM	Yes	Non-multilevel
<i>Presbytis hosei</i>	7.5	OM	UK	Non-multilevel
<i>Trachypithecus obscurus</i>	17	MM	Yes	Non-multilevel
<i>Trachypithecus geei</i>	10.7	OM	Yes	Multilevel
<i>Trachypithecus vetulus</i>	8.9	OM	Yes	Non-multilevel
<i>Trachypithecus johnii</i>	7	MM	Yes	Non-multilevel
<i>Trachypithecus phayrei</i>	14.3	MM	UK	Non-multilevel
<i>Trachypithecus leucocephalus</i>	10.3	OM	UK	Non-multilevel
<i>Trachypithecus pileatus</i>	8.6	OM	Yes	Multilevel
<i>Trachypithecus francoisi</i>	9.5	MM	UK	Non-multilevel
<i>Semnopithecus entellus</i>	21.2	MM	Yes	MM-MF
<i>Semnopithecus schistaceus</i>	23.7	MM	UK	MM-MF
<i>Semnopithecus priam</i>	29.4	MM	UK	MM-MF
<i>Simias concolor</i>	5.2	OM	No	Non-multilevel
<i>Rhinopithecus bieti</i>	8.3	OM	Yes	Multilevel
<i>Rhinopithecus roxellana</i>	13	OM	Yes	Multilevel
<i>Rhinopithecus brelichi</i>	6.2	OM	Yes	Multilevel
<i>Rhinopithecus avunculus</i>	12.9	OM	Yes	Multilevel
<i>Pygathrix nigripes</i>	11.3	MM	UK	Multilevel
<i>Nasalis larvatus</i>	13.4	OM	Yes	Multilevel

Table 1 – An overview of the unit size (mean # of animals), unit composition (one-male or multi-male), the presence of AMUs (yes, no or unknown) (Newton & Dunbar 1994) and social organization of the Asian Colobines for which sufficient data are on hand. Social organization is described as multilevel, non-multilevel or multi-male multi-female (MM-MF). Table adjusted from (Grueter & Van Schaik 2009).

In addition to the most basic units in the social organization of Colobines, the OMU, AMUs play an important role in the system as well. In an AMU, group members are frequently juvenile, while the middle-aged and old males are more often found in OMUs. In Colobines, all male groups have been observed in 17 species (Murai 2004). For instance, for the Eastern black-and-white Colobus (*Colobus guereza*) the maturation of younger animals and immigration of foreign males can lead to the formation of these groups (Oates & Davies 1994). Many Colobine populations, e.g. langur species, banded-leaf monkeys and red-leaf monkeys, also have extra-troop males, who join other units or bands than their natal unit and try to get access to its females (Newton & Dunbar 1994).

Table 1 gives an overview of the similarities and differences between the social organization of the proboscis monkey and the other Colobinae. While some genera, like the *Semnopithecus*, do not seem to share any social aspects, others are very similar to the proboscis monkey. The snub-nosed monkey (*Rhinopithecus*) comes closest to the proboscis monkey regarding social organization (Kirkpatrick *et al.* 1998). Both species are known to have a multilevel society, with large range overlaps between units (Bennett & Davies 1994). The Yunnan snub-nosed monkey (*Rhinopithecus bieti*) society consists of mostly OMUs, but AMUs were observed as well. Those OMUs and the occasional AMU join together to form a band, in which 15 to 18 units can be found (Kirkpatrick *et al.* 1998). Sub-adult males of the Yunnan snub-nosed monkey join AMUs as well and may switch between one-male and all-male units within the band (Kirkpatrick *et al.* 1998). Depending on the season, aggression between males was observed between units within a band, which is similar to what occurs in other Colobine species (Kirkpatrick *et al.* 1998; Struhsaker 2000). However, another snub-nosed monkey species with similar social organization, the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*), does not show much inter-unit aggression and there seems to be no clear hierarchy between the units (Zhang *et al.* 2008). Within an OMU not much aggression is observed for most Colobines, including the snub-nosed monkeys (Struhsaker & Leland 1987; Kirkpatrick *et al.* 1998; Zhang *et al.* 2008). Regarding aggression during takeovers, lack of knowledge makes it impossible to form an opinion on this subject. It is known that after a takeover, a new resident male snub-nosed monkeys will not receive any support from its females during fights (Zhang *et al.* 2008).

In conclusion, it has become clear that it is definitely not possible to consider all Asian Colobines as one regarding social organization and attention should be given to all separate species to be able to form a conclusion on their social system. The multilevel society with fission-fusion structures of the snub-nosed monkeys suggests that, among the Colobines, they are most similar to the proboscis monkey.

Baboons: Judging Similarity in Social Organization

Looking at species with a similar social organization, but without a close phylogenetic relation, can create another view on the proboscis monkey's social organization. The multilevel society and fission-fusion structures, as mentioned before, have frequently been observed in several species of the tribe *Papionini*, namely gelada baboons (*Theropithecus gelada*), hamadryas baboons (*Papio hamadryas*) as well as drills (*Mandrillus leucophaeus*) and mandrills (*Mandrillus sphinx*) (Stammbach 1987). This section will take a closer look at their social behaviour and group composition to find out more about the similarities and dissimilarities to the proboscis monkey.

The social organization for most baboon species is generally a large group of animals, living in single level multi-male groups. In these groups, the females form the foundation of the group and the males can switch between groups to find mates for breeding (Barton 2000). Nonetheless, bonds between males and females of the *Papio* are of high importance. For the males it is a reproductive certainty and for the females it ensures protection when necessary (Dunbar 1987). However, the hamadryas and gelada baboons show a different social organization to other *Papio*, which is more similar to the organization of the snub-nosed monkey species.

Hamadryas baboons live in multilevel societies with fission-fusion activities, in which all animals are members of an OMU. Frequently however, two or three OMUs join together into a clan, which are often formed during foraging (Stammbach 1987). Clans can join to form a band, in which they have social interactions. During night times, bands can come together at a sleeping site and compose a troop (Kummer 1984). In contrast to most baboon species, females of the patrilineal hamadryas baboon transfer between units instead of the males (Barton 2000). These females do not share as strong relationships with each other as they do in other baboon species (Barton 2000). In contrast to the large clans of snub-nosed monkeys, the hamadryas clan exists of only two to three OMUs, making it easier to evaluate the position of the males. Within the clan, males can have four possible roles (Figure 3). First there is a unit leader per unit, most often an adult male. There can be one or more followers of the clan, who can be divided into two categories, namely leaders of initial units or bachelors. An initial unit is a pair of a male and a female individual forming a small unit within an OMU. Initial unit leaders are looking for a takeover opportunity when they have reached maturity. The other type of follower, the bachelor, is often a sub-adult male that simply follows the clan. Another male within a clan can be an aged male, often the former leader of one of the units, who remains with its clan.

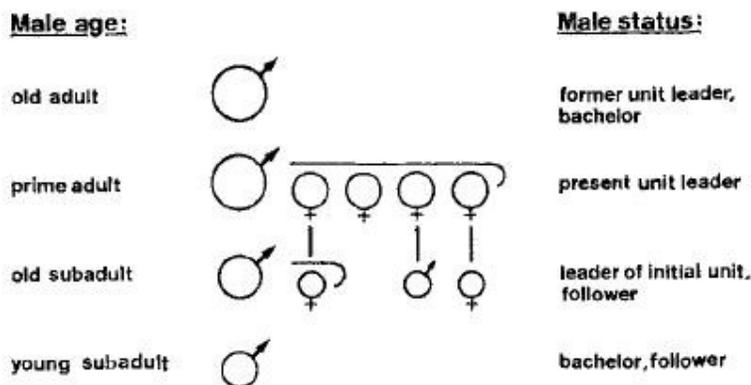


Figure 3 – The four roles of the males within a hamadryas baboon clan. An old adult within a clan is often a former group leader. There are prime adults as the current unit leaders. And there can be several followers, who can be subcategorized into two groups, namely leaders of the initial unit or bachelors (Kummer 1984).

The unit leader will have control over the females and monopolize them against other males (Kummer 1984). Group takeovers are mostly done by males returning to their natal unit when reaching adulthood, where they create a bond with a female of this group and form its own group. Between males, fights may be elicited to try and take over a unit as well, during these fights females may separate and new OMUs can be formed (Abegglen 1984; Stambach 1987). Furthermore, between units of a clan not a lot of aggression is reported. On the other hand, within units aggression may take place, especially herding can be performed in an aggressive manner (Stambach 1987)

In geladas, OMUs can join together to form a band as well, however contrasting to hamadryas baboons, their band membership is not as constant (Stambach 1987). Males may also join an AMU when they are not in an OMU, which is similar to what snub-nosed monkeys do, but not often observed for hamadryas baboons (Stambach 1987). Joining and leaving an AMU occurs when the unit associates with an OMU and males can attempt a takeover this or join the AMU as a follower (Kawai *et al.* 1983). When food is less available, OMUs and AMUs can form a herd, comparable to a troop. OMU takeovers can be strategic as well as aggressive for this species. According to the “follower strategy” gelada males may join an OMU in the role of a follower, but may take over several of the leader’s females and begin his own group, which is similar to the behaviour of hamadryas males. Another way to take over a unit is by simply attacking a weaker unit leader and become leader of the group after winning the fight (Stambach 1987). Aggression between units occurs rarely, similar to hamadryas baboon. For geladas, aggression within units is uncommon as well, which is in contrast to the hamadryas baboons (Stambach 1987) Gelada baboons seem to have a similar set up as hamadryas with some functional differences, for instance gelada baboons are

matrilineal whereas hamadryas are patrilineal, resulting in a larger role for the males in the hamadryas society than with geladas (Kawai *et al.* 1983).

Older reports mention that mandrills and drills live in OMUs as well and meet in larger groups from time to time (Stammbach 1987; Barton 2000). More recent reports however, state that there is no evidence of OMUs in the mandrill society (Abernethy *et al.* 2002). Older mandrill and drill males could be living solitary. Additionally, AMUs have not been observed for these species (Stammbach 1987). It remains difficult to come to a conclusion since not many studies have been done on these animals. A reason for this is that these monkeys are difficult to follow in the wild due to low visibility in their habitat (Abernethy *et al.* 2002). Researchers do state that females and their infants live together in groups and are joined by males during the breeding season, which is in agreement to the suggestion that males might live solitary (Abernethy *et al.* 2002). Concluding, the social organization of the mandrills and drills is still unclear on multiple levels and needs more studying to be able to form a conclusion.

While the discussed baboon species are a lot more similar in their social organization than the many Colobinae species, it has become clear that they have more differences than might be expected. Looking at the mandrills and drills, their social organization may not be as similar to the proboscis monkey as expected. If, as suggested by later studies, the OMU is not their basic unit, they may only slightly resemble the social organization of the proboscis monkey. The lack of knowledge of the social organization makes it impossible to compare to the proboscis monkey adequately. The hamadryas and gelada baboons however show similarities in social organization to the proboscis monkey, i.e. multilevel societies with the OMU as a basic unit. The main difference between those two is the absence of AMUs within the hamadryas system. Another important difference is the extent of the role of the males in the groups, since male hamadryas have a lot more influence in the unit than male geladas, for which the proboscis monkey is similar to the geladas. Table 2 gives an overview of the several aspects of the social organization of these four baboon species and the proboscis monkey. This shows most similarities between the proboscis monkey and the gelada baboons, as concluded before.

Species	Unit size	Unit composition	AMU	Social organization
<i>Theropithecus gelada</i>	10	OM	Yes	Multilevel
<i>Papio hamadryas</i>	7.3	OM	No	Multilevel
<i>Mandrillus leucophaeus</i>	15-20	UK	No	Multilevel
<i>Mandrillus sphinx</i>	20-25	UK	No	Multilevel
<i>Nasalis larvatus</i>	13.4	OM	Yes	Multilevel

Table 2 – An overview of the average unit size, unit composition (one-male or multi-male), the presence of AMUs and social organization of four baboon species (Kummer 1984; Stammbach 1987; Abernethy *et al.* 2002). UK stands for unknown.

Discussion

Proboscis monkey: more similar to colobine or baboon social organization

In this thesis a phylogenetic evaluation and an evaluation of species with similar social structures were done, comparing the two to the social organization of the proboscis monkey. This created the opportunity to critically discuss its resemblance to the Colobus species as well as species with similar social societies, i.e. baboons. The many different social organizations of the Colobinae make it difficult to form one conclusion on the social organization of the genus. It does however show that the Sichuan and Yunnan snub-nosed monkeys can be potential models for the proboscis monkey. The multilevel society that they exhibit is observed for the proboscis monkey as well (Yeager 1991; Boonratana 2000). Multilevel societies are also what baboons are known for, especially hamadryas and gelada baboons. This section will evaluate whether the snub-nosed monkeys or the baboon species provide a better model for the social organization of the proboscis monkey.

Starting with to the comparison between the proboscis monkey and the snub-nosed species, their multilevel societies are very similar. The fission-fusion activities that are observed in the snub-nosed monkey society were not mentioned by earlier studies on the proboscis monkey. Part of the studies do mention observations of this type of behaviour (Kawabe & Mano 1972; Macdonald 1982; Newton & Dunbar 1994), but others state the contrary (Kern 1964; Boonratana 2000). More recently, the social organization of the proboscis monkey was described in more detail, eliminating this uncertainty (Boonratana 2000). Researchers of this study state “*Nasalis larvatus* have a flexible social structure with a one-male multi-female (or polygynous) group as the basic social unit. Furthermore, there is a secondary level of social organization—the band—with (fission–fusion of stable one-male groups within bands.” Thus, this type of social organization is similar to the snub-nosed monkeys as well as hamadryas and (Macdonald 1982) gelada baboons (Kawai *et al.* 1983; Yeager 1991).

Another similarity between the two is the amount of aggression observed. Generally for snub-nosed monkeys, not a lot of aggression has been observed between individuals that are in a unit together (Kern 1964; Kawabe & Mano 1972; Salter *et al.* 1985; Struhsaker & Leland 1987; Kirkpatrick *et al.* 1998; Zhang *et al.* 2008). Between units, territorial aggression might take place for the Yunnan snub-nosed monkey, but is not often recorded for the Sichuan snub-nosed monkey (Struhsaker 2000; Zhang *et al.* 2008). Looking at the baboon species, the hamadryas baboons do exhibit aggressive behaviour within a unit, but are also tolerant to other units. Regarding another type of aggression, for baboons several studies have been done on the situation during takeovers, which suggested that the males are known for their violent attacks against the unit leader of their own or others groups

(Abegglen 1984; Stambach 1987). Unfortunately, lacking information on aggression during snub-nosed and proboscis monkey takeovers inhibits the possibility to compare them to the baboons on this subject.

In literature, when snub-nosed monkeys are discussed for their social organization, often a reference to baboon species is made as well (Barton 2000; Zhang *et al.* 2008). When looking at the mandrill and drill species though, there are too many unclear parts of the social organization to form a conclusion and make a reliable comparison to the proboscis monkey. The hamadryas and gelada baboons are more frequently studied and show many similarities to the proboscis monkey in social organization. The extensive multilevel societies that the hamadryas baboons have and the resulting large troops are not necessarily mentioned in studies on the proboscis monkey. The hamadryas baboon's multilevel society consists of more levels (Stambach 1987; Barton 2000) than the described two levels (OMUs within bands) of the proboscis monkey (Boonratana 2000).

Both the gelada and the hamadryas baboons have comparable parts of social organization to the proboscis monkey, but the gelada may be the best comparison to the proboscis monkey for the *Papio* genus. Very important for this decision is the presence of AMUs in the gelada baboon society, which is not mentioned in studies on the hamadryas baboon. This however is reported for the proboscis monkey and plays a great role in the maturation of the males (Stambach 1987). Adding that the hamadryas baboons are patrilineal, this is not the case for the proboscis monkey. In this monkey's social system, switching between units is often performed by the males and only occasionally by a female animal, which is also described for the gelada baboon (Stambach 1987; Murai *et al.* 2007). Looking at these similarities, it seems that out of the four *Papio* the gelada baboon comes closest to the proboscis monkey regarding social organization.

To sum up, the snub-nosed monkey and the gelada baboons show many resemblances to the proboscis monkey in social organization. Both primate species rarely show aggression within and between units. The relatively higher number of levels to the society of the geladas compared to the two-level organization of the snub-nosed monkeys makes the snub-nosed monkey more similar to the society of the proboscis monkey regarding social organization (Stambach 1987; Kirkpatrick *et al.* 1998). This leads to the conclusion that the proboscis monkey in captivity should be adjusted to the situation of the snub-nosed monkeys in captivity.

Captivity

In captivity it is understandable that fission-fusion structures cannot take place. Surplus males are most often single housed, since it has become obvious that keeping more than one adult male in a group, creating a multi-male multi-female group, would lead to an aggressive and stressful environment for the animals. Housing animals alone however, increases the care and space needed. The formation of captive AMUs seems to be a successful answer to this problem, especially since this is a natural solution. As mentioned before, only a small number of studies has been done regarding the social organization of the proboscis monkey in captivity, all describing OMUs. Recently however, Singapore Zoo has successfully created an AMU in captivity, which solves many of the problems, e.g. surplus males and housing space (Fàbregas & Guillén & Salazar 2007; Sha *et al.* 2012). Another species that was studied on the formation of an AMU in captivity is the white crowned mangabeys (*Cercocebus atys lunulatus*) at Valencia Zoo. This study concluded that when the males are socially compatible, this is a very feasible solution to surplus males. A group of male lion-tailed macaques (*Macaca silenus*) was successfully kept in an AMU, with fewer disadvantages than experienced with males housed solitary or in a multi-male multi-female group (Manns 2000). Proboscis monkeys were observed when a group of six males were joined together forming an AMU (Sha *et al.* 2012). This study noted all aggressive and affiliative behaviours and showed that after six weeks of introduction, the aggressive behaviour showed a decline while affiliative behaviour then increased and a hierarchy appeared (Sha *et al.* 2012).

Conclusion

Coming back to the original comparison, the best model for the social organization of the proboscis monkey is the snub-nosed monkey. With its two-layered multilevel society and low aggression levels within and between units, its social organization is similar to the proboscis monkey. Combining this information with knowledge of the proboscis monkey in captivity, results in a recommendation to keep the proboscis monkey in artificial AMUs. The formation of an OMU in captivity results in a much higher stress levels, as parts of their natural behaviour, e.g. fission-fusion activities to control the number of males within a group, are suppressed.

Broadening the understanding of the social group structures of the proboscis monkey in the wild can help optimizing the situation for their counterparts in captivity. When this Colobine can be kept in an artificial environment without much difficulty, zoos can maintain breeding programs and cooperate against the extinction of this species in the wild.

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