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FEMALE PRIMATES –
ARE GORILLAS SPECIAL?
AN INTRODUCTION.

Socioecological models on female primate social relationships

Social organizations are constructs emerging from pattern and quality of social interactions and individual behavioral strategies (Hinde 1974, 1976, van Hooff 1988). Social relationships allow members of a community the prediction of conspecific behavior to frame more efficient interactions (van Schaik & Aureli 2000). Female social relationships will be the emphasis of this study. The current socioecological model assumes within-species competition as a primary factor in the evolution of sociality (van Schaik 1989, van Hooff & van Schaik 1994, Sterck et al. 1997). Van Schaik and van Hooff (1983) have argued that the spatial-temporal distribution pattern of females is mainly determined by ecological factors such as food distribution and predation pressure. For females, food is seen as the key resource for reproductive success (Trivers 1972, Wrangham 1979). For example, to avoid competition over food, a solitary life would be most advantageous. However, other constraints, such as predator presence ("predator-defense" theory, Harcourt 1981c, Dunbar 1988, Treves 1999) and the need for protection for themselves and their offspring, may force females to live in groups (van Schaik 1983, van Schaik & Kappeler 1997, "conspecific-threat hypothesis": Treves 1998). Males are expected to adapt to female distribution and demands, as females are the key resource to male reproductive success (Wrangham 1980, van Schaik 1996).

Wrangham (1980) invented the terms "female- and non-female-bonded" societies, based on the main cohesive social units in a group, mostly represented by matrilines that can increase their inclusive fitness by helping kin. According to this definition, species with female dispersal can also be classified as female-bonded, if female-female dyads build the core of the group. These classifications were extended by other authors, who included predation and infanticide as important factors for female reproductive success (van Schaik 1989, 1996, van Hooff & van Schaik 1992, Sterck et al. 1997). However, large-bodied primates face reduced predation risk (Cheney & Wrangham 1987, Janson 1998). Based on sexual selection, socioecological theory predicts the majority of behavioral traits and was tested on a variety of primate taxa with differing results (for example: *Saimiri oerstedii* and *S. boliviensis*: Mitchell et al. 1991, *Saimiri*: Boinski et al. 2002, *Presbytis entellus*: Borries 1993, Koenig et al. 1998, *Presbytis thomasi:* Sterck 1995, *Macaca fascicularis*: van Schaik & van Noordwijk 1988, *Pan troglodytes verus*: Wittig & Boesch 2003, *Pan troglodytes schweinfurthii*: Williams et al. 2002, *Gorilla beringei beringei*: Watts 2003, comparative: Janson 1988, Chapman et al. 1989, Sterck 1999, Johnson et al. 2002).

Four competitive regimes, influencing social organization and behavior, are outlined. These organizations are mainly based on the intensity of within- and between-group competition (either scramble or contest, van Schaik 1989), shaped by female group transfer activities. Basically, dispersal appears facilitated, if the food situation is relaxed, predation pressure is neglectable and cooperation with other group members does not augment access to (food) resources. Therefore female-dispersal species are expected to form only weak ties among the mostly unrelated females and egalitarian structures ("dispersal-egalitarian"). Female philopatric species, the majority of primate taxa, can either establish nepotistic relationships with strong within-group competition ("resident-nepotistic"), the opposite with egalitarian group structure but intense between-group competition ("resident-egalitarian") or a system with both intense within- and between-group competition, where matrilines support each other in contests, form stable bonds and where tolerance more than aggressive traits are features of high ranking individuals ("resident-nepotistic-tolerant", Sterck et al. 1997). A discussion on recent theoretical considerations in the light of the above models was given by Isbell & Young (2002). Current classifications for ape taxa are presented in Table 1.

Table 1. Classifications of great ape female social relationships.

	Social system	*Food distribution*	*Social category*[4,5]
Gorilla [1, 2, 3]	One-male/multi-male Polygynous	Herbaceous: abundant, fruit: patchy, seasonal	Non-female-bonded, Dispersal-egalitarian Male/Female transfer
Pan troglodytes [6, 7, 8, 9, 10]	Multi-male/multi-female Fission-fusion	Patchy/clumped, variable in size, seasonal	Variable non-female-bonded, male bonds and male philopatry (Nepotistic-despotic)
Pan paniscus [8, 11]	Multi-male/multi-female	Herbaceous: abundant, fruit: large patches	Female-bonded Dispersal-egalitarian Male philopatry
Pongo pygmaeus [12, 13, 14]	Solitary Individual fission-fusion	Fruit: patchy	Non-female-bonded Female tolerant? Female philopatry

1 Tutin 1996, 2 Watts 2001, 2003, 3 Robbins 2001, 4 Wrangham 1980, 5 Sterck et al. 1997, 6 Pusey et al. 1997, 7 Wittig 1993, 8 Boesch 1996, 9 Boesch 2002, 10 Wrangham 2000, 11 Parish 1994, 1996, 12 van Schaik & van Hooff 1996, 13 van Schaik 1999b, 14 Utami et al 1997.

Group living holds benefits for primates such as predator vigilance, aberration and defense (Alexander 1974, van Schaik 1983), cooperative defense of (food) resources, cooperative infant care and infant peer socialization. However, costs to the individuals also arise, such as less effective foraging, increased resource competition and, consequently a higher possibility for aggression (van Schaik 1983, 1989, Janson & Goldsmith 1995, Chapman & Chapman 2000, but see Sussman & Garber 2005), as well as energy-consuming maintenance of social

relationships. Optimal group sizes are expected where benefits and costs balance each other (van Schaik & van Hooff 1983). Hostility of resident towards immigrant females in transfer species seems to support the optimal group size theory (Cheney 1987, Nishida 1989, Watts 1994b). Aggression is expected to increase with group size as a consequence of more competitors for limited resources and is widely seen as an important factor in female evolution ("competitive strategizing creature": Blaffer Hrdy 1981, Silk 1993, Isbell & van Vuren 1996, Koenig 2002). Nevertheless, aggressive behavior can have more causes and might also result from proximate frustrations. Additionally, for each parameter, for each individual the optimum might vary and for the group as a unit, it might change over time when environmental circumstances and group composition vary. Besides food distribution, these social factors might co-influence dispersal decisions of females.

Gorilla females in the wild

Most publications on free-ranging gorillas have been conducted on a few groups of mountain gorillas (Stewart et al. 2001). These groups are non-territorial, highly herbivorous and folivorous, and experience a relaxed food situation (Watts 1985). Although the mountain area in which these groups live is small and isolated, and has an exceptional climate and vegetation, results from these populations have been generalized for all (sub-) species (genera revised: Groves 2001, 2003). Only during the last decade reports on western lowland gorillas became available (summarized by Tutin 1996, 2003).

Preliminary results on lowland gorilla populations as well as the only long-term study in Gabon (Tutin & White 1998) showed, that the habitat situation leads to marked differences not only from mountain gorillas, but also between populations (Doran & McNeilage 2001). The most important ecological difference between lowland and mountain species is the availability and use of fruit. Whereas the diet of mountain gorillas contains only small amounts of fruit (in 36% of all fecal samples, Goldsmith 2003), populations in Gabon, Central African Republic and Republic of Congo consumed fruit in up to 75% of observed feedings and in almost all fecal samples fruit remains were present (Tutin 2003, Remis 2003). In addition, they also consumed fibrous and herbaceous foods, in volume depending on seasonal availability of fruit.

Large differences in social traits have been found between different lowland gorilla populations (Doran & McNeilage 1998, 2001). Groups range from multi-male units, that undergo

seasonal fission (Goldsmith 1996, Olejniczak 1996), to exclusively one-male units (Tutin 1996, Magliocca et al. 1999) and unexpectedly large associations (n=32, Bermejo 1997). Table 2 sums the current findings on socioecological differences between the gorilla (sub-)species.

Additional findings such as the peaceful intermingling of groups at swampy feeding sites (bais) and proposed dispersed male networks in western lowland gorillas (Bradley et al. 2004) are in contrast with presumptions based on frugivory-theory. Doran & McNeilage (2001) assumed that a more frugivorous diet favours female philopatry, as potential for monopolizable foods favors establishment of cooperative bonds preferably with relatives. Therefore they discussed plasticity in this behavioral trait. In mountain gorillas females are known to stay in their natal group, if incest can be avoided, e.g.,by the presence of unrelated mature males (Watts 2001, 2003, Sicotte 2001). However, western gorilla females seem to transfer even more than mountain gorillas and favor small groups (Stokes et al. 2003, Stokes 2004), which is in line with theoretical predictions. Although leopard predation has been verified for lowland gorillas in recent years (Fay et al. 1995, Watson 2000) and was also reported for mountain gorillas in the past (Kawai & Mizuhara 1959), selection pressure by large carnivores seems to have only minor influence on these large primates (Janson 1998).

Are gorillas special?

The large variety of environments that are inhabited by gorillas could have favored selection for behavioral flexibility. Within the ape taxa only common chimpanzees have similarly diverse habitats, though these differ more in humidity (dry savannas to tropical forests, Boesch 2002), whereas gorilla habitats differ climatically also due to vertical differentiation (Doran & McNeilage 1998, 2001). Western gorillas (*Gorilla gorilla: G.g. gorilla* and *G.g. diehli*) have possibly split from their eastern relatives (*Gorilla beringei: G.b. beringei* with populations Virunga and Bwindi, *G.b. graueri*) about six million years ago, though their genetic differences are not as large as those between the common chimpanzee (*Pan troglodytes*) and the bonobo (*Pan paniscus*) (Ruvolo et al. 1994, Garner & Ryder 1996, Jensen-Seaman et al. 2003).

Table 2. Socioecological differences among gorilla (sub-) species.

	Gorilla gorilla	*Gorilla b. graueri*	*Gorilla b. beringei*	Reference
Altitude (meter)	0-500, up to 1500m	600-2600	Virungas: 2300-4507 Bwindi: 1160-2600	Yamagiwa 1996, Oates et al. 2003, Ganas et al. 2004
Frugivory[a] (fecal samples containing fruit)	Up to 99.8%	89-96.5%	Virungas: na, low Bwindi: 36%	Yamagiwa et al. 1996, Remis 1997, 2003, Doran et al. 2002, Goldsmith 2003, Ganas et al. 2004, Rogers et al. 2004
Average group size (range)	(Total range: 2-32) Bai Hokou: 8.7-10.1 (3-18) Gabon: 10 (4-23) Mbeli Bai: 5.5	4.8-5.7 (up to 42)	Virungas: 9.2 (>40) Bwindi: 9.7-10.2 (3-25)	Sholley 1991, Tutin et al. 1992, Parnell 2002, Goldsmith 1996, 2003, Yamagiwa 2003, Olejniczak 1996
Multi-male groups	Predominantly (partly multi-male at Bai Hokou: 51.8%, Mbeli Bai, Lossi)	8-14%	Virungas: 26-40% Bwindi: 40-46%	Yamagiwa et al. 1993, McNeilage et al. 1998, Robbins 2001, Goldsmith 2003, Yamagiwa 2003
Fission	Bai Hokou: daily/seasonally Afi Mountains susp.	Yes	Yes	Remis 1997, Goldsmith 2003, Oates et al. 2003, Robbins 2003, Yamagiwa 2005
Fusion[b]	Few (Bai Hokou seasonally, Losso overnight, Afi Mount. susp.)	?	Yes	Remis 1997, Robbins 1995, 2003, Goldsmith 1996, 2003, Oates et al. 2003, Bermejo 2004
All-male bands	?, few non-reproductive groups	?	Yes	Harcourt 1988, Robbins et al. 2004
Solitary males	Yes	Yes	Yes	Fossey 1984, Yamagiwa & Mwanza 1994, Tutin 1996, Robbins et al. 2004
Male-male competition	Differing	Differing	High	Yamagiwa 2001, Sicotte 1993, Bermejo 2004, Bradley et al. 2004, Magliocca & Gautier-Hion 2004, Stokes 2004
Female transfer	Yes	Yes	Yes	Harcourt 1978, Yamagiwa et al. 1996, Stokes 2004
Group cohesion	Differing (poaching pressure)	Strong	Strong	Goldsmith 2003, Stokes 2004
Infanticide	Probable	Probable	Yes	Fossey 1984, Watts 1989, Schuler pers. com. 2003, Stokes et al. 2003
Predation/Poaching	High	High	Low	Plumptre & Williamson 2001, Wilkie et al. 2001, Plumptre et al. 2003

?: no reports yet, na: not available, a: seasonal variations, b: fission-fusion periods can precede true group fissioning, Goldsmith 1996, 2003.

Mountain gorillas are known for their inability to adapt to captive conditions (Fossey 1983); their adaptation to the present altitude range levels, to which they were forced by habitat destruction (Plumptre & Williamson 2001), seems to be incomplete (Mudakikwa et al. 2001). It needs to be questioned, if this gorilla subspecies has to be regarded as a specialist and the others due to their behavioral plasticity, as generalists (Jones 2005). Conclusively, the environmental variation, the different dietary adaptations give unique opportunity to study the possible consequences of different habitats and feeding regimes on social behavior of a highly cognitive ape.

Gorilla females in zoos

By the end of 2003 a total of 821 gorillas (446 females) were kept in 143 zoos/institutions worldwide (only members of studbook registered facilities, Schmidt & Hilsberg 2004). Older and founder individuals were wild caught until 1973 CITES restricted trade of endangered wild animals and was ratified successively by 150 nations today. As most individuals were caught as youngsters they did not have the opportunity for full socialization and therefore often lacked skills, e.g., natural maternal behavior. Although in the early years knowledge on natural behavior and environmental conditions of gorillas was scarce, zoological institutions tried to transfer upcoming findings from mountain gorillas onto their mostly western lowland gorilla orphans. Today, heterogeneous groups with one silverback and several adult females are the main exhibited social structure, although pairs and solitary silverbacks also still occur. All-male groups were established as well (Stoinski et al. 2004), even though none have yet been found for western gorillas in the wild. In zoos females are mostly transferred to other groups when they reach maturity, if their father is still in their natal group. Secondary transfer is not that common, though females are exchanged if reproduction is hampered by other than physiological conditions or because of group management decisions. Thus, one important difference from natural conditions is that there is **no free female choice for time of transfer, and for mates, groups and territory**.

Most captive gorilla females have long-term group residency. Older founder individuals have remained together with their group mates since infancy. In some groups daughters remain with their mothers. **Therefore female philopatry or long-term residency, as it is represented in lesser degree in the wild, is artificially established** and could create the potential to establish relationships among females with features representing flexible outputs of their genetic dispositions.

Feeding regimes in zoos have changed over time, but still vary between institutions with respect to food items given, feeding times and the spatial distribution of food. Formerly high (citrus) fruit containing diets changed to mainly vegetables and browse after publication of results from mountain gorillas and tests that revealed a correlation between fruit intake and regurgitation behavior (Ruempler 1992). Remis (2003) found gorillas to have a high dietary flexibility with needs for highly fibrous food, protein content and fructose concentrations. Limited movement possibility and increase of activity endorse the provision of low protein- and energy-containing greens in zoos. Though the food situation would normally be assumed to be relaxed, because every individual will receive sufficient quantities, **different food offering methods, either dispersed or clumped, can greatly influence group situations during feedings**, e.g., provoke aggression and dominance behavior to monopolize high quality food items. Though these situations are artificial, they point at the behavioral possibilities of the species under different circumstances.

Spatial limitations and housing conditions (e.g., night separation) are another main artificial factor thought to affect individual behavior. Proximity arrangements as well as movements have to be adjusted to these limits in every situation. As possibilities to escape (e.g., from conspecific harassment) are restricted, behavioral tactics to reduce their causes might develop.

This study

Contrary to the wild, especially regarding western gorillas, captive conditions offer the best opportunities to study social interactions. Taking all the above-mentioned restrictions into account, the zoo can be viewed as another form of environment (see also Hosey 2005). The understanding of social structure in captivity has practical applications for future management planning and decisions. A large set of observational studies has already compared behaviors displayed in zoos with those in the wild, mostly with mountain gorillas (Gorilla ethograms by GBAG 1991). Wide agreement exists that behavioral elements are largely if not completely equal. However, complex social behavior and pattern depend on context and circumstances and may differ due to group and environmental conditions.

In the present study social interactions in four different zoo populations will be investigated. **Characteristics of relationships, their establishment and maintenance especially among**

adult females are of main interest. It will be examined, whether expression of relationships in captivity differs from those previously described in the wild (for mountain gorillas by Watts 1994a) and expected by the current socioecological model (Sterck et al. 1997). **Dyadic interactions and their long-term fluctuations** are compared as they are seen as the basis of relationships. The silverback might influence relationships among females, so special interest is placed on male-female interactions and the male role, especially in female conflicts (following Harcourt 1979a, Watts 1997, 2003).

Different (interacting) social parameters, investigated under normal and under stressful situations, are assumed to allow a conclusive assessment of the dyadic relationships:

The existence of social hierarchies among females, based on frequency and direction of agonism, is analyzed (following Watts 1994a).

Conflicts on group and individual levels are investigated via aggression, its dyadic frequency, intensity and context and associated affiliation.

Affiliation, unexpected among unrelated females, its frequency, direction and context is examined. **Nearest neighbor proximity** is considered as an additional factor for social affinity (following Robbins 2001, Watts 2001).

Comparing and connecting dyadic agonism and affiliation data will be done to **distinguish between good and bad relationships.**

Conflict management is investigated, as conflict restoration is thought to be expressed only between beneficial individuals, thus pointing at the existence of valuable relationships (following de Waal & van Roosmalen 1979, Watts 1995a, 1995b).

Furthermore, **integration processes** are studied regarding their development in captivity and their similarity to natural situations (following Harcourt et al. 1976, Harcourt 1978a, Watts 1991, 1992, 1994b). Here the interest is placed on the establishment of relationships by the introduced females with the male and the other females as well as the resident female´s reactions on the immigrant.