

# Great Ape Social Systems

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## Abstract

For decades, the social systems of the great ape species were described as being fundamentally different, but long-term field studies have questioned this idea. Although orangutans seem to be less social than the African apes, they have the ability to socialize and spend much time in contact with conspecifics if ecological conditions permit. Although the social behavior of chimpanzees and bonobos seems very different, their social structure is similar. The social systems of all great apes have common traits. They are characterized by weak ties, female transfer is common, they have a tendency toward fission–fusion grouping and a complex social network, females lack sharply defined dominance relations, and intrasexual bonds among non-kin can be relatively strong. There is remarkable intraspecific variability in social organization and structure; differences in ecological conditions seem to be very important in determining this. Frugivory especially requires a mobile and flexible social system. Compared to the great apes, humans show even greater variability.

## Introduction

Great apes share a common ancestor, they live in similar habitats (at least some populations), they are rather large, and they have slow life histories. Despite these similarities, they developed different social structures. What are the similarities? What are the differences and why did they develop? What social structure might the common ancestor have had? What does this mean for *Homo*, which emerged from within the great apes?

These questions have occupied primatologists for decades. Many hypotheses and models were developed and had to be abandoned because the growing evidence from field research did not support them. Some questions cannot be answered satisfactorily yet, but researchers have a much better idea now of the social systems of man's closest relatives. This knowledge is summarized here. Ecology and life history are also briefly portrayed for each species because they are key factors for the understanding of group structures and dynamics.

## Primate Social Systems

Animals may live in groups to increase their survival and reproductive success, but these groups have different structures for each species. To explain social systems, Kappeler and van Schaik (2002) distinguish three components: social organization (group size and organization), mating

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system, and social structure (relationships between group members). These three components are used here to clarify the social structures of the ape species.

Dunbar (1988) lists four reasons why primates should associate (stay and move) with conspecifics: better protection against predators, defense of resources, foraging efficiency, and improved caregiving opportunities. But sociality also has costs, especially higher intraspecific competition. Competition means usually competition for food (Kummer 1971; Wrangham 1979). Large groups deplete food more quickly and have to travel further in a day; this may influence female grouping patterns and restrict travel and sociality of females with infants (Sommer and Reichard 2000).

Folivores do not need to travel far each day and can live in relatively large groups without high levels of competition. The distance a group of a frugivore species has to travel is related to group size, so food distribution limits the number of group members (at least during feeding). Therefore, frugivores should either live in small groups or in fluctuating grouping patterns.

According to Dunbar (1988), several other factors may also influence primate group structure, at least theoretically. An important factor in this respect is the risk of male infanticide. Females with long lactation (like great apes) face an increased risk of infanticide, particularly when a reproductively capable male comes into a position of top dominance (van Schaik 2000). Usually male infanticide is seen, especially in one-male groups, as a strategy to increase reproductive success: the female will become receptive again sooner and the bond between the partners will be strengthened.

Regarding reproductive systems, the ape species have traditionally been classified as follows (Sommer and Reichard 2000):

- One male-many females (*polygyny*): gorillas
- One male-one female (*monogamy*): gibbons
- Many males-many females (*polygynandry*): chimpanzees
- Many males-one female (*polyandry*): not generally present in apes

As in this list, certain social systems have often been attributed to certain mating systems, but this is much too simple, not only in apes but also in primates in general. A social unit has its own history; a group may be polygynous or polyandrous, for example, and temporarily this may mean monogamy, but one individual may have several successive partners during its lifetime. Moreover, primates, and especially the great apes, show considerable flexibility and variability in their social behavior.

Finally, grouping levels may form a hierarchy. In great apes, the fission-fusion society is such a multilevel social system. Fission-fusion means that groups with different size and different composition may form for limited periods of time but that above this lowest grouping level, there is a higher, stable social unit. According to Lehmann et al. (2007) the advantage of fission-fusion societies is that the community size can increase.

## The “Lesser” Apes

Although this chapter concentrates on the family Hominidae [used here to include great apes as well as humans], the sister family Hylobatidae will be briefly discussed. Gibbons are much smaller than the great apes: they weigh about 5–11 kg, with the siamang being the largest species. They live mostly in evergreen rain forest, with some populations in semideciduous and mixed evergreen forest. They are strictly arboreal and are primarily frugivorous.

**Table 12.1** Great ape species and subspecies and their distribution

Species/subspecies	Distribution	Study sites mentioned here	Habitat
<i>Pongo abelii</i> Sumatran orangutan	Sumatra	Gunung Leuser (Ketambe, Suaq Balimbing)	Rain forest, swamp forest
<i>Pongo pygmaeus</i> Bornean orangutan			
<i>Pongo pygmaeus</i> <i>pygmaeus</i> Northwest Bornean orangutan	Sarawak, northwest Kalimantan		Rain forest, swamp forest
<i>Pongo pygmaeus</i> <i>wurmbii</i> Bornean orangutan	Southern west Kalimantan, Central Kalimantan	Tanjung Puting	Rain forest, swamp forest
<i>Pongo pygmaeus</i> <i>morio</i> Bornean orangutan	East Kalimantan, Sabah Northeast	Kutai	Rain forest, swamp forest
<i>Gorilla beringei</i> -eastern gorilla			
<i>Gorilla beringei</i> <i>beringei</i> mountain gorilla	Virunga Volcanoes, Bwindi (Uganda)	Virunga Volcanoes, Bwindi	Montane forest, occasionally grassland
<i>Gorilla beringei</i> <i>graueri</i> eastern lowland gorilla, Grauer's gorilla	Eastern D. R. Congo	Kahuzi-Biega (mountains), Utu, Masisi (extinct)	Lowland rain forest, montane forest, occasionally swamps
<i>Gorilla gorilla</i> -western gorilla			
<i>Gorilla gorilla</i> <i>diehli</i> Cross River gorilla	Cross River area (Nigeria/ Cameroon)	Cross River National Park, Afi, Takamanda	Lowland rain forest, montane forest
<i>Gorilla gorilla</i> <i>gorilla</i> Western lowland gorilla	From Cameroon to Cabinda and D. R. Congo in the west to the Central African Republic and the Congo Republic in the east	Lopé, Nouabalé-Ndoki (Mbeli Bai), Dzanga-Sangha (Bai Hokou), Lossi, Odzala, Río Muni, Lokoué Bai	Lowland rain forest, occasionally grassland and swamps
<i>Pan troglodytes</i> -chimpanzee			
<i>Pan troglodytes</i> <i>schweinfurthii</i> Eastern chimpanzee	D. R. Congo, north of the Congo River from its junction with the Oubangui into South Sudan and the Ituri region to the Rutshuru district, Uganda, Rwanda, Burundi, Tanzania	Gombe, Mahale, Bwindi, Budongo, Kibale, Semliki, Kahuzi-Biega	Rain forest, woodland, gallery forest, semideciduous forest, lowland and montane rain forest
<i>Pan troglodytes</i> <i>troglodytes</i> Central chimpanzee	From the Congo River mouth to the Congo Republic and the Central African Republic to Cameroon, north to the Sanaga River	Lossi, Lopé, Río Muni, Ndoki	Rain forest
<i>Pan troglodytes</i> <i>elliotti</i> East Nigeria-West Cameroon chimpanzee	Nigeria and Cameroon to the Sanaga River	Gashaka	Lowland forest, montane forest, woodland

(continued)

**Great Ape Social Systems** Social systems, Table 12.1 (continued)

Species/subspecies	Distribution	Study sites mentioned here	Habitat
<i>Pan troglodytes</i> versus West African chimpanzee	West Africa to Togo in the east	Taï, Assirik, Bossou	Savanna, deciduous forest, rain forest
<i>Pan paniscus</i> Bonobo	D. R. Congo, south of the Congo River	Lomako, Wamba, Lukuru	Rain forest, swamp forest, occasionally grassland, dry forest

Taxonomy according to IUCN 2012

For a long time gibbons were regarded as one of the few monogamous primate taxa, but this concept has been questioned. Change or replacement of a partner occurs in many species; in Khao Yai (Thailand), where the population density is very high, there is intense competition for females. The majority of adults copulate or attempt to copulate with partners other than their mates. Social polyandry is not uncommon, and male immigration into existing monogamous groups is observed. Extensive overlap of territories and a wide range of affiliative interactions with neighbors have been described in several gibbon species (Sommer and Reichard 2000). They show a high interspecies variation in social structure, but even if Brockelman et al. (1998) question it, their basic social structure seems to be the nuclear family unit.

Traditionally, the male-female relationship was regarded as pair-bonded, but it seems that gibbons rather live in small groups, most probably because selective pressures do not permit large groups. At least in some species, these social units are not really two-adult groups, although it is the norm. There is a remarkable intraspecific flexibility in social organization and affiliation (Reichard and Barelli 2008). Sommer and Reichard (2000) suggest that male gibbons associate with females in order to provide a constraint to roving males and thus protect their offspring from infanticide.

## The Great Apes

The species of great apes, and their distributions, are summarized in the table below:

### Orangutans (Genus *Pongo*)

Bornean and Sumatran orangutans are today usually classed as two distinct species (Table 12.1). There seem to be characteristic differences between the two species in behavior and social organization.

### Ecology

Orangutans live in rainforest habitats with a high tree species diversity from sea-level swamp forests to mountain slopes (Galdikas 1988; Knott 1999). They prefer the lowland forest up to about 1,000 m, usually close to streams and rivers as well as swamps. Galdikas (1988) lists 317 food types for Tanjung Puting. The orangutan diet consists of 61 % fruit; figs are their staple food. They eat meat (small mammals) on rare occasions (Rijksen and Meijaard 1999). Part of their habitat is characterized by extreme fluctuations in the type and quantity of fruit available, and this results in dramatic differences in nutritional intake and body weight (Knott 1999).

Orangutans require a large area that typically includes varied habitats. Resident females have stable, overlapping home ranges with an area of 0.5–6 km<sup>2</sup> in Borneo and 1–3 km<sup>2</sup> in Sumatra. The ranges are not actively defended and overlap considerably. The size of a resident adult male's home range is 1–8 km<sup>2</sup> on Borneo and 6–10 km<sup>2</sup> on Sumatra. It is neither exclusive nor stable (van Schaik and van Hooff 1996; Rijksen and Meijaard 1999; Singleton and van Schaik 2002; Stoinski et al. 2009). Daily travel distances vary from 90 m to 3.1 km (mean: 0.79 km) in Tanjung Puting.

Orangutans are the largest arboreal animals. Females move almost exclusively at between 10- and 25-m height in the trees. In Tanjung Puting, males sometimes walk on the ground, where they also forage and rest, but not in Sumatra, where tigers occur (Sugardjito et al. 1987; Galdikas 1988).

### **Life Histories and Dispersal**

Orangutans may be nursed until 6 years old, longer than any other ape species. The mean interbirth interval in Sumatra is 8–9 years and in Borneo 6–7.7 years (Wich et al. 2009). Females may conceive from about 11 years (Knott 1999). Fully adult (flanged) Bornean males weigh 86.2 kg on average and females 38.7 kg; a single Sumatran male weighed 86.2 kg and Sumatran females on average 38.3 kg (Markham and Groves 1990). Apparently mature but unflanged males weigh about 60–70 kg. In captivity, orangutans have reached as much as 58 years of age, whereas in the wild their maximum age is estimated at 45 years (Leighton et al. 1995).

On reaching adulthood, males develop typical secondary sexual characteristics: flanged cheeks and a big throat sac which enables them to produce loud calls (“flanged” males). Some males show an extended subadult appearance (“unflanged” males) in some cases until the age of 30. This parallel existence of two morphs of mature males is called bimaturism (Utami Atmoko and van Hooff 2004). Orangutan male bimaturism is socially influenced; the close presence of a flanged male suppresses the development of secondary sexual characteristics in subordinate males (van Hooff 1995).

Females often stay in ranges that overlap or are close to their natal area (Galdikas 1984; Singleton and van Schaik 2002). Despite these observations, Utami et al. (2002) found that adult males and females are mostly unrelated in Sumatra – this means that both sexes disperse. Males generally seem to disperse more widely (van Schaik and van Hooff 1996; Morrogh-Bernard et al. 2011; van Noordwijk et al. 2012).

Regarding their ranging behavior, Rijksen and Meijaard (1999) discern three types of orangutans: residents, who stay in the same area for years; commuters, who appear regularly and have a very large home range; and wanderers, who are seen very infrequently and seem to have no home range at all. There are considerable between-site differences in the percentage of these types. In some sites in Sumatra, no residents are found at all. In Ketambe, commuters are the majority of the population (Rijksen and Meijaard 1999; van Schaik 1999).

### **Size and Structure of Associations**

In both species of orangutans, the individuals move independently most of the time. Usually, trees do not provide enough food for several adults. It is difficult to get statistical data on the sizes of associations, because all field studies bias toward larger party sizes, since they are found more easily. The mean daily party size is 1.67 independent individuals in Suaq Balimbing, and the largest sustained party size that has been observed so far was 10.67 (van Schaik 1999).

It is sometimes difficult to decide whether orangutan associations can be called social or whether the apes just meet during their search for food and tolerate the presence of each other. According to Galdikas (1984), in Kutai only 6 out of 13 groups could be considered “social”: a consorting adult pair and two female-offspring units. In Tanjung Puting, Galdikas (1995) observed that 94 % of the

time adolescent females who are in contact with others included true social interaction; the rest is nonsocial aggregation. In other age/sex classes, roughly 80–90 % of associations are true social groupings.

The most common grouping is one subadult male and one unreceptive adolescent female (Galdikas 1988). Subadult males and adolescent females spend about 40 % of their time in contact with other units in Tanjung Puting, adult males 16.8 %, and adult females 13.5 % (Galdikas 1995). Adult females in Borneo are far more solitary than those in Sumatra; this reflects the difference in average orangutan density (van Schaik 1999). Fully adult males suffer energetically from association and thus are extremely solitary (van Schaik and van Hooff 1996; Knott 2009). The largest stable parties in Suaq Balimbing develop when females converge upon a dominant male. Sexual associations seem to last longer there and involve more animals than elsewhere (van Schaik 1999).

### **Male-Female Relationships and Mating Strategies**

Contacts of adolescent females with adult males in Tanjung Puting are almost totally restricted to consortships which the female initiates, maintains, and terminates. In general, adult females either avoid contact with males or ignore them, while adolescent females (9–14 years) spend 56 % of their contact time exclusively with males. Toward adult males, nonreceptive adolescent and adult females show avoidance or indifference; if they are receptive, however, they are highly motivated to maintain contact with the seemingly indifferent adult males and may respond to their long calls by immediate approach. With subadult males, adolescent females have long-term associations with no copulation, which may be called friendships, as well as short associations, but no consortships (Wich et al. 2006). The subadult males are responsible for maintaining contact with nonreceptive adolescent females, and sometimes they travel with them for weeks (Galdikas 1984, 1995).

There are two behavioral tactics in the mating strategy of male orangutans: resident flanged males sit, utter long calls, and wait for females (residents, commuters, and wanderers), while unflanged and nonresident flanged males actively search for females and mate with them, irrespective of their receptivity (Utami Atmoko and van Hooff 2004; Stumpf et al. 2008; Knott 2009). Rijksen and Meijaard (1999) assume that these “rapes” are a sexual strategy of young males because the ascent to a higher social status is associated with long-lasting sexual relationships with several females, and this status may be the prerequisite for the development of the full sexual characteristics (Utami et al. 2002). During consortship, the partners travel closely for days or even weeks, usually with the adult male following (Galdikas 1984; Singleton and van Schaik 2002). Severe mating competition is usual among fully adult orangutan males, but no infanticide attempts have ever been seen so far.

Both mating tactics are successful. A paternity analysis in Ketambe, Sumatra, showed that all but one of 11 infants were sired by resident males; out of these ten infants, six were sired by unflanged males (Utami et al. 2002). There is more variation in orangutan mating patterns than previously thought (Utami Atmoko et al. 2009a). In general, however, unflanged males seem to have a slightly lower reproductive success (Satkoski et al. 2004).

### **Female-Female Relationships**

Competition for access to limited resources is rare. In Sumatra, where the population density is high, female home ranges overlap considerably and the rates of association between females are high compared to Borneo (Singleton and van Schaik 2002; Knott et al. 2008). The longest association Galdikas (1984) observed between two adult females in Tanjung Puting was 3 days and 2 nights. Sometimes females travel together, but few direct interactions are observed. Their

behavior toward each other varies from aggression and avoidance to affiliative activities, but only very rarely does a female touch another female affiliatively.

Adolescent females often travel together after encounters. The longest association Galdikas (1995) saw lasted at least 10 days. Although adult females are often intolerant to and may attack adolescent females, the adolescents try to associate with them.

### **Male-Male Relationships**

Flanged males avoid each other. They produce long calls that carry for up to 1 km, especially when they approach another individual, after they have defeated another adult male or before they travel over long distances. When adult males come close to each other, agonistic interactions are observed. They have the highest incidence of disfigurements among orangutans, presumably from injurious fights. They dominate unflanged males but may tolerate them as long as they keep a certain distance (van Schaik and van Hooff 1996; Utami Atmoko et al. 2009b).

### **Discussion: Genus *Pongo***

An older model of orangutan social relationships is that a fully adult male controls a relatively large range that includes the smaller ranges of several females. Calculations proved, however, that a male can maximally defend 0.37–0.57 km<sup>2</sup>, which is less than the size of a single female's range. Moreover, adult male ranges overlap and mating is promiscuous (van Schaik and van Hooff 1996).

Orangutans have been regarded as solitary, but they have the ability to socialize and spend much time in contact with conspecifics if ecological conditions permit. That they are not antisocial is documented from zoos, where they have been kept in rather large groups (Poole 1987). Restrictions on group size must therefore lie in the environment in the wild (Harrison and Chivers 2007).

To associate with conspecifics in feeding parties is costly if the food in one tree is not sufficient for several adults (especially for large males). But social contacts are important, particularly for the development of various behaviors and of social competence and relationships. Females with new offspring therefore form “nursery groups” in which new and weaned offspring can socialize (Galdikas 1995; van Schaik 1999; van Noordwijk et al. 2012). Infants learn there how to behave correctly toward conspecifics. Even in independent immature animals, social contact is still necessary for further development. According to Galdikas (1995), adolescent females use social contacts to establish their own home range and to form relationships with the individuals in adjacent ranges. Sugardjito et al. (1987) discuss more benefits of grouping.

Orangutans show the greatest degree of sexual dimorphism of all great apes. Such an extreme dimorphism may be a result of female choice or male-male competition. Other species with such sexual dimorphism are usually either living in one-male groups or have a lek-type mating system. Rijksen and Meijaard (1999) suggest that orangutans have a very complex lek-type mating system. Males meet in a “social arena,” an area with especially abundant food resources, where the ranges of several residents overlap and where commuters and wanderers visit regularly. In that arena they emit long calls to attract females.

Two models for the description of the orangutan social system are discussed by van Schaik and van Hooff (1996): either a roving male promiscuity system (an estrous female attracts multiple males who compete vehemently for sexual access to her) with no higher-level social unit or a spatially dispersed but socially distinct community organized around one or more large adult males. Both models have weaknesses: well-defined communities do not seem to exist in any orang population and orangutan females do not mate with any available male. They seem to show distinct preferences; individual relationships and bonding are important (Galdikas 1984; van Schaik and van Hooff 1996; Rijksen and Meijaard 1999; van Schaik 1999; Utami et al. 2002; Stumpf

et al. 2008; Utami Atmoko et al. 2009a). The roving male promiscuity system seems to be closer to the situation of the Bornean orangutans, and the socially distinct community system organized around a dominant male fits better for the Sumatran population (Singleton and van Schaik 2002; Mitra Setia et al. 2009).

Although orangutan communities comparable to those of chimpanzees do not exist, orangutans obviously have a social network. Residents and commuters in a certain area seem to know each other well, while wanderers are strangers to them. An explanation could be provided by a suggestion by Rijksen and Meijaard (1999) and van Schaik (1999) that the individual-based fission–fusion social system that is characteristic for chimpanzees may also be typical for orangutan societies; the differences are in degree rather than in quality.

## **Gorillas (Genus *Gorilla*)**

Eastern and western gorillas are today usually classed as two distinct species (Table 12.1). Long-term studies are available now for both species from several sites.

### **Ecology**

Gorillas live in a variety of habitats: lowland rain forest, swamp forest, marshy clearings (bais), and montane forest. The lowest densities of western lowland gorillas are observed in areas without Marantaceae and Zingiberaceae, their preferred food are plants, and the highest densities in Marantaceae and swamp forest (Poulsen and Clark 2004; Rogers et al. 2004).

Mountain gorillas mainly feed on green plant parts, whereas lowland gorillas eat a lot of fruit (but still markedly less than chimpanzees and orangutans). Utilization of fruit and of herbaceous vegetation varies seasonally. Western lowland gorillas eat about 250 food items with up to about 100 fruit species, while the mountain gorillas of the Virunga Volcanoes eat only up to 72 different plant species and very few fruits (Tutin and Fernandez 1993; McNeilage 2001; Doran et al. 2002a). Gorillas do not kill vertebrates but eat small animals, mainly insects.

Gorillas do not occupy territories. Their annual home range covers about 8 km<sup>2</sup> in the Virunga gorillas, about 30–40 km<sup>2</sup> in Grauer's gorillas, and 11–30 km<sup>2</sup> in western lowland gorillas. The size depends on the distribution of food sources and group size; home ranges overlap (Tutin 1996; Remis 1997; McNeilage 2001; Yamagiwa et al. 2003a, 2012; Bermejo 2004). In general, gorilla groups move an average of 0.5–2 km a day to forage. Folivorous gorilla populations in montane forest show a shorter daily journey length than more frugivorous populations (Yamagiwa et al. 2003a, b; Robbins et al. 2006).

Apart from humans, gorillas do not really have “predators.” The only predator is the leopard (Tutin and Fernandez 1991; Fay et al. 1995). They live primarily on the ground, particularly in the Virunga Volcanoes, where females spend only 7 % of the time above the ground and males 2 % (Doran and McNeilage 1998). Silverback males do not often leave the ground because of their great weight. Gorillas sleep on bare earth or in nests, which they build on the ground or in trees (Poulsen and Clark 2004).

### **Life Histories and Dispersal**

Gorilla infants are nursed for at least 2–3 years in Virunga gorillas, which develop faster than other populations, and for 4 years in western lowland gorillas; the interbirth interval is about 4–5 years (Breuer et al. 2009). Gorillas grow faster and breed more rapidly than other hominids (Groves and Meder 2001). Females may first reproduce between about 8 and 9 years of age in the wild (Watts 1991; Robbins et al. 2004). Males are fully grown at approximately 15 years of age and are called silverbacks. Young mature males without the secondary sexual characteristics are called

**Table 12.2** Gorilla group sizes (including unweaned immatures)

Region	Group size		Sample size	Number of silverbacks		Source	
	Mean	Range		Mean			
<i>Gorilla gorilla gorilla</i>							
Mt. Alen, Río Muni	7.13	2–12	8			Jones and Sabater Pí (1971)	
Abumnzok-Añinzok, Río Muni	6.4	3–19	5			Jones and Sabater Pí (1971)	
Ndoki, Congo	7.3	5–12	7			Mitani et al. (1993)	
Lokoué Bai, Congo	7.7	2–15	45			Gatti et al. (2004)	
Mbeli Bai, Congo	8.4	2–16	14	1.1		Parnell (2002)	
Maya Nord, Odzala, Congo	11.2	2–22	31	1.0		Magliocca et al. (1999)	
Lossi, Congo	17	7–32	8			Bermejo (1999)	
Lopé, Gabon	9.3	4–15	4	1.25		Tutin et al. (1992)	
<i>Gorilla beringei graueri</i>							
Kahuzi-Biega, mountains	14.3	3–42	12	1.2		Yamagiwa (1983)	
	15.6	6–37	14	1.1		Murnyak (1981)	
	10.0	2–24	25			Yamagiwa et al. (1993)	
Kahuzi-Biega, lowland (Utu)	15	4–25	6			Cordier (Schaller 1963)	
Masisi	8	3–11	3			Yamagiwa et al. (1989)	
<i>Gorilla beringei beringei</i>							
Virunga Volcanoes	16.9	8.8 5–27	3–21	10	28	1.7 1.4	Schaller (1963), Weber and Vedder (1983)
	10.9	3–47	32			1.9	Kalpers et al. (2003)
	12.5	2–47	36				Gray et al. (2010)
Bwindi, Uganda	9.9	2–23	28	1.9			McNeilage et al. (2001)
	8.8	5–14	12	1.75			Harcourt (1981)
	10.7	2–27	36				Robbins et al. (2011)

blackbacks. Western lowland gorilla males have a mean weight of 149 kg and females 71.5 kg, mountain gorilla males weigh 157 kg and females 97.7 kg, and Grauer's gorilla males 171 kg and females 80 kg (Meder 1993; Rowe 1996). Adults have a relatively short life expectancy; silverback males, in particular, seem to have a hard life and die young (Groves and Meder 2001). In the wild, they probably reach 40–45 years; in captivity, several individuals have lived more than 50 years.

Reaching adulthood, female gorillas usually leave the group they were born in and join a new unit. They emigrate only if they encounter another male and may transfer several times before they settle down in a certain group (Watts 1996; Sicotte 2001; Stokes et al. 2003). In Kahuzi-Biega, the simultaneous transfer of several individuals was observed (Yamagiwa and Kahekwa 2001; Yamagiwa et al. 2009).

In western gorillas and Grauer's gorillas, male emigration is common, while among mountain gorillas less than 50 % of the males emigrate (Stoinski et al. 2009a). If they leave, they either become solitary or join all-male groups in some populations (Watts 2000; Yamagiwa et al. 2003a; Robbins et al. 2004). In western lowland gorillas (Lokoué Bai, Congo), even subadults and

juveniles may emigrate (Gatti et al. 2004). Solitary males may travel very long distances (Douadi et al. 2007).

### **Size and Structure of Social Units**

In a gorilla group there is a clear hierarchy. The leading silverback has the highest rank, and adult females are dominant over young animals. In most populations, groups usually consist of one adult male, several females, and their offspring (Magliocca et al. 1999; Yamagiwa et al. 2003a; Gatti et al. 2004). In the Virunga mountains, in Bwindi and Bai Hokou, however, a large percentage of the groups include more than one adult male (Table 12.2; Goldsmith 2003; Kalpers et al. 2003; Yamagiwa et al. 2012).

As groups contain more females than males, many males are “left over.” Gatti et al. (2004) found that at Lokoué Bai, 42 % of the silverbacks are unmated: 31 % are solitary and 11 % live in nonbreeding groups. Solitary males make up 5–10 % of the western lowland gorilla populations. Among eastern gorillas, the percentage seems to be lower: up to 3.5 % in Kahuzi-Biega and 1.8–4.0 % in mountain gorillas.

Gorillas occasionally form all-male groups, usually with one mature male and a few younger males. Such nonreproductive groups have a similar size to breeding groups; they have been observed in western lowland as well as mountain gorillas, although not in Grauer’s gorillas (Robbins et al. 2004; Levréro et al. 2006). These groups as units may be long-lasting, but their membership changes quite often due to male migrations. They seem to be transition units in both gorilla species (Gatti et al. 2004; Levréro et al. 2006).

Gorilla groups can have very different histories (Robbins 2001). When the dominant male dies, the group may disperse if no subordinate silverback is there to take over the leadership; if there are two younger silverbacks, the group may split. Parnell (2002) lists five stages in the development of a typical western lowland gorilla group: nascent (one silverback + one female without offspring), infant (one silverback + one or more females with dependent offspring), juvenile (one silverback + one or more females with a range of offspring), mature (one silverback + one or more females and a range of offspring from infants to young silverbacks), and senescent (one old silverback, few or no females, only older offspring). Group takeovers by outside males have not been reported so far (Robbins et al. 2004), but in zoos new males have been introduced successfully to established groups in many cases.

The size of gorilla groups is very variable but similar among the subspecies (Table 12.2). An average group contains about nine to ten members (Parnell 2002; Yamagiwa et al. 2003a). Possibly groups can grow especially large where the density of their staple food is very high (Robbins et al. 2006). The largest group observed so far was Pablo’s group in Rwanda with 65 members.

### **Male-Female Relationships and Mating Strategies**

In the social system of gorillas, the high cohesiveness of a group is usually attributed to the attractiveness of the leading male to females (Yamagiwa et al. 2003a, but see Stokes 2004). Adult male-adult female relationships are considered to be the “core” of the social group; they vary depending on kinship, length of tenure, and reproductive status. Male aggression to females is common and often can be regarded as “courtship aggression.” It is higher if the female is in estrus; females usually respond submissively (Robbins 2003; Bradley et al. 2005).

Wrangham (1979) suggests that a gorilla group represents a “permanent consortship.” Adult females usually prefer to mate with the leading male and subadult females with subordinate males (Robbins 1999; Bradley et al. 2005; Stoinski et al. 2009b). Females in multimale groups often

copulate with more than one male, despite interference by dominants (Sicotte 2001); this may confuse paternity and induce all the males to protect the infants against infanticide.

If a mountain gorilla mother transfers between groups while she has a baby, if a dominant male dies, or if another silverback male takes over the group, the baby is frequently killed by the new male (Fossey 1984; Watts 1989). Infanticide causes 37 % of infant deaths in the gorillas of the Virunga Volcanoes in one-male groups (Bradley et al. 2005; Robbins et al. 2007). Recently, evidence for infanticides was reported for Kahuzi-Biega too; possibly it had been suppressed earlier because the males of neighboring groups were related (Yamagiwa and Kahekwa 2004). Infanticide is suspected also in several cases in western lowland gorillas, when infants disappeared (Yamagiwa et al. 2009).

### **Female-Female Relationships**

Dominance relations between females are weak, their rank depending on factors such as how long they have been in the group (Watts 2001; Kapsalis 2004). Females in large groups sometimes harass new immigrants, and aggression between females is not unusual (Watts 1996).

As females usually leave their natal group to join another group, it was long assumed that all females in gorilla groups are unrelated. In mountain gorillas, however, more than 70 % of the females spend at least some of their reproductive careers with female relatives. In western lowland gorillas, Bradley et al. (2007) found that 40 % of the adult females had an adult female relative in the same group. Female maternal relatives are close associates, often interacting affinitively and supporting each other (Watts 1996, 2000, 2001).

### **Male-Male relationships**

As between females, there are few affiliative interactions among adult males. Severe contact aggression between males within a group is not usual (Sicotte 1994; Stoinski et al. 2009a).

Patrilineal kinship is important for mountain gorilla males because they often remain in their natal group instead of dispersing. There they assist their fathers in resisting threats or incursions from extragroup males (Robbins 1995). Mature followers and older adolescents cooperate with dominant males against extragroup males (Watts 2000). Dominant males try to prevent these followers, however, from mating with females other than the dominants' daughters. Coalitions of brothers may occur but are probably uncommon (Watts 1996).

### **Intergroup Interactions**

The home ranges of various gorilla groups and of lone silverback males overlap, so encounters are frequent, but the leaders of breeding groups generally avoid them. In mountain gorillas on average, about one encounter per month is observed; it often includes aggression between silverback males. They try to drive competitors away by displaying or attacking (Yamagiwa 1987; Watts 1991; Robbins 2003). During such encounters, extragroup matings have been observed (Sicotte 2001).

Western lowland gorilla males generally show less contact aggression during encounters than mountain gorillas. They often meet in swamps or fruiting trees; the groups may feed together without hostility (Tutin 1996; Magliocca and Gautier-Hion 2004). They occasionally intermingle peacefully and even may nest together for one night (Kuroda et al. 1996; Doran and McNeilage 1998; Bermejo 2004). In Lossi, silverbacks often react aggressively to lone males, but usually they tolerate other groups – their reaction varies, however, and depends on the identity of the silverback (Bermejo 2004).

### **Discussion: Genus *Gorilla***

Differences in ecological conditions seem to be more important in determining the social system of a gorilla population than its taxonomy. Mean group sizes seem to be similar across the genus *Gorilla* (Table 12.2), but in populations with a highly folivorous diet, the groups may become larger (Goldsmith 2003).

There seems to be a considerable influence of fruit availability on ranging and grouping patterns. During the fruiting season, large groups travel farther than small groups in western lowland gorillas as well as Bwindi gorillas. To reduce competition, the groups may spread more widely during feeding and/or form temporary foraging subgroups in western lowland gorillas and Grauer's gorillas (Tutin 1996; Remis 1997; Parnell 2002; Goldsmith 2003; Yamagiwa et al. 2003a), which may feed and even nest more than 1 km away from the rest of the group (Bermejo 2004).

Parnell (2002) assumes that a high proportion of multimale groups in some populations may have developed because solitary males face unusually high odds against establishing a group and the current demographic conditions deter maturing males from emigration. As multimale groups provide better protection from infanticide, females may prefer groups with more than one male in the future (Watts 1996, 2000; Yamagiwa et al. 2003a; Yamagiwa and Kahekwa 2004). Dominant males may tolerate the presence of mating activities of younger males to reduce the risk of later infanticide (Robbins 1995).

Maryanski (1987) introduced the hypothesis that gorillas, like chimpanzees, live in an "open-group system": several gorilla groups and lone males share a home range where they meet preferred groups, socialize, and then depart. There is no evidence that a higher unit like the chimpanzee community exists in gorillas, but in some gorilla populations, there do seem to be strong ties between different groups. Yamagiwa and Kahekwa (2004) observed group fission in Kahuzi-Biega, which resulted in several neighboring groups with related males.

It seems that two types of association among related males evolved in gorillas: association within a group and tolerance between males of neighboring groups. The occurrence of infanticide may promote the former, and its absence may promote the latter. The social structure of gorillas may be very flexible and allow them to choose either type of social organization, even in the same population (Yamagiwa and Kahekwa 2004).

### **Chimpanzees (Genus *Pan*)**

Although the two species of the genus *Pan* (the "common" or robust chimpanzee and the "pygmy" or gracile chimpanzee, or bonobo) share many characteristics – physical as well as social – there are marked differences. These presumably result from their separation by the Congo River. One of the common characters distinguishing them from the other apes is a low degree of sexual dimorphism in body size, but instead a large swelling of the anogenital region in females and large testicles and penises in males.

### **Chimpanzee (*Pan troglodytes*)**

#### **Ecology**

Chimpanzees have been studied at a number of sites (Table 12.1). They live in a wide variety of habitats in tropical Africa, from rain forest to closed and open forest, gallery forest, open savanna and grassland, as well as montane rain forest up to 2,400 m. In Ndoki, Poulsen and Clark (2004) found the highest density in swamp forest.

Chimpanzees are mainly frugivorous. Their diet consists of 48–82 % fruit, the rest consisting of leaves and other plant parts, and also more animals than other great apes, including insects as well as vertebrates, which are hunted communally (Goodall 1986; Chapman et al. 1994). The number of

**Table 12.3** Mean party and community size in chimpanzees (including unweaned immatures)

Population	Mean party size	Range	n	Community size	Source
<i>Pan troglodytes schweinfurthii</i>					
Gombe, Tanzania	5.6		498	50	Boesch (1996)
Mahale, Tanzania	6.1		218	29	Boesch (1996)
	4.0	1–24	3,818		Itoh and Nishida (2007)
Kibale, Uganda	10.3	1–47	827	140	Basabose (2004)
Budongo, Uganda	6.3	1–30	1,824	46	Newton-Fisher et al. (2000)
Kahuzi-Biega, D. R. Congo	4.43	1–13	71	22	Basabose (2004)
<i>Pan troglodytes troglodytes</i>					
Ndoki, Congo	7.0		32		Malenky et al. (1994)
Mt. Alen, Río Muni	4.7	2–7	3		Jones and Sabater Pí (1971)
Mt. Okoro Biko, Río Muni	11.2	4–23	5		Jones and Sabater Pí (1971)
<i>Pan troglodytes verus</i>					
Taï, Côte d'Ivoire	8.3	1–41	2,912	76	Boesch (1996)
Taï (during fruit scarcity)	5.75		395		Doran (1997)
Bossou, Guinea	4.0	1–9	426	20	Sakura (1994)
Assirik, Senegal	5.3		267	28	Boesch (1996)
<i>Pan paniscus</i>					
Lomako	4.33	1–8	87	10	White (1988)
	7.15	2–17	26	22	White (1988)
	9.69	1–18	26	21	White (1988)
	7.9	1– > 50	268	>50	Badrian and Badrian (1984)
Wamba	16.9	1–54	147	58	Kuroda (1979)
	11.2				Mulavwa et al. (2008)

plant food items ranges from 55 to 328, depending on the habitat. Their diet varies seasonally, and this results in seasonal body weight fluctuations (Nishida 1990; Tutin and Fernandez 1993; Basabose 2002).

The home ranges (or territories) of chimpanzee communities vary according to habitat, season, community size, and the risk of encountering neighboring communities. The mean size is 21.6 km<sup>2</sup>. In open landscapes, where food is dispersed widely, the density is very low and the home range extraordinarily large, up to 560 km<sup>2</sup>. Home ranges of neighboring communities overlap (Yamagiwa 1999; Boesch and Boesch-Achermann 2000).

Within the community's home range, each adult has his/her own core area. Most females show strong fidelity to an area once they settle there as an adult (Williams et al. 2002b, 2004). Males have larger home ranges than females (Hasegawa 1990; Chapman and Wrangham 1993; Lehmann and Boesch 2005). The mean daily travel distance of individuals is about 3 km (Doran 1997; Boesch and Boesch-Achermann 2000).

In Taï, leopards attack chimpanzee; at other sites, lions prey on them (Tsukahara 1993; Boesch and Boesch-Achermann 2000). About 50 % of the day chimpanzees stay above ground level. They spend the night in nests that are usually built in trees up to 50-m high (Poulsen and Clark 2004),

although terrestrial nesting has also been observed in some areas, for example, in Guinea (Koops et al. 2004).

### Life Histories and Dispersal

Chimpanzee infants are nursed for about 3–4 years. The interbirth interval is usually 4–7 years (Nishida et al. 1990; Boesch and Boesch-Achermann 2000). Females may first conceive at about 9–11 years.

The mean weight of adult male *Pan troglodytes troglodytes* is 53 kg, of females 43.8 kg; *Pan troglodytes schweinfurthii* males weigh 40.5 kg and females 32.9 kg (Groves 2001), but even within each subspecies, there is great variation both within and between populations.

The maximal age of wild chimpanzees is not yet very well known. Boesch and Boesch-Achermann (2000) assume that they may reach 50 years. In captivity, they have lived for almost 60 years.

In most populations, females usually leave their natal groups upon maturity. At Gombe, most or all adolescent females visit other communities, and some may even conceive there, but only 50 % of them emigrate permanently, the others returning to their natal communities (Pusey et al. 1997). In Taï, on the other hand, almost all females transfer (Boesch and Boesch-Achermann 2000). In Mahale, the transfer process lasts from 6 months to 2 years, while the females associate and mate with the males of the two communities, and 13 % of the females transfer more than once there (Nishida et al. 1990). Male chimpanzees do not emigrate and cannot migrate between communities (Goodall 1986). Nevertheless, captive chimpanzees can be induced to accept new males into their group (Wilson and Wrangham 2003).

### Size and Structure of Social Units

Chimpanzees live in fission-fusion groups within their communities. They have two levels of social unit: the smaller association unit is the party or subgroup – temporary and very variable – and the higher-level unit is the (stable) community or unit group (Table 12.3). Members of a community meet occasionally (fusion) and travel for longer or shorter periods in parties until they separate again (fission). On average, a party stays constant in size and composition for 24 min in Taï, in Gombe for 69, in Bossou for 126, and in Budongo for 14 min (Boesch and Boesch-Achermann 2000).

In Gombe, the average party size is 3.5 for females only, 10.7 for mixed parties, and 4.0 for males only. Single-sex parties are significantly smaller than mixed-sex parties, and parties with more estrous females contain more males (Williams et al. 2002a). Estrous females are more gregarious than other classes, and they are especially associated with males (Goodall 1986; Pepper et al. 1999).

In several populations, nursery parties – several females with their infants – have been observed. In Gombe, females spend 65 % of their time alone or with their offspring, in Kibale even 70 %, while in Taï they are alone only 18 % of their time when fruits are abundant (Wrangham et al. 1996; Pusey et al. 1997; Lehmann and Boesch 2004). During fruit scarcity, their day range is reduced and the mean party size decreased (Doran 1997). In Mahale and Kibale, food availability and the number of estrous females are positively correlated with party size (Mitani et al. 2002), but in Budongo, Newton-Fisher et al. (2000) found no positive correlation, and Basabose (2004) found in Kahuzi-Biega that fruit abundance per se does not affect party size but seasonality and fruit distribution do.

Party size is also determined by their function. During hunts for vertebrate prey, such as monkeys in Kibale, Watts and Mitani (2002) found a significant positive relationship between

hunting party size and the number of kills per hunt. Success also increases with the number of males per hunting party at Gombe and Tai.

Party size depends also on community size; in large communities parties occasionally are larger than a whole small community. Therefore, Boesch and Boesch-Achermann (2000) suggest that relative mean party sizes should be compared. According to their calculation, chimpanzees have a relative mean party size of 9–21 % of the community size.

The community size may lie between 20 and 150 members. It must contain at least one adult male, but a higher number of males is usual, often more than ten. It seems that small communities retain a fission-fusion structure, but this loses much of its flexibility and the parties remain stable for much longer periods of time than in larger communities.

### **Male-Female Relationships and Mating Strategies**

Relationships between male and female chimpanzees are usually not very close. Grooming between them, for example, is rather infrequent compared with male-male grooming. Constant and frequent proximity is particularly found in mother-son dyads.

Chimpanzee females use a tactical strategy of mating promiscuously to confuse paternity (Stumpf et al. 2008). In Gombe, consortships have been observed in all males, and 25 % of conceptions occur during consortships (Constable et al. 2001). In Mahale, however, they are very rare and only 8.3 % of conceptions are the result of consortship (Hasegawa and Hiraiwa-Hasegawa 1990), while in Tai only one offspring was conceived during consortship; half of the males and 56 % of the females are never seen to consort.

Matsumoto-Oda (2002) reported from Mahale that females copulate more often with continuously affiliative males; therefore, males interact with anestrus females to increase the chance of mating when they are in estrus. Most authors, however, found persistent coercing male aggression for eastern chimpanzees and the females most frequently solicited the most aggressive males (Muller et al. 2011). Prime males dominate all adult females and often try to monopolize them. Estrus females are more selective in their partners (Stumpf and Boesch 2006) and most frequently stay around the alpha male in Mahale and Kibale (Takahata 1990a; Muller et al. 2011). In Gombe, the alpha male is responsible for 36–45 % of all conceptions and high-ranking males for 50 %; in Tai, 71 % of all infants are sired by high-ranking males (Constable et al. 2001; Boesch et al. 2006).

According to Williams et al. (2002b), male aggression in boundary areas forces the females to be members of their community by settling in the center of their home range. Male coercion of females is an important element, and violence toward unfamiliar females near the edges of the defended range is particularly fierce. Nevertheless, estrus females sometimes disappear for a few days and may make temporary visits to neighboring males (Boesch and Boesch-Achermann 2000). In Gombe, 13 % of copulations are with males from other communities (Goodall 1986). These extracommunity matings do not very often result in conception: in Tai, extragroup paternity was found only for 7 % of the offspring (one infant), and in Gombe, all tested offspring were sired by males of the same community (Constable et al. 2001; Vigilant et al. 2001).

Infanticide has been observed in several chimpanzee populations, especially in Mahale (Nishida et al. 1990). In Tai and Gombe, infanticide and cannibalism by females were observed (Pusey et al. 1997; Boesch and Boesch-Achermann 2000; Pusey et al. 2008). In Gombe and Mahale, more cases of infanticide were recorded within the community than between communities. These cases do not provide any evidence that infanticide is a successful male reproductive strategy in chimpanzees (Wilson and Wrangham 2003).

### **Female-Female Relationships**

High-ranking females are the most social with other females; low-ranking females are the least. This suggests that contest competition is an important aspect of female association patterns. In Mahale and Gombe, immigrant females experience aggression from resident females (Williams et al. 2002a, b; Pusey et al. 2008).

But females may also have affiliative relationships (Lehmann and Boesch 2008; Langergraber et al. 2009). In Tai, close female associations (friendships) can last for years and are very stable; some pairs spend up to 79 % of their time together. According to Boesch and Boesch-Achermann (2000), higher intrasexual competition and higher involvement in the social interactions of males make it profitable for females in Tai to develop long-term friendships with other females and to form stable alliances.

### **Male-Male Relationships**

Male chimpanzees associate more strongly with one another than do females with other females and males with females. They form coalitions in all populations studied (Boesch and Boesch-Achermann 2000; Newton-Fisher 2002), and apart from coalitions, friendship between males has also been observed (Nishida and Hosaka 1996). Which individuals form affiliative relationships is not clear; genetic studies in Kibale showed that maternal kinship is not strongly associated with male-male association (Kapsalis 2004).

Among the males there is a linear dominance hierarchy, and rank reversal generally results from dyadic fights (Takahata 1990b; Muller 2002). The alpha male is the most active groomer; he tends to move first and be followed by subordinates (Takahata 1990b). In Tai, the leader of a community announces his presence by drumming; this also gives information to other individuals about the direction and speed of group movement (Boesch and Boesch-Achermann 2000).

Agonistic confrontations between males are observed regularly, and they are most aggressive between the two highest-ranking males. Coalitions in attacks are frequent; in Tai it is mostly low-ranking males coalescing against dominant individuals (Boesch and Boesch-Achermann 2000). Coalitions are also formed for hunting, for the intragroup control of widely dispersed females, and to monitor territorial borders (Stanford 1998).

### **Intergroup Interactions**

Most interactions of chimpanzee males with neighboring communities involve only auditory contact-pant-hoots, a long-distance call. These pant-hoots are also used to advertise their presence and numerical strength. Males almost always show fear or hostility to strange males (Wilson and Wrangham 2003).

Chimpanzee males invest considerable time and energy in defending the home range of their community or locating their neighbors; the home range is controlled by groups of at least four males on a weekly basis in Tai (Boesch and Boesch-Achermann 2000). During those patrols, they remain silent and actively search for signs of the neighbors. They make incursions into the home ranges of the neighbor communities, sometimes of more than 1 km, and if they encounter strange males, they attack them. In Tai, they are sometimes joined by females (Lehmann and Boesch 2005). Not only males are attacked but females too, except for tumescent females (Pusey 2001; Williams et al. 2004; Watts et al. 2006). Females with or without infants often join attacks, but they tend to avoid direct physical contact with members of the other community.

Hostile intercommunity relations have been observed at all sites. Intraspecific violence is one of the leading causes of mortality for eastern chimpanzees (Wilson et al. 2004). At Gombe and Mahale, the destruction of a small community by a larger one, including systematic attacks and

killing of individuals by males from a larger community, has been observed. Wilson and Wrangham (2003) provide a good overview of such intercommunity conflicts. So far, there is no consistent evidence from the field that the communities find more or better sexual partners and new resources as a result of the fights (Boesch and Boesch-Acher 2000, but see Mitani et al. 2010). Extensive female transfer after a violent fight between communities was observed only in Mahale (Wilson and Wrangham 2003). In Gombe, adult parous females join other communities only when all males of their community have been killed.

Williams et al. (2004) conclude that male chimpanzees cooperatively defend territories that contain food resources for themselves, their long-term female mates, and their offspring, and they try to extend the size of the community's home range because a larger area means greater availability of food and higher female reproduction. Infanticide during intercommunity encounters can also be interpreted as the removal of future competitors. Concerning intercommunity killings by adult males, data from various study sites most strongly support the hypothesis that attackers reduce the future coalition strength of rival communities.

### **Bonobo (*Pan paniscus*)**

The most important sites where bonobos have been studied are listed in Table 12.1.

#### **Ecology**

The typical habitat for bonobos is the lowland rain forests and swamp forests of the Congo Basin. In some areas, they also live in dry forest and visit grassland. They eat up to 147 food items; 72–90 % of their diet consists of fruits (Kano and Mulavwa 1984; White 1992; Yamagiwa 2004). The amount of meat consumption is not as high as in some chimpanzee populations but seems to fall within the general range of chimpanzees. Bonobos (including females) hunt small mammals, usually solitarily (Fruth and Hohmann 2002; Surbeck and Hohmann 2008).

In Wamba as well as in Lomako, the home ranges of communities overlap extensively (Idani 1990; Hohmann and Fruth 2002). Their size lies between 22 and 58 km<sup>2</sup> in Wamba (Idani 1990). Each adult has an individual home range or core area within the community's home range (White 1996).

Bonobos may experience lower leopard predation pressure than chimpanzees because they spend more time off the ground (Boesch 1991). Outside the forest, they seem to be very careful; if they feed on fruit in the grassland, they remain quiet (Myers Thompson 2002).

#### **Life Histories and Dispersal**

Bonobo infants are weaned at 3–4 years of age, and the interbirth interval is about 4–7 years (Lee 1999; Yamagiwa 2004). Females conceive for the first time at about 10–14 years. Adult males have a mean weight of 39.2 kg, and females weigh 31.5 kg (Groves 1986).

Females transfer to other communities as older juveniles or early adolescents (Furuichi 1989). Paternity analyses suggest that there must be a large exchange of females between communities (Gerloff et al. 1999). Males tend to stay in their natal community. Occasionally, they may transfer to other communities, but this is rare (Hohmann 2001).

#### **Size and Structure of Social Units**

Much like common chimpanzees, bonobos live in a fission-fusion social system. Parties usually contain mature individuals of both sexes with more females than males. The proportion of all-female parties in Lomako is high and of all-male parties low (Hohmann and Fruth 2002). If

estrous females are present, the proportion of males increases (Hohmann and Fruth 2002). Lone individuals are rare – usually males travel alone (White 1996).

Party sizes are determined by food availability: if more fruits are available and if the food patch is large, the parties grow larger. Males disperse when food becomes scarce, but females do not (White 1998; Furuichi et al. 2008). As bonobo food includes herbaceous plants that are abundant in the rain forest during all seasons, feeding competition is low.

In general, bonobo parties are large in Lomako and Wamba, compared to chimpanzees. While chimpanzee parties are 9–21 % of the community size, bonobo parties consist of 21–89 % of the community. Bonobo parties last longer than those of the chimpanzees at Tai and Gombe (in Wamba 86 min, in Lomako 102 min; Boesch and Boesch-Achermann 2000).

Community sizes in Wamba are very variable, ranging from 33 to more than 100 members (Idani 1990). The cohesion of community members is high, and they stay together most of the time. In Lomako, several parties may congregate in the evening to nest in proximity to each other (Hohmann and Fruth 2002). Community members may be separated by kilometers for days or weeks (White 1996).

### **Male-Female Relationships and Mating Strategies**

It is usually stated that in bonobo communities, either females are dominant over males or both sexes are codominant/egalitarian (Gerloff et al. 1999), but recent studies suggest that males dominate females – except for feeding situations (White and Wood 2007). Long-term bonds are found predominantly between heterosexual dyads and involve not only close kin but also unrelated individuals. Relatives associate and groom more often, however, and kinship ties are important between males and females. The highest association rates are observed between adult females and their adult sons: males receive agonistic aid from their mothers in conflicts with other males (Hohmann et al. 1999; Kapsalis 2004). Aggression by males toward females is less intense than in chimpanzees. Females may form alliances to attack males (Furuichi 1989; Hohmann and Fruth 2002).

Bonobo mating is opportunistic and promiscuous and involves no or little aggression between males. The maximal swelling lasts for a large proportion of the cycle; therefore, males establish long-term bonds with females that exceed tumescence (Fruth et al. 1999). Nevertheless, sexual coercion is found in some populations; high-ranking males have a strong tendency to monopolize tumescent females and they sire more offspring (Kano 1996; Gerloff et al. 1999; White and Wood 2007; Surbeck et al. 2011). In low- and mid-ranking males, the mother's presence increases mating success (Surbeck et al. 2011).

Extracommunity copulations are not uncommon, and females are rarely prevented from mating with members of neighboring communities. The number of infants sired by nonresident males is low; more than 80 % of the infants in Lomako are fathered by resident males. No infanticide was observed so far in bonobos (Fruth et al. 1999; Gerloff et al. 1999).

### **Female-Female Relationships**

Female bonobos are more affiliative and cohesive with each other than chimpanzees. Contact frequencies between females are higher than between females and males or between males. They associate and forage in larger parties for most of the year, share food, and support each other in food defense (Hohmann and Fruth 2002). These affiliative bonds are not particularly observed between related females; female associations are not based on kinship (Kapsalis 2004).

Female bonobos groom less than male-male and male-female dyads but show a unique behavior called genito-genital rubbing, especially in the context of feeding: two females embrace each other

ventro-ventrally and rub their genital swellings together with rapid sideways movements. The function of this behavior was discussed by various authors, such as Hohmann and Fruth (2000), who observed genito-genital rubbing six times as often as female-female aggression. According to their analysis it serves reconciliation and tension regulation.

### **Male-Male Relationships**

Although strong bonds between males exist, especially at Wamba, they are less prominent than the bonds among females (Hohmann and Fruth 2002). Unlike chimpanzee males, bonobo males have even fewer contacts with other males than with females (White 1998). High-association rates are observed between maternally related adult brothers (Kapsalis 2004). Alliances are unusual between males (Hohmann et al. 1999). The males establish dominance relationships with each other, but aggression is less intense than in chimpanzees and conflicts are often settled in a nonagonistic way (Hohmann and Fruth 2002; Surbeck et al. 2011).

### **Intergroup Interactions**

Bonobo communities do not seem to search for and contact neighboring communities. Lomako males have never been seen to make border patrols (Hohmann and Fruth 2002). In Wamba, intergroup encounters vary from group fights to peaceful intermingling. In general, encounters are peaceful and communities may spend hours together. Females take the initiative in the temporary fusion of communities. During these community meetings, males keep a certain distance from the males of the other group. The most prominent form of intergroup interaction between males and females is copulation, and relations between resident and unknown females are characterized by friendly contacts (Idani 1990; Kano 1996; Gerloff et al. 1999).

There are frequently aggressive interactions between males when they approach, but direct body contact and cooperative attacks are rare; the aggressive interactions are never as fierce as those reported for chimpanzees (Idani 1990; Hohmann and Fruth 2002). Agonistic aid during conflicts between members of different communities has never been reported. Severe aggression does occur, however, when mixed-sex parties encounter unknown males; in such a case, the strangers are charged by the males and also by the females (Hohmann et al. 1999). No fatal aggression was observed between bonobo communities at Wamba (Kano 1996).

### **Discussion: Genus *Pan***

Usually the chimpanzee social system has been regarded as male-bonded, with strong kinship ties between the males of a community but no relationships between the females. Experience from various field sites does not always support this idea and indicates that it is much more complicated and variable. In Tai, males within a community are on average not significantly more related than females, and the group members have more relatives within their home community than outside (Vigilant et al. 2001). Association patterns do not support the view of strong bonds between males in general (Pepper et al. 1999).

Tai chimpanzees may be bisexually bonded, while other populations are male-bonded, and more cooperation is found in Tai than in eastern chimpanzees. The reasons are presumably differences in habitat. Boesch and Boesch-Achermann (2000) assume that the forest environment allows or forces bonobos and chimpanzees to build larger and more cohesive parties. Doran et al. (2002b) hypothesize that permanent female association with males is a female counterstrategy to infanticide risk and that more infanticide occurs in habitats with considerable annual variance in fruit production. Bonobos live in a still more stable environment than Tai chimpanzees – this may lead to even more stable party sizes (Doran 1997). Bonobo parties seem to be large compared to

chimpanzees (Table 12.3), but the within-species variation is larger than the interspecies variation (Hohmann and Fruth 2002; Furuichi 2009).

Bonobo communities seem to be composed of unrelated females who are highly affiliative with each other and related males who are not highly affiliative with each other; females directly control competition with homosexual behavior (Boesch and Boesch-Achermann 2000). Aggression between males and between the sexes is less intense than in chimpanzees, and conflicts are often settled in a nonagonistic way. Bonobos in general have more relaxed relationships than chimpanzees that do not depend on kinship, as paternity studies show that there is no matrilineal organization (Gerloff et al. 1999).

The typical chimpanzee/bonobo social structure is a multimale group with a fission-fusion structure. Similarities are obvious with respect to party size and association patterns. Female bonding in bonobos does not exceed that of some chimpanzee populations; differences between the two species are the proportion of female party members and the frequency of mixed parties (Hohmann and Fruth 2002). Chimpanzees as well as bonobos have the potential for great social variability, with considerable capacity for cooperation, reciprocal interactions, and coalitional behavior (Boesch and Boesch-Achermann 2000).

Despite the common basis, the two species show some differences in social behavior. Wrangham et al. (1996) think that this can partly be explained by the differences in feeding competition: chimpanzees and gorillas live sympatrically in many areas while bonobos do not have a great ape competitor.

## Sympatric Ape Populations

Sympatric apes share a great part of their diet – in Asia as well as in Africa (Morgan and Sanz 2006; Vogel et al. 2009; Yamagiwa et al. 2012). This is especially visible in fruits. Sugardjito et al. (1987) observed some competition between orangutans and siamangs in Gunung Leuser, and one benefit of grouping for Sumatran orangutans may be that siamangs cannot drive the youngsters away from fruiting trees. More obvious, however, is the interspecific competition between chimpanzees and gorillas in Africa.

The dietary overlap between gorillas and chimpanzees ranges from about 50 % at Kahuzi-Biega to 60–80 % at Lopé and Ndoki. In Kahuzi-Biega, all fruit species eaten by gorillas are also eaten by chimpanzees. Overt interspecific competition between chimpanzees and gorillas has not been observed at any site; instead, competition avoidance is commonly seen (Kuroda et al. 1996; Morgan and Sanz 2006; Head et al. 2011). Interspecies relationships are more peaceful than intergroup relationships within the two species (Yamagiwa et al. 2003b). In Gabon, Okayasu (2004) observed close interactions between gorillas and chimpanzees; occasionally the groups would mix and play and even sleep at the same site.

During fruit scarcity, gorillas increase the proportion of herbaceous vegetation in their diet, while chimpanzees as obligatory frugivores continue to search for fruit. The two species obviously find different niches (Yamagiwa et al. 2003b, 2012), and some habitats are used almost exclusively by one species (Tutin and Fernandez 1993; Malenky et al. 1994; Kuroda et al. 1996; Rogers et al. 2004).

Kuroda et al. (1996) suggest that the low population densities of gorillas and chimpanzees in Lopé and Kahuzi-Biega might partly be due to competition. Possibly interspecific competition over food affects foraging strategies and may have caused divergence in grouping patterns. The larger party sizes of bonobos are possible because of the high density of terrestrial herbaceous vegetation;

as gorillas mainly eat these plants, sympatric chimpanzees may be forced to take a different foraging strategy and to form smaller parties (Wrangham et al. 1996; Yamagiwa and Takenoshita 2004). The effects of competition have not been analyzed yet, but they are difficult to study – also because additional competitors like elephants have to be considered (Rogers et al. 2004).

## Conclusions and the Genus *Homo*

Although some great ape populations have been studied for decades, their social systems are not yet completely understood. The Asian apes seem to be less social than the African apes; this may be due to food types and distributions in Southeast Asian forest, which may differ strongly from African forests. All great apes lead “individual-centered lives,” but they need interaction with familiar conspecifics. Despite their tendency to congregate, their social structure is characterized by weak ties, compared to female philopatric primates.

Female transfer is common to all species. They have a tendency toward fission-fusion grouping; females lack sharply defined dominance relations, and intrasexual bonds among non-kin can be relatively strong. Van Noordwijk et al. (2012) hypothesize that this ability to form and maintain bonds has freed females from the necessity to be strictly philopatric. It is difficult to assign a social system to each ape species (or to the family Hominidae in general) because there is remarkable intraspecific variability in social organization and structure. Especially frugivory requires a mobile and flexible population.

Compared to the great apes, humans show an even greater variability in social structure – nevertheless, there are certain trends across all human societies (Rodseth et al. 1991): males maintain consanguineal kin ties; females maintain consanguineal kin ties; males cooperate in conflicts against other males; and females also cooperate but rarely in physical conflicts with other females.

According to Knauff (1991), simple human societies are decentralized, and there tends to be active and assiduous devaluation of adult male status differentiation. Among complex hunter-gatherers and with the advent of sedentism and horticulture/agriculture, male status differentiation increased. There seems to be a similarity between great apes and middle-range human societies in terms of competitive male dominance hierarchies. Such dominance relations may not be particularly adaptive in environments of low resource density and predictability; this may have led to the simple egalitarian hunter-gatherer societies that nowadays live in extreme environments.

Most human societies are characterized by female-biased dispersal and male philopatry. Long-term pair bonds between males and females are common, although their form, strength, and duration vary between societies. Moreover, these bonds are not identical with mating and grouping patterns (Pusey 2001). And according to the cooperative breeding model, these bonds allowed the increase of brain size during the development of *Homo* (Hrdy 2005; van Schaik and Burkart 2010; Isler and van Schaik 2012).

There has been much speculation on the “natural” human mating system. Although fossils of man’s early ancestors show extreme sexual dimorphism, modern human males are only about 15 % larger than females; the relative size of testes in humans is much smaller than in chimpanzees and comparable to “monogamous” or one-male group species. Polygamy with only some males producing many offspring thus cannot be the common mating system in humans, but social monogamy is not common either (Low 2003). According to Plavcan (2012) size dimorphism is not a robust indicator for breeding systems.

The social system of humans certainly has several levels, like the social system of *Pan* (Layton et al. 2012). Dunbar (1993) developed the hypothesis that there is a species-specific upper limit to group size that is set by cognitive constraints. This would mean that human groups can be much larger than those of the great apes. According to Dunbar, group size depends on the maximum number of individuals with whom an individual can maintain personal contact. He discerns (in modern hunter-gatherer societies) the group levels overnight camp (30–50 members), band/village (100–200 members), and tribe (1,000–2,000 members). Dunbar's overnight camp certainly is not the smallest human grouping above the individual. Rodseth et al. (1991) and Pusey (2001) state that the majority of human societies consist of conjugal families united in stable communities, but also relatively autonomous families. Apart from these units, associations of men usually play an important role too (Rodseth 2012).

But what is the central, stable component of the human social system? Even ape specialists have contradictory opinions. De Waal (2001) thinks that the nuclear family is the basic social grouping of humans and that this unit is unique to the species *Homo sapiens*, although Low (2003) states that it is rather unusual in human societies. Perhaps the nuclear family is an especially successful social structure in modern industrialized societies. Ghiglieri (1989) calls the social structure of humans a multimale kin group, a stable, semiclosed fission-fusion community.

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