

2 BACKGROUND

2.1 Distribution and status of feral gorillas

The following paragraphs briefly discuss distribution, habitat, ecology, and behavior of the all gorilla subspecies, with emphasis on the western lowland gorillas. Gorillas were previously seen as one species and were subdivided into three geographically isolated subspecies, the western lowland gorilla (*Gorilla g. gorilla*), the eastern lowland gorilla (*Gorilla g. graueri*), and the mountain gorilla (*Gorilla g. beringei*) (Groves, 1971). Figure 1 denotes the distribution of these three gorilla subspecies.

More recently, the IUCN/SSC Primate Specialist Group proposed a new classification, describing two species and four subspecies (Stewart et al., 2001). According to this classification, the western lowland gorillas should be divided into the western lowland gorilla (*Gorilla g. gorilla*) and the Cross River gorilla (*Gorilla g. diehli*). The later is only found in Nigeria, consisting of approximately 150-200 gorillas, thus these gorillas are considered critically endangered (Oates, 2000).

Furthermore, an ongoing debate discusses as whether the mountain gorillas should be split into two subspecies. According to Sarmiento et al., (1996): “Limited morphological and ecological comparison between the Virunga and Bwindi gorillas suggest that they should not be considered the same subspecies.” On the other hand, Garner and Ryder, (1996) argue that there is no genetic evidence available which would support a classification into two subspecies. The latest findings postulate the presence of two species, *Gorilla gorilla* and *Gorilla beringei* (Groves, 2001, 2003) with the later being subdivided into the two subspecies, mountain gorillas (*Gorilla beringei beringei*) and eastern lowland gorillas (*Gorilla beringei graueri*). Due to the ongoing debate, in the following chapters the author will stay with the thus far used species name of *Gorilla gorilla beringei* for the mountain gorillas. Table 1 presents an overview of the recommended classification according to Groves (2001).

The best-known and most-studied subspecies in the wild are the mountain gorillas. They are found in the Virunga Volcanoes region, within the countries of

Congo (former Zaire), Rwanda, and Uganda (Fossey, 1983) and in the Biwindi Forest Reserve, Kigezi District, in southwestern Uganda (Groves and Scott, 1979; Fig. 1). Various long-term studies have been carried out on their ecology, development, and social behavior (i.e., Fossey, 1979, 1983; Harcourt, 1979a; Schaller, 1963).

Census data from 1989 indicates that the mountain gorilla population in southwest Uganda, the Bwindi Impenetrable National Park, consisted of approximately 320 animals (Butynski et al., 1990). Thus, together with the 320 gorillas in the Virunga Volcanoes region of Rwanda, Uganda, and Democratic Republic of Congo, the total number of mountain gorillas was estimated to be 640 animals (Butynski et al., 1990). Surveys, more recent, indicate that the total number of mountain gorillas is approximately 600 for the population of the Virunga Volcanos of Rwanda, Uganda and the Democratic Republic of Congo and for the population of the Bwindi Impenetrable National Park, Uganda (Sholley, 1991; McNeilage et al., 1998).

The eastern lowland gorillas inhabit both lowland and certain highland forests of northeastern Congo, east of Lualaba River and west of the Albertine Rift (Groves and Scott, 1979; Fig. 1). The population size at the Kahuzi-Biega National Park, Zaire (now Congo) was estimated at 258 animals, with a density of 1.03 individuals/km² (Yamagiwa et al., 1993). The total population size for the eastern lowland gorilla is estimated to be 17,000 located in various isolated populations (Harcourt, 1996; Hall et al., 1998).

The western lowland gorillas are found in the tropical forests of Nigeria, Cameroon, Equatorial Guinea, Gabon, the Central African Republic and the Congo (Mitani, 1992; Remis, 1997a; Yamagiwa and Goodall, 1992; Fig. 1). Blom et al. (1992) estimated the gorilla population size in Gabon at approximately 35,000 animals. The authors described the conservation status of these gorillas as not threatened, and noted that they are only moderately hunted in this country. Information based on WF/IUCN data indicates that there are 1000 – 2000 gorillas in Equatorial Guinea, and equal numbers are suggested for Cameroon. The total population size is estimated to be about 110,000 animals (Harcourt, 1996).

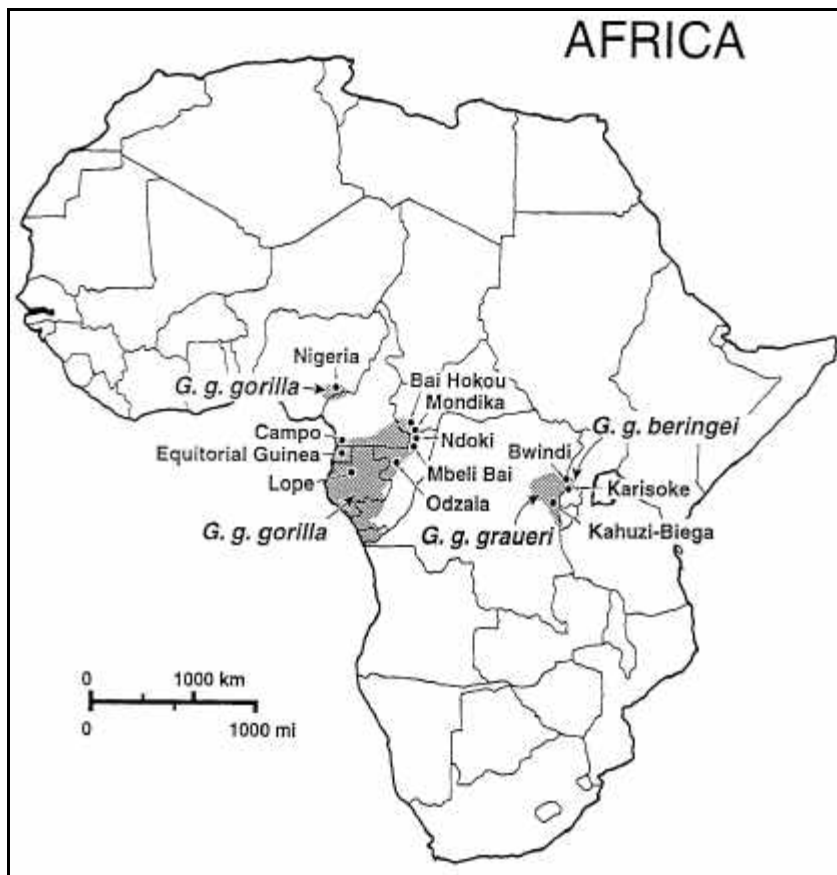


Fig. 1: Distribution of *Gorilla gorilla* sp. and the major gorilla research sites (taken from Stewart et al., 2001).

Table 1: Gorilla classification, an overview of the two species and four subspecies, based on the suggestions by Groves (2001).

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| Western gorillas | <i>Gorilla gorilla gorilla</i> |
| Cross River gorilla | <i>Gorilla gorilla diehli</i> |
| Mountain gorillas | <i>Gorilla gorilla beringei</i> and <i>Gorilla beringei beringei</i> |
| Eastern lowland gorillas | <i>Gorilla gorilla graueri</i> and <i>Gorilla beringei graueri</i> |

The population density of western lowland gorillas was estimated in various regions of Central Africa and varies from low densities of 0.2 individuals/km² (Fay and Agnagna, 1992; Furuichi et al., 1997; Matthews and Matthews, 2000; Tutin and Fernandez, 1984) to high densities of 1-3 individuals/km² (Blom et al., 2001; Fay, 1989; Stohmayer and Ekobo, 1991; Tutin and Fernandez, 1984; WCS, 1996; White, 1992; Williamson and Usongo, 1995). Highest densities were so far recorded in Odzala National Park (5.4 gorillas/km²) in the Republic of Congo (Bermejo, 1999) and in the Dzanga-Ndoki Park (1.6 gorillas/km²) in the Central African Republic (Blom et al., 2001).

The density of western lowland gorillas is often significantly lower in primary forest than in secondary forest with a dense layer of monocotyledons of the families Zingiberaceae and Marantaceae, which provide an important food source for gorillas (Fay and Agnagna, 1992; Furuichi et al., 1997; Hall et al., 1998; Tutin and Fernandez, 1984), but high densities can also be found in primary forests with abundant swamp forest (Nishihara, 1995; Fay and Agnagna, 1992).

While Mitani (1992) notes that out of 17 sightings the majority consisted of groups with three or fewer animals, Parnell (2002) presents data on 14 groups with a mean group size of 8.4 ± 4.3 . In the Lopé Reserve in central Gabon the median group size was ten animals, with two large groups of 15 and 16 animals, with two silverback males (Tutin et al., 1992). The home range size varies between a "minimum" of 3.9 to 8.1 km² and a "maximum" of 7.3 to 14.4 km² (Tutin et al., 1992). The total population size is estimated to be about 110 000 animals (Harcourt, 1996).

The lowland gorillas (*Gorilla gorilla sp.*) were until recently classified as "vulnerable" throughout their range, according to the 1994 IUCN Red List (Groombridge, 1993) and the mountain gorillas (*Gorilla g. beringei*) were listed as "endangered." Due to the increased threats, all gorilla subspecies are now recognized as "endangered" according to the International Union for Conservation of Nature (IUCN) definition (IUCN, 2000). According to Plumptre et al. (2003) "The major threats to gorillas can be categorized as: 1) habitat loss, modification, or fragmentation (e.g. logging activities); 2) hunting or poaching; 3) disease transmission from humans;

and 4) war or political unrest.” Oko (1992) described the major threats to gorillas as hunting for their meat. In addition, the adults of the group are killed by poachers to obtain baby gorillas as pets or for the international trade. Other threats include mining activities and inland petroleum exploitation; all of which decrease the available habitat for the gorillas.

2.2 Ecology of free-ranging gorillas

The diet of mountain gorillas consists mainly of leaves, stems, and pits (Watts, 1990a). Most of the mountain gorilla foods are highly digestible, rich in protein, and low in fiber and condensed tannins. These food items represent 90% of the actual food intake of mountain gorillas. Compared to the other two subspecies, the diet of the mountain gorillas can be viewed as the least diverse. This may well reflect that the favorite food items for the mountain gorillas are very abundant throughout their habitat. Another possibility for their dietary pattern is that it could reflect lower plant species diversity in the Virungas, compared to the gorilla habitats at lower altitudes.

The eastern lowland gorillas, which inhabit regions of eastern Congo (Yamagiwa and Goodall, 1992; see also Fig. 1), have a dietary pattern similar to that of mountain gorillas (Watts, 1990a). Additionally, those eastern lowland gorillas, which live at lower altitudes in the tropical forests, show a higher fruit intake in their diet than gorillas living in montane forests (Yamagiwa et al., 1993).

Studies on western lowland gorillas have been carried out within the last couple of years in the Likouala swamps of the northeastern Congo (Fay et al., 1989), and at the 'Station d'Etudes des Gorilles et Chimpanzés' in the Lopé Reserve in central Gabon (Williamson et al., 1990; Rogers et al., 1992; Fig. 1). Furthermore, observations have been attempted in the remote area of the Ndoki Forest, located at the frontier between Cameroon, the Central African Republic, and the Congo (Mitani, 1992; Nishihara, 1992; Fig. 1) and at Bai Hoköu in the Dzanga-Ndoki National Park (Goldsmith, 1999; Remis, 1997b).

In contrast to the previous described subspecies, the diet of western lowland gorillas consists mainly of fruit (54%) (Nishihara, 1992). Thus, fruit represent the majority of food intake for these gorillas (Williamson et al., 1990). The amount of fruit intake seems to be related to seasonal variations in fruit availability. Nishihara (1992) states that gorillas eat more fruit during the wet season (i.e., 77 % fruit in August), and they relied more on fibrous food during the dry season (i.e., 6% fruit during January). This pattern reflects the abundance of fruits during the wet season

and the limited availability of fruits during the dry season. A similar feeding pattern has been observed for eastern lowland gorillas, which live at lower altitudes (Yamagiwa et al., 1992).

Tutin and Fernandez (1985) compared food items eaten by chimpanzees and western lowland gorillas in Gabon. Their results showed that fruit made up 67% of the food consumed by gorillas. For chimpanzees, in comparison, the total fruit proportion of their diet consisted of 78% of the total food intake. Thus, if fruit is available, these gorillas are nearly as frugivorous as chimpanzees. Besides feeding on fruit and plant material, gorillas forage for insects also, as shown by Tutin and Fernandez (1992).

2.3 Social behavior of free-ranging gorillas

2.3.1 Social structures

The majority of the available information on gorillas refers to the long-term studies on mountain gorillas (i.e. Fossey, 1983; Harcourt 1979a, b; Schaller, 1963; Watts, 1983). Thus, the following paragraphs on group compositions, the social structures and behaviors of gorillas, focus mainly on observations on Mountain gorillas (*Gorilla g. beringei*), due to the lack of extensive behavioral observations on western lowland gorillas.

Gorillas are among those primate species, characterized by great sexual dimorphism. Males weigh on average about 160 kg and females weigh approximately 95 kg (Stewart and Harcourt, 1987). Sexual dimorphism becomes apparent once the males reach adulthood. The various age categories for gorillas referred to in this research are based on the classifications by Stewart and Harcourt (1987). Gorillas from ages of 0 – 3 years are considered infants, from 3 – 6 years they are classified as juveniles; and subadults are gorillas ages 6 – 8 years. Since males and females mature at a different rate, females are considered adults when they are eight years and older. They come into estrus between seven and eight years and the first conception in the

wild occurs at about 10 years of age. Males are considered blackbacks at the ages of 8 – 13, and they are considered fully-grown by 15 years. Since upon maturity, males develop the characteristic silver saddle, they also referred to as “silverbacks”. As far as dominance relationships are concerned, older males are dominant over younger males (Schaller, 1963).

A mountain gorilla group consists of 6-17 animals with an average of nine animals, one adult male, several adult females and subsequent offspring of both sexes (Maple and Hoff, 1982; Stewart and Harcourt, 1987; Lukas et al., 1996). Such a group structure is also referred to as “harem” or polygyne group (Meder, 1993). Besides such one-male units, groups with two adult males or several adolescent males, so called “blackbacks” are also common (Maple and Hoff, 1982). Either such multimale groups consist of an older and of a younger silverback, which are likely father and son (Stewart and Harcourt, 1987) or such groups consist of several silverbacks, which are likely closely related to each other, such as half or full brothers (Robbins, 1995). The group structure of a multimale group might change to a one-male group once adolescent males mature and eventually emigrate (Robbins, 1995). Among western lowland gorillas, the observed group size ranges from 5 to 16 individuals, depending on the region where they have been observed (Jones and Sabater Pi, 1971 [Equatorial Guinea]; Tutin, 1996 [Congo]; Tutin et al., 1992 [Gabon]).

The majority of gorilla groups are usually one-male groups, where younger males live at the periphery of the group until they eventually leave the group around sexual maturity. Then they become either solitary animals or join a bachelor group (Maple and Hoff, 1982; Lukas et al., 1996; Yamagiwa, 1986). The latter will be discussed in more detail in the following chapter. Approximately 60% of the mountain gorilla population are one-male groups and adult solitary males make up as much as 10% (Harcourt, Fossey and Sabater Pi, 1981), the rest will either stay within their natal group and reproduce, or join bachelor groups (Stewart and Harcourt, 1987).

In mountain gorillas, not only males usually leave their natal group; females as well leave their group by transferring either to another social group or to a lone silverback (Harcourt et al., 1976; Harcourt, 1978; Pusey and Packer, 1987; Yamagiwa,

1983; Moore, 1984). Female transfer had also been observed in eastern lowland gorillas (Yamagiwa, 1983) and western lowland gorillas (Parnell, 1999; Tutin, 1996). Female transfer occurs when a group meets another group or a solitary young male. Whereas females join breeding groups, emigrating males hardly join such groups after they emigrate from their natal group (Harcourt, 1978), because of the intense competition for females.

Usually, intra-group aggression is low, consisting mainly of aggressive vocalizations, such as cough-grunts, as described by Stewart and Harcourt (1987). Once sexual mature males leave their natal group, they attempt to attract females during encounters with other groups, usually accompanied by agonistic displays, such as chest beating, throwing of foliage, etc. In some instances, fights with physical contact have also been observed (Harcourt, 1987). Usually, these “solitary males” have to travel a long time before they are actually able to form their own social group (Fossey, 1974).

One reason why young adult males leave their natal group might be that they have few mating opportunities within their group or that the group leading silverback will not tolerate the young male’s attempts to copulate (Harcourt, 1981; Harcourt et al., 1981; Fossey, 1982; Stewart and Harcourt, 1987; Watts, 1990b). The latter is related to the intense male-male reproductive competition within a group with more than one sexually mature male (Harcourt et al., 1981; Watts, 1990b), which can lead to physical fights and inflicting wounds upon each other (Harcourt, 1978, 1981). An adult male’s main social interactions within a group are primarily based on his relationships with the adult females, where the females maintain the proximity to the leading silverback. As far as his relationship towards immatures is concerned, a silverback is very tolerant and very protective towards them (Stewart and Harcourt, 1987).

Since the main objective of this project is concerned with males, the following paragraphs will describe in more detail the role of males within a social group and why solitary males may join all-male groups.

2.3.2 All-male groups

Besides mountain gorillas, all-male groups have been observed in many other primate species (e.g. gray langurs (*Presbytis entellus*), Rajpurohit et al., 1995; hanuman langurs (*Presbytis entellus*), Ross, 1993; geladas (*Theropithecus gelada*), Kummer, 1975). Pusey and Packer (1987) describe in detail the occurrence of all-male groups among various species of primates (e.g. various macaques species). Forming an all-male group can be an alternative solution to a solitary life for many males, such as when they might not be able to remain in their natal group due to high male-male competition. The reason why males join all-male groups in the wild might be as a response to predation pressure or to maximize foraging efforts (Rajpurohit et al., 1995).

Since this research project is concerned with the behavioral dynamics within captive all-male groups, the following paragraphs will describe the available background information of the bachelor groups in the Virungas.

As previously noted, males may either choose to join bachelor groups or become solitary males. Stewart and Harcourt (1987) state, “In the Virungas, all-male groups may make up as much as 10% of all groups of two or more animals.” When comparing the ranging patterns of solitary males with all-male groups, it seems that solitary males do not avoid contact with social groups whereas all-males groups avoid the vicinity of other social groups (Yamagiwa, 1987).

All-male groups may form after the disintegration of a group, i.e. when the silverback has died (Stewart and Harcourt, 1987). Fossey (1983) described in more detail the demise of two groups after the leading silverback of one group had been shot and the subsequent formation of an all-male group. The formation of an all-male group might be “an evolutionary response to predations” and thus would explain why immature males built all-male groups (Robbins, 1995; Schaller, 1963). Further studies on free-ranging all-male groups of mountain gorillas were conducted by Yamagiwa (1987, 1992) and Robbins (1995, 1996). The size of the home range of an all-male group is similar to the range observed of one-male and multi-male groups (4.0 – 8.1

km²) (Fossey and Harcourt, 1976) and thus, larger than the range covered by solitary males (1.5 – 5.25 km²) (Caro, 1976; Yamagiwa, 1986).

Yamagiwa (1987) described the social structures and behaviors of an all-male group of mountain gorillas, which consisted of six unrelated males (including two silverbacks) staying together for about three years. He noted that “the daily activities of the six males involved were highly synchronized, and they spent a considerable part of their day within 10 m of one another both during feeding and resting phases.” Yamagiwa (1987) stated that the following factors played an important role in the groups social relationships: “(1) the homosexual attractiveness of the subadults; (2) loser-support and mediating behavior; and (3) their responses to other social units.” The responses to other social groups were characterized by males avoiding the proximity to such groups.

Robbins (1996) compared the behaviors of males in all-male groups of mountain gorillas with the behaviors of males in heterosexual groups. She found that males in all-male groups spent more time alone during resting and feeding times, engaged more often in high aggression (aggressive interactions with body contact such as hits) and moderate aggression (chest beating and strut-walking), but less in mild aggression (vocalization) when compared with males in heterosexual groups. However, social affiliative interactions were more frequently observed among the gorillas of the all-male group and occurred between all group members. Homosexual behaviors were observed only in the all-male group, as noted by Yamagiwa (1987) in his observation of subadult and juvenile males. Robbins (1996) argued, “all-male gorilla groups may provide an environment in which males can further develop social skills that they would be unable to obtain as lone males and possibly gain protection against predators.” In such an environment, young males mature and eventually going to emigrate once they are silverbacks to become solitary males and to form possibly a social group of their own (Robbins, 2001). For instance, when the dominant male of her study group emigrated in 1993 (Robbins, 2001) the rest of this all-male group disintegrated shortly afterwards (Robbins, personal communication, 2003).

2.4 Status in captivity

The status of captive gorillas, the move of individuals between institutions such as zoos, is managed by various Species Survival Committees and through regional and international studbooks. The European gorilla populations are managed by the Gorilla-EEP (European Endangered Species Program for the Gorilla) (Kirchshofer, 1994). The North American gorilla populations are managed by the Gorilla-SSP, which stands for “the Gorilla Species Survival Plan”, founded in 1983 (Conway et al., 1985).

The following information is based on data from the International Studbook of the gorilla (Hilsberg, 2003). As of December 2002, there were 825 western lowland gorillas (375 males, 450 females) kept worldwide in zoos or research facilities. The rate and ratio of births among captive gorillas in 2002 was 23 males and 11 females. Based on the information of the International Studbook for the Gorilla, approximately 32 males were kept solitary worldwide, however, no further information is provided whether some of these males are kept as a group or solitary. In Europe, six zoos by the end of 2002 held all-male groups (Schmidt, personal communication, 2003) with two additional groups planned for 2004. Thus far, nine all-male groups exist in North American Zoos in 1997 (Lukas, personal communication, 1997).

Gorillas in zoological gardens have been widely studied with respect to the influences of rearing history (Gold, 1986, 1992; Mallinson, 1983; Meder, 1985 a,b, 1987, 1989), physical environments (Goerke et al., 1987; Gold, 1992; Gould and Bres, 1986; Maple and Stine, 1982; Meder, 1992; Ogden et al., 1990) and age (Beck and Powers, 1988; Gold, 1992; Meder, 1989) have on the behavioral development of these animals.

The majority of gorillas kept in zoological gardens are western lowland gorillas (*Gorilla g. gorilla*), with the exception of a group of eastern lowland gorillas (*Gorilla g. graueri*) at the Zoo of Antwerpen (Belgium) (Kirchshofer, 1994). Since the birth rate was approximately 1:1 (in 2002 twice as many males as females were born, see above), and zoos keep mainly one-male groups or even numbered pairs, these institutions today face a “surplus” of male gorillas that cannot be integrated into

existing social groups (Lukas et al., 1996; Schmidt, personal communication, 1996; Symington, 1993). Zoos have various possibilities to deal with this “problem”, such as: euthanasia (Graham, 1996), to keep them as solitary animals, or to form all-male groups (Johnstone-Scott, 1988). As an alternative to the controversial euthanasia, usually zoos keep them solitary (Burks, 1995; Burks and Maple, 1995; Hearn and Trotta, 1993). However, this should be avoided considering the high social needs of gorillas.

Watts and Meder (1996) point out the main reasons for the establishment of all-male groups in zoological gardens: the animals do not lose the important social contact to their conspecifics, since they stay in social association and remain socially competent. This is primarily important for the integration into social groups once the males become adults. Additionally, all-male groups represent an important and suitable potential genetic pool to maintain the species and genetic variation. Hence, a male who has been part of an all-male group should be “easier” to integrate into a social group or to be able to start a new group. Such a gorilla male would subsequently contribute to the survival of the species.

The establishment of all-male groups is also important from the zoo perspective as keeping of males solitary is limited by available space. Additionally, an all-male group represents also an interesting, entertaining and an educational value when compared to single housed highly social animals (Porton and White, 1996). The formation of a gorilla group, involves the introductions of gorillas to previously unknown conspecifics, which will be discussed in the following section.

2.4.1 Introductions of juvenile and adolescent gorillas

The behavioral development of infant and juvenile gorillas in various zoos have been reported by various researchers in relation to interactions with group members, aspects of mother-rearing vs. hand-rearing and gender differences (i.e.: Gold, 1992; Hoff et al., 1981; Meder, 1985a, 1987, 1990; Mitchell, 1989; Niemitz, 1995; Nitsch, 1995, 1996). An understanding of development of infant gorillas within their social group is necessary to facilitate the successful integration of hand-reared gorillas into a social group.

The processes of slowly integrating gorilla infants, juveniles or adults have been described by various researchers (Bowen, 1981; Burks et al., 2001; Elsacker et al., 1990; Johnstone-Scott, 1984, 1992; Meder, 1985a, 1990; Nitsch, 1995, 1996). Such processes usually started out by allowing the animals to get to know each other while still separated. Eventually, the to-be-integrated animals were introduced to an adult female for a short period each day. This should allow the animals to bond gradually with one another during this period of introduction. As Jendry and Absi (1989) pointed out, "... it is important to end these daily sessions at a point when the animals appear relaxed, so that the experience for all animals remain positive." As a final step, the animals are integrated to the rest of the group, except the silverback. The introduction of the silverback to the whole group represented the concluding part of the integration process.

For successful group formation, it is important to allow the animals to become familiar to the new situation, by proceeding gradually and slowly with the process of the introduction, to avoid aggression, and to provide the animals with a positive experience (Nitsch, 1995). Meder (1987, 1990) observed the introduction of five hand-reared gorillas to social groups at three locations. In her study, the animals ranged from one to three years of age at the time of introduction. Furthermore, the introductions were handled in different ways. The occurrence of social play with all members of a group was interpreted as an indication of a "successful integration," especially when it occurred with the silverback male (Meder, 1990).

2.4.2 Establishment of all-male groups of gorillas in zoos

Information on the establishment of all-male groups in zoological gardens is thus far available from the gorilla group at the St. Louis Zoo (Porten, 1990 a, b; Porten & White, 1996), from Loro Park in Tenerife (Downman, 1998) and from the Zoo Atlanta (Lukas et al., 1996).

St. Louis Zoo started with the formation of an all-male group in 1987, after this zoo had been selected by the Gorilla SSP to initiate such a project. By 1990, they had a stable group of four males. During this period, seven males had been part of this group until the right combination of males was found. They first introduced two males to each other before they added a third male. After carrying out various introductions, some males had to be taken out of group due to the occurrence of high aggression toward one another. They found that "... the age, size, rearing history, personality of the individual and formation of coalitions are all factors that impact the likelihood of a successful introduction" (Porton & White, 1996).

Lukas et al. (1996) documented the formation of an all-male group at the Zoo Atlanta, USA, (two subadult males and one juvenile male). Behavioral data were collected on three unrelated males, and two sub-adults and one juvenile male. The decision to choose younger gorillas was based on their opinion that "the successful development of an all-male group may involve the introduction of juvenile or sub-adult individuals, as older males can be dangerously aggressive to one another, leading to stress or injury" (Lukas et al., 1996). Because the group consisted of three gorillas, two of them eventually formed a coalition and excluded the third one, particularly during social play. They concluded, "Results have shown that this introduction differed in many respects from the introductions that have previously taken place at Zoo Atlanta involving bisexual groups. The period, in which aggression increased following introductions was longer than usual, and the regurgitation and reingestion observed by one of the males dropped dramatically following the introduction" (Lukas et al., 1996).

Loro Park in Tenerife also started the group formation of the all-male gorilla group in 1992 with a subadult and a juvenile gorilla (Downman, 1998). Over the course of three years, four additional gorillas (two juveniles, one subadult and one silverback) were introduced to one another, similar to the procedure at St. Louis. At the final stage, the silverback was introduced to the group. All introductions were carried out in off-show areas. When it was apparent that all gorillas were getting along with each other, they were given access to the outside enclosure. Before that, each gorilla had access to the outside enclosure to become familiar with the new surroundings. Coalitions between individual group members were found mainly between the youngest gorillas. See the following chapter for more details on the individual group members.