5 DISCUSSION

The following pages discuss the results of this study in comparison to the relevant literature and outlines recommendations for future group formations and management of all-male groups in captivity. The main objective of this research project concerned the implications of housing all-male groups of western lowland gorillas in zoological gardens and the development of the social behavioral dynamics between individual group members within an established group.

5.1 Group formation at Paignton Zoo

The following section discusses, the group formation at Paignton Zoo focusing on the development of the relationships between the individual group members and how the initial process of the group formation influenced the expressions of social and non-social behaviors among the males.

As described in the previous chapter, the two silverbacks Claus and Pertinax were chosen to be the founders of the new all-male group at Paignton Zoo because of their familiarity with one another. While they were still at the Cologne Zoo and part of a heterosexual group, both males stayed at the boundaries of the social group and as far away from each other as possible, occupying opposite ends of the enclosure. A similar pattern was noted by Chalmeau and Peignot (1998) who found that within a group containing two silverbacks at the same age, that these males stayed as far away from each other as possible. This eventually decreased the tension between them and subsequently avoided serious fights between the males. At the zoo of Apenheul (The Netherlands), a young silverback also kept his distance from the social unit, which consisted of females and offspring at various ages that stayed in close proximity to the resident silverback (personal observation at the Zoo of Apenheul, 2002). This is similar to what can be seen among free-ranging mountain gorillas (Fossey, 1983). This behavioral pattern plus the presence of a leading silverback male who interfered when

these young silverbacks displayed towards each other may have reduced the tension between Claus and Pertinax. Once both silverbacks arrived at Paignton Zoo, Claus was the one who had apparent difficulties becoming accustomed to the new surroundings whereas Pertinax started to explore the new enclosure immediately. Furthermore, both males avoided each other whenever possible. An earlier study by Meder (1985), while they were still juveniles, described their adjustment, to the than new enclosure at the Cologne Zoo: Claus was the one being more explorative whereas Pertinax had more difficulties adjusting to the new environment. Additionally, Meder noted that Claus was the preferred play partner for the other youngsters and that Pertinax was able to retain his dominance by forming an alliance with Claus. After the arrival of the males at Paignton Zoo, it appeared that Pertinax behaved as the dominant male, characterized by his exploratory behavior.

As mentioned previously, Claus and Pertinax possibly behaved in such a way, because when they were at Cologne Zoo, the leading silverback Kim interfered or supported one of them whenever both young silverbacks displayed towards each other. Thus, when these young silverbacks found themselves in a new social environment their relationship was very likely influenced by the absence of the leading silverback. Hoff et al. (1982) described that after the removal of a silverback male, aggression among the remaining females increased drastically and consisted of "aggressive displays (chest-beat, stiff stance, stiff walk, tight lip, etc.)." Once the male was returned to the group, the rate of aggressive behaviors of the silverback towards the females increased whereas the aggressive behaviors among the females decreased.

Previous studies that dealt with the process of growing up between two gorillas, often involved male-female dyads. Brown and Wagster (1986) presented data on the socialization process of a 13-year-old female gorilla. Upon reaching maturity, the female became aggressive towards a male with whom she was raised. Eventually the male was moved to another zoo and the female was introduced to three younger gorillas from Yerkes Primate Center. Hardin et al. (1969) stated that some pairs who grow up together interacted aggressively towards one another once they became adults. The occurrence of aggressive behaviors between maturing males within a social group

has also been observed among mountain gorillas (Harcourt, 1987). A similar pattern was observed between Claus and Pertinax after their arrival at Paignton Zoo, with an increase of aggressive behaviors after the arrival of Richard and Avahli, despite the familiarity between the silverbacks. Therefore, it is important to consider that even if males grow up together, eventually they will fight over dominance status once they become adults, and this will increase the tension within the social unit. This finding is also supported by Lukas et al. (1996) who stated "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. Related males, or those who have been reared in the same family group, may occupy the same habitat as they grow older without problems that arise from introducing unrelated adults males." Additionally, ongoing agonistic interactions can eventually lead to persistent stress (Aureli et al., 1989), which can have a negative impact on the relationship between group members (Watts, 1995b). Therefore, for the successful formation of an all-male group, it is beneficial to start with subadult and juvenile males and preferably not more than one adult male, the younger males will become adults in a familiar social environment.

The changes and adjustment to the new social environment plus the new enclosure very likely created the tension between both males, which was expressed in aggressive encounters between them. From the beginning, Pertinax occupied the upper level within the enclosure (L1, see also Fig. 14 at page 27), and was subsequently challenged by Claus. In addition, the arrival of the juveniles Richard and Avahli, just a few days after the arrival of the silverbacks might have caused additional stress for the males. The separation of the two silverbacks at the time of arrival of the juveniles had an additional effect on the tension between these two males. Particularly for Claus, who he was separated from Pertinax and had neither visual contact to Pertinax nor to the new males. Thus, the arrival of the juveniles, soon after the silverbacks had arrived, reduced the time available for Claus and Pertinax to adjust to their new situation. This might have been the cause of the subsequent observed serious fight between Claus and Pertinax, leading to the separation of the two males. Thus, not only the introduction of new group members should proceed gradually but also the

adjustment period to a new environment. Sunde and Sievert (1995) described the process of forming a new group consisting with one male and two females, by introducing a new female to the pair. The authors pointed out that stepwise introductions of individuals and the consideration of the individuality of each animal is a very important factor for a successful group formation. The importance of a gradual introduction was also pointed out by Elsacker et al. (1990), describing the introduction of two adult eastern lowland gorillas (Gorilla gorilla graueri), over a course of about two years, into a social group at the zoo of Antwerp, Belgium and noted: "By gradually proceeding the introduction, thereby giving the animals time to adapt to the new situations but not making it too slow and frustrating, we have united the individuals to their own comfort." Thus, it is equally important to allow the animals to become familiar to the new situation, by a gradual process of the introduction, which decreases aggressive behaviors between the group members (Nitsch, 1996; Winslow et al., 1992). This procedure was applied to Richard and Avahli who had time to become accustomed to one another once they arrived at Paignton Zoo, as it was hoped that Richard would support Avahli once they were together with the adult males.

The group formation of the all-male group at Loro Park, in comparison, was carried out by introducing individual gorillas to each other and eventually having all six males together. This took about two years from the arrival of the first gorilla until the last gorillas (Downman, 1998). Thus, giving the individuals enough time to familiarize themselves with the new situation and proceed on an individual basis is most important for the formation of an all-male group more than for mixed gender group formation.

Changes with group composition or the environment are very likely to have an influence on the personality of a gorilla, which was affirmed by a nationwide survey of zoo personal (Gold and Maple, 1994). These observations were supported by the expressed behaviors of Claus and Pertinax after their arrival at Paignton Zoo. Within a short time period, they had to adjust to a new social situation and a new environment by being by themselves. Increase in aggressive behaviors among gorillas after changes in the group membership was described by Hoff et.al (1996). They stated that: "It is

typical for gorillas to exhibit aggressive displays and contact aggression when group composition is changed." Among feral gorillas, aggressive behaviors between adult males occur more often between males from different groups than between males within a group (Fossey, 1972, 1974; Harcourt et al., 1976; Harcourt, 1978). The high and moderate aggression observed between Claus and Pertinax upon their arrival at Paignton Zoo might very well reflect their attempt to establish a new dominance relationship between each other (Robbins, 1996).

The experiences of the group formation at the St. Louis Zoo (Porton and White, 1996) and from Paignton Zoo showed several factors are relevant and important for a successful start of an all-male group. These factors are the age of the to be integrated animals, the size of the group and most importantly the individual personality of each group member as well as the formation of coalitions between individual animals. An additional important factor is related to the size, design and furnishing of the enclosure to provide the animals with amble opportunities to withdraw from each other's view whenever necessary. Furthermore, it is equally important, particular for adult male gorillas, to have the possibility to overview their "territory" from each given point within the enclosure.

5.1.1 Non-social behaviors

Group formations, particularly among all-male groups, present stressful situations and are likely to have an effect on the non-social as well as on the social behaviors of all animals involved. However, since the observations prior and post group formation were separated by approximately five months, differences in various behaviors observed by both juveniles might reflect changes due to their development.

Idle behaviors increased for all three gorillas after the formation of the group. Particularly, Avahli became quieter after the group formation, as could be seen in an increase of idle behaviors and a decrease in locomotive behaviors. At the same time,

he was seen to retreat quite often from the rest of the group to higher elevations within the show den or to stay outside on the island all day long. For instance, during the course of the observations, Avahli spent 220 min (3,67 hours) on the Island post introduction and was joined by Richard only for 80 min. The rest of the time he was alone. Possibly, he retreated from the presence of Pertinax, but this can also be related to his rearing history. As mentioned previously, he was hand-reared and did not spent time with adult gorillas before he came to Paignton. This could be seen whenever Pertinax moved towards him or changed his position, Avahli stayed as far away as possible. Studies concerned with the differences between hand-reared and motherreared infant gorillas show that hand-reared gorillas spent more time resting than mother-reared animals (Gold, 1992). Richard's increase in idle behaviors might well be related to his decrease in play interactions with Avahli while he spent more time watching Pertinax. After the introduction of two young females into the social group idle behaviors also increased (Nitsch, 1995) whereas Hoff et. al (1996) found that idle behaviors decreased after changes in group memberships. The increase in idle behaviors of the juvenile males reflects also the decrease in social affiliative interactions between them. Additionally, spending more time resting might also be helpful to overcome the stressful events of an introduction and eventually to become familiar with the new situation.

The time spent foraging and feeding (ingestion) decreased for all three gorillas during the period post group formation, mostly for Pertinax, which could be related due to Pertinax's increase of stereotypic behaviors. Although the food supply stayed the same for all animals, they spent less time with feeding than prior to group formation. Additionally, post group formation the animals received the "larger" food items, such as whole cabbage mainly to keep Pertinax occupied to influence his stereotypic behaviors. Thus, the animals also spent less time with foraging for smaller food items. Avahli spent a lot of time at one of the upper posts. He retreated frequently from Pertinax by climbing up the posts where food was not available. Similar patterns were observed after the introduction of two hand-reared females to a social group, where feeding behavior decreased after the introduction (Nitsch, 1995,

1996). Thus, the time after the introduction obviously represents a stressful period that correlates to a decrease in feeding activities.

Time spent in locomotive behaviors decreased for Avahli during post group formation, but stayed nearly the same for Pertinax and Richard prior and post group formation. Gold (1992) showed in his study, which involved 20 infant gorillas ranging in age from 14 to 36 months, that hand-reared infants were more active than mother-reared infants. A similar result was obtained by Meder (1989), who pointed out that the hand-reared animals in her study engaged more in locomotive activities than mother-reared gorillas. However, among older animals, the observed locomotor activity was equal to mother-reared animals. Hoff et. al (1996) observed an increase in locomotive behaviors after changes in group memberships. Thus, there appears to be no clear distinction between hand-reared and mother-reared animals in terms of locomotor activities. In Nitsch's (1995, 1996) studies concerning the introduction of two female gorillas, locomotive behaviors for one female increased whereas for the other female it decreased post introduction. Avahli's decrease in locomotive activities is very likely related to the increase in idle as well as stereotypic behaviors.

Self-directed behaviors increased for Pertinax and Richard post group formation, and decreased slightly for Avahli during the period after the group formation. Self-directed behaviors decreased for one of the females post introduction (Nitsch, 1995). Stoinski et. al (2001) showed in her comparison of two all-male groups of gorillas that one of the groups, which consisted of two juveniles and one silverback, spent more time with self-directed behaviors than a group consisting of three juveniles. Richard spent most of his time autogrooming and scratching himself while he was watching Pertinax at the same time, especially, since Avahli retreated when they were together with Pertinax.

Object play decreased for all three gorillas, but more so for Pertinax, which could be related to his marked increase in stereotypic behaviors. Pertinax spent a considerable amount of time manipulating cardboard boxes prior to group formation. Since he started to ingest these and subsequently regurgitated this material, it was decided to remove cardboard boxes as enrichment items. The lack of objects and his

increase in stereotypic behaviors very likely contributed to this observed drop in object play activities. For Richard and Avahli, post group formation, the supply of enrichment items was limited. Towards the end of the study various enrichment items, such as browse and a puzzle feeder, was provided, primarily to occupy Pertinax. Once these enrichment items became available, Pertinax started to use them immediately, and eventually his behaviors were copied by Richard whereas Avahli did not try them. The availability and variety of objects may have had an effect on the time spent playing. For instance, one juvenile gorilla spent a considerable time playing with objects post introduction since they had been given plenty of boxes, burlap etc. post introduction. However, prior to the introduction, few objects were available, thus reducing the time spent in this behavior (Nitsch, 1995, 1996).

Solitary play also decreased for both juveniles, but slightly more for Avahli than for Richard. Avahli's decrease in solitary play is likely a result of his increase in stereotypic and idle behaviors. A similar pattern was also observed for two infant female gorillas subsequent to their introduction to a social group (Nitsch 1995, 1996). Richard as well as Avahli spent more time with solitary play when they were by themselves, which suggests that they were more relaxed during these times.

5.1.2 Aberrant and stereotypic behaviors

Aberrant and stereotypic behaviors increased for Pertinax as well as for Avahli post group formation. As Marriner and Drickamer (1994) pointed out: "The causes and functions of stereotyped behavior are uncertain, but many hypotheses have been proposed. First, stereotyped behavior may be a response to a lack of sensory input." Such "sensory input" facilitates the development of normal behaviors; however, if animals lack this input, stereotypic behaviors, such as "self-grasping and rocking" can manifest itself (Berkson, 1967; Capitano, 1986). Stereotypic behaviors were defined "... as the uniform repetition of a motor pattern that occurs at a higher frequency than

considered typical for a species when observed in a natural environment (Immelmann and Beer, 1989; Walsh et al., 1982)."

The behaviors observed among the gorillas at Paignton Zoo included regurgitation and reingestion, hair and skin plucking, hugging oneself, rocking behavior and ear covering. Aberrant behaviors such as regurgitation and reingestion have been studied widely by various researchers (e.g. Akers and Schildkraut, 1985; Gould and Bres, 1986; Lukas, 1999; Lukas et al., 1999; Marriner and Dickamer, 1994). This behavior seems to occur among captive gorillas only and has never been observed among feral gorillas (Bourne, 1975; Fossey, 1979; Fossey and Harcourt, 1976; Harcourt, 1979 a, b; Harcourt and Stewart, 1978; Schaller, 1963). Stress and boredom seem to be major causes for the expression of this behavior among gorillas in captivity (Akers and Schildkraut, 1985).

Gould and Bres (1986) noted during their study that the occurrence of regurgitation and reingestion is related to the individual rearing history, since mainly hand-reared gorillas showed this behavior more frequently compared to mother-reared gorillas. Thus, the rearing history of primates plays a major role in the expression of behavior such as regurgitation and reingestion (Marriner and Drickamer, 1994). Gould and Bres (1986) noted, "Provisioning of browse decreased R+R and increased feeding time...".

At Paignton Zoo, Pertinax started to express regurgitation and reingestion when he was separated from Claus for the first time. Both silverbacks did not show this behavior while they had been at the Cologne Zoo (Rümpler, personal communication, 1997). The gorilla group at the Cologne Zoo did not express regurgitation and reingestion due to a change in diet, which includes largely browse and vegetables (Rümpler, 1992). As previously mentioned, stress as well as individuality and possibly a whole complex set of factors (e.g. boredom) seem to play a major role in whether gorillas engage in regurgitation and reingestion. Thus, it does not seem surprising that one gorilla expressed this behavior and the other did not.

The slight occurrence of Richard's performing regurgitation and reingestion might be because he learned or copied this behavior from Pertinax, since he did not show this behavior prior to the group formation. During their study, Nash et al. (1999) found occurrences of stereotypic behaviors in relation to rearing and holding situations of chimpanzees "...that animals may learn some abnormal behaviors from each other just as they learn appropriate behaviors". That juvenile primates might learn to perform stereotypic behaviors from older animals within the group has been described also for chimpanzees by various researchers (Bloomsmith et al., 1994; Fritz, 1986; Fritz et al., 1992).

Lukas et al. (1999) stated: "Replacing R/R with appropriate foraging behavior is particularly important if youngsters are learning this behavior through social observation. The results of this study suggest that infant and juvenile gorillas do observe adults while they regurgitate and further consume regurgitant they obtain from a regurgitating adult. On several occasions, infant and juvenile gorillas were observed watching an adult engage in R/R and subsequently assuming similar body postures and movements while expectorating and reconsuming what appeared to be saliva."

After the departure of Claus, when he was sent to Bristol Zoo, Pertinax started to spent considerable time with hair and skin plucking of his ankles. Towards the end of the observation period, changes in the routine as well as enrichment items were implemented to keep Pertinax occupied and to distract him. The changes in the routine included, spreading out additional supply of scattered feed, placing the food outside on the Island to encourage Pertinax to go outside and forage for food. Furthermore, the daily "Tea time" was dropped during the week, since it became apparent that Pertinax waited anxiously for his treat and during these times his regurgitation and reingestion increased. Enrichment was provided by the implementation of a puzzle feeder, which was filled for instance, with mashed potatoes. In order to reach the content of the puzzle feeder, branches were supplied. Pertinax immediately took hold of them and stripped off the leaves and subsequently used the prepared "sticks" as tools.

Occasionally, Pertinax was also seen to sit in a corner and cover his ears with both hands, possibly as a response to the "stressful" situation for him. This "ear-covering" behavior has also been described by Woods (1996) as stereotypic behavior. Johnstone-Scott (1998) described this behavior, which has been observed in various gorillas worldwide, as follows: "Despite maintaining a predominantly playful and mischievous nature, shortly after Jambo's death Hlala Kahilli had developed a habit of drawing her forearms or wrists up around either side of her head, thus covering her ears. It was a behavior displayed by the young female whenever a stressful situation arose, or one that subsequently made her feel insecure, a not uncommon 'neurosis' among captive gorillas".

As described in the quantitative chapter, Avahli started to push objects, preferably straw, repetitively in front of him after the group formation. This was seen only during ad libitum observations, not during data collection. During the group formation with two hand-reared female gorillas, one of the females also started to express this behavior after group formation (Nitsch, 1995). Meder (1985a, 1987) also observed this behavior among hand-reared gorillas during her study. She observed this behavior only when the animals were in stressful situations. Group formation was apparently a stressful situation for Avahli. Bowen (1980) described the occurrence of stereotypic behaviors among three hand-reared gorillas after they moved to a new enclosure. Stressful events also caused the expression and the increase of stereotypic behaviors among hand-reared chimpanzees (Davenport and Rogers, 1970). Especially after the group formation, Avahli spent his time, outside on the island by himself whenever possible. He was often seen holding onto a piece of burlap or covering himself with it. Holding onto a blanket seems to decrease stress and provides comfort (Davenport, 1979).

Therefore, gradually adjusting the group formation process is particular important for an inexperienced hand-reared juvenile gorilla, such as Avahli. Furthermore, sociable group-reared males, such as Richard, adjust more easily into an all-male group (Gold and Maple, 1994).

5.1.3 Social affiliative behaviors

The occurrence of social play between juvenile primates can be viewed as an indication of the socialization of an individual within its social group (Harlow et al., 1971; Poirier, 1969). Social affiliative behaviors or social play between Richard and Avahli decreased drastically upon the formation of the group and appeared to be related to the increased time Richard spent watching Pertinax and an increase of time spent retreating from Avahli. After the group formation, the juveniles only spent the afternoons together with Pertinax. During this time, Richard was watching Pertinax, whereas Avahli either retreated to the Island or climbed up one of the logs. In the morning, Richard and Avahli were by themselves. Thus, Richard and Avahli took advantage of this and played with each other during these times. This suggested that both were more relaxed during these times. Once they were together with Pertinax all day, social affiliative play dropped considerably. The decrease of social affiliative behaviors was also observed after the introduction of two infant females to a social group (Nitsch, 1995, 1996). Since the animals had not been together for a long time, when data was obtained, it is very likely that social affiliative behavior will increase. During a comparison of two all-male groups, Stoinski et.al (2001) found no differences in the occurrence of social affiliative behaviors independent of the presence of the silverback, except that the juveniles engaged more often in this behavior than the silverback. At Paignton Zoo, Pertinax did not engage in social affiliative play with Richard and Avahli during the course of this study.

5.1.4 Sexual behaviors

Sexual behavioral interactions between the males at Paignton Zoo were not seen during this period. Only Avahli engaged occasionally in masturbation, but neither Pertinax nor Richard showed this behavior. This is similar to what had been observed by Stoinski et. al (2001) who noted the absence of homosexual behavior between the silverback and subadults and the low frequency between subadults in both groups. On

the contrary, Yamagiwa (1987) observed homosexual behaviors frequently among the free-ranging all-male group and argued that "frequent homosexual interactions" were indicative of all-male groups. That these behaviors were not observed at Paignton Zoo might be also related to the fact that this group had just been recently introduced to each other at the time of observation.

5.1.5 Aggressive behaviors

Moderate aggression was very low prior and post of the introduction, and remained very much the same for Pertinax. For Richard and Avahli this behavior decreased during the period after the group formation. Richard and Avahli were engaged in annoying up Claus by banging at the door prior to group formation, behavior also described as "rough-up" by Porton and White (1996). As a response, Claus displayed and banged at the door as well. However, Richard and Avahli did not show such agonistic displays prior to the group formation towards Pertinax, probably because he did not show a reaction to it. Apparently, both juveniles "enjoyed" to wind up Claus and differentiated between both silverbacks, thus, seemed to put themselves into the position of somebody, which is also described as "empathy" (Niemitz and Niemitz, 1999).

Moderate aggression prior to group formation was mainly directed towards Claus by all three gorillas. Post group formation, Pertinax displayed towards the juveniles, mainly towards Avahli who lacked the experience of a group-reared male. This was apparent when he was approached by Pertinax and did not show submissive behaviors, which in turn lead to a display charge by Pertinax towards Avahli. Gold (1992) studied non-social behavior among 20 infant lowland gorillas at the ages of 14 to 36 months and concluded that: "One of the primary behavioral differences found between the human-reared and mother-reared infants was the seemingly inappropriate contextual use of display behavior by the human-reared infants". The improper use of display behaviors of hand-reared gorillas has been noted by various researchers (i.e.,

Johnstone-Scott, 1984; Meder, 1985, 1989; Rogers, 1973; Schaller, 1963). Inexperienced young gorillas do receive more aggression from the silverback than socially experienced males and thus, increase the overall occurrence of aggressive behaviors within the group.

5.1.6 Coalitions and agonistic support

While at Cologne Zoo, Claus and Pertinax supported each other during agonistic encounters towards Kim, the leading silverback. This was very rare but is similar to what can be seen among feral mountain gorillas, where brothers seldom form coalitions (Watts, 1996). However, occasionally Claus and Kim build a coalition against Pertinax during aggressive interactions. Prior to the birth of the youngest group member Goma, at the time of this study, Claus and Pertinax supported each other far more frequently than after the birth of Goma (Klaus Pyszora, personal communication, 1997). Thus, the relationship between these two young silverbacks had changed prior to their move to Paignton.

After the group formation, once Pertinax, Richard and Avahli were together for about three months, whenever Pertinax went after Avahli, Richard joined in and supported Avahli. Occasionally, Richard displayed towards Pertinax in these instances and eventually chased him away. The importance of the establishment of such coalitions had been described for feral mountain gorillas (Yamagiwa, 1987; Robbins, 1996) and for groups in captivity by Porton and White (1996). Furthermore, such coalitions facilitate the coexistence between the males within all-male groups, described also as "loser-support" and "mediating behaviors" (Yamagiwa, 1987). Thus, introducing Richard and Avahli first to one another and allowing them to get to know each other and bond was and advantageous strategy prior to the introduction to the adult male. This ensured that Richard and Avahli had formed a coalition and as pointed out by Porton and White (1996) lead to the support of Avahli by Richard when Avahli was attacked by Pertinax.

5.1.7 Enclosure utilization

When Claus and Pertinax arrived at Paignton Zoo, Pertinax immediately occupied the upper level (L1) whereas Claus was at the central level (L2) (see Fig. 14 on page 27). Due to the layout of the enclosure, it was not possible to have a clear view from the central level to the upper level; thus, both silverbacks could not always see one another. However, at Cologne Zoo, both had visual contact with each other at all times, if they chose to. The enclosure layout at Paignton Zoo, in comparison, did not allow visual contact of each other due to the differences in height between the individual levels (see Fig. 15 for details on page 27). It is important for gorillas to be able not only to retreat from each other's view but also to be able to see the rest of the group. As pointed out by Jonstone-Scott (1992): "... there is no doubt that the size and design of the complex, and particularly that of the outside enclosure, served to minimize the inevitable stressful encounters by providing adequate flight distance".

Pertinax spent the majority of his time prior and post group formation at the upper level (L1), whereas for Richard his preferred area was the central level (L2) prior to the group formation and the upper level (L1) post group formation. Richard's increased stay at the top level (L1) after group formation could be related to the fact that Pertinax spent most of his time in this area and Richard kept watching him, since he appeared quite interested in the behavior of the silverback. When Richard and Avahli were alone in the mornings during the first couple of weeks after the group formation, both spent their time at the upper level in rough and tumble play interactions.

Avahli, on the other hand, spent most his time at the central level (L2) as well at the upper level (L1) prior to the group formation. Once all three were together, Avahli spent the majority of his time outside alone on the Island and when he was inside, he spent his time up at the climbing structures. This is in concordance with his attempts to retreat from the presence of Pertinax. Avahli's increased preference for the climbing structures after the group formation (prior to group formation: 13.4 %; post to group formation: 25.0 %) seems to be related to the fact that these structures offered a possibility of allowing him to keep a great distance to the silverback. As Marriner and

Drickamer (1994) noted: "Species-specific requirements, such as diet, habitat, and sociality, must be taken into account when designing enclosures and environmental enrichment devices." It is important to facilitate species typical behaviors and eventually reduce time spent in stereotypic behaviors, especially for all-male groups.

5.2 Loro Park

The following paragraphs discuss the results of the social behavioral dynamics, the occurrence of stereotypic behaviors and the enclosure utilization of the group at Loro Park, in comparison to free-ranging all-male groups.

5.2.1 Social affiliative behaviors at Loro Park

The results revealed that all males at Loro Park frequently engaged in social affiliative behaviors. Social play occurred between almost all males, with the exception of the silverback. High rates of social interactions also characterized the allmale group of mountain gorillas (Robbins, 1996). Additionally, she found that affiliative interactions between members of an all-male group of mountain gorillas occurred more often than in heterosexual groups. By looking at the proportion, each male took part in social affiliative behaviors; the highest rates were expressed by the social reared male Maayabu and the youngest group members. Social play between particular between Maayabu and Noel are likely underestimated, since both retreated to the areas near the building structures, were they could not always be seen. The social affiliative behaviors among the group at Loro Park can be mainly attributed to the group-reared male, Maayabu who actively solicited affiliative behaviors from all group members, especially from the older ones. Staying in close proximity and resting in contact with the silverback largely characterized Maayabu's relationship with him. Among free-ranging mountain gorillas, play was mainly observed between the subadults (Yamagiwa, 1987), although infrequently with the younger blackbacks (Robbins, 1996). Thus, among mountain gorillas, the males of all-male groups stayed in closer proximity (Yamagiwa, 1987) and affiliated even more (Robbins, 1996) when compared with heterosexual groups (Harcourt, 1979a).

The social competence of Maayabu when interacting with others can be attributed to his rearing history, being the only group-reared gorilla in this group. His

positive influence on the group dynamics strengthens the notion that socially competent gorillas are beneficial and important for the long-term management of an all-male group of gorillas in captivity (Porton and White, 1996). Thus, social competent males, such as Maayabu, have a positive effect on the social group dynamics by integrating the rest of the group in social affiliative activities.

Experiences of all-male groups in group formations showed that socially skilled males are an important factor for such all-male groups (Porton and White, 1996). Additionally, the importance of having a sociable male in an all-male group was pointed out by Gold and Maple's (1994) study of personality and management in gorillas who stated: "Based on past bachelor group formations, it is known that males with a history of aggressiveness have trouble living in an all-male situation. Sociable males, on the other hand, tend to adapt easily to a bachelor group".

By looking at the individual group members, Schorsch was never seen to take part in playful activities, despite Maayabu's frequent attempts, to invite him. The reasons why Schorsch never engaged in social affiliative play could be related to his previous history. As mentioned previously, he was hand reared and primarily were kept solitary before he became part of this all-male group. Although he appeared to be integrated into this group, his social interactions were mainly a result of the initiatives by the other group members rather than himself. Stoinski et al. (2001) argued that the observed low level of social behavior expressed by a silverback gorilla in an all-male group "could reflect some level of social incompetence resulting from his early rearing history". Thus, all-male groups can provide the necessary environment to enhance social behavior between these males and subsequent acquisition of social skills, which they need once they become part of a heterosexual group.

Grooming was seen only on one occasion between Maayabu and Ivo; with Maayabu grooming Ivo, thus, it occurred very seldom. Maayabu often actively seeked out the proximity of Schorsch during resting periods. However, both males rarely had physical contact. According to one of the keepers, Maayabu and Schorsch shared one sleeping den during the night (Alvarez, personal communication, 1998) and apparently engaged more often in affiliative contacts than when they were in the outside

enclosure. Grooming occurred very seldom among the free-ranging all-male groups (Harcourt, 1988; Robbins, 1996; Yamagiwa, 1987).

5.2.2 Sexual behaviors

Sexual behaviors at Loro Park were observed only on rare occasions during ad libitum observations between Ivo and Rafiki and Ivo and Polepole. For instance, twice Ivo was observed soliciting Rafiki by presenting towards him. In response, Rafiki attempted to mount Ivo and performed pelvic thrusts. Downman (1999) also observed few instances of homosexual behaviors between Ivo, Polepole and Rafiki. He argued that this might be "a dominance display by Ivo over the younger animals". Additionally, Ivo and Maayabu engaged occasionally in sexual behaviors. Among free-ranging mountain gorillas, Yamagiwa (1987) pointed out that "frequent homosexual interactions" were indicative of all-male groups allowing them to stay together. He observed that it was usually older males that mounted younger males, and he described how this allowed older males to retain "ownership" over the younger males. During one incident, a similar situation had been seen between Noel and Polepole, where Noel mounted Polepole. Masturbation by Schorsch was frequently observed, and it was directed mainly towards female visitors (and observers).

Overall, the occurrence of sexual behaviors among the all-male group at Loro Park was very low in comparison to the information on free-ranging all-male groups of gorillas as described by Yamagiwa (1987). Stoinski et al. (2001) also noted lower rates of homosexual behavior between two captive all-male groups than among their wild conspecifics. Furthermore, she also observed that the silverback, as was the case at Loro Park, never was involved in homosexual behaviors. Robbins (1996) never observed homosexual behaviors among the silverbacks in heterosexual groups. She argued that the observed differences in sexual behaviors between her study and the one by Yamagiwa (1987) was that Yamagiwa observed homosexual behaviors mainly

between subadult and juvenile males whereas the all-male group observed by Robbins (1996) did not contain these age groups. At Loro Park, homosexual behaviors were also observed between juveniles, subadults, and blackbacks. Homosexual behaviors were observed also among the males of the all-male group at St. Louis Zoo, involving all age groups (Porton and White, 1996).

5.2.3 Agonistic behaviors

When looking at interacting pairs, the majority of agonistic behaviors were seen between Noel and Ivo (Fig.38 and 39), especially when the animals were not able to retreat from each other and got too close to one another. It was then that tension built up between them, and they displayed towards each other. From observational data and *ad libitum* sampling, a total of 29 aggressive interactions between the males at Loro Park were observed. Of these, 16 (55.2 %) were directed from Noel to Schorsch, 6 (20.7 %) from Noel to Maayabu, 4 (13.8 %) from Noel to Ivo, 2 (6.9 %) from Ivo to Noel, and one interaction (3.5 %) was directed from Maayabu to Noel (Fig. 41).

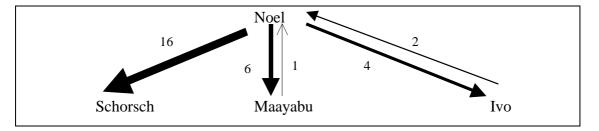


Fig. 41: Direction and number of agonistic behaviors of the males at Loro Park.

Yamagiwa (1987) observed the highest rate of agonistic behaviors between the silverbacks of the all-male group, during which these males were frequently wounded. He also noted that the younger males received more aggression than the older ones and showed the older gorillas were more aggressive. During Robbins (1996) study, the ages of the males ranged from 11 to 13 years were similar to Noel and Ivo's age. She found that the males of free-ranging all-male groups engaged more in moderate and

high aggression than the males of heterosexual groups. However, high aggressive behaviors among the males of the heterosexual groups were more serious (i.e. biting), whereas the all-male group's high aggression involved more hitting and kicking one another.

At Loro Park, Noel frequently challenged Schorsch and apparently viewed Ivo as a "rival," which resulted in frequent displays between Noel and Ivo. Neubauer and Heckner-Bisping (1999) also observed Noel frequently challenging Schorsch; thus, Schorsch was mainly the receptor of aggressive behaviors. Additionally, Schorsch hardly intervened when the three blackbacks had agonistic interactions.

Wounds, as an indication for high aggression, were rarely observed among the males at Loro Park during the course of observation. Only Ivo and Noel showed occasional minor scratches. The displays between Noel and Ivo can be viewed as an attempt to establish a dominance relationship between them. Noel's frequent displays towards Schorsch, the leading silverback, were very likely an attempt to challenge his dominant status. Robbins (1996) also attributed the high occurrence of chest beating and strut-walking displays, similar to the situation at Loro Park, as an attempt to establish dominance between the individual males. By looking at the occurrences of high and moderate aggression in relation to proximity to each other, she observed a higher rate of these behavioral categories when the males spent more time in proximity to each other. In a captive setting, however, the males seemed to increase the distance between themselves, i.e. by hiding from each other's view. Although, Maayabu was occasionally involved in agonistic interactions, his role was more as a mediator because he had good relationships with all males in the group. Apparently, he was able to intervene and to display towards various group members without facing consequences.

5.2.4 Coalitions and agonistic support

Agonistic support and interventions have been described as indicative of all-male groups by various researchers, such as Yamagiwa (1987), Robbins (1996), Lukas et. al (1996) and Porton and White (1996). These behaviors allow several males to coexist in such a group. Although, among multi male groups of mountain gorillas, usually males do not develop alliances, as seen among chimpanzees, occasionally adolescent males form coalitions with related silverbacks (Watts and Pusey, 1993).

Among free-ranging mountain gorillas Watts (1997) observed that related females did support each other whereas unrelated females rarely supported one another. He stated: "Females mostly supported other females with whom they had affinitive relationships against those they often engaged in dyadic aggression". This could also be seen in the relationship between Schorsch and Maayabu, who was the only male with whom Schorsch engaged in affinitive interactions.

The males at Loro Park did not reconcile after an aggressive interaction, which is similar to free-ranging mountain gorillas where only females would engage in affiliative interactions with the leading male (Watts, 1995a). Furthermore, after aggressive interactions between Noel and Ivo, both males avoided each other and retreated to the opposite side of the enclosure. Since adult males within a group, like Noel and Ivo, hardly tolerate each other, the observed lack of reconciliation between these two was expected (Harcourt and Stewart, 1981; Watts, 1991; Watts and Pusey, 1993). During one observed incident, Maayabu padded Noel's shoulder after they displayed towards each other. This is described by Watts (1995b) as an "attempted appeasement or a request for reassurance that aggression had ceased." He argued that the kind of behavior expressed by Maayabu might be an effort to confirm his relationship and alliance with Noel.

A total of 11 instances of agonistic support were seen during these aggressive interactions, of which Maayabu supported Schorsch 6 times (54.6 %) mainly during agonistic encounters between Schorsch and Noel. Maayabu supported Noel 3 times (27.3 %) and Schorsch supported Maayabu during 2 (18.2 %) instances. Agonistic

interventions were seen with Maayabu intervening 4 times (66.7 %) between Schorsch and Noel. Schorsch intervened in twice the disputes between Maayabu and Noel (33.3 %). For instance, Maayabu frequently intervened by displaying and charging towards one of the opponents. Unfortunately, it was not possible to determine vocalizations as described by Yamagiwa (1987), who noted that "Dyadic interactions in antagonistic contexts usually attracted other animals and often elicited their supporting behaviors, which included chasing with vocalizations, charging with chestbeating and physical contacts as observed in aggressive behaviors". Furthermore, he described that a third male frequently supported the one who received aggression, which he termed "loser-support" and that enables males to coexist within an all-male group. The subadults received the most support whereas the blackbacks gave support. However, at Loro Park, the silverback received the majority of agonistic support from the blackback Maayabu. Coalitions were seen mainly between the silverback and one of the blackbacks and among juveniles. Robbins (1996) rarely observed agonistic interventions and argued that these behaviors "do not appear to play a strong role in male-male relationships". She attributed the differences between her findings and Yamagiwa's (1987) to the different age structures of the groups observed. The group structure at Loro Park more closely resembled the one observed by Yamagiwa (1987), containing adults and subadults than the group of adult males observed by Robbins (1996). Thus, within a group containing males of various age classes, the animals employ similar mechanisms to coexist in an-male group as has been described for freeranging all-male groups.

5.2.5 Stereotypic behaviors

Aberrant behavior such as coprophagy was exhibited only by Schorsch whereas stereotypic behaviors, such as rocking and hair plucking, were seen being done by Rafiki and occasionally by Schorsch. Schorsch and occasionally Noel and Rafiki were observed regurgitating and reingesting. Coprophagy has been observed to

occur among mountain gorillas (Fossey and Harcourt, 1976) but also among gorillas in captivity (Akers and Schildkraut, 1985). The occurrence of coprophagy among feral gorillas has been attributed to adverse weather conditions and the subsequent lack of foraging possibilities. For captive gorillas, it has been argued that the occurrence of this behavior appears more often in hand-reared animals than in mother-reared ones (Nash et. al, 1999). Hair plucking by Rafiki is also described by Downman (1998) as well as by Neubauer and Heckner-Bisping (1999). This behavior, started before this study took place, and he had not fully recovered at the time of this study. Although he played often and boisterously with Maayabu, he was excluded during play sessions between Maayabu and Polepole. Rafiki would sit at a distance and watch them play. Schorsch occasionally plucked the hair and skin on his hands and wrists until a small wound could be seen. However, it was not possible to determine with certainty whether he was in a stressful situation at that moment. Since Schorsch preferred the places near the public windows, the presence of the public might have caused some stress for him.

5.2.6 Enclosure utilization

Almost all males preferred the larger terrace over the smaller one. This could be related to the fact that the smaller one had become part of the whole enclosure just a year prior to this study, and the animals were still used to it (Downman, 1999). However, interestingly, it was Noel and Ivo who occupied noticeably separate parts of the enclosure (Fig. 40), and this was very likely related to the high rate of aggressive behaviors and the increased tension between both males whenever they were in close proximity to each other. Such an enclosure offers abundant possibilities to retreat from each other. This is especially important when one considers that size, design and supplied enrichment of an enclosure for all-male groups of gorillas plays an essential role allowing several adult males to coexist at a low risk level and thus, subsequently at a low rate of aggression. The importance of hiding places and complex enclosures for

the successful management of gorilla groups in zoos has been pointed out by various researchers (e.g., Maple and Finlay, 1989; Ogden et.al, 1993; Wiesner, 1995). Such visual barriers enable the gorillas not only to retreat from each other's view, but also to retreat from the public if necessary (Hediger, 1950). Additionally, such complex enclosures are beneficial for the psychological well being of gorillas since this species seems to be very sensitive to the stress of captivity (Maple and Finlay, 1989; Miller-Schroeder and Paterson, 1989).

5.2.7 Enrichment

The availability of various enrichment devices is as important as a complex structured enclosure for the long-term management of all-male groups in captivity. The presence of enrichment items, such as the implementation of fishing boards, within the enclosure at Loro Park offered the possibility to evaluate its effects on the behaviors of the individuals of this group.

At various places, throughout the enclosure, fishing boards had been inserted into tree trunks, where yogurt, jam, honey and a chocolate mix were placed every day. The gorillas were provided with twigs and palm fronts, which they use as tools to obtain the contents from the fishing boards. Usually the palm fronts were manipulated by removing the leaves and breaking off pieces of the leafstalk until the tool had the "right" size. Downman (1999) described that when these fishing boards were implemented that Maayabu was the first gorilla that used them immediately. Gradually this behavior was adapted by the rest of the group, with the exception of Schorsch. During this study, he was seen only on very rare occasions trying to obtain some of the contents of the fishing boards by using his fingers versus tools.

Maayabu made the most intense use of the provided enrichment at Loro Park (Fig. 42) followed by the juveniles Polepole and Rafiki. However, Noel and Ivo could be seen preparing tools and used them successfully at the fishing boards. The

implementation of enrichment seems to be very beneficial for all-male groups since it keeps them occupied and as a result, leads to a reduction of aggressive behaviors with a positive effect on the expression of stereotypic behaviors.

Wilson (1982), who studied the influence of captive environments on the activity level of great apes, found that stationary and temporary factors, in particular, were very important for gorillas and beneficial for their activity level. Furthermore, enrichment items can reduce boredom and aggressive behaviors (Conwan, 1998) and can have a positive effect by increasing activity, such as object manipulation and object play (Wright, 1995). In this study, the availability of fishing boards and an abundance of plant material from which the gorillas manufactured sticks seemed to have had a positive effect on their behavioral relationships, i.e. the low rate of aggressive behaviors between the individual group members.

As mentioned in chapter 3, various waterfalls and ponds were incorporated in the enclosure, and proved popular among some group members. Maayabu, eventually started to use one of these waterfalls for his "morning shower" (see also Fig. 43) where he sat directly underneath the waterfall and spent approximately 10 minutes or more at a time, while occasionally tapping on his shoulder or his back or just letting the water run over his head. After his "shower," occasionally he approached either Polepole or Rafiki to start a play session, which caused them to run off and subsequently they ended up chasing one another. It appeared that the juveniles were not particularly fond of getting wet. However, Rafiki did enter the pool on the smaller terrace and splashed water towards the public. Water can also play an important role as an additional enrichment item to increase activity and promote social interactions between individual group members (Brown et al., 1982). Therefore, future designs of enclosures should include an abundance of enrichment items, movable as well as stationary, and incorporate small ponds or waterfalls in the floor plan to reduce boredom and to promote activity among group members. Besides, the availability of enrichment items, a place to retreat from each other's view is equally important, particularly for an allmale group.

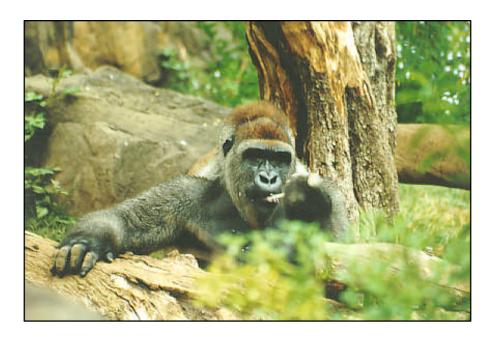


Fig. 42: Maayabu fishing for yoghurt at Loro Park.



Fig. 43: Maayabu taking a "shower" at Loro Park.

5.3 Concluding Remarks

More and more zoological gardens have started to house all-male groups of western lowland gorillas as an answer to the present "surplus" of male gorillas. This is due to the successful breeding programs of zoos worldwide and the solitary housing of single males. The occurrence of all-male groups among free-ranging mountain gorillas supported this housing arrangement. The purpose of this research project was to study the social behavioral dynamics of all-male groups of western lowland gorillas in captivity and to provide recommendations for the establishment and long-term management of such all-male groups in captivity.

The first part of the project focused on the formation of an all-male group and what could be learned from it, particularly for the building of future all-male groups, in terms of group composition and introduction procedures. The study group at Paignton Zoo started out with two young silverbacks, Claus and Pertinax, as it was believed that the familiarity between them would be beneficial for successful group formation. Eventually, the changes in social structure as well as the adjustment to the new surroundings might have been the causes for the observed fights and the subsequent removal of one of the males. These events prolonged the group formation process, and these stressful situations are very likely responsible for the occurrence of various stereotypic behaviors of Pertinax. The introduction of subadult males, Richard and Avahli, to one another and allowing enough time for them to bond and support each other, proved to be very beneficial in the end. As a result, the young sub adult male Richard supported Avahli towards Pertinax during agonistic interactions.

Thus, socially inexperienced hand-reared gorillas should gain social experience through contact with group-reared gorillas before being introduced to an all-male group and this will reduce stressful situations and prevent the manifestation of stereotypic behaviors. In successful introductions, it is important to proceed with the introduction gradually, particular in all-male groups, allowing the animals to became familiar with each other but also to an eventually new environment.

The second part of this research focused on social behaviors, especially the utilization of the enclosure of an established all-male group of six males. The main

differences in relation to the group formation of an all-male group were that the all-male group at Loro Park was founded with adolescent males, followed by the introduction of juvenile males and finally the silverback while the Paignton group started with the two silverbacks. The very calm nature of the Loro Park silverback as well as the mediating behavior of the group-reared male contributed positively to the successful group formation and long-term management of this group.

At both locations, enrichment items, such as fishing boards and plant material, proved beneficial for the group dynamics and the psychological well being of the gorillas. The gorillas at Loro Park took full advantage of the provided enrichment. Fishing boards and palm fronds are being utilized as tools and for nest building. The waterfalls and pools are being utilized by some, if not all males.

Concluding, this project showed that for a successful group formation and long-term management of such groups, it is advisable to start a group with younger males at various ages with at least one, preferably more males with social experience (e.g. group-reared). This point strengthens the argument that housing socially experienced males, as part of bachelor groups is important. Subsequently, it should be worth investigating if such sociable males could be also part of a multi-male group.

The enclosure should, when possible, be spacious and provide the possibility for the animals to retreat from each other's view. Besides space requirements, it is equally important that the enclosure is designed in such a way that if they should get into a fight, each male will have the opportunity to retreat freely and not be "cornered." Additionally, gorillas, especially the silverback, prefer to have vantage points from where they can overview the enclosure and the rest of the group. Availability of enrichment items that occupy the individual leads to a reduction of stress, aggression and a decreased manifestation of stereotypic behaviors.

In relation to the frequent membership changes observed among the feral all-male group, there is an indication that for all-male groups in captivity those males should be transferred out of the group as soon as they reach maturity. During the course of this study, this was supported by the observation of the transfers of Claus to another zoo and Ivo to the Artis Zoo of Amsterdam. Claus and Ivo are examples that

illustrate the point that adult males may need to be transferred and zoological gardens should be prepared for this possibility. This requires long term planning to avoid possible solitary housing of these "surplus" males. After all, the current practice of housing these males in solitary arrangements was one of the reasons various zoos initiated bachelor groups. Therefore, long-term management needs to consider this and plan for it while in the stage of selecting subadult and immature males for new all-male groups.

This research led to the following recommendations on the formation and longterm management of all-male groups in captivity:

- It is advisable to start an all-male group with males at various ages, such as blackbacks, subadults and juveniles and not more than one adult male. This will reduce the risk of high aggression between males and will lead to an expected higher rate of social affiliative behaviors. This, in turn, makes bachelor groups very attractive, interesting and educational to the public.
- If males are being introduced for the first time to a new enclosure, it is necessary to provide sufficient time to allow them to adjust to their new surroundings.
- At the minimum, at least one male should be group-reared, thus, having substantial social experience with group living. This is beneficial for the social dynamics of the group, by increasing the rate of social affiliative behaviors.
- During the initial introduction of new group members, limited contact
 between the individuals via mesh or partly opened doors is preferable.
 Furthermore, the availability of an abundance of displacement items, such
 as cardboard boxes etc, is important since these items give the males
 something to do resulting in the reduction of aggression towards one
 another.
- Enrichment items and various objects keep the individuals occupied, thus,
 reducing stereotypic behaviors and reduce boredom.

• The complex design of the enclosure with abundant opportunities to retreat from each other's view is very important for the successful long-term management of such groups.

Further long-term research is needed to determine which various factors have an impact on the social dynamics within an all-male group, especially since the majority of the all-male groups in captivity contain mainly blackbacks and sub adult males. Such a study would be able to determine whether it is always necessary for males to leave their group once they become adults or if and under which circumstances males could stay within a group. Measuring stress hormones to determine the individual stress level in relation to the position of each male within the group would be illuminating. Furthermore, more research is needed on solitary males in captivity and how this situation affects their behaviors.

In conclusion, it can be said that an all-male group consisting of males at different ages, which engage frequently in social affiliative behaviors, can be housed successfully in captivity, providing an interesting, entertaining and educational opportunity for the public. Nonetheless, long term planning is critical, since an all-male group is characterized by membership changes, and zoos have to be prepared to find new places for their males as they mature.