CHARLES UNIVERSITY IN PRAGUE

FACULTY OF HUMANITY SCIENCES

PROJECT REPORT FOR THE BACHELOR OF SCIENCE DEGREE

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A BEHAVIOURAL STUDY OF CAPTIVE WESTERN LOWLAND GORILLA (*GORILLA GORILLA GORILLA*) AT BRISTOL ZOOLOGICAL GARDENS – SOCIAL BEHAVIOUR / RELATIONSHIPS WITHIN A SOCIAL GROUP

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BRISTOL, MAY 2008

ACKNOWLEDGEMENTS

I would like to thank Mgr. Marina A. Vančatová and Doc. RNDr. Václav Vančata, CSc**.** for their invaluable advice and guidance. My thanks go also to Richard Marvan for check-sheet design which was originally used for observation of captive chimpanzees. Special thanks to Mel Gage, Assistant Curator of Mammals, BZG, for her time, inspirational talks and patience. I also owe a debt of gratitude to Dr. Sue Dow who provided me with valuable materials on the Bristol gorilla group, and the gorilla keepers, namely Lynsey, Vicky, Jo and Toby for their readiness to help. I am grateful to the Bristol Zoological Gardens for providing a supportive and professional atmosphere to conduct my research.

Last, but not least, I thank my partner David and my brother Roman as this work would not have been possible without their constant support, inquisitive questions and love.

Declaration

Hereby, I declare that I have completed this dissertation by myself under supervision of Mgr. Marina A. Vančatová and I have stated all used information sources. I give my consent to publish this work in either electronic or print version.

Bristol, 30.4.2008

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1 INTRODUCTION

1.1 Gorilla Socioecology

Gorillas are found in 10 equatorial African countries, in a broad diversity of habitats ranging from coastal lowland forests to high-altitude, Afromontane rain forests (Figure 1.).

There are two species of gorilla, separated from one another by the inner Congo Basin. According to Colin Groves in 2001 each species has two subspecies (Caldecott and Ferriss 2005; Harcourt et al. 2007):

1) The **Eastern gorilla (*Gorilla beringei*)** is divided into the:

a) Eastern lowland gorilla (*Gorilla beringei graueri*)

b) Mountain gorilla (*Gorilla beringei beringei*)

2) The **Western gorilla (*Gorilla gorilla*)** is divided into the:

a) Western lowland gorilla (*Gorilla gorilla gorilla*)

b) Cross River gorilla (*Gorilla gorilla diehli*)

However, the number of species and subspecies is a subject to debate. “Our taxonomy is not definitive; taxonomy never is.” (P. Grubb in Harcourt et al. 2007, pp. 69).

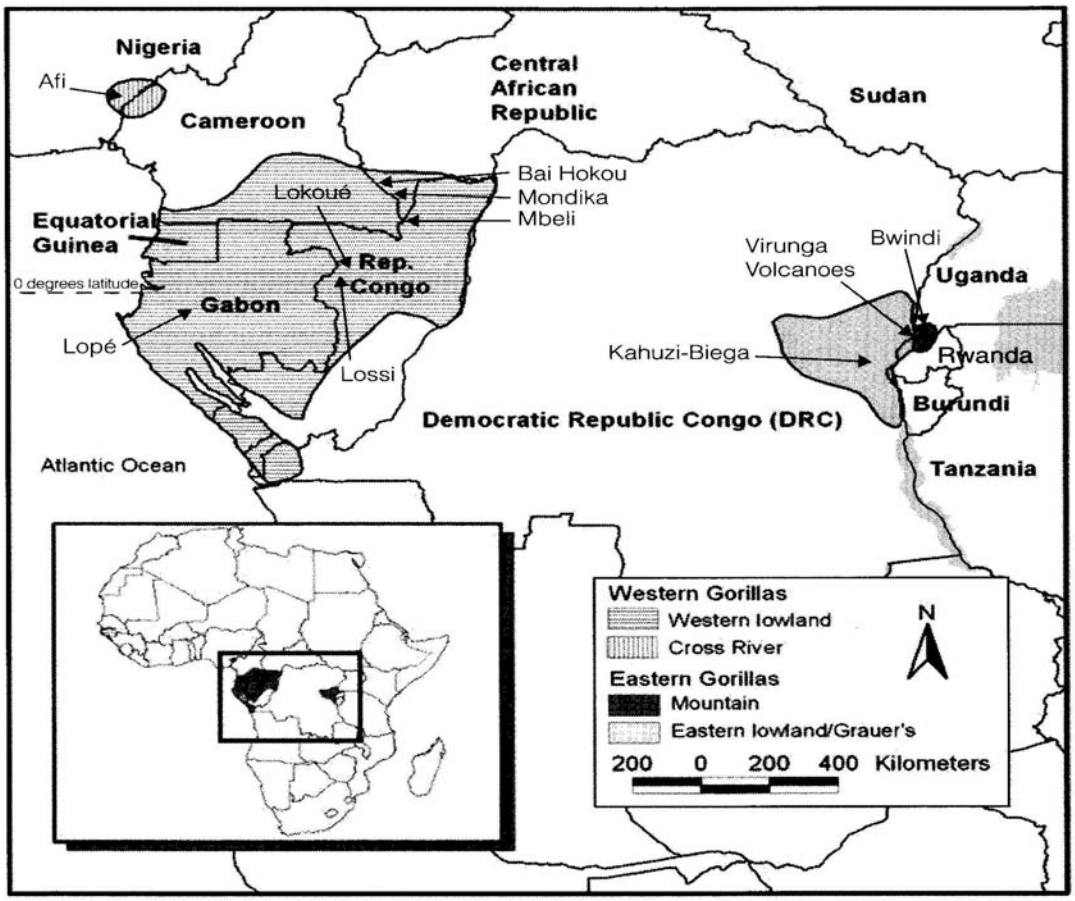

Figure 1. *Extent of gorilla distribution in Africa. Arrows indicate sites, shading encompasses general regions of distribution, but gorillas occur discontinuously within these areas. Source: Harcourt et al. (2007), pp. 66.*

The majority of information on gorillas has come from a very small population of mountain gorillas studied for over 35 years at Karisoke Research Centre, Rwanda (Robbins 2007). Because of the difficulty of habituating lowland gorillas, only a limited number of studies involving direct observations have been conducted and much remains unknown. The differences in social organization, group composition, and behaviour in the two species have been hypothesized to be a function of ecological variables like habitat, resource availability, diet, and foraging strategies (Watts 1996; Parnell 2002; Yamagiwa 2003). Research in field as well as in captivity proves that we cannot assume that all knowledge of the behaviour and demography of mountain gorillas applies to all gorilla populations. (Harcourt et al. 2007; Campbell et al. 2007; Robbins 2007).

Given their large brain and body size, gorillas have a long maturation time and are long-lived, have long inter-birth intervals, and reproduce relatively few times in their lives (Campbell et al. 2007). Almost all gorillas in all populations live in cohesive groups consisting of adults of both sexes and their offspring. These groups are usually led and protected by a mature male who has a silvery mantle down his back and therefore known as *silverback*; immature males are called *blackbacks* and are subordinate to the resident silverback and rarely mate (Robbins 1995; Strier 2000). Median group size does not differ significantly between gorilla subspecies (Figure 2.) (Godwin 1994; Harcourt et al. 2007).

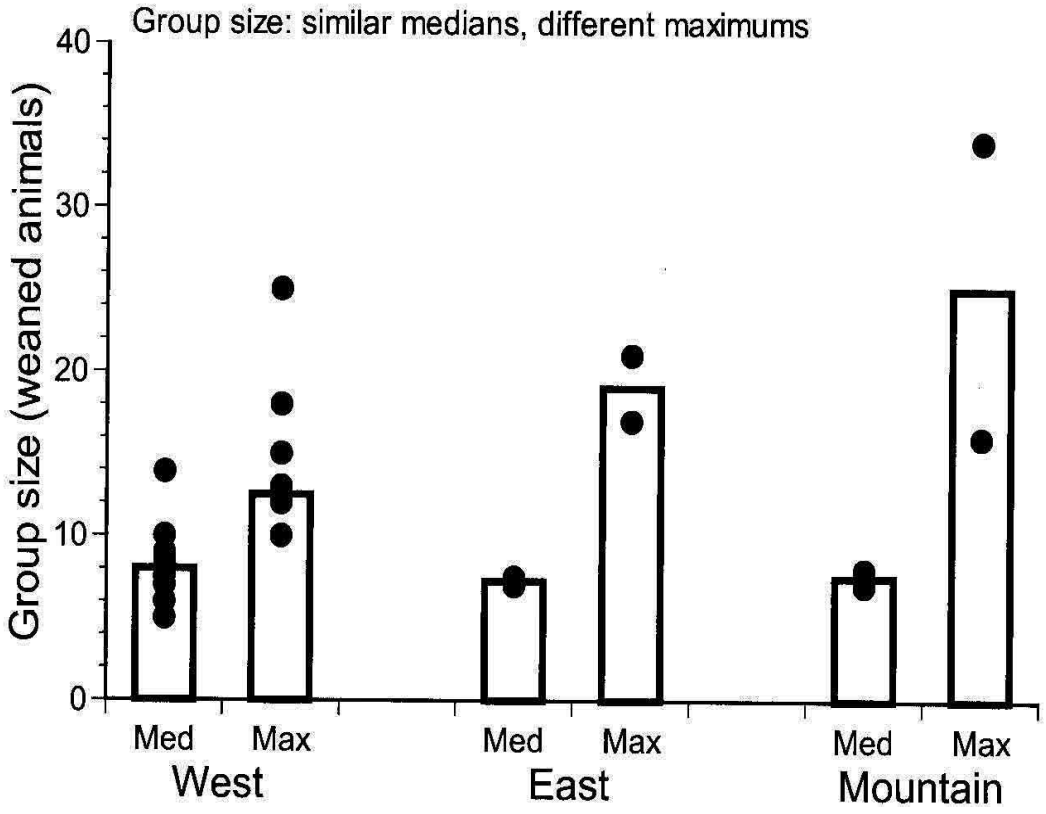

Figure 2. *Gorilla group sizes. Median (Med) and maximum (Max) group size for different gorilla populations (represented by a dot on the graph), and medians for three subspecies (bar), western (West), eastern lowland (East), and mountain. Only weaned individuals are considered because infants can be missed in censuses. For each population only data from one census are shown. Source: Harcourt et al. 2007, pp. 114.*

The great apes are the largest of all primates, and gorillas are the largest of the apes. They are also, along with orangutans, among the most sexually dimorphic primates (Figure 3.). Male gorillas are not only far larger than females (for weight comparison see section 1.2.1), but develop distinctive secondary sexual characteristics that include huge sagittal (down the middle) and nuchal (across the top of the back) crests on their skulls for attachment of jaw muscles, and relatively large canines (Godwin 1994; Caldecott et al. 2005). As mentioned above, a silver back is also a visual signal of full maturity. Another feature that differs between males and females is the quality of their chest-beat. The behaviour is most developed in adult males (although both males and females beat their chest in times of excitement) and is an important part of their aggressive display. Silverback's chest-beat is amplified by inflatable air pouches that are extensions of the larynx (Harcourt et al. 2007)

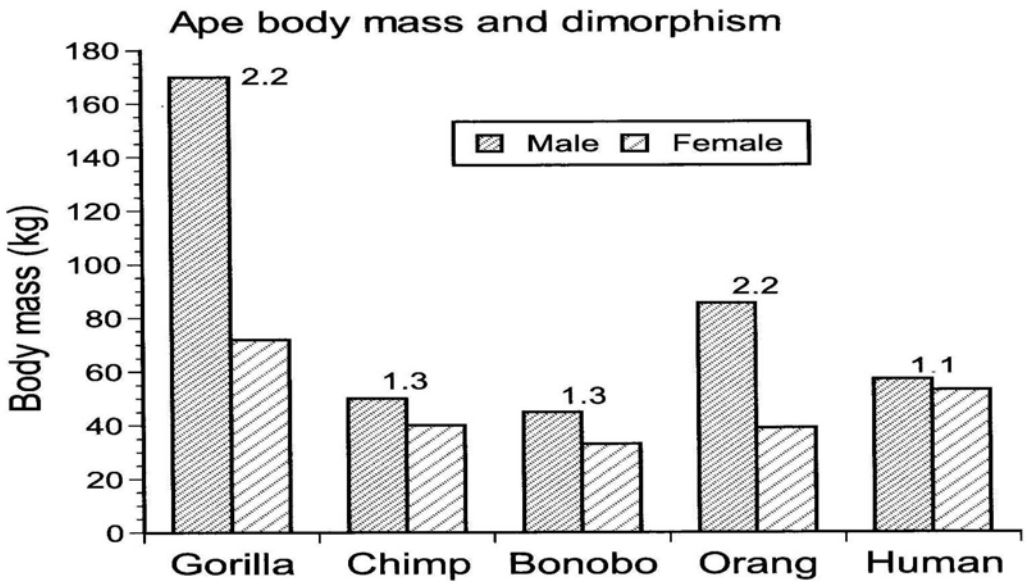

Figure 3. *Mean body mass, in kilograms, of male and female great apes and, for the sake of comparison, humans. Numbers next to male histograms indicate ratio of M / F weights, that is, degree of sexual dimorphism. Data are for wild animals when available but also includes some data from captivity. The values for humans come from four hunter-gatherer societies. Source: Harcourt et al. 2007, pp. 76.*

Age / sex classifications typically used for gorillas include *infants* (0 – 3.5 years; by 3-year-old they are usually weaned and their mother has returned to sexual cycling),

juveniles (3.5 – 6 years; they have been weaned but have not yet reached puberty), *subadults* (6 – 8 years; that is between puberty and fertility), *adult females* (>8 years; sexually fully active females), *blackback males* (8 – 12 years; young adolescent males whose hair on their backs becomes shorter and gradually turns silvery white), and *silverback males* (>12 years; dominant breeders). Females become sexually active at approximately age 6 and go through a period of adolescent sterility for usually at least 2 years (Stewart et al. 1987; Campbell et al. 2007; Harcourt et al. 2007).

Female gorillas become sexually active only for 1 to 3 days in each 25 to 40-day sexual cycle. Females with young infants also have a long period of about three years of lactational amenorrhea when they become sexually inactive (Yamagiwa 1987).

Gorillas have been observed on many occasions using tools, such as stones, sticks, twigs, and in captivity also blankets (Natale et al. 1988; Nakamichi 1999). They are highly intelligent animals with complex psychological processes (Godwin 1994; de Waal 1996; Lyttle 1997) and capable to learn inter-species communication in captivity (Godwin 1994; The Gorilla Foundation 2008).

1.2 Mountain Gorillas

1.2.1 Ecology

The habitat of the mountain gorilla (*Gorilla beringei beringei*) consists of high altitude mountain forests in the Albertine Rift of east / central Africa. Mountain gorillas feed mainly on terrestrial herbaceous vegetation - leaves, shoots, and stems of terrestrial herbs, and they have also been observed eating insects such as driver ants (Watts 1989). These are abundant and widely distributed resources, and so there is very little within-group feeding competition (Watts 1996; Harcourt et al. 2007).

1.2.2 Social Structure

Mountain gorillas live in single or multi - male groups. Males and females generally transfer out of their natal groups once they reach sexual maturity to avoid

inbreeding. Females transfer directly into another group, whereas males become solitary, or join all-male "bachelor" groups (Watts 1996). Male - female relationships are thought to form the core of mountain gorilla sociality for a number of reasons (Watts 1996; Vančatová and Vančata 2002; Harcourt et al. 2007; Campbell et al. 2007):

a) Both sexes engage in natal transfer, resulting in adults that are generally unrelated and unfamiliar. This tends to discourage male - male and female - female affinitive bonds.

b) Males mediate in female - female conflicts, and provide protection against infanticide. Thus, males are valuable social partners for females.

c) Males compete for access to females and thus tend to coexist through tolerance or avoidance, rather than male-male affiliative bonds.

d) Abundant and non-monopolizable food resources produce few opportunities for contest competition between females. Thus, there is no selection for feeding aggression (since this will not lead to greater resource acquisition), no alliance formation, and unclear female dominance hierarchies.

e) Most unrelated females do not groom each other, or help each other in conflict. Therefore, a failure to reconcile after an agonistic interaction does not imply a loss of a "valuable" partner.

In multi-male mountain gorilla groups, dominant males mate more than subordinate silverbacks but subordinates do mate, including at the likely time of conception (Robbins 1999).

1.2.3 Dispersal Patterns

New social groups form when females transfer to lone silverbacks. Such groups remain one-male until male offspring mature into silverbacks, and the group is then multi-male. Multi-male groups return to a one-male structure if males emigrate, the original adult male dies, or the group fissions. When the silverback of a one-male group dies, the group disintegrates. If a breeding group loses all of its adult females, it becomes an all-male, or non-reproductive, group.

All-male groups may also form through a merger of immature males (evicted from a heterosexual group taken over by a new silverback following the death of the previous silverback) and a solitary silverback. All-male groups can become heterosexual if a female transfers into them. If a dominant male loses all of his group members, he becomes a lone silverback. Take-overs by outsider males of established groups containing a mature silverback have not been reported for any gorilla population (Yamagiwa 1987; Robbins 2007; Harcourt et al. 2007; Campbell et al. 2007).

Direct observations suggest that immature females have more opportunities to move between breeding groups than immature males. The distribution of kin dyadic relationships within and between groups does not, however, support this hypothesis. At larger geographical scales, dispersal is likely to be easier for males than females because of the solitary phase most blackbacks experience before founding their own breeding group (Douadi et al. 2007).

1.3 Western Lowland Gorilla

1.3.1 Ecology

The Western lowland gorilla inhabits primary and secondary tropical forests (moist lowland with dense ground-level herbaceous growth), within parts of central Africa, specifically Angola (Cabinda), Cameroon, Gabon, Congo, Central African Republic, Angola and Equatorial Guinea (Caldecott and Ferriss 2005). Staple foods are pith, stems, bark, roots, leaves, and shoots (*herbaceous terrestrial vegetation) (*Remis 2003; Harcourt et al. 2007); fruit component of the diet is generally high but varies with seasonal availability (Rogers et al. 2004). Western lowland gorillas have also been seen to eat at least 20 species of invertebrate. Most of the insects eaten are termites and ants, and, more rarely, caterpillars, grubs, and larvae from dead wood (Rogers et al. 2004; Caldecott and Ferriss 2005). Once fully mature the captive males weigh between 157 – 237kg and captive females weigh 66 – 136kg (Godwin 1994; Woodland Park Zoo 2007). In wild the mean weight ranges for males between 140 – 160 kg, and for females usually between 70 - 110kg (Harcourt et al. 2007).

The abundance and distribution of food resources differ from that of mountain gorilla habitat. First, terrestrial herbaceous vegetation is less abundant and more sparsely distributed (Watts 1996). Second, in some lowland habitats, abundant aquatic herbs or *Marantaceae* forests occur. Third and most importantly, fruit is abundant, and comprises a large portion of the diet of the Western lowland gorilla (Watts 1996; Harcourt et al. 2007).

Western lowland gorillas are typically found at a density of about 0.25 per square kilometre. At some sites, this can be as many as three or, exceptionally, five gorillas per square kilometre; poor habitat may host as few as 0.1 per square kilometre (Caldecott and Ferriss 2005). It is difficult to observe Western lowland gorillas in their natural habitat, as little light filters through the canopy, and the understory is often choked with dense vegetation. Meeting gorillas under such circumstances can be alarming to both humans and gorillas alike. Therefore, collecting unbiased data is almost impossible. Primatologists discovered marshy clearings in the forest, called by local people *bai.* Several studies of *bais* (treeless clearing situated around a watercourse, the substrate is often extremely swampy with floating vegetation on the surface; the primary activity of gorillas while at *bais* is feeding) were subsequently undertaken in Congo, CAR, and Gabon (Parnell 2005).

There is no distinct breeding season for this sub-species. Males in the wild reach sexual maturity at 8 – 9 years old, but are not thought of as fully mature silverbacks until 15 years old. Females in the wild reach sexual maturity at 7 - 8 years old and usually they have one infant per reproductive cycle (approximately every four years). They often have their first offspring at about 10.5 years old. Gestation is 250 – 270 days (Strier 2000; Cowlishaw and Dunbar 2000).

Western lowland gorillas have shorter, sleeker and greyer or browner hair than the mountain gorillas, and their head hair tends to have red tones, with the crest and nape hair of adult males usually being a striking chestnut colour (Picture 1. and 2.). The mountain gorilla has a more developed sagittal crest along the midline of the skulls than the Western (Caldecott et al. 2005).

Picture 1. *Mountain gorilla. Source: Godwin (1994); © Craig R. Sholley*

Picture 2. *Western lowland gorilla in BZG, 2008. Source: Lenka Bednarikova*

1.3.2 Social Structure

Groups of reproductively active Western lowland gorillas almost always contain only one dominant, silverback adult, plus three or four females, and four or five offspring. There have been rare reports of groups with more than one silverback, and only one report of all-male groups (Caldecott and Ferriss 2005). Total group size ranges from two to 32 individuals, with an average four to six adults, although up to 52 nests have been recorded as belonging to a single group. Larger groups typically contain a higher proportion of adult females (Ferriss and Miles 2005). The group size is influenced by ecological variables such as food availability and predation pressure, and by a range of ontogenetic and social influences (Parnell 2002). Within this structure there is female hierarchy which is established by the length of time each female has been in the group, her age and reproductive success (Nakamichi et al. 2001; Robbins et al. 2005; Campbell et al. 2007). The silverback is often the father of all offspring in the group (extra-group copulations have been observed only very rarely) and infants remain with their natal group for up to 8 years. It is not uncommon to find females that have recently left their family group looking for solitary silverbacks, with whom to establish a social group (Parnell 2002; Campbell et al. 2007).

Doran and McNeilage (Robbins 2007; Campbell et al. 2007) found that although the overall social structure and group size for Western lowland gorillas did not differ from that of mountain gorillas, multi-male groups occur less often. In addition, consumption of a patchy resource like fruit and the presence of swamps result in greater group spread during foraging, greater average day ranges and home range sizes, reduced group cohesion, and more frequent inter-group encounters in Western lowland gorillas.

Further evidence for the variation in social dynamics between the two subspecies can be seen in captive studies of Western lowland gorillas. As mentioned earlier, male - female bonds form the core of mountain gorilla society. But, studies of captive Western lowland gorillas show a different pattern, with females spending significantly more time with other females, or alone than with silverbacks (Nakamichi et al. 2001; Harcourt et al. 2007).

1.4 Female Strategies and Gorilla Society

Harcourt et al. (2007) argue that a relative lack of competition in the foliage-eating gorilla allows females to be in groups, and that a relative lack of benefits of cooperation allows female to leave the group in which they were born.

Grouping and emigration are explained by the unusually strong influence of the males. Females benefit by associating with a large, powerful male, twice their size, for protection against predation and for protection against infanticidal, non-father males. Breeding females emigrate if the male is not powerful enough and perhaps also if they have to share the male's protection with too many other females. Females born into the group are forced to emigrate to avoid inbreeding when their fathers manage to remain as the main breeding male in the group beyond the age of maturity of the female.

Thus, in gorilla society there is a strong influence of males on the distribution of females. "The distribution of food determines what gorilla females can do, while the males then determine what the females actually do." (Harcourt et al. 2007, pp. 145).

It is not clear on which basis females choose mates, but they are likely to include male qualities such as strength or experience, which enhance his ability and willingness to protect a female and her offspring, and possibly more subtle behaviours such as a male's tolerance or affiliation toward her infants (Sicotte 2002; Harcourt et al. 2007).

In regards to female – female relationships, Martha Robbins and her colleagues (2005) have summarised results over three decades in Karisoke Research Centre. Dominant hierarchies, by which is meant linear hierarchy, are detectable in female gorillas. However, while hierarchies are certainly detectable in some gorilla groups, it is by no means the case that they are always obvious. Some clearly dominant individuals exist, and some clearly subordinate ones, too. But among several other individuals, no differences in competitive ability are clear, in part because many females compete too infrequently for a difference to be seen.

1.5 Male Strategies and Gorilla Society

According to Harcourt et al. (2007) female gorillas occur at so low a density, and they and males travel so slowly, that a male is forced to associate permanently with females in order to ensure that he is in the presence of a female when she is in oestrus. It then pays the male to protect the resource that he is tied to, the females and their offspring.

Contest between non-group males is the primary stage for mating competition but also males residing in the same group compete to mate. The intensity of that competition, and the benefits that dominant males might gain from tolerating young subordinates, influence whether young males emigrate or remain in the group with other males. There they must wait in line for top rank and the breeding advantages of this position (Yamagiwa 1987; Harcourt et al. 2007). Robbins et al. (2005) argue that female choice also plays a role in the relative benefits to males of dispersal or philopatry, specifically, female's preferences for single or multi-male groups.

1.6 Cladogram and Gorilla Species Taxonomical Position

1.6.1 Cladogram

The starting point of cladistic analysis is a group of species and molecular, morphological, or other data characterizing those species. The end result is a tree-like relationship-diagram called a *cladogram* (Figure 4.). The cladogram graphically represents a hypothetical evolutionary process. Cladograms are subject to revision as additional data becomes available (Hartwig 2007).

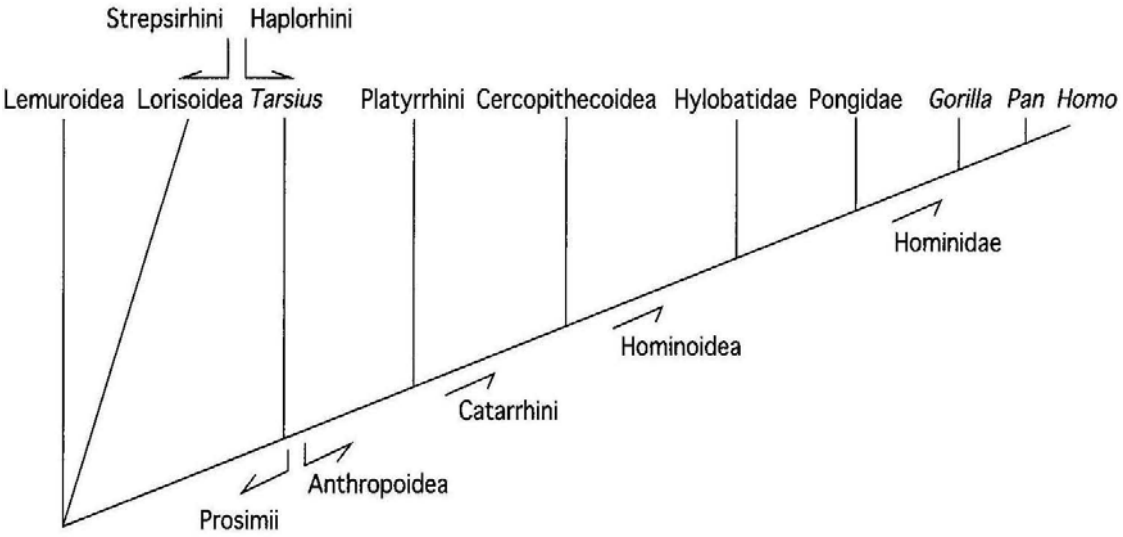

Figure 4. *A macrophylogeny of living primates. This diagram applies higher taxonomic category terms to a standard cladogram design in order to express conventional interpretations of the relative time at which complementary categories arose or diverged from one another. Implicit in the diagram is the belief that major taxonomic groups of primates experienced sequential dichotomous divisions. Source: Hartwig (2007) in Campbell et al. (2007), pp. 18.*

1.6.2 Taxonomy

Gorillas belong to the family Hominidae, which includes all the great apes – chimpanzees, gorillas, orangutans – along with humans. The orangutans of Asia separated from the common ape-human ancestor earlier than did chimpanzees or gorillas and are classed in their own subfamily, Ponginae. Humans and the African apes are classed together in the subfamily Homininae, which is divided into the three genera of *Gorilla*, *Pan*, and *Homo* (Appendix 1.) (Smuts et al. 1987). The latest genetic analyses indicate that *Pan* and *Homo* are more closely related to each other than either is to *Gorilla* (Hartcourt et al. 2007).

1.7 Endangered Species

According to The IUCN Red List of Threatened Species, Western lowland gorilla is classified as Critically Endangered under criterion A4, a population reduction of more than 80% over three generations (where a generation is estimated as 22 years). The listing is based on exceptionally high levels of hunting and disease-induced mortality (over 90% in some large remote areas, including the second largest protected population at Minkébé), which combined are estimated to have caused its abundance to decline by more than 60% alone over the last 20 to 25 years.

Most protected areas have serious poaching problems and almost half of the habitat under protected status has been hard hit by Ebola. If the current Ebola epizootic continues at the same rate and trajectory, then the decline in Western gorilla abundance in all protected areas is projected to be on the order of 45% for the 20-year period spanning 1992 – 2011 (not accounting for other threat factors such as hunting).

Gorilla reproductive rates are extremely low (maximum intristic rate of increase about 3%) and therefore, even an immediate cessation of Ebola mortality and a drastic reduction in the rate of hunting would not result in rapid population recovery. Under the most optimistic scenarios, population recovery would require about 75 years, while much sooner (perhaps 20 to 30 years) habitat loss and degradation from agriculture, timber extraction, mining and possibly climate change will become a major threat. Thus, a population reduction of more than 80% over three generations is likely.

Recommended further reading on this issue and history of humans - gorillas relationship: Gorillas by Sarah Godwin (1994); Primate Conservation Biology by Guy Cowlishaw et al. (2000); Matthews et al. (2004); The IUCN Red List of Threatened Species (2008).

2 PREVIOUS RESEARCH

2.1 Previous Research in Bristol Zoological Gardens (BZG)

There are five Western lowland gorillas in Bristol Zoological Gardens; the group and their habitat will be introduced in detail in the following chapter.

Stephanie Turnbull (Turnbull 2007) has conducted a research with aims to identify differences in behaviour between BZG's four gorillas (one silverback, two adult females, one 2-year-old male, and one 6-month-old male who was not considered as a focal gorilla as he was still fully dependent on his mother) to determine if the group behaves differently at different times of day and at different times during the study period; to assess enclosure use by the gorillas, identifying any preferential areas; to compare enclosure use data from her study with data from previous studies; and to assess social interactions within the group.

The main results of this research were as follows:

a) **Levels of social interaction differ between each of gorillas.** Jock spent more of his time with Romina as his nearest neighbour (NN) as oppose to Salome. This was consistent with research of Whitehouse in BZG (Whitehouse 2006). However, findings did not correlate with Nakamichi conclusions regarding captive gorilla social groups, where the dominant female is the female who has been in the group the longest and therefore establishes a relationship with the silverback (Nakamichi et al. 2001); as Romina arrived at BZG in 2002 and Salome in 1998. Jock, the silverback, was the latest arrival, joining in 2003. Jock also spent very little time alone which was supported by the findings from NNNN (nearest neighbour's nearest neighbour) analysis. Salome spent a large amount of her time (41.53%) alone with her offspring (she isolated herself with Komale). Namoki and Romina spent the majority of their time as NN. Namoki has never been observed further than 10 metres away from any member of the group. Romina was very rarely observed near Salome. This minimal interaction between adult females is supported by the findings of Nakamichi et al (2001).

b) **Jock, Romina and Salome differ in their behaviour**. However, all demonstrate behaviours associated with relaxation. In some circumstances behaviours have changed since the Whitehouse's previous research (Whitehouse 2006), which is probably due to increasing independence of Namoki and the birth of Komale.

c) **Most of the gorillas exhibit a preference for certain areas within the enclosure**. Salome prefers areas out-of-sight from visitors and Jock prefers central areas where he can view the rest of the group. All the gorillas spent more time outdoors toward the end of the study, probably due to higher temperatures and longer daylight hours.

d) **Social interactions occur between all the gorillas.** Jock spent a proportion of his time with each of the females and Namoki. Namoki demonstrated his dependence on Romina by remaining close to her the majority of the time. The females spent very little time interacting.

e) **No atypical behaviours were observed**. The enclosure provides suitable space for an infant to explore as well as spaces for a new mother to avoid disturbance by the public.

2.2 Other Previous Research

As mentioned in Introduction, recent research of Western lowland gorillas, shows a different life history patterns and substantially more complicated and more adaptable social structure compared to that of mountain gorillas (Yamagiva 2003; Robbins 2007).

2.2.1 Research in the Wild

Gorilla society is based on cohesive groups usually containing one adult male, several breeding females (median of 3) and their offspring (Harcourt et al. 2007). Previous studies have shown that the number of individuals in a basic social unit of Western lowland gorillas usually does not exceed 14 individuals (Parnell 2002), which is significantly smaller group size than in mountain gorillas, and they also tend to form less cohesive groups (Yamagiwa 2003; Harcourt 2007). According to Yamagiwa et al.

(2003) the within-group competition may determine the upper limit of group size in lowland habitats with scarce undergrowth.

Parnell's study (2002) has reported that the all-male groups in Western lowland gorillas are rather rare. On the other hand, although Gatti at el. (2004) did confirm those observations, they also reported occurrence of temporary all-male groups which is closely connected with the male migration among groups.

Both sexes normally leave the group of their birth; females immediately join a silverback, either group-living or solitary, while dispersing male usually wander alone, or associate with other bachelors, until they attract females and form their own breeding group. Females migrate not only from their native group but also from the groups where they had lived as adult breeding females, and usually they migrate from larger groups to smaller ones (Caldecott el al. 2005; Harcourt et al. 2007; Robbins 2007).

Harcourt et al. (2007) consider as ones of the most important social contrasts between Western lowland and mountain gorillas the difference in infanticide occurrence and inter-group encounters; "Infanticide appears to be less predictable in other populations than it is in mountain gorillas …", "… at some Western sites, peaceful encounters between groups (including lone males) are relatively frequent". (Harcourt et al. 2007, p.113).

In 2004 was published Stokes's study in intra-group social relations among females and males in wild Western lowland gorillas. Stokes reported that there is no clear evidence for dominance hierarchy among females and agonistic behaviour among them is very variable. Silverback's dominance towards females was very clear and of similar nature to that reported in mountain gorillas in Virunga Volcanoes, Karisoke Research Centre. One of Stokes's conclusions was that protection behaviour of a silverback male is the most important aspect to females and their drive to create social groups with silverback.

According to Yamagiwa et al.'s study (2003) Western lowland gorilla females do not tend to form all-female groups and they have gregarious tendency.

They have also reported that females and males create two types of groups:

a) breeding groups with exclusively one silverback male

b) temporary non-breeding groups

Yamagiwa et al. (2003) also note that there are some similarities between Western lowland gorillas and chimpanzees, such as frugivorous diet and sub-groups.

2.2.2 Research in Captivity

Captive research has contributed to our knowledge of gorilla behaviour, although behaviour of captive animals may be influenced by factors specific to captivity, such as boredom or inability to evade group members (Harcourt et al. 2007). Captive research has provided invaluable data, for example, on maternal behaviour and infant development (Beck 1984; Hoff et al. 1994; Nakamichi et al. 2001 b; Nakamichi et al. 2004; Nowell et al. 2007), intra-group social interactions (Fischer et al. 1978; Hoff et al. 1996; Hoff et al. 1998; McCann et al. 1999; Enciso et al. 1999; Nakamichi et al. 2001 a; Stein 2001; Stoinski et al. 2003; Scott and Lockard 2006 and 2007), play behaviour (Meder 1990; Palagi et al. 2007); post-conflict behaviour (Cordoni et al. 2006; Koyama et al. 2006) and habitat use (Hoff et al. 1994; Hoff et al. 1995; Hoff et al. 1997).

Amongst the conclusions from the above mentioned studies are:

a) **Silverback is a leading male**. If the silverback gets too old, a blackback can take a leading role in the group and assume responsibilities much earlier than he would in the wild (Stein 2001).

b) **Mother - infant contacts play important role in infant social learning, and are essential part of the social group**. Also mother – grandmother interactions are highly valuable and can contribute to successful natural breeding of offspring (Nakamichi et al. 2004; Nowell et al. 2007).

c) **Social behaviour of captive Western lowland gorilla groups is rather adaptable**; post-conflict mechanisms, such as reconciliation and consolation, commonly take place, and the silverback participates in conflict management (Hoff et al. 1998; Koyama et al. 2006; Cordoni et al. 2006).

d) **There are clear effects of environmental conditions on behaviour**. Hoff et al. in 1997 reported clear behavioural differences between indoor and outdoor conditions; particularly aggression was high in indoor areas.

e) **Habitat use**, both indoor and outdoor areas, is influenced by the social structure of the group and social interactions among conspecifics (Stoinski et al. 2001).

3 BRISTOL ZOOLOGICAL GARDENS (BZG)

The Bristol Zoo Gardens, as a modern and progressive zoo, are engaged in education, research and conservation, with the aim of maintaining healthy animals that behave in a natural way. They maintain and defend biodiversity through breeding endangered species, conserving threatened species and habitats and promoting a wider understanding of the natural world (Bristol Zoo Gardens 2008).

3.1 Gorillas in Bristol Zoological Gardens

The gorillas at BZG are part of an international conservation breeding programme for Western lowland gorillas. Currently there is a family group consisting of five gorillas (Jock, Romina, Namoki, Salome and Komale) (Appendix 2.), which is similar in size to a family group in the wild.

Jock is the 24-year-old, 195kg silverback male of the group, born 31 May 1983. He joined BZG breeding group of Western lowland gorilla in July 2003 as an inexperienced adult male and since then he has fathered two offspring, one male and one female. Jock arrived at BZG from London zoo after they were unable to introduce him to their females due to his aggressive behaviour (BZG exchanged males with London zoo). Previous to London zoo Jock was in the bachelor (all-male) group at La Palmyra zoo in France. Despite many months and different variations of introductions, Jock still showed abnormal aggressive behaviour on introduction to the females and therefore, the decision to attempt medical therapy was made. He was treated with anti psychotic drugs used for humans suffering from schizophrenia for a period of eight months. This treatment was a complete success; Jock has been un-medicated now for three years and is behaving appropriately towards the females.

Romina is a 28-year-old female, born 18 Apr 1980 in Rome, who is famous for undergoing the first ever cataract operation performed in Europe on an adult gorilla (arranged by the BZG in 2002). Romina was born with congenital cataracts and has spent her whole life partially blind (ophthalmologists were able to determine that she

had peripheral vision only). During the operation Romina's cataracts were removed and replaced with artificial silicon lens. This enabled her to interact more effectively with the other gorillas and following her successful mating with Jock, resulted in the birth of Namoki in 2005.

Namoki is a 3-year-old female, born 17 May 2008 as the first infant in the group. In one previous study at BZG Namoki was not included in the research due to her dependence on Romina (Whitehouse 2006). She is a very social, playful, independent and healthy juvenile, interacting with all members of the group.

Salome is a 31-year-old hand-reared female who was conceived at BZG in 1975 but was born on 16 July 1976 at London zoo. She is a very genetically valuable gorilla as her father's parents came from the wild. In April 1988 Salome gave birth to her first offspring at Chessington zoo; it was a male and died when he was 8-year-old. Ten years later she returned to BZG, where in 2004, after a long time of investigation of her oestrus cycle and regular miscarriages, she was started on a course of fertility treatment. The condition is known as diminished ovarian reserve - a premature menopause condition also affecting fertility in humans. The fertility treatment (a drug containing clomifene), normally used on women, was successful and after three months Salome conceived Komale, her only surviving offspring. The birth is believed to be the first fertility treatment for gorillas of its kind.

Salome came to BZG significantly overweight and has been on special diet ever since.

Komale is a 15-month-old male, born 15 Dec 2006 as the second male infant in the group. At the start (January 2008) of this project Komale spent most of his time in very close proximity to Salome who was very protective towards him. Later on (February – March 2008) he started enjoying more independency but still in very close proximity to Salome. Komale, although developing well, appears a little slow and small for his age. To eliminate any possible abnormalities, samples will be taken during his routine health check and sent for detailed examination (planned for June 2008).

3.2 Enclosure

The zoo habitat – or exhibit – is comprised of Gorilla Island (outside enclosure) (Appendix 3), and Gorilla House (inside enclosure) (Appendix 4).

Gorilla Island contains approximately 3,500 square metres of usable space and there is continuous electric fencing around it to protect both gorillas and public. Neighbouring enclosure is a naturalistic marmoset's habitat. Around the whole Gorilla Island is a flowing river which is inhabited by few species of ducks. The habitat has flat and sloped areas and contains a variety of mature trees, larger bushes and logs, and there is also a grass substrate. Additionally, there is a spacious shed with ropes and straw which can provide a space to hide from public sight, and a large wooden construction for climbing. There is also a small stream running across the island. The Gorilla Island is connected with the Gorilla House via three entrances and the gorillas can use them freely most of the time.

The inside enclosure is comprised of four large rooms with elevated upper floor; one of these rooms is a so called "isolation area" where gorillas can seek complete privacy from the public view and partially from the rest of the group. The lighting is both natural (skylights) and artificial. There are six iron nests and three large rope nests with plenty of straw; fresh straw is put in the nests every morning. As part of the habitat enrichment plan there is (L3 area) an artificial termite nest where the keepers regularly insert yoghurt or peanut butter, and in the U3 area there is a wooden desk on the wall, with many holes where the keepers insert nuts or any dried fruit. There are lots of ropes that can be used for locomotion around the enclosure. The upper areas U1 and U8 are connected via a bridge that can also provide the gorillas with a hiding space away from public view.

Both of the enclosures provide plenty of space for both free locomotion and play. Also, the keepers regularly enrich the habitat by providing "toys" such as blankets, cloths, cardboard boxes and leafy twigs.

The keepers interact with the gorillas on daily basis (feeding and playing through the bars in keepers' area) and train them once a week so that the gorillas can present

them with various parts of their body for examination, and biological samples can be taken.

3.3 Feeding

The gorillas are usually fed three times a day – around 10am, 12.30pm and 3pm. The times are approximate and can differ dependently on the weather and urgent duties of the keepers.

The morning feeding usually takes place in the outside enclosure. The keepers scatter primate chow, fruit and vegetables all around the island. While the gorillas forage and feed outside, the entrance doors to the inside enclosure are closed as the keepers clean up the Gorilla House.

The 12.30pm feeding also usually takes place in the outside enclosure when one of the two keepers is giving a presentation on the gorilla group to the public while the other keeper throws fruit and vegetables to gorillas.

The 3pm feeding usually takes place in the inside enclosure. At the beginning (January, February 2008) of this study the gorillas were separated for feeding as follows: Jock in L4, Salome with Komale in L5, and Romina with Namoki in the isolation area. Later on (February, March 2008) Jock, Romina and Namoki were fed together (although Romina and Namoki stayed on the elevated upper floor), and Salome with Komale were still fed in L5 area. Komale was always fed by the keeper from her hand and, as mentioned in 3.1 section, Salome is on special diet as she has come to the BZG significantly overweight. For the gorillas menu example please see Appendix 5.

4 RESEARCH OBJECTIVES AND HYPOTHESES

4.1 Objectives

The main objective of this project was to study social behaviour of Western lowland gorillas in the Bristol Zoological Gardens, UK, focusing mainly on the affiliative, agonistic, parental, play, dominant, and submissive behaviours with a special regard to the social structure in the group.

Social behaviour is a complex of behaviours relating to maintenance of positive or neutral social relationships in a group, including social contacts amongst conspecifics' social grooming, and genitalia presentation to the group members of the opposite or the same sex in order to confirm the hierarchy status within the group. The social behaviour consists of, but is not limited to: social grooming, greetings, embracing, reconciliation, consolation, kin behaviour, protective behaviour, social copulation, and some non-reproductive heterosexual and homosexual behaviour (Vančata 2003).

Affiliative behaviour is a complex of social behaviours with purpose of maintaining or gaining positive social relationships typically within a social group, including social grooming, parental behaviour, social play, close proximity, copulation, touching and embracing, greeting, reconciliation, consolation, and protective behaviour (McFarland 2006).

Agonistic behaviour is a complex of aggression, threat, appeasement, and avoidance that often occurs during encounters between members of the same species or social group. Agonistic behaviour is usually typical of the species, often taking the form of characteristic displays (McFarland 2006). To agonistic behaviour belong such actions whose direct purpose is to enforce one's interests; mark or defend one's territory; maintain, gain or stop contact with another group or a member of one's own group; show one's dominance towards member or members of a group; gain or defend food resources; defend or monopolize female or females; defend own or conspecific's offspring; defend oneself against an attack; attack a predator or another social group of

potential competitors. Agonistic behaviour is not limited only to aggressive or violent forms of behaviours; it also includes non-physical threats, displays, territorial behaviour and chasing; and cannibalism and infanticide (Vančata 2003).

Dominant behaviour is a feature of social behaviour through which individuals acquire a high status in a group, usually as a result of aggression. Dominant individuals tend to use their status to gain priority in access to resources, such as food, resting sites or mates (McFarland 2006).

Submissive behaviour falls to the category of agonistic behaviour and it explicitly includes behaviours such as subordinance, retreat and conciliation. Submissive behaviour is displayed towards a dominant individual in order to avoid fight, confirm one's status within the group hierarchy, or maintain positive or neutral social relationships (McFarland 2006).

Parental behaviour is a complex of maternal and paternal behaviours aimed at offspring wellbeing and development, including grooming, suckling, and protective behaviour (Vančata 2003; McFarland 2006).

Play is an aspect of juvenile behaviour, in which the (usually) young animal spends time in apparently pointless activity, such as friendly fighting, sex without coition, hunting without prey etc. Play is often accompanied by a characteristic facial expression and characteristically energetic movement. Although play seems to be functionless, it may be a type of rehearsal or practice for activities that will become important later in life. It may also be a form of exploration of both the physical and the social environment. Play may include all sorts of object manipulation, chasing, display behaviour, competing with conspecifics, but also solitary play (Vančata 2003; McFarland 2006).

4.2 Hypotheses

For the use of this study it has been hypothesised the following:

1) ***Silverback male is strictly dominant to all adult females***.

a) Male is strictly dominant towards all females in both feeding and social context.

b) Females are distinctly submissive to the male in majority situations and contacts.

2) ***There is no clear hierarchy among females in the captive Western lowland gorilla group***.

5 METHOD

5.1 Apparatus

The following apparatus were used:

a) Stop-watch Casio HS - 3

b) Pre-printed check-sheets (Appendix 6)

c) Camcorder Sony DCR-DVD 306, 25 x Optical Zoom

5.2 Sampling Method

Data was collected using focal-animal sampling method (Altmann 1974) and recorded in check-sheets (Appendix 6). First 20 hours of observation was recorded on camcorder and data was analysed from DVDs into the check-sheets. All occurrences of the actions or interactions specified in the ethogram (section 5.2.1) were recorded during 15-minute intervals for each of the group member. It was attempted to record any social behaviour involving the focal animal, including which individual(s) initiated certain behaviour and the reaction of the other individual(s). The observed behaviours were grouped into affiliative, agonistic, dominant, submissive behaviour, parental and play (although only the first four categories were used for the purpose of this study).

The duration of the behaviour was recorded whenever possible. Dependant on the duration all the behaviours were divided into long-term ($\geq$ 2 minutes) and short-term ($<$ 2 minutes) however, this was not taken into account for the statistic.

Independently on the focal sampling and ethogram any unusual or interesting behaviour, such as regurgitation, coprophagy or masturbation was recorded. When appropriate or necessary, additional observational notes were also recorded in the bottom of the check-sheet.

The study started at the beginning of January 2008 and finished at the end of March 2008. The gorilla group was observed twice or three times a week for the whole day. Most data are from between 9am and 4.30pm.

As some sections of the outdoor and indoor facility were out of sight, the data collection was stopped until the focal animal appeared again.

Altogether 105 hours of observation (420 fifteen-minute focal samplings) have been collected; 21 hours per each member of the group.

5.2.1 Ethogram

The ethogram (Figure 5.) has been compiled based on the Collection of Gorilla Ethograms (1991) and under supervision of Mgr. Marina A. Vančatová.

Figure 5. *Ethogram of Bristol Western Lowland Gorilla Group*

(di) Displacement:	individual or individuals move away after or during approach by a conspecific; the initiator can but does not have to occupy the original location of the displaced animal
(fa) Flee upon aggression:	individual or individuals run away after an agonistic / aggressive action of conspecific(s)
(dd) Display direct:	behaviour specifically directed to another individual(s) involving chest beating, wall or ground beating, throwing items, running, swinging on ropes/bars/branch, vocalizing (hooting)
(dn) Display non-direct:	behaviour not specifically directed to another individual(s) involving chest beating, wall or ground beating, throwing items, running, swinging on ropes/bars/branch, vocalizing (hooting)
(lo) Locomotion:	movements that displace the whole body of the animal; moving from one place to another
(gr) Grooming context:	grooming behaviour between two or more members of the group; also

	recorded any other behaviour mentioned in the ethogram that happened in connection to grooming
(fc) Feeding context:	any behaviour mentioned in the ethogram that happened in connection to feeding, typically agonistic or affiliative behaviour
(ag) Agonistic behaviour:	physical contact between two or more members of the group resulting from attack and involving hits, kicks, bites, slaps, push, or pinches; and/or threatening behaviour in the form of pig-grunts, roars, growls, or screams directed toward specific member(s) of the group; and/or non-physical contact directed toward specific member(s) of the group such as charge, rush charge, threat, stiff quadrupedal stance, stare, rigid quadrupedal walk, and/or chase
(co) Copulation:	male mounts female in any orientation; and/or attempts to make genital contact with female in any posture
(fo) Following:	individual moves in the direction of a moving animal; and/or joins another individual(s)
(to) Touching:	any physical contact between two or more members of the group that is not one of the other physical social behaviours
(em) Embracing:	individual encircling with arms another individual in clear attempt to seek comfort/reassurance (typically in parental behaviour context)
(pl) Play:	chasing and/or non-agonistic physical contact between two or more members of the group; and/or object manipulation, throw at, arm shake, circle, clapping, and/or rolling around by oneself; and/or repetitive, exaggerated, disjointed, and seemingly non-purposeful behaviour involving two or more individuals, behaviour accompanied by the “play face”
(cf) Common feeding:	putting food and/or water into mouth; all activities that are involved in handling and ingesting food
(cs) Coalitionary support:	individual(s) support another member(s) of the group against agonistic action of a third party

(cb) Comforting behaviour:	activities that have to do with body care, including grooming, scratching, shaking, stretching, and yawning; and/or cushioning oneself with substrate/straw
(pa) Parental	any behaviour aimed at individual's (mother's or father's) offspring wellbeing, including protection, providing feeding (breast feeding), comforting, back ride, restrain, retrieve, tripedal walk and/or wean

5.2.2 Data Analyses

Separate analyses for each member of the group were conducted in order to see their social behaviours and interactions. *Chi-square* test was used to determine the statistical significance in linear hierarchy within the group.

Focal-sampling data was used to determine the overall number of social interactions between group members, and to determine responsibility for initiation of behaviour.

Data analyses were focused on agonistic and affiliative behaviours. Play and parental behaviours were not included in affiliative behaviour.

Software MatMan 1.1 and OpenOffice.org Calc were used for data analysis. MatMan was used to determine linear hierarchy. To determine the linear hierarchy it had to be calculated the linearity indices of Kendall *(K*) and Landau (*h*), and an adjusted Landau index (*h'*) that is corrected for the number of 'unknown' relationships (i.e. dyads with no interactions). All three indices increase from 0 to 1 as a hierarchy improves from random to completely linear (1 describing complete linearity) (Witting et al. 2003).

While *h* basically compares the number of dyads in which A dominates B to the total number of dyads, *K* basically compares the number of circular triads with the total number of dyads. Linearity is evidenced when the proportion of circular triads is less than expected by chance based on a *Chi-square* distribution (MatMan manual pp.34; Witting et al. 2003).

According to the MatMan manual the ideal group size should be ≥12 to obtain reliable results. Also, small sample sizes and ambiguous relationships decrease the probability of statistically proving the linearity.

Linearity in a set of binary dominance relationships depends on the number of established relationships and on the degree to which these relationships are transitive. If for every pair of animals, A and B, either A dominates B or B dominates A, and if for every three animals A, B and C in the group, A dominates B and B dominates C implies A dominates C, then there is perfect linearity in the set of dominance relationships. The individuals can then be ranked into a fully linear hierarchy. When some triads form circular triangles and/or when some dyads have an unknown or tied relationship the degree of linearity decreases (Robbins et al. 2005).

5.3 Observation Conditions

All data has been collected from the public viewing area (both inside and outside enclosures).

6 RESULTS

Altogether 643 agonistic (physical and non-physical aggressive behaviour in any context including displacements) actions were observed and the linear hierarchy was calculated as follows:

Linear Hierarchy

Matrix	**Agonistic**	
Matrix total	643	
Landau's linearity index (h)	0.5	
Linearity index h' (corrected for unknown relationships)	0.65	
Expected value of h or h'	0.5	
Maximum number of circular triads	5	
Expected number of circular triads	2.5	
Actual number of circular triads	2.5	
Kendall's coefficient of linearity (K)	0.5	
Chi-square value (degrees of freedom)	64	60
Directional consistency index	0.99	
Number and % of unknown relationships	3	30.00%
Number of one-way relationships	5	50.00%
Number and % of two-way relationships	2	20.00%
Number and % of tied relationships	0	0.00%
Total number of relationships	10	100%

Landau's index *h* and Kendall's index *K* equal 0.5. Expected number of circular triads is 2.5 and the Actual number of circular triads is also 2.5 therefore linearity is not evidenced or rather weak with a probability of type 1 error of 0.34. There are 50% of one-way relationships and 20% of two-way relationships.

Linear hierarchy in Bristol gorillas will be further discussed in chapter 7.

6.1 There Is No Clear Hierarchy Among Females

Salome has never displayed any agonistic or dominant behaviour towards Romina, while Romina has on many occasions (164 times) displayed agonistic or dominant behaviour towards Salome (Figure 6.). Thus, the above hypothesis has been disproved.

Legend:

Rom = Romina
Sal = Salome
Joc = Jock
Nam = Namoki
Kom = Komale

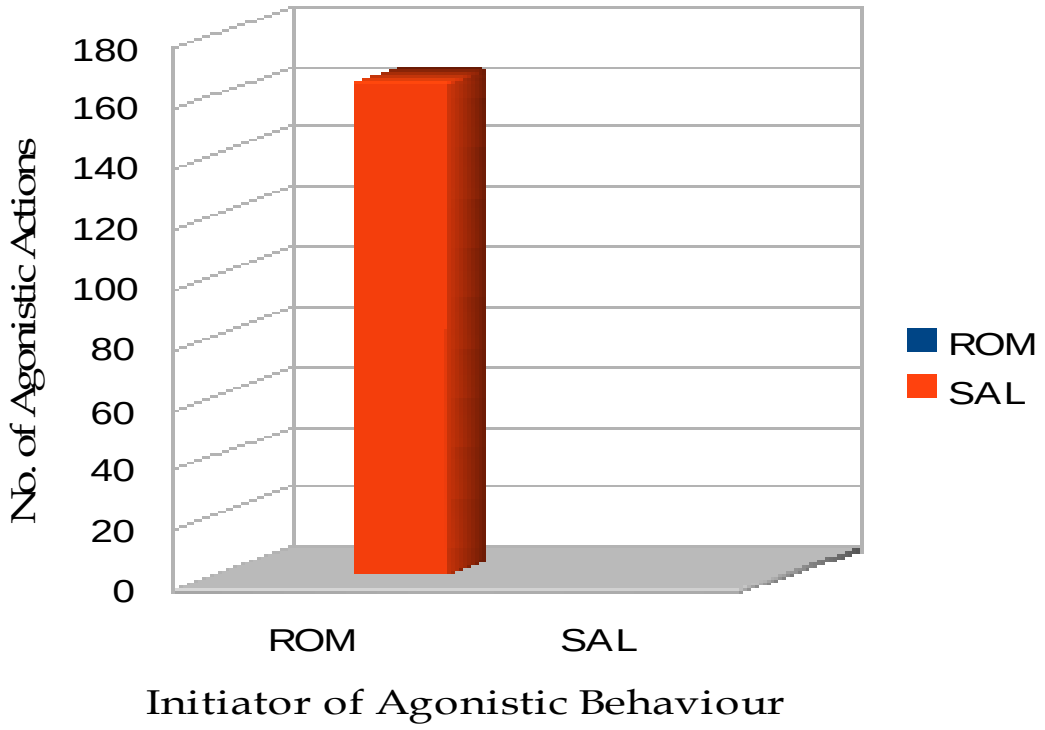

Figure 6. *Agonistic behaviour between Romina and Salome.*

Salome has never displayed any affiliative behaviour towards Romina, while Romina has once displayed affiliative behaviour towards Salome. This happened in coalition support against Jock's aggression towards Salome (Figure 7.).

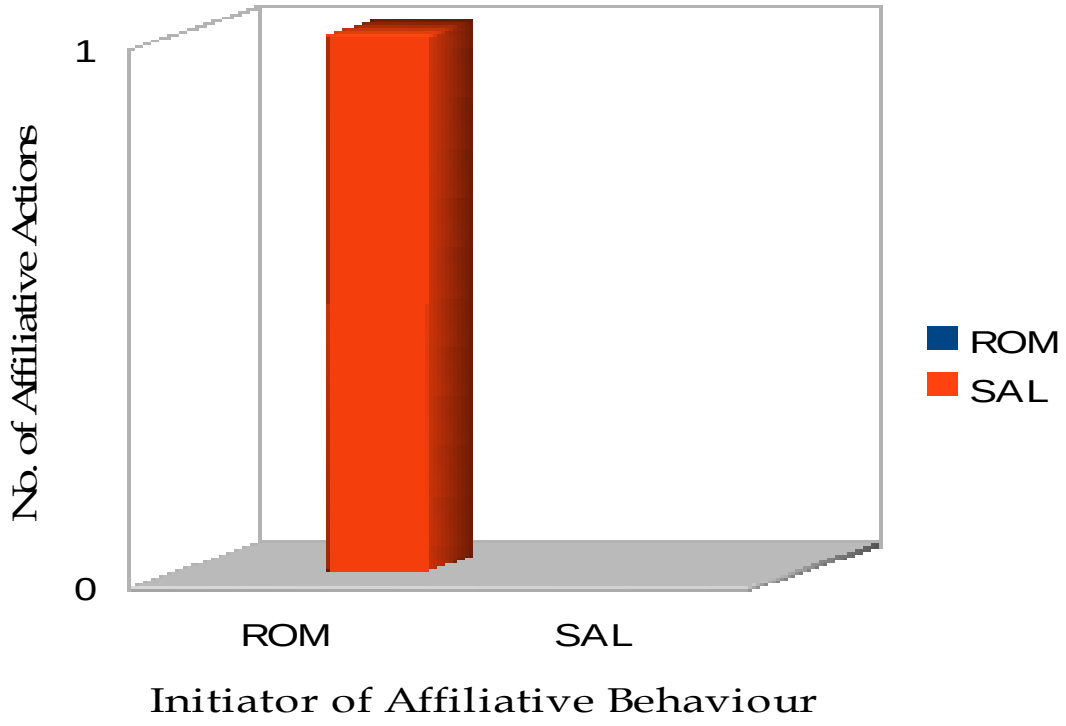

Figure 7. *Affiliative behaviour between Romina and Salome*.

6.2 Silverback male is strictly dominant to all adult females

a) ***Male is strictly dominant towards all females in both feeding and social context.***

Jock displayed the largest amount of agonistic actions; 57% out of which was towards Romina, 31% towards Salome, and 12% towards Namoki. No agonistic action towards Komale was observed. No member of the group has ever displayed any sort of agonistic behaviour towards Jock (Figure 8.). Thus, the above hypothesis has been proved.

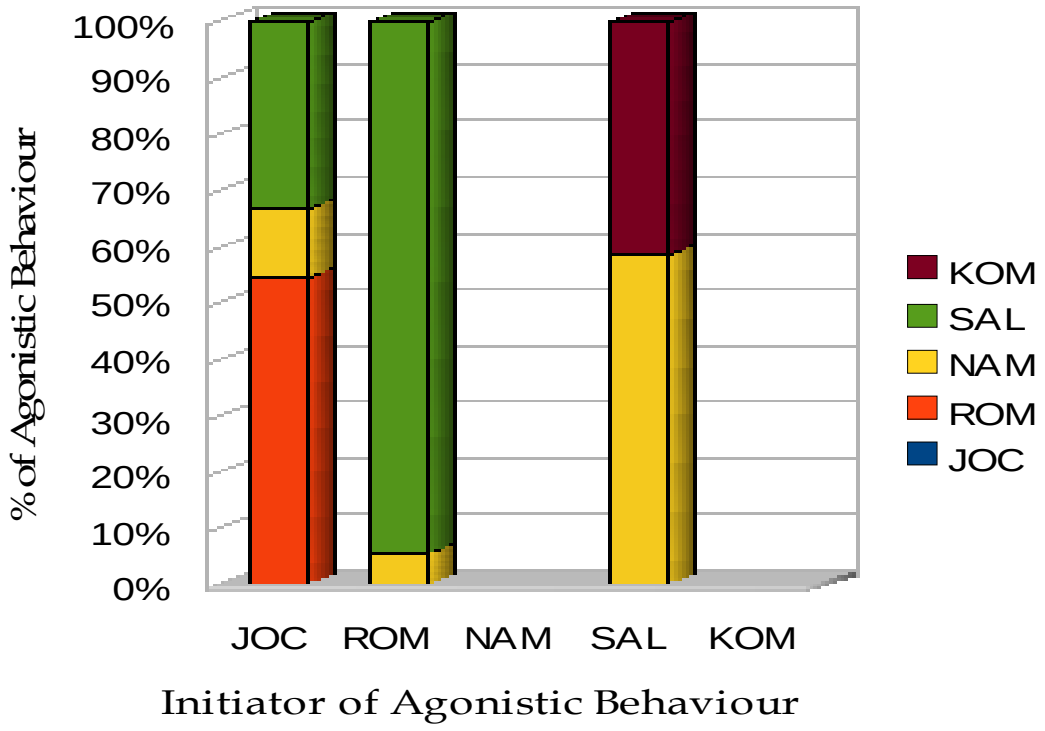

Figure 8. *Agonistic behaviour among BZG gorillas.*

Jock has initiated affiliative behaviour more often to Romina (214 times) than to Salome (114 times). Romina has initiated affiliative behaviour towards Jock (5 times) more often than to Salome (once). Salome has never initiated any sort of affiliative behaviour neither towards Jock or Romina (Figure 9.).

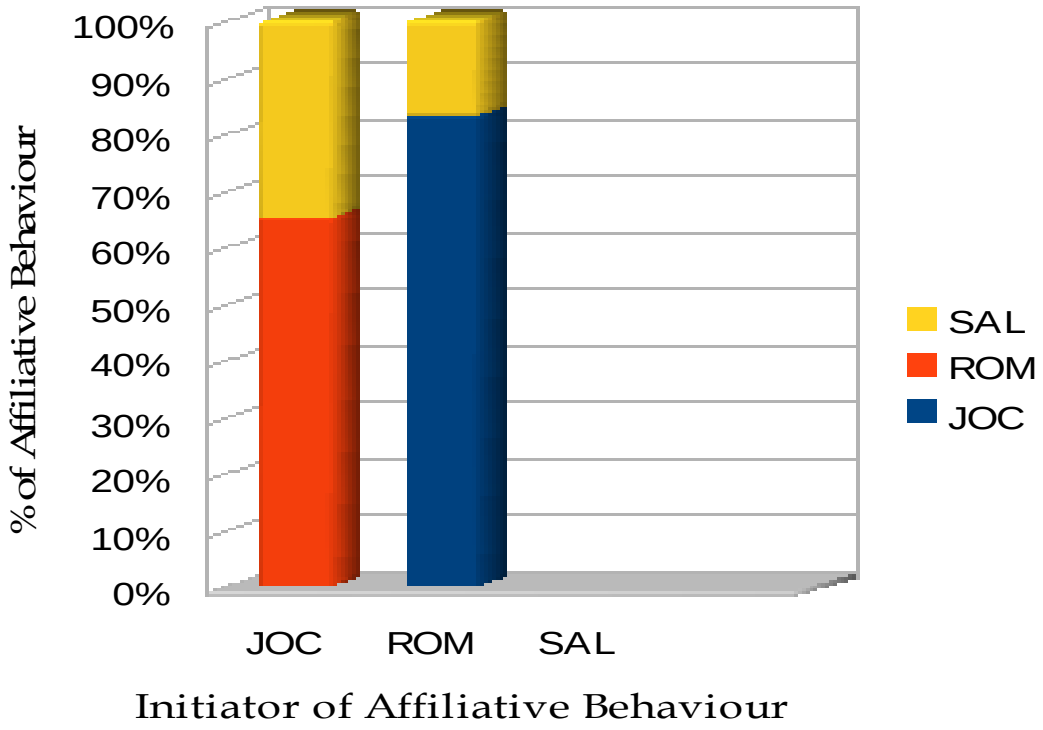

Figure 9. *Affiliative behaviour among BZG gorillas.*

b) ***Females are distinctly submissive to the male in majority situations and contacts.***

Jock has never displayed any sort of submissive behaviour towards any member of the group, while Romina has been submissive towards Jock 65 times, Salome 33 times and Namoki 13 times. Submissiveness was displayed in both feeding and social context. From Komale no submissive behaviour towards Jock was observed (Figure 10.). Thus, the above hypothesis has been proved.

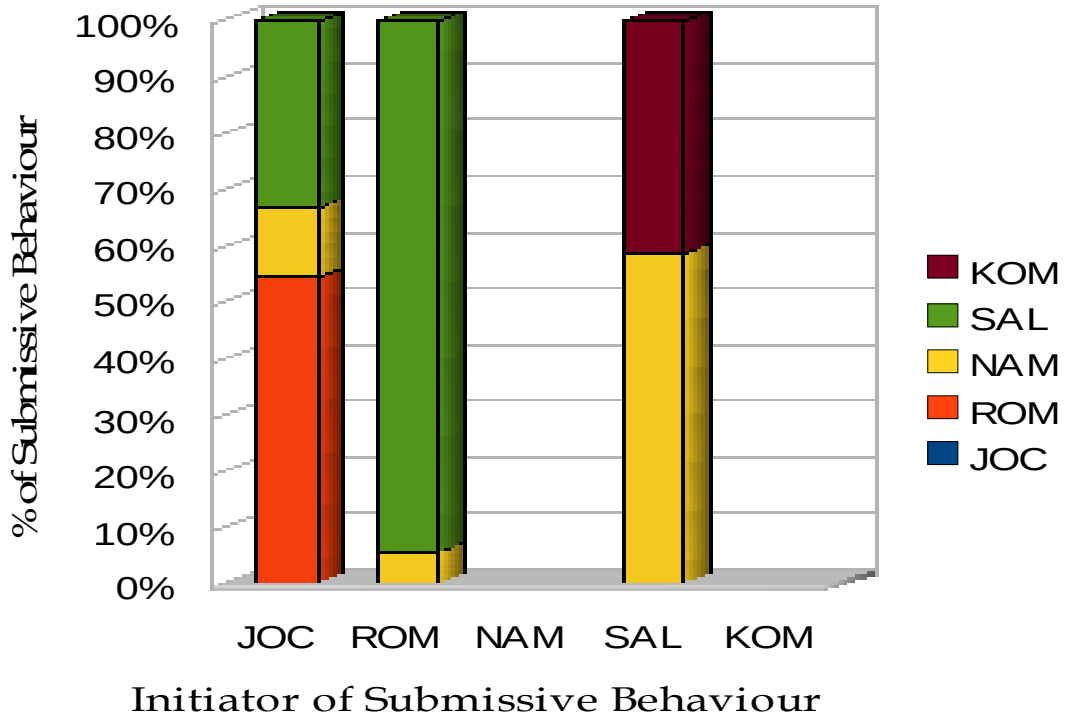

Figure 10. *Submissive behaviour among BZG gorillas.*

7 DISCUSSION

In this study, social relationships within Bristol Western lowland gorilla group were observed; special attention was paid to dominant, submissive, affiliative and agonistic behaviours. The data indicates that there is a social hierarchy with the silverback being a head of group. It was also found that there is a hierarchy among females.

7.1 Hierarchy in the Group

Strictly, in a statistical sense, speaking there is rather weak evidence of linear hierarchy in the Bristol gorilla group (Chapter 6.). However, the small size of the group should be taken into account and we should not entirely rely on the statistical analyses. Therefore in the following we will rely on visual analyses of chart data.

The data in the charts (Chapter 6.) clearly shows the dominance hierarchy within the gorilla group, with Jock being the group dominant animal. This corresponds with findings both in the wild and in captivity (e.g. Fischer et al. 1978; Harcourt et al. 1987; Watts 1994; Watts 1996; Hoff et al. 1997; Enciso et al. 1999; Nakamichi et al. 2001 a; Sicotte 2002; Vančata 2003; Yamagiwa et al. 2003; Gatti et al. 2004; and many others).

Gorillas are social animals and live in cohesive groups consisting of typically one fully adult male, three to five adult females and immature animals of various ages. In all well studied populations, groups are remarkably stable, with adult male(s) and females living together for years (Robbins 2007; Harcourt et al. 2007). According to Harcourt et al. (2007) it is fair to conclude that "… in general, gorilla society is based on a single-male system" (pp.115). In accordance to such a structure in wild population, the captivity population of Bristol Western lowland gorillas creates such a social unit, i.e. silverback male, two adult females and their offspring that the silverback fathered.

Although the BZG's gorilla group might seem to be small in numbers (5 individuals), the group size is corresponding with group size of Western lowland gorillas in the wild where the median for silverback is 1, for blackback 0.8, adult

females 3.5, infants 2, and ratio of infants to adult females in a group is 0.6. (Harcourt et al. 2007).

The BZG's gorilla group displays all signs of wellbeing and appears to be well settled (Mel Gage, Assistant Curator of Mammals, BZG).

7.2 Silverback Male is Strictly Dominant to Adult Females

Dominance is a feature of social organisation in which some individuals acquire a high status, usually as a result of aggression, while other individuals retain a low status. Dominant individuals tend to use their status to gain priority in access to resources, such as food and mates. Subordinate individuals show typical appeasement behaviour, sometimes without any sign of fear. The dominant animal may simply supplant the subordinate at a feeding site as a matter of routine (McFarland 2006). Dominance has been defined as "… an attribute of the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member, and a default yielding response of its opponent rather than escalation" (Robbins et al. 2005).

7.2.1 Silverback Is Strictly Dominant to Adult Females Both in Social and Feeding Context

The results of this study (Figure 10.) showed that the silverback male is clearly dominant to the two females and, additionally, to the older offspring Namoki in both social and feeding context. There was no agonistic interaction between the younger offspring Komale and Jock. There were affiliative actions between Jock and Komale observed, but mostly Komale has initiated those (26 affiliative actions; 3 out of which were initiated by Jock). The finding that the silverback male is dominant to adult females in his group is in accordance with numerous previous researches both in wild and in captivity (e.g. Enciso at el. 1999; Nakamichi et al. 2001 a; Stein 2001; Sicotte 2002; Vančata 2003; Yamagiwa 2003; Koyama et al. 2006; Cordoni et al. 2006; Robbins 2007; Harcourt et al. 2007; and many others).

According to Stein (2001), Alexander Harcourt reported in 1979 that the timing of group activities, the direction of travel, and the overall cohesiveness of the group is determined by the dominant adult male. “While the dominant male appears to be solely responsible for maintenance of daily operations and the cohesiveness of the group, the adult females and immatures are responsible for maintaining the relationship – through proximity – with the silverback.” (Stein 2001, pp. 178).

The results of my study could not confirm Harcourt’s report as Jock was the one who approached females significantly more often than they approached him (Figure 9.). On the other hand, the immatures regularly sought proximity to the silverback and often left their mothers to do so (Namoki significantly more often than Komale due to his independence on his mother) which is in accordance with above mentioned Harcourt’s research. Also, Jock’s usual place for resting was in such an area (L4/L5) where he had good view on all members of the group. This might be pointing at Jock’s efforts to maintain overall cohesiveness of the family.

In the wild, resident males compete with extra-group males for long term access to females. Females transfer between groups and group cohesion is maintained through the bonds that form between a male and the adult females in his group. Male - female relationships are differentiated depending on female length of residence in the group, kinship, reproductive state, and male status (Watts 1996; Sicotte 2002; Harcourt et al. 2007; Robbins 2007).

According to Sicotte’s (2002) research in the wild, the silverback male’s aggression towards females regularly takes the form of male display in order to

a) demonstrate his fighting abilities, or his qualities as a protector, since dominant males are the ones offering long term protection to females against infanticide and predators.

b) decrease potential competitive inequities between females (long term resident dominant females received a higher proportion of displays from the dominant males).

c) provision females of an occasion to confirm their sub-ordinance to a male (there was an association between female appeasement reactions and male displays).

Oestrous females did not receive a higher proportion of male displays, and there was no association between male display and copulation, suggesting that male displays are not a form of courtship aggression aimed at influencing mating in the short term.

Obviously, the conditions in captivity differ radically to those in the wild and therefore it might be difficult to compare Sicotte's research with my project. Nevertheless, Jock, the BZG's silverback, has regularly charged at Salome in protection of Komale and Namoki. Mostly, it was a case of misunderstanding on Jock's behalf – the two offspring often played with each other in close proximity (approximately 1 metre) to Salome who was always making sure that Namoki does not hurt Komale. Occasionally, Namoki, being older and considerably stronger, was too rough during the game and Komale screamed. Instantly, Jock ran to the group and aggressively charged at Salome, including bites and violent hits, as he thought that she is the one who is hurting one of the offspring. After a few incidents Salome always made sure that she is in Jock's view when the two offspring are playing together. Jock's reaction as a protector supports Sicotte's first conclusion.

Also, Jock's reactions and agonistic displays are in accordance with Sicotte's second finding, although from obvious reasons the females in captivity cannot transfer to another group and therefore there is no need as such for the silverback to "decrease potential competitive inequities between females"; also, Jock came to the group as the last member and therefore both of the females have the same tenure to him. Jock displays more agonistic behaviour to Romina who is the dominant female in the group (description in details in section 7.3) nevertheless he is significantly more physically aggressive to Salome. While Jock's agonistic behaviour towards Romina consisted mostly of displacements, "cough grunts", bluff charges and mild hits, his agonistic behaviour towards Salome consisted mostly of aggressive charges, such as chasing, running at, repeated charges, bites, violent hits, but also included displacements, "cough grunts" and mild hits.

After analysing the collected data for a certain period and discussion with Mel Gage, Assistant Curator of Mammals, BZG, it became clear that there is a significant correlation between Jock's aggressive charges at Salome and Romina's oestrus. This is contrary to the above mentioned Sicotte's research in the wild suggesting that male

displays are not a form of courtship aggression aimed at influencing mating in the short term.

Jock also displayed his dominance in feeding context on many occasions. First of all, he occupied the best feeding spot in the outside enclosure and no member of the group could approach him within approximately 5 metres radius during feeding time. Secondly, when the group was about to move from inside to outside enclosure for feeding and only one door was open, Jock blocked the exit and did not let any conspecific out. The rest of the group waited for few minutes until Jock left and then followed him outside. Thirdly, it was always Jock who started eating first. Lastly, no member of the group approached Jock while he was feeding. There were four occasions when Namoki tried to steal Jock's food behind his back. Jock charged at Namoki but did let her run away with the food. This has never happened with any of the females. This is in accordance with Enciso at el.'s (1999) study who described great tolerance of silverbacks to their offspring.

7.2.2 Females Are Distinctly Submissive to the Male

There is clear evidence that both adult females in the group are distinctly submissive to the silverback (Figure 10.).

The analysed data are in accordance to Harcourt et al. (2007), who summarised that all silverbacks, even young subordinate ones, are dominant to females. Females avoid even the non-aggressive approaches of adult males, sometimes almost fearfully, while the silverback never avoids a female, is never submissive to a female, and very rarely is threatened by any female. "This complete dominance comes about only when males reach twelve years or so, by which time they are much larger than females, and beginning to develop their silver back" (pp. 131).

The full range of female reactions to male interactions comprised behaviours such as emitting an aggressive "cough grunt", showing no reaction or leaving the proximity of the male, simply by departing or by retreating. Females could also avoid the male or scream. Also, when being charged at by the male, females could display

submissiveness by adopting postures that appear to make them vulnerable, or giving intense grumbling or humming vocalizations (Robbins et al. 2005; Harcourt et al. 2007).

According to Sicotte (2002) and Harcourt et al. (2007) the motivation for females to display submissive behaviour is to stop the display aggression, prevent its escalation, or reduce the likelihood of its reoccurrence. Sicotte (2002) asked a question "why would females need to confirm their subordinance status in a species where males should be confident that they could displace any female in a competitive situation, by virtue of size alone and because of the lack of female - female alliances?" He argued that submissive behaviour can also carry information on the strength of the bond between a female and her long term mate, and hence the likelihood of the female remaining with the male in this female-emigrant species. This argument could explain the fact that Romina has been submissive to Jock more often than Salome even though Jock has not been as physically aggressive to her as to Salome.

7.3 There Is No Clear Hierarchy Among Females

The chart data provide evidence of a dominance hierarchy among BZG's gorilla females (Figures 6. and 7.).

Salome has never displaced Romina, nor has she ever displayed any agonistic behaviour towards her. Romina, on the other hand, has 164 times displayed agonistic behaviour, including numerous displacements towards Salome. Also, there was only one affiliative action between the two females recorded.

This one observed affiliative action happened when the group was foraging in the outside habitat. Romina started following Salome but kept distance of approximately 4 metres for a few minutes. Then Salome holding Komale in her left arm sat down; Romina approached the mother - infant couple and sat down about one metre away from them. Romina was clearly interested in Komale who was clinging on his mother's arm. Salome has let Romina watch him for about 10 seconds; then she left with Komale on her arm and continued in foraging. Romina did not follow anymore.

During the 3-month research Romina has never been observed supporting Salome against Jock's aggressive actions. Furthermore, she has even on numerous occasions

joined Jock in his aggressive behaviour towards Salome. Although this has not been observed during this study, according to the keepers Salome, on the other hand, does support or tries to protect Romina against Jock's aggression.

This finding does not correlate with previous research, such as Scott et al.'s (2007) who observed captive Western lowland female gorilla agonistic relationships and reported that Howletts female gorillas seem to be forming political alliances amongst each other: all members of the group almost exclusively supported familiar adult females.

High status females (HSFs) usually gain their status through long-term residency, reproductive success and age (Robbins et al. 2005). HSFs in the Scott et al.'s (2006) study rarely engaged in agonistic behaviour with other HSFs. Instead, they were more likely to direct aggression and other agonistic behaviours towards the low status females (LSFs). Also, a submissive response to female agonism was observed specifically in LSFs towards the HSFs, and the Howletts female gorillas did not show any pattern of reciprocity in initiated agonism that Watts (1994) described in mountain gorillas.

This supports the finding in Bristol female gorillas who display such a pattern in agonistic behaviours, Romina being the HSF and Salome the LSF.

Also, Scott et al. (2006) reported that the distinction between HSFs and LSFs were most evident during roof feedings, when HSFs were successful at keeping LSFs away from the food patch (their own access already being considerably reduced by the presence of the silverback).

This pattern was also evident in Bristol female gorillas during the 12.30pm feeding in the outside enclosure when typically Salome sat in the shed waiting for keepers to throw some food very close to her while Romina was occupying most foraging space (except about 5 metres radius around Jock).

According to Scott et al.'s (2006) conclusions, the agonistic behaviour patterns among Howletts gorillas supports the hypothesis that the style of feeding, in providing highly valued foods in a clumped, defendable area, can lead to greater competition between females, resulting in stronger dominance hierarchies.

In addition, Scott et al. (2006) mention that in conditions of social tension, primates may also direct aggression towards an opponent that presents little risk, such as a low ranking, new female immigrant with no allies, and the latter may have also served as a convenient scapegoat.

This partly would and would not be the case in Bristol gorillas. The finding is relevant in the sense that Salome appears to serve as a scapegoat to both Romina and Jock. Although there are no data collected specifically on this matter, during 105 hours observation and after many discussions with the keepers, it seems that Jock might be occasionally using Salome as some kind of "tension release tool" as he directed most of his aggressive actions towards Salome when Romina was in oestrus and did not let him mate with her. Also during such periods Romina displaced Salome more often and therefore Salome also might be serving to Romina as a convenient scapegoat.

On the other hand, Romina is younger than Salome and came to BZG three years later than Salome (Jock joined the females after two years they have been together with another silverback). This should therefore result in Salome's higher status over Romina but the opposite has happened.

There are at least two possible explanations to Romina's higher status:

a) Romina was reproductively more successful than Salome as she gave birth to the first offspring in the group

b) Romina has limited social skills, possibly due to early cataracts which inhibited a lot of natural behaviour and limited involvement in group situations when she was young (Mel Gage, Assistant Curator of Mammals, BZG)

As odd as it might seem, there might be some true value in the latter argument. Romina was basically blind when she came to BZG. The BZG staff recognised that she was suffering from cataract in both eyes and arranged an operation in 2002 which was 100% successful and the only remainder of her previous blindness is her left index finger that is, out of habit, constantly sticking out (she used to use her index finger like the white stick of blind people to move around enclosures). According to the keepers, immediately following cataract removal surgery she started enjoying exploring her surroundings and socially interacting with other gorillas. Therefore it might be just a

case of Romina's misunderstanding of "how to be a gorilla" which is resulting in her supporting Jock's aggressive actions towards Salome, and her displacing Salome, as displacement could be taken as an result of any approach, even a friendly one.

Obviously, this hypothesis might not be relevant but all aspects should be taken into account.

7.4 Limitation of the Study

The Bristol gorilla group has been observed for a 3-month period which might not be sufficient from at least three reasons:

a) three-month observation might not cover all or majority of various social aspects and behaviours of the group, and therefore the collected data might not be representative enough

b) as the observation took place from the beginning of January to the end of March the gorilla behaviour might have been influenced by the cold weather which forced them to spend more time in the inside enclosure with much limited space in comparison to outside enclosure (Hoff at el. 1994; Hoff et al. 1996)

c) although the Bristol gorilla group is rather small in size (which matches natural conditions in the wild), there is a possibility that not all interactions between the gorillas have been noticed by the observer

Also, the protective glass of the inside enclosure is 36mm thick and does not let through most noises including gorilla social vocalisation. Vocalisation in gorillas is an important part of their communication and females often make a "grumble" vocalisation as an apparent signal of submission to silverbacks; they also grumble after receiving aggression from other females, although this happens more rarely (Lyttle 1997; Robbins et al. 2005).

7.5 Future Directions

Future research would be highly valuable in terms of group social dynamics development. Romina's offspring is three years old and completely weaned therefore Romina is in the position to conceive again. A third offspring will bring extra dynamics into the group and it would be interesting to observe Namoki's reactions to having share her mother's attention.

It would be beneficial to focus also on nearest neighbour proximity as this is good indication of social relationships within a group (Stoinski et al. 2003). Also taking into account Turnbull's (2007) research incorporating the nearest neighbour proximity in Bristol gorillas, it would provide us with comparison between previous and present situation.

Also, Komale appears to be getting stronger, more independent from Salome, and more curious about his father. It would be beneficial to observe his progress, especially if the planned DNA tests confirm some sort of genetic disorder.

8 CONCLUSIONS

Due to the unique background of the group (3.1 section) we are not entitled to draw any general conclusions on population of Western lowland gorillas in captivity. Nevertheless, with fair confidence (Chapter 6), we can report the following:

a) The Western lowland gorillas in Bristol Zoological Gardens live in a cohesive group with linear social hierarchy.

b) The silverback male is a clear leader of the group and is dominant towards females in both social and feeding context.

c) There is also social hierarchy among the two females – Romina is dominant towards Salome in both social and feeding context.

Results of the data analyses (Chapter 6) confirmed the first hypothesis while the second hypothesis was disproved.

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10 APPENDICES

Appendix 1. *Taxonomy and Social Organization of Living Primates (Section of Apes and Humans only) Source: Smuts et al (1987), pp. 504 - 505.*

APES AND HUMANS		Grouping Pattern	Inter-group Pattern
Hominoidea			
Hylobatidae			
Hylobates agilis	Agile gibbon	Mon	
Hylobates concolor	Black – or white – checked gibbon	Mon	
Hylobates hoolock	Hoolock gibbon	Mon	
Hylobates klossii	Kloss's gibbon	Mon	
Hylobates lar	Whitehanded or lar gibbon	Mon	
Hylobates moloch	Sovery or moloch gibbon	Mon	
Hylobates muelleri	Mueller's gibbon	Mon	
Hylobates pileatus	Pileated gibbon	Mon	
Hylobates (Symphalangus)			
syndactylus	Siamang	Mon	
Pongidae			
Gorilla gorilla beringei	Mountain gorilla	Sm-V	F
Gorilla gorilla gorilla	Western lowland gorilla	Sm-V	?
Gorilla gorilla graueri	Eastern lowland gorilla	Sm-V	?
Pan paniscus	Bonobo or pygmy chimpanzee	C-i	F?
Pan troglodytes	Chimpanzee	C-i	F
Pongo pygmaeus	Orangutan	Sol	F
Hominidae			
Homo sapiens	Human	C-i	F, B

Grouping Pattern

C-i = community – closed social network (containing several breeding female and males) within which individuals forage partly independently.

Mon = monogamous pairs, travelling as a family group.

Sm-V = small groups, having variable number of resident adult males, from one to many.

Sol = individual forage solitarily.

Inter-group Transfer

F = primarily females transfer between breeding units.

B = both sexes show a strong tendency to transfer between breeding units

Data are given only for groups (or communities) having more than one breeding female.

Appendix 2. *Taxon Report for Gorilla gorilla gorilla in Bristol Zoological Gardens. Source: BZG, 2008.*

Report Start Date 01/01/2005 — **Taxon Report for Gorilla gorilla gorilla** — Report End Date 03/04/2008

2741 SAL **Gorilla gorilla gorilla** **IZY EndangeredApp.** **Western lowland gorilla**

Date in	Acquisition - Provider/local Id	Holder	Disposition - Recipient/local Id
3 Nov 1998	Loan In from LONDON RP-A1	BRISTOL	

Sex-Contraception:	Female -	Birth type:	Captive Born
Hybrid status:	Not a hybrid	Birth Location:	Zoological Society of London
Enclosure:	GORILLA	Birth date - Age:	16 Jul 1976 - 31Y, 8M, 17D
Sire:	1628 at BRISTOL	Dam:	A2779 at LONDON RP
Rearing:	Hand	Global Studbook #:	620/129

Regional Studbook #:59 – FZG

7925 ROM **Gorilla gorilla gorilla** **IZY EndangeredApp.** **Western lowland gorilla**

Date in	Acquisition - Provider/local Id	Holder	Disposition - Recipient/local Id
28 Nov 2001	Loan In from ROMA-3	BRISTOL	

Sex-Contraception:	Female -	Birth type:	Captive Born
Hybrid status:	Not a hybrid	Birth Location:	Fondazione Bioparco di Roma
Enclosure:	GORILLA	Birth date - Age:	18 Apr 1980 - 27Y, 11M, 15D
Sire:	1 at ROMA	Dam:	STB283 at ROMA
Rearing:	Parent	Global Studbook #:	726/193 - EAZA

8555 JOC **Gorilla gorilla gorilla** **IZY EndangeredApp.** **Western lowland gorilla**

Date in	Acquisition - Provider/local Id	Holder	Disposition - Recipient/local Id
25 Jun 2003	Loan In from LONDON RP-498	BRISTOL	

Sex-Contraception:	Male -	Birth type:	Captive Born
Hybrid status:	Not a hybrid	Birth Location:	Zoo de La Palmyre
Enclosure:	GORILLA	Birth date - Age:	31 May 1983 - 24Y, 10M, 3D
Sire:	BALOU at LA PALMYR	Dam:	NATACH at LA PALMYR
Rearing:	Parent	Global Studbook #:	825/281

9018 NAM **Gorilla gorilla gorilla** **IZY EndangeredApp.** **Western lowland gorilla**

Date in	Acquisition - Provider/local Id	Holder	Disposition - Recipient/local Id
17 May 2005	Birth	BRISTOL	

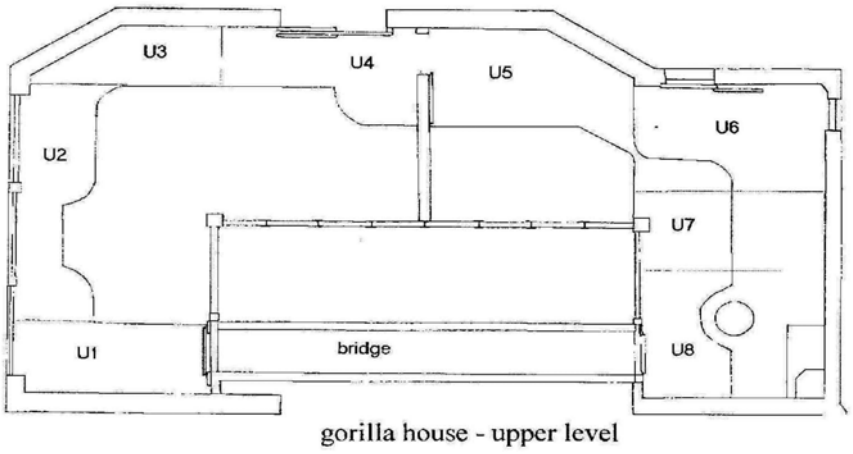
Sex-Contraception:	Male -	Birth type:	Captive Born
Hybrid status:	Not a hybrid	Birth Location:	Bristol, Clifton, & W. of England Zool
Enclosure:	GORILLA	Birth date - Age:	17 May 2005 - 2Y, 10M, 17D
Sire:	8555 at BRISTOL	Dam:	7925 at BRISTOL
Rearing:	Parent		

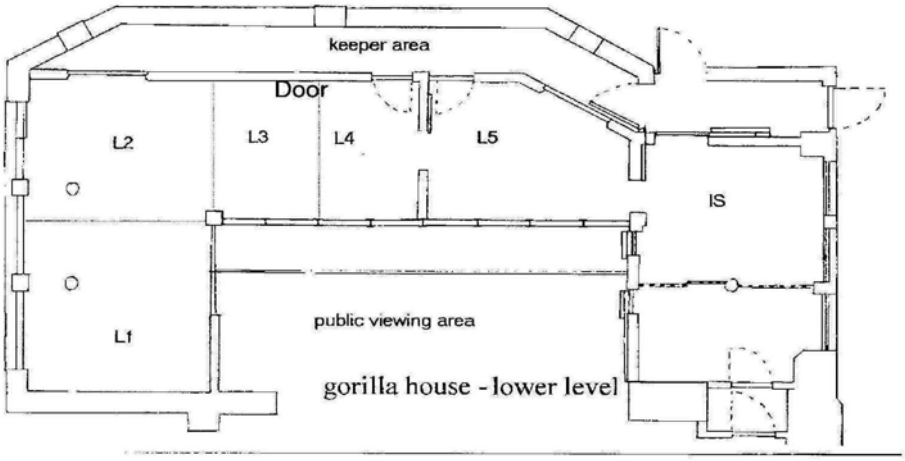
9582 KOM **Gorilla gorilla gorilla** **IZY EndangeredApp.** **Western lowland gorilla**

Date in	Acquisition - Provider/local Id	Holder	Disposition - Recipient/local Id
15 Dec 2006	Birth	BRISTOL	

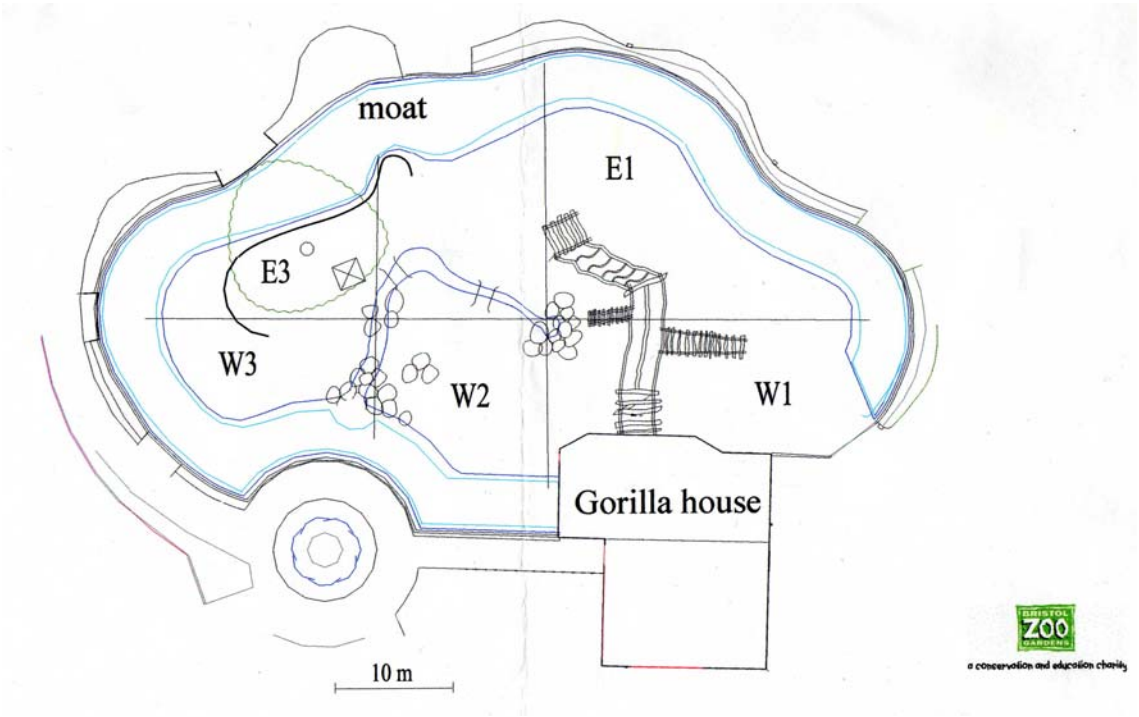
Sex-Contraception:	Male -	Birth type:	Captive Born
Hybrid status:	Not a hybrid	Birth Location:	Bristol, Clifton, & W. of England Zool
Enclosure:	GORILLA	Birth date - Age:	15 Dec 2006 - 1Y, 3M, 18D
Sire:	8555 at BRISTOL	Dam:	2741 at BRISTOL
Rearing:	Parent		

Appendix 3. ***Gorilla House in Bristol Zoological Gardens. Source: BZG, 2008.***





Appendix 4. ***Gorilla Island in Bristol Zoological Gardens. Source: BZG, 2008.***



Appendix 5. ***An example of BZG's gorilla menu. Source: BZG 2008.***

Gorilla Teas August 2007

Menu 1	Menu 2	Menu 3	Menu 4
Jock	Jock	Jock	Jock
1 yoghurt		1 yoghurt	
1 fennel	6 ½ tomatoes	8 tomatoes	6½ tomatoes
8 tomatoes	2 2/3 red/yellow peppers	1 orange	2 hard boiled eggs
2 2/3 carrots	2 2/3 leeks	2 2/3 corn on the cob	4 carrots
2 2/3 corn on the cob	2 2/3 packs of baby corn	2 2/3 handful of beans	1 1/3 celery
3 chicory	2 2/3 chicory	2 2/3 chicory	3 chicory
4 satsumas	1 1/3 orange	4 peaches or nectarines	4 satsumas
2 2/3 apples	1 1/3 apple	2 2/3 apples	1 1/3 apple
2 2/3 red/yellow peppers	1 1/3 pear	2 2/3 parsnips	1 1/3 pear
3 bunches of basil	2 hard boiled eggs	2 2/3 red or yellow peppers	2 2/3 red/yellow peppers
1 ½ leafy lettuce	2 2/3 bunches of chives	2 2/3 bunches of basil	3 bunches of chives
1 ½ Iceberg lettuce	2 2/3 leafy lettuces	1 1/3 leafy lettuce	3 leafy lettuces
		1 1/3 iceberg lettuce	
Romina	Romina	Romina	Romina
	1 1/3 red/yellow pepper	1 1/3 red or yellow pepper	3 tomatoes
½ fennel	3 tomatoes	3 tomatoes	1 1/3 red/yellow pepper
3 tomatoes	2/3 cucumber	2/3 grapefruit	2/3 cucumber
1 1/3 red or yellow pepper	1 1/3 chicory	2 chicory	2 chicory
2 chicory	1 1/3 pear	1 1/3 apple	1 1/3 pear
1 1/3 apple	3 satsumas	1½ peach or nectarine	1 bunch of grapes
1 1/3 orange	1 1/3 pack of baby corn	1 handful of beans	1 1/3 celery
1 1/3 corn on the cob	2 2/3 carrots	1 1/3 carrots	3 carrots
2 2/3 carrots	1 1/3 leek	1 1/3 parsnip	2 hard boiled eggs
2 iceberg lettuce	2 hard boiled eggs	1 yoghurt	2 leafy lettuce
2 bunch of basil	1 1/3 bunch of chives	2 bunch of basil	2 bunch of chives
1 yoghurt	1 1/3 leafy lettuce	2 iceberg lettuce	
Salome	Salome	Salome	Salome
3 tomatoes	1½ red/yellow peppers	1½ red or yellow peppers	1½ red or yellow peppers
½ fennel	3 tomatoes	3 tomatoes	3 tomatoes
2 chicory	2/3 cucumber	2/3 grapefruit	2/3 cucumber
1½ apples	3 chicory	2 chicory	3 chicory
1½ oranges	1½ pears	3 apples	1½ pears
1½ corn on the cob	3 satsumas	3 peaches or nectarines	1½ small bunches grapes
3 carrots	1½ pack of baby corn	3 handful of beans	1½ celery
1½ red or yellow peppers	3 carrots	3 carrots	3 carrots
1 yoghurt	1½ leeks	1½ parsnips	4 bunches of chives
4 bunches of basil	2 hard boiled eggs	3 leafy lettuces	1½ leafy lettuces
3 leafy lettuces	1½ leafy lettuces	4 bunches of basil	2 hard boiled eggs
	4 bunches of chives	1 yoghurt	
Namoki	Namoki	Namoki	Namoki
1/3 iceberg lettuce	1/3 leafy lettuce	1/3 iceberg lettuce	1/3 leafy lettuce
1 tomato	1 tomato	1 tomato	1 tomato
13 grapes	13 grapes	13 grapes	13 grapes
2/3 orange	1½ satsuma	1 1/3 peach	2/3 kiwi
1/3 apple	1/3 pear	1/3 apple	1 1/3 nectarine
1/3 carrot	1/3 parsnip	1/3 carrot	1/3 parsnip
1 1/3 banana	1 1/3 banana	1 1/3 banana	1 1/3 banana
7 beans	7 beans	7 beans	7 beans
1 yoghurt	1 boiled egg	1 yoghurt	1 boiled egg

Pellet – total 1050g
Jock – 350g
Romina – 300g
Salome – 350g

6 large cooked potatoes to be delivered to section in 1 tub please.

Appendix 6. ***Check-sheet used for recording behavioural data*.**

Checksheet No:

Date - Time:

Focal animal:

Reactions: **dominant - D**
submisive - S
other - O

I	Initiation	**fo**	Following
di	Displacement	**to**	Touching
fa	Flee upon aggression	**em**	Embracing
dd	Display direct	**pl**	Playing
dn	Display non-direct	**cf**	Common feeding
lo	Locommotion	**cs**	Coalitionary support
gr	Grooming context	**cb**	Comforting beh.
fc	Food context	**pa**	Parental beh.
ag	Agonistic behaviour		
co	Copulation		

JOC	Jock silveback
ROM	Romina
SAL	Salome
NAM	Namoki (son of Sal)
KOM	Komala (son of Rom)

Focal sampling (whole-day-focal-follow)

I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	pa
			D S O		fa	dn	gr	ag	fo	em	cf	cb	
I	Name	◁ : ▶	Name	I	di	dd	lo	fc	co	to	pl	cs	
			D S O		fa	dn	gr	ag	fo	em	cf	cb	

Notes/Comments:..
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