Male – male social interactions in breeder and bachelor groups of gorillas (*Gorilla gorilla*): An indication of behavioural flexibility

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I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

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Abstract

The establishment of bachelor gorilla groups in captivity, along with the continued success of the captive breeding programme provides an opportunity for research on social interactions in two differing circumstances. This thesis focuses on male – male social interactions. Emphasis is placed on dominance and affiliative behaviours and gives indications of the level of behavioural flexibility within both breeder and bachelor gorilla groups.

Evaluation of behavioural diversity, to validate the use of multi-institutional research, confirms that behavioural phenomena, such as the effect of age class, are not masked by the potential confound of differing husbandry practices and enclosure design between institutions.

It was found that males in bachelor groups express significantly lower frequencies of both dominance and aggressive behaviours than males in breeder groups. A Relationship Quality Index (RQI, based on the ration of dominance to affiliative behaviours) was developed and again bachelor males exhibited a significantly lower RQI, indicating that bachelor males express a greater frequency of dominance behaviours than affiliative behaviours. This may have a direct impact on the social development of young males, and potentially their social competence in later life, a significant finding for the management of gorillas in captivity. In addition, it can be suggested that affiliative behaviours, which may work to repair damage to social bonds, may not be performed to the same extent in bachelor groups, suggesting that the ‘value’ of social bonds within a bachelor group may be reduced.

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Chapter 1: Introduction

1 Introduction

Although there has been a large body of research published on gorillas in wild situations, the focus has been strongly toward the mountain gorilla of the Virungas (*Gorilla beringei beringei*) as this is where the majority of conservation efforts and subsequently research on gorillas have been aimed (Harcourt and Stewart, 2007). Until relatively recently there was very little research being undertaken on the western gorilla (*Gorilla gorilla*), due to difficulties in accessibility of their habitats and political or social instability within their range countries. Within recent years there has been a steady increase in published research on western gorillas (Levrero *et al*, 2006; Olejniczak, 1996; Parnell, 2002) but even so the bulk of our knowledge about gorilla behaviour still comes from the mountain gorilla research. However the western gorilla is the species held within zoological institutes, providing a valuable research resource. Within the past ten years there have been an increasing number of zoos establishing bachelor gorilla groups to provide housing for males considered 'surplus' to the breeding programme at the current time. The establishment of these groups, along with the continued success of captive breeding groups and the broadening field of zoo based research provides an opportunity for research into western gorilla social systems.

1.1 Gorillas in the wild

1.1.1 Taxonomy, ecology and habitat

Gorillas are the largest of the living primates with a natural distribution confined to central Africa. There are two recognised species of gorilla, the western (*Gorilla gorilla*) and the mountain gorilla (*Gorilla beringei*), each of which has been divided into subsequent subspecies. The mountain gorilla is divided into the eastern gorilla

(*Gorilla beringei graueri*) and the mountain gorilla (*G. b. beringei*). The Bwindi mountain gorilla is currently listed with the Virunga mountain gorilla, although there is debate as to whether it is more closely related to the eastern gorilla or alternatively deserves its own subspecies. The western species is currently divided into the western lowland gorilla (*G. gorilla gorilla*) and the Cross river gorilla (*G. g. deihli*) (Groves, 2001; Clifford *et al*, 2004).

To date the majority of information available on gorillas from the wild has been gathered from the long-term studies of the Virunga mountain gorillas (Harcourt and Stewart, 2007). In addition there are research initiatives for both the eastern and the Bwindi mountain gorillas. Within recent years there has been an increase in published research on western gorillas (Doran-Sheehy and Boesch, 2004; Levrero *et al*, 2006; Olejniczak, 1996; Parnell, 2002), however there are still comparatively few papers. It was originally thought that group size and composition was very similar between the two species and, from comparison between wild mountain and zoo housed western gorillas, behaviours and vocalisations appeared very similar as well (Harcourt, 1988). However recent research on wild western gorilla populations suggests that variation in habitat leads to marked differences not just between western and mountain, but also between populations of western gorillas (Tutin, 1996; Doran and McNeilage, 2001).

Both species of gorillas are highly social primates, living in typically small polygynous family groups dominated by a ‘silverback’ male, although both multi-male and all male groups have been documented (Levrero *et al*, 2006; Robbins, 1995, 2001, 2007; Stewart and Harcourt, 1987; Yamagiwa, 1987, 1992). The number of females present in the group can vary depending on the resources available and the ability of the silverback to maintain control of the group. The average group size for both western and eastern gorillas is 8 – 10 individuals, with a range of 2 – 40 plus individuals

(Robbins, 2007; Tutin, 1996), although the western gorilla appears to show greater variation in social structure with groups ranging from multi-male units which show seasonal fission (Olejniczak, 1996) to more traditional one-male units (Magliocca, Querouil and Gautier-Hion, 1999; Tutin, 1996). The social structure of the western gorilla can also become dispersed in some environmental conditions such as the swampy sites known as 'bais', where groups will intermingle peacefully whilst feeding (Bradley *et al*, 2004).

Gorillas show marked sexual dimorphism on reaching maturity, with males often becoming almost twice the size and weight of the female (Harcourt and Stewart, 2007). Male offspring are classed as juvenile or sub-adult to an age of 10 years. From the age of 10 to 13/14 years, they are termed blackback. The development of secondary sexual characteristics in the male is indicated by the development of the silverback from the age of 13/14 years (Robbins, 1996). This is the growth of silvery grey hairs running across the saddle and lower back, and stretching down the thighs. This indicates full maturity in the male gorilla.

1.1.2 Conservation status

Gorillas are classed as critically endangered (IUCN, 2007) throughout their range, particularly where the populations are fragmented into small ranges. The major threat to their existence is the expanding bushmeat trade, which is facilitated by extensive logging within home ranges. Estimates now indicate that at current rates of decline gorillas will be functionally extinct in the wild within the next 10 – 15 years.

1.1.3 Gorilla behaviour (socio-ecology) – an overview

Mountain gorilla groups will typically show morning and afternoon peaks of daily activity (locomoting and feeding) with a midday rest period (Stewart and Harcourt, 1987). The direction of travel and timing of group activities will generally be determined by the silverback. The general pattern will be a spreading out of the group and moving slowly through the forest and feeding as they go.

Although intra-group aggression is generally low in gorilla families, consisting mainly of cough-grunt vocalisations, levels of these vocalisations are raised during feeding times. In addition, it has been observed that during resting phases, the inter-individual distance is far less than during feeding periods. The increased level of aggressive vocalisation and greater social distances suggest that even when food is evenly dispersed and abundant, feeding competition can still occur (Stewart and Harcourt, 1987).

Gorillas are generally considered to be terrestrial and when locomoting in search of food or new areas will move quadrupedally, knuckle walking on their arms. However the western gorilla, in particular, will spend a considerable amount of time within the forest canopy, especially in the fruiting season. Even adult silverbacks will climb to the highest levels and move through the canopy from tree to tree, although not for long distances. It has been observed that females spend a higher proportion of time in an arboreal situation than males, and that younger age classes spend more time in an arboreal situation than adults (Doran, 1996).

A high proportion of a gorilla's daily activity will be taken up in resting behaviour. The digestive physiology of the gorilla is adapted to a diet consisting largely of highly fibrous terrestrial herbaceous vegetation and food retention time is long indicating the necessity for a more sedentary mode of life to ensure efficient absorption of nutritional requirements from the food source (Tutin, 1996). During the daily rest periods, loose day nests may be constructed. However this is also the time, when the group tends to cluster close to the silverback, that affiliative interactions, such as grooming, are highest (Stewart and Harcourt, 1987). Grooming patterns can be extremely varied between groups of gorillas. In mountain gorillas it has often been observed to take place frequently between the adult females of a group and the silverback, but less frequently between the females themselves (Robbins, 1999).

The stability of mountain gorilla groups is highly dependent on the relationship of the silverback with his females. The females will stay closer to the silverback than to any other adult within the family group and the proximity of a female to the silverback increases dramatically after parturition (Harcourt and Stewart, 2007; Robbins, 1999; Stewart and Harcourt, 1987). This proximity is thought to aid in infant defence from extra-group males on the periphery of the group (Harcourt and Stewart, 2007).

The relationship of juveniles to the adults, particularly the silverback is also a key factor of mountain gorilla families. During the first two to three years of life, infants are kept close to the mother and not allowed to stray far. Between the ages of three and four infants will undergo weaning and the female begin to come into oestrous again. At this point the young gorillas will begin to build associations with other members of the family group (Stewart and Harcourt, 1987). Although the silverback is rarely seen to initiate contact with juveniles or carry them whilst moving, it is clear that the juveniles will maintain a level of proximity with the silverback. The silverback will often tolerate this, allowing play fights to occur around him and, in some circumstances, the juveniles to rest on top of him (Robbins, 2007). The silverback will also become protective of the juveniles both in the case of threats from outside the group and within the group (Harcourt and Stewart, 2007; Stewart and Harcourt, 1987).

1.1.4 Dispersal and philopatry

In both gorilla species, males and females will disperse from the natal group upon reaching sexual maturity (approx. 8 years) and transfer to new social groupings, unlike the majority of other primates. In addition, a female may undertake secondary transfer (i.e. transfer between groups) at a later stage of her life (Watts, 1996; Stokes, Parnell and Olejniczak, 2003) and several females within the research groups studied have been seen to reproduce in more than one group (Watts, 1996). Females who remain to breed in their natal group usually do so when a sexually mature male other than their father is also present (Robbins, 2007; Watts, 1996).

Although the mountain gorillas are typically classified as having a one-male mating system research undertaken in 1999 with the Virunga mountain gorillas indicates that up to 40% of the social units consist of multi-male groups. In multi-male groups subordinate males have been observed to mate with females and there is male-male competition. It was first thought that subordinate males would only mate with the infertile, nulliparous females, however further research has indicated that subordinates may mate with younger daughters of the dominant silverback and with other fertile females when not in proximity to the dominant silverback (Robbins, 1999; Watts, 1990). More recently paternity analysis of multi-male groups of Virunga mountain gorillas suggests that the second ranked male will sire an average of 15% of the group's offspring (Bradley *et al*, 2005). This finding has led to the suggestion that multi-male groups should be considered as "long-term assemblages of related and unrelated individuals...similar to chimpanzee groups..." (Bradley *et al*, 2005).

Mating harassment can be viewed as a form of male mating competition and varies widely in amount between species. Research in mountain gorillas has indicated that mating harassment occurred in 33% of the matings observed (Robbins, 1999).

Aggression observed in mating harassment reflected the overall pattern of aggression observed; mild aggression with infrequent contact. Investigation into the paternity of offspring groups is needed to determine the reproductive costs and benefits to the males within a multi-male group. However there may be an additional benefit to the dominant silverback in having a related male to cooperate in the defence of females from unrelated infanticidal males (Robbins, 1999).

Male emigration from a natal group is also a common event, although subsequent transfer into a new group is very rare. In situations where the silverback is old or infirm, young males may remain in the natal group as sub dominant silverbacks, ready to takeover when the old male dies. In a few similar situations, young males have transferred into a group with an older silverback male present, however, this is a less common phenomenon as male immigration and the takeover of a mixed-sex group is rare (in the mountain gorilla) (Stewart and Harcourt, 1987).

In the mountain gorilla young males emigrating from their natal groups will often spend time in a solitary situation. In this state they will usually follow an established mixed-sex group, remaining on the periphery. If the opportunity arises, the solitary male may then make a bid for one of the females within the group. Solitary males attract females from established mixed-sex groups through intense male – male competition. This is characterised by visual displays (chest beating, foliage slapping, charge displays) and on occasion by fights with physical contact. The female will generally move to the periphery of her group during the process of transfer, and within a few days remove herself from the current group to the new male.

Not all male gorillas remain solitary when emigrating from the natal group. Several will form a bachelor group in a loose association with other solitary males. These gorillas have formed sometimes long lasting but not intrinsically stable groups on the death of the silverback and the transfer of the females to an unrelated group (Yamagiwa, 1987; Levrero *et al*, 2006)

Bachelor groups – the situation in the wild

The presence of bachelor groups has been documented in many species of mammal (e.g. feral horses (*Equus caballus*), Feh, 2001; elephants (*Loxodonta africana*), Sitati, Walpole, Smith and Leader-Williams, 2003; African buffalo (*Syncerus caffer*), Cross, Lloyd-Smith and Getz, 2005) as well as other primates (Hanuman langurs (*Presbytis entellus*), Rajpurohit, Sommer and Mohnot, 1995; gelada baboons (*Theropithecus gelada*), Mori, 1979; and macaques (*Macaca sp*), Pusey and Packer, 1987). In many species the existence of bachelor groups is part of the 'fission-fusion' nature of their social organisation e.g. adult African buffalo males will often move from mixed sex groups to smaller bachelor groups (Cross, Lloyd-Smith and Getz, 2005). However, in some species bachelor bands may be short lived and have specific motivation e.g. male squirrel monkeys form bachelor 'migration alliances' in order to transfer between troops (Mitchell, 1994).

Although bachelor groups of mountain gorillas had been identified during the 1980's (Harcourt, 1978; Robbins, 2001; Yamagiwa, 1987), bachelor groups of western gorillas were not identified until 2004 (Gatti, Levrero, Ménard and Gautier-Hion, 2004; Levrero *et al*, 2006)

The majority of data from the wild is centred on the mountain gorilla populations from the Virunga volcanoes in Rwanda and Zaire. Census data taken at Karisoke research centre (Virungas) during the 1980's indicated that approximately 10% of the gorilla groups within the conservation area consisted entirely of males.

Whilst no silverback has been seen to join a bachelor group within the mountain gorilla population, blackbacks and sub adults have been seen to join groups without being seriously attacked by the resident males (Harcourt, 1988; Yamagiwa, 1987). Groups have also been seen to be formed from the remains of an established mixed-sex group after the death of the silverback and the transfer of the females to an alternate mixed-sex group. The remaining young males formed the core of a bachelor group with additional solitary males joining at a later date. The oldest observed to immigrate to date has been approx. 10 years of age (Yamagiwa, 1987).

Although bachelor mountain gorilla groups have been reported to exist for years (one for over nine years), (Harcourt, 1988) the groups can be seen to be fluid in composition with membership changing over time. The degree of stability within a bachelor group probably depends on the males' ability to attract females. The arrival of a female in the bachelor group has a significant effect on the behaviour of individuals. The levels of aggression dramatically rise and the subordinate individuals tend to emigrate from the group as they mature (Harcourt, 1988).

Levrero *et al* (2006) have suggested that bachelor western gorilla groups (also termed non-breeding groups) are temporary, unstable structures characterised by many transfers between groups. They documented formation of bachelor groups to include disintegration of breeding groups through death or emigration of females, and the association of males transferring from natal groups. Levrero *et al* (2006) also suggested that bachelor groups represent an alternative strategy for young males leaving natal groups (to gain social experience whilst achieving some protection from potential predators [also Robbins, 2007]), and that aging males may benefit from the presence of maturing youngsters.

1.2 Western gorillas in captivity

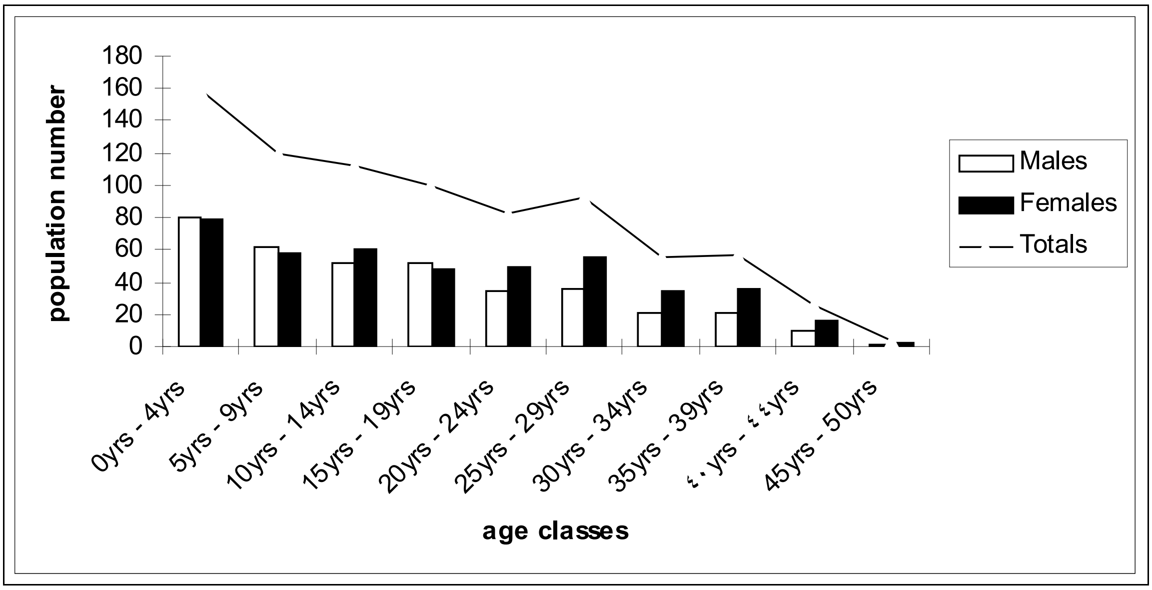
1.2.1 Gorilla populations in captivity

The captive population is generally classified as western lowland (*G. g. g.*) but as yet there has been no genetic analysis to assess to possibility of captive cross breeding between the western lowland and the Cross river subspecies, therefore within this thesis captive gorillas will be referred to as western gorillas (*G. gorilla*).

The western gorilla is one of many species of endangered animals managed in a co-operative breeding programme in institutions worldwide. The breeding programmes run on both a regional basis – the European breeding programme, EEP and the American species survival plan, SSP, and internationally. The captive population of gorillas is stable and expanding with an increasing birth success rate (Fig. 1.1). However the continued success of the programmes relies on the provision of adequate diet, large stimulating enclosures and the establishment of suitable social groupings (McCann and Rothman, 1999). Because of the nature of the gorilla's natural habitat, this is not always possible to achieve within the confines of a zoo.

In recent years the birth rate in captivity has increased and the percentage of hand reared infants has decreased although maternal competence can still be a major problem.

Fig. 1.1 Status of the living captive gorilla population in European and North American zoos (International studbook 2002)



1.2.2 Housing and husbandry techniques

The provision of acceptable environments for apes in captivity is a concept which is continually evolving within the zoo world. In 1974 a bench mark paper was written by Robert Sommer concerning the effects of confinement. The paper coined the phrase "hard" architecture to describe environments that were barren, oppressive or restrictive in any form. These environments often include mesh enclosures with concrete floors and minimal cage furniture. The conclusion that “the animals are degraded by these environments and that the resultant adaptations are rarely in the best interest of either the individual or the society concerned” was established (Sommer, 1974).

Many zoos have been trying to move away from the concept of "hard" environments towards a "soft" outlook. Typically today the move is towards moated enclosures (either dry moats or water moats), removing the mesh from between the animal and the public. This technique, although very successful from the public point of view, can lead to difficulties particularly for primates (mainly arboreal). Many zoos that have opted for the pleasant view of a moated enclosure then find that they have great difficulty in providing the height dimensions necessary for species-specific behaviour. Zoos with "hard" steel mesh cages can provide adequate stimulation for the animals through provision of complex cage furniture, manipulable materials and plenty of space also allowing the housing of a number of social companions. In these cases the initially "hard" external view of the cages is "softened" by the provision of enrichment and social grouping to promote species typical social interactions, comfort and well-being. The "hard" steel mesh also automatically allows the generation of the height dimension that is so important for these animals. The space available for locomotion can be calculated by volume of the enclosure rather than area.

Within the zoo environment the majority of mammalian taxa can benefit from the provision of enrichment or appropriate enclosure furniture. There is evidence that the more "intelligent" animals will exhibit higher levels of "boredom" in captivity and will therefore display a higher need for stimulation in their environment (Maple and Perkins, 1996). Further to this the concepts of "exploration" and "curiosity" can be added. In a now landmark study, the addition of deep woodchip litter into primate enclosures decreased the amount of time spent in fighting and inactivity and increased exploratory behaviours. When foodstuffs were then hidden in the woodchip, further behavioural improvements were seen (Chamove *et al*, 1982).

Research carried out within the North American region assessing environmental influences on the activity levels of captive apes has indicated that enrichment of an impoverished area can increase the activity levels of gorillas. The survey, carried out between 43 groups of gorillas indicated that the factor most highly related to activity in gorilla groups was the presence of other individuals. However this was closely followed by the presence of stationary and temporary objects within the enclosure (Wilson, 1982). This indicates that a successful environment for captive gorillas would consist of an enriched, naturalistic area where enclosure furnishing could be added and removed at intervals to maintain novelty and complexity.

Post occupancy evaluation of zoo environments can play an integral role in ensuring the efficacy of enclosure design for the three user groups: visitors, animals and staff (Stoinski, Hoff and Maple, 2002). Post occupancy evaluations conducted at Atlanta Zoo carried out in 1988, when four groups of gorillas were first introduced to new naturalistic enclosures, and then repeated after ten years examined the relationship of space use patterns and environmental structures as well as the effect of temperature and social factors on space use. It was found that the gorillas spent significantly more time near buildings than expected and that this space use pattern masked preferences for the natural objects (trees and rocks) also in the enclosure. It was also observed that there was a positive relationship between time spent close to the buildings and the temperature. The gorillas spent more time close to the buildings when it was hot and less when it was cold (Stoinski, Hoff and Maple, 2001).

1.2.3 Parent vs hand rearing

Experimental separations of primate mothers from infants have shown that presence of the mother has a critical effect on the normal development of primate infants (reviewed in Weaver and de Waal, 2002), with even ‘mild’ separations causing less play, fewer social partners and less complex socializing (Capitanio and Reite, 1984). Rhesus macaques with a history of social disturbances during ontogeny have great difficulties functioning in groups, exhibiting disturbed social functioning (e.g.

repeated aggression against certain individuals and a lack of grooming partners for others) and, in some cases, stereotyped behaviours (Ljunberg and Westlund, 2000).

Although hand rearing appears to have no effect on the reproductive success of zoo-born male gorillas (Ryan, Thompson, Roth and Gold, 2002), in an assessment of the behaviour of bachelor groups in the U.S., two groups comprising of only hand-reared animals exhibited almost a complete lack of affiliative behaviours (Stoinski *et al*, 2004b). As yet there is no data on whether this lack of affiliative behaviours is a source of stress for the individuals or will compromise their social competence when integrated to another group. However it is known that both captive all-male groups with mother-reared animals present (Stoinski, Kuhar, Lukas and Maple, 2004a, 2004b) and wild mountain gorilla bachelor groups (Yamagiwa, 1987; Robbins, 1996) do exhibit affiliative interactions, suggesting that captive all-male groups comprising of only hand-reared animals may not encourage affiliative behaviours.

There is literature focusing on the importance of peer orientated behaviours in the social development of primates (de Waal and Johanowicz, 1993; Pereira and Fairbanks, 1993; Roney and Maestriperi, 2003). Ljunberg and Westlund (2000) have suggested that early socialization with peers has important consequences for the development of more typical socialization patterns (social grooming, aggression and activity levels) in primates with early social disturbances. McCann and Rothman (1999) observed that when introducing a number of hand-reared infants to a captive group of western lowland gorillas, the infants associated more strongly with other infants, particularly when related. This has led to the recommendation to establish a peer group when introducing hand reared infants to established groups and could be equally applicable to bachelor or breeder groups.

1.2.3 Bachelor groups in captivity

The establishment of bachelor groups in captivity has been begun in response to concerns over the numbers of males born in the captive breeding program. Traditionally, gorillas are housed in single adult male: multi-female groups and sub-adult males are moved before reaching adulthood and becoming a threat to the silverback male. Whereas the integration of young females to established groups is frequently successful, there are few cases of sexually mature males co-existing with unrelated males of similar ages. This has limited the moves between zoos to straight male-male swaps, the formation of new groups and replacement of males that have died.

During the annual meeting of the Anthropoid Ape Advisory Panel in 1988, the subject of establishing bachelor groups was discussed. Collections interested in establishing groups of gorillas were asked to consider the possibility of providing facilities suitable for bachelor groups of gorillas (Johnstone-Scott, 1988).

The establishment of bachelor groups was considered to be a way of achieving long term benefits for the captive breeding population:

1. Reducing stress related problems caused by the presence of mature males in addition to the silverback
2. Minimising the risk of inbreeding.
3. Prevention of the de-socialization of males which would otherwise be kept alone
4. Provide a social environment for animals that were already in isolated situations.

The presence of bachelor groups would also provide an opportunity for research into a very different aspect of gorilla society, and the potential for comparisons of evolutionary and facultative explanations for variation in behaviour.

The establishment of bachelor groups in the wild is thought to usually consist of animals at sexual maturity, and so establishment of bachelor groups in captivity was considered to be most feasible with gorillas of a similar age group. As males between 6 and 9 years are generally considered to be the most adaptable to change, this age group has been considered to be the optimum. However, the introduction of at least one fully mature male has been suggested to be a benefit to the grouping. Suggestions that the establishment of a sub-adult group and then the introduction of a mature male were made to offset any advantage of age and weight over the youngsters the adult may have.

The benefit of collections new to the breeding program housing bachelor groups of gorillas was the establishment of new facilities designed to cope with a different aspect of gorilla society. The design of the enclosure must accommodate the need of the individual characters. A number of strategically placed shut-offs are advisable to allow the ability for separation and isolation if necessary, in addition with doors on a ratchet slide mechanism, shut-offs can be maintained so that sub-adults and blackbacks can use them, whilst silverbacks are prevented from access. The design of the enclosure must also include the provision of “run-arounds” i.e. ensuring that an animal that may be being chased will not be trapped in a dead end section of the enclosure. As the gorillas will also “play-chase” this design provision can also increase very simply the complexity of the enclosure and allow increased play behaviour to be exhibited.

Over the last few years a number of bachelor groups have been formed both in Europe and the United States in an attempt to address the problem of excess numbers of males.

1.3 Social Interactions

1.3.1 Social systems and social conflict

Individuals living within a group can derive certain benefits from the presence of others within the group (Janson, 1992). These benefits can be very wide ranging (e.g. female and infant defence, Robbins 1995; Watts, 1996). However, social living also increases the risk of a conflict of interest and competition between group members (Bernstein, 2007; Walters and Seyfarth, 1987) which may lead to aggression.

Our view of social conflict has been altered and enhanced by the body of research conducted on primate societies (e.g. Aureli and de Waal, 2000; Bernstein, 2007; Mallavarapu, Stoinski, Bloomsmith and Maple, 2006; Watts, 1995a; Watts, 1995b). It can now be viewed as a normal and recurring feature of social life, which varies greatly in form but always has a consequence for the participants and the other members of the social group (e.g. Aureli, Cords and van Schaik, 2002; Aureli and de Waal, 2000; Bernstein, 2007; de Waal and Yosihara, 1983). Social conflict can impact on reproductive fitness and physical well-being but can also impact on the selection of travel routes, whether to lead or follow as well as selection of feeding or sleeping areas (Mason, 1993). It has also been suggested that social conflict can lead to the evolution of rituals and rules of social conduct (such as ritualised greetings) and influence social bonds (Colmenares, Hofer and East, 2000).

Conflict, competition and aggression can be defined as separate issues within a social situation (Bernstein, 2007; Mason, 1993). A conflict of interest can arise in situations where two individuals may want to engage in differing activities (e.g. one individual may want to play fight, the other doesn't) or in competition over limited resources. A conflict of interest implies a clash or incompatibility between factions within the group. It inherently identifies at least two individuals with differing needs.

In the example of primate group life, a conflict of interest is most often manifest as an interruption in the ordered flow of social events in the group life (Mason 1993). This may lead to a range of potential behavioural responses to gain conflict resolution (de Waal, 1996; de Waal, 2000).

1.3.2 Aggression

Traditionally aggression has been viewed as a negative social behaviour leading to deconstruction of social bonds (de Waal, 2000; Popp and DeVore, 1979). Indications that losers of aggressive conflicts tend to avoid winners, and that distance between individuals is maintained by hostile reactions to incursion of space lead to the assumption that there is a dispersive impact of aggression. This led to the establishment of the dispersal hypothesis (Lorenz, 1963), where aggression works as a spacing mechanism. In this scenario aggressive behaviour causes the loser to avoid the winner and predicts a decreased probability of contact and an increase in distance between the individuals involved. This would obviously have a negative effect on the cohesion of a social grouping, imposing distances upon individuals, and may jeopardize the benefits of group living (Janson, 1992). The need to clarify potential conflicts of interest and indicate relative positions within the social hierarchy leads to necessary communication of differences between individuals and so aggression can be viewed as a means of negotiation between individuals (Aureli and de Waal, 2000). However, behavioural mechanisms that may mitigate damage caused by aggressive conflict resolution (termed reconciliation and consolation) may be strongly selected for in group living animals (Arnold and Aureli, 2007; Aureli and de Waal, 2000; Das, Penke and van Hooff, 1997).

However, preventing the disturbance of a social relationship can be achieved more effectively if aggressive interactions do not occur. A conflict of interest can be managed by alternative methods such as tolerance or avoidance. These behaviours are often subtle and difficult to observe but may involve grooming to ease tempers, or simply walking away from a situation (de Waal and Aureli, 2000). Tolerance behaviours can often be identified in situations of crowding, where coping strategies to deal with the potential for increased aggression have been exhibited (Judge, 2006; see behavioural flexibility below)

Aggression in wild bachelor groups

Although in recent years there has been research published on western gorilla bachelor groups (Levrero *et al*, 2006) there is still little information on social interactions within these groups, so again most of our information comes from mountain gorilla bachelor groups. Harcourt (1988) found most aggression within the bachelor mountain gorilla groups was in the form of cough-grunts and chest-beat displays, however some physical fighting was observed and wounding did occur. The levels of aggression were not higher than in mixed-sex groups, and were lower than that seen in competition between strange males when approaching a family group (Harcourt, 1988). However, the aggression exhibited did correlate with the dominance hierarchy within the group (i.e. the silverbacks exhibited more aggression than the black backs, and the black backs exhibited more than the sub adults) although aggression was rarely observed in similarly aged individuals except between black backs (Yamagiwa, 1987).

In addition, the Virunga mountain groups exhibited intervention by a third party, particularly on behalf of sub dominant animals, in more than 50% of contests. Even silverbacks would be threatened by sub adults in this fashion (Harcourt, 1988) involving cough-grunt vocalisations, chest-beat charges and some physical contact (Yamagiwa, 1987).

Aggression in captive gorilla bachelor groups

Preliminary comparisons have been carried out between bachelor groups of gorillas established in the United States (Stoinski, Hoff, Lukas and Maple, 2001). This research has suggested that there were no significant differences in agonistic behaviours in the two groups studied, but that agonistic / aggressive behaviours were at a lower level than affiliative behaviours.

1.3.3 Affiliation

The evaluation of affiliative behaviours has underpinned a large proportion of the research into the social complexity of many social species, particularly non –human primates (Roney and Maestripieri, 2003). Affiliative behaviours are often termed 'positive interactions' and within the primates can include grooming, social resting and play fighting.

Social rank and dominance hierarchies can be seen to affect the distribution of affiliative behaviour within a group. High ranking individuals generally initiate affiliative interactions (particularly grooming) at a far lower rate and receive affiliative interactions at an increased rate in comparison to lower ranking individuals (de Waal and Luttrell, 1985; Mehlman and Chapais, 1988; Silk, 1982, 1992).

The distribution of affiliative interactions within a primate group can also be strongly influenced by the reproductive status of the females within that group (Mehlman and Chapais, 1988). Seasonal breeders will become the focus of increased grooming behaviour from males (i.e. will receive higher levels of grooming) in the breeder season. Even in non-seasonal breeders the oestrous cycle and the formation of consortships can lead to higher levels of grooming behaviour. In this situation it has been suggested that increased grooming behaviour reduces the risk of aggression, allows the increased proximity necessary for mating to occur and can temporarily impact on social status within groups (Mehlman and Chapais, 1988). This has been observed in hamadryas baboon harems where females in oestrous both give higher levels of grooming directed towards the alpha male and receive higher levels from the male, and have been observed to 'leapfrog' positions within the female hierarchy (Kummer, 1995).

It seems likely that the benefit received by the initiator of an affiliative interaction is social tolerance, so that a low ranking animal initiating an affiliative interaction with a higher ranking animal is able to maintain proximity and thereby some level of protection or sharing of resources (Roney and Maestripieri, 2003). However there is a lack of easily interpretable data on a causal relationship between affiliative behaviours and agonistic support, partly because these interactions often occur at a low rate and can be separated by long time intervals. Tolerance may not be the only benefit to establishing an affiliative relationship. Within mountain gorilla groups it appears that male infants who establish a strong bond with the silverback and maintain that through adolescence are more likely to inherit leadership of the group whereas those male infants who do not establish such as strong bond are more likely to emigrate from the group (Harcourt, 1981).

It has been suggested that social development is strongly affected by the experiences within a peer group. Therefore the acquisition and development of affiliative behaviours can be paramount to an individual's development. Research has indicated that individuals that are deprived from social interaction with peer groups may exhibit reduced social competence in adult life (Pereira and Fairbanks, 1993; Roney and Maestriperi, 2003; de Waal and Johanowicz, 1993)

Affiliative behaviour in wild bachelor groups

Affiliative behaviours within bachelor groups often consist of grooming and play. Observations of the bachelor groups in the Virungas have indicated that affiliative behaviours can be observed at a higher level than in mixed-sex groups. On average a bachelor male was within 5m of at least one other male for 60% of the day, although within 5m of two males for less than 10% of the time. In addition, although the total amount of grooming was low, 92% was of subordinates by dominants (Harcourt, 1988).

The silverbacks within the bachelor groups were not seen to initiate play episodes, but did participate in play initiated by the younger individuals. In particular the sub adults would initiate play and, although the black backs would intrude upon these sessions, the silverbacks were not observed to do so (Yamagiwa, 1987).

Affiliative behaviours in captive bachelor gorilla groups

Comparisons of levels of affiliative behaviours between captive bachelor groups housed in U.S. zoos readily compared to observed patterns in bachelor Virunga mountain gorilla groups. (Stoinski, Hoff, Lukas and Maple, 2001; Stoinski, Kuhar, Lukas and Maple, 2004a). The proximity data showed that the percentage of time spent in contact or at distances within 1m of other individuals was greater in the captive bachelor groups than in captive breeding groups either between male – male or male – female dyads. This again was found to be similar when compared to results from wild bachelor and breeding groups (Stoinski, Hoff, Lukas and Maple, 2001). The young animals in the captive groups were also seen to spend more time in close association with each other rather than with the silverback and were thought to be primarily responsible for the cohesion within the group (Stoinski, Hoff, Lukas and Maple, 2001; Stoinski, Kuhar, Lukas and Maple, 2004a).

This preliminary work suggests that bachelor groups can be used successfully at some periods during a gorilla's life span, however further longitudinal research is needed (Stoinski, Kuhar, Lukas and Maple, 2004a).

Homosexual behaviours in wild bachelor groups

The majority of non-agonistic interactions observed during the Karisoke based research involved homosexual behaviour (Yamagiwa, 1987). More than half the approaches to the silverbacks made by the lower age classes were carried out in a homosexual context, some of which resulted in mounting with pelvic thrusts as seen in copulation in mixed-sex groups (Yamagiwa, 1987). Silverbacks were not seen to be mounted by the lower age classes although, on occasion, the sub adults were seen to mount the blackbacks (Robbins, 1999). Mounting would either be initiated by the mounter's intensive approach with copulatory pants or by the mountee with soliciting approach behaviour (Yamagiwa, 1987).

In many primate social systems male – male mounting behaviour has been seen in the context of dominance rank and high social tension or stress, or as submissive behaviour on the part of the mountee and reassurance behaviour on the part of the mounter (Goodall, 1986). The observations of male – male mounting in the bachelor groups of Virunga mountain gorillas did not occur in situations of high stress or social tension, suggesting that its function is not to decrease stress (Yamagiwa, 1987). Yamagiwa (1987) also suggested that the high cohesiveness of the bachelor group he studied was due in part to the frequent homosexual interactions, although the reduced inter-individual distance resulted in frequent aggression between the silverbacks within the group. This suggests that male gorillas in bachelor groups increased their sexual activities and copulated in a homosexual context. As such, this aspect of gorilla bachelor group activities clearly differs from other primate species (Robbins, 1999).

Homosexual behaviour in captive gorilla groups

Despite observations from the wild of frequent homosexual behaviour between silverbacks and sub-adults, preliminary observations of two bachelor groups in captivity showed a lower rate of sexual activity generally and none observed between the silverback and sub-adult. This deviation from the patterns observed in the wild was thought to be due to the rearing history of the silverback, a hand reared individual (Stoinski, Hoff, Lukas and Maple, 2001).

1.3.4 Behavioural Flexibility

Behavioural flexibility is described as reversible, within-individual alternative behavioural phenotypes in response to external stimuli (Jones, 2005). Behavioural flexibility is assumed to be functionally adaptive, with numerous factors influencing an individual's decisions to behave in one way or another. Behavioural flexibility can be seen as a 'toolbox' of potential responses. The response selected is thought to be dependent on a range of variables including a function of its fitness value (Jones, 2005).

Behavioural flexibility has been suggested in the fluctuations of thresholds for female dispersal in response to environmental resources in Japanese macaques (*Macaca fuscata*) and mantled howler monkeys (*Alouatta palliata*), conflict management strategies in macaques, social cognition in capuchins (*Cebus apella*), display in mantled howler monkeys (*A. palliata*) (Jones, 2005).

Research on behavioural responses to conditions of crowding grew from the classic experiments on crowding in rats (Calhoun, 1962; reviewed in Judge, 2000) resulting in high aggression, among other effects. Research on the effect of crowding in primates has revealed a far more complex picture. There is documentation of primates changing a number of behavioural responses in crowded conditions; rates of aggression, affiliative behaviours and submissive behaviours can either increase or decrease (Judge, 2006). Varying behavioural mechanisms have been suggested to enable animals to cope with the potential for increased aggression within crowded situations; increased grooming and submission with no increase in heavy aggression in chimpanzees (*Pan troglodytes*) ('tension-reduction' strategy, Nieuwenhuijsen and de Waal, 1982), increased submissive displays and social huddling with increased mild but not heavy aggression in rhesus macaques (*Macaca mulatta*) ('conflict avoidance' strategy, Judge and de Waal, 1993), decreased aggression, submission and grooming in short term crowding in chimpanzees ('inhibition' strategy, Aureli and de Waal, 1997). In periods where crowding can be seen as short term animals may not have the time to develop more active strategies and may need to increase avoidance behaviours and inhibit interactions (Judge, 2006). The modification of behaviour patterns in either long-term or short-term situations of crowding can be seen as examples of behavioural flexibility in response to the social environment.

An interaction of the social environment and environmental resources can also encourage behavioural flexibility. The diversity of social groupings for western gorillas from multi-male units with seasonal fission (Olejniczak, 1996) to one-male units (Tutin, 1996; Magliocca, Querouil and Gautier-Hion, 1999) and bachelor groups (Levrero *et al*, 2006), demonstrates the flexibility of western gorilla social dynamics. These groups are also flexible in their level of cohesion and social behaviours when surrounding environmental conditions allow, e.g. groups become dispersed and intermingle peacefully whilst feeding in swampy 'bais' (Bradley *et al*, 2004). The large variety of environments inhabited by western gorillas may have favoured selection for social and behavioural flexibility (Weiche, 2006).

1.4 Aims of the research

It is reasonable to expect that a modern institution (such as those selected for research here), with good enclosure design and well developed husbandry and enrichment programmes which allow for the expression of natural behaviours, will provide an interesting and appropriate situation in which to carry out research.

Although there have been suggestions that behavioural phenomena documented in captivity may be an artefact of the environment (Sommer, Denham and Little, 2002), more recent publications have argued that research in captivity can be equally justified in the identification of behavioural phenomena (Aureli, Cords and van Schaik, 2002; Colmenares, 2006).

The establishment of bachelor gorilla groups and the continued success of the captive breeding population in zoological institutions provide the opportunity to carry out research on social interactions between males in two differing circumstances, the presence and the absence of a resource (females). In addition, there is a lack of knowledge of social interactions between males in bachelor groups in western gorillas. Assessment of social interactions of males in captivity can provide information on gorilla behaviour which has proved difficult to obtain in the wild.

This thesis has the following aims:

- To demonstrate that multi-institutional research can be used within zoo research enabling the identification of known behavioural phenomena (chapter 3).
- To examine the social spacing of the males, levels of association and hierarchies within breeder and bachelor groups. The presence of females within the breeder

group can be viewed as a resource that may create a need for control. Therefore the presence of females in the group may influence the social spacing and dominance hierarchies of the males (chapter 4).

- To examine the levels of aggressive and affiliative behaviours within breeder and bachelor groups. The presence of females can be viewed as a resource where the benefits of maintaining access outweigh the potential costs (injury, damage to social bonds) of aggressive behaviour (chapter 5).
- To examine longitudinal data from Paignton Zoo for indications of behavioural flexibility dependant on the composition of the social environment (chapter 6).

Chapter 2: Methods

2.1 Group descriptions and individuals

2.1.1 Sampling considerations

With continuing improvements in captive care, naturalistic enclosures and social groupings, zoos can be seen as a middle ground for research between highly controllable but unnatural laboratory conditions and the difficulty of working with animals in the field (Plowman, 2006). Although zoo-based research can give access to a range of animals not usually available, and in conditions that can be manipulated to some extent, there are often difficulties. The majority of individual zoos do not hold large enough collections to ensure a sufficient sample size. The desire to rectify small sample sizes and the lack of independence of data from animals in a single enclosure can lead the researcher to potential methodological dilemmas such as pseudoreplication (Hurlbert, 1984, Kuhar, 2006).

Pseudoreplication

Pseudoreplication has been defined as “the use of inferential statistics to test for treatment effects with data from experiments where either treatments are not replicated (though samples may be) or replicates are not statistically independent” (Hurlbert, 1984), and would include situations where an individual contributes multiple measurements to an analysis which does not employ repeated measures statistics (Kuhar, 2006). In order to increase sample size without risking this ‘simple pseudoreplication’ (Hurlbert, 1984), multi-institutional research can be implemented.

In order to achieve an acceptable sample size, without incurring pseudoreplication, six bachelor groups were selected, each holding a minimum of four animals. Due to difficulties encountered during the introduction of a subadult to one of the groups, data were only collected at five bachelor groups. In addition, research was carried out in six groups of gorillas established as breeder groups, where each contained one or more young males in addition to the silverback (see Tables 2.1 and 2.2 below). Care was taken to select groups with enclosure and husbandry practices as similar as possible (enclosure photographs are included in Appendix I).

2.1.2 Bachelor groups

The establishment of bachelor groups in captivity is a management response to concerns over the numbers of males born in the captive breeding programme (Johnstone-Scott, 1988). At this time there was very little information from the wild on the formation of bachelor groups. Research from the Virunga mountain gorilla population provided two examples of the establishment of bachelor groups, the death of a silverback male and subsequent emigration of the females, and the fission of a breeder group (Yamagiwa, 1987).

In captivity, the establishment of bachelor groups is thought to be more easily achieved with younger animals. As males between 6 and 9 years are generally considered to be the most adaptable to change, this age group is considered the optimum for group formation, with the subsequent introduction of a fully mature male (Bemment and Pullen, 2006; Johnstone-Scott, 1988). There is a tendency for captive bachelor groups to consist of animals that are not related and have had no interactions with each other before being placed within the bachelor group.

Levrero *et al* (2006) detailed the histories of 14 non-breeding groups (including bachelor groups) in Lokoué clearing, Republic of Congo. Within these groups 33 different compositions of non-breeding group were observed. This research indicated that immatures migrated among non-breeding groups regardless of relatedness, but some immatures do associate with related silverbacks (Levrero, 2006).

Table 2.1 Bachelor gorillas observed during this research

Institution	Name	Social status (at time of research)	Age months (at time of research)	Stbk No	Mean kinship*[3] (with grp)	Rearing	Sire	Dam
Paignton	Pertinax	Silverback	247	792	0	hand	unk	477
	Mambie	Blackback *[1]	179	1162	0	hand	497	635
	Richard	Blackback	132	1169	0	parent	337	804
	Asato	Blackback	133	1166	0	parent	111	90
	Awali	Sub-adult	116	1279	0	hand	185	972
	Mapema	Sub-adult *[2]	96	1405	0	parent	855	1073
	Damisi	Sub-adult *[2]	84	1428	0	parent	337	804
Boissiere du Doré	Mambie	Silverback *[1]	179	1162	0	hand	497	635
	Atanga	Blackback	132	1348	0	hand	842	723
	Vimoto	Blackback	131	1357	0	parent	654	662
	Yeboah	Sub-adult	109	1429	0	parent	839	520
	Kambuka	Sub-adult	105	1447	0	hand	857	961
Port Lympne	Bonz	Silverback	205	1071	0.125	hand	458	683
	Boumi	Silverback	197	1082	0.125	hand	458	371
	Ambam	Silverback	187	1127	0.125	hand	458	367
	Djimu	Blackback	155	1246	0.063	parent	577	779
	Kush	Blackback	156	1244	0.063	parent	577	386
Disney	Gus	Silverback	296	771	0.167	hand	216	217
	Kejana	Silverback	179	1185	0.167	parent	771	791
	Zawadi	Silverback	176	1190	0.083	hand	749	660
	Spike	Blackback	152	1305	0.083	hand	599	660
Loro Parque	Schorsch	Silverback	380	435	0	unk	253	178
	Noel	Silverback	203	942	0	hand	183	565
	Mayaabu	Blackback	184	1063	0	parent	255	241
	Pole Pole	Blackback	167	1106	0.125	hand	654	724
	Rafiki	Sub-adult	150	1177	0.125	hand	654	724

*[1] Mambie started at Paignton and then went to Boissiere du Doré. Data point from Paignton with Mambie excluded from cross-zoo comparisons but used in longitudinal analysis in chapter 6.

*[2] Damisi and Mapema both arrived at Paignton after initial observations. Data only used for longitudinal analysis in chapter 6.

*[3] Calculation of Mean Kinship is described on page 62.

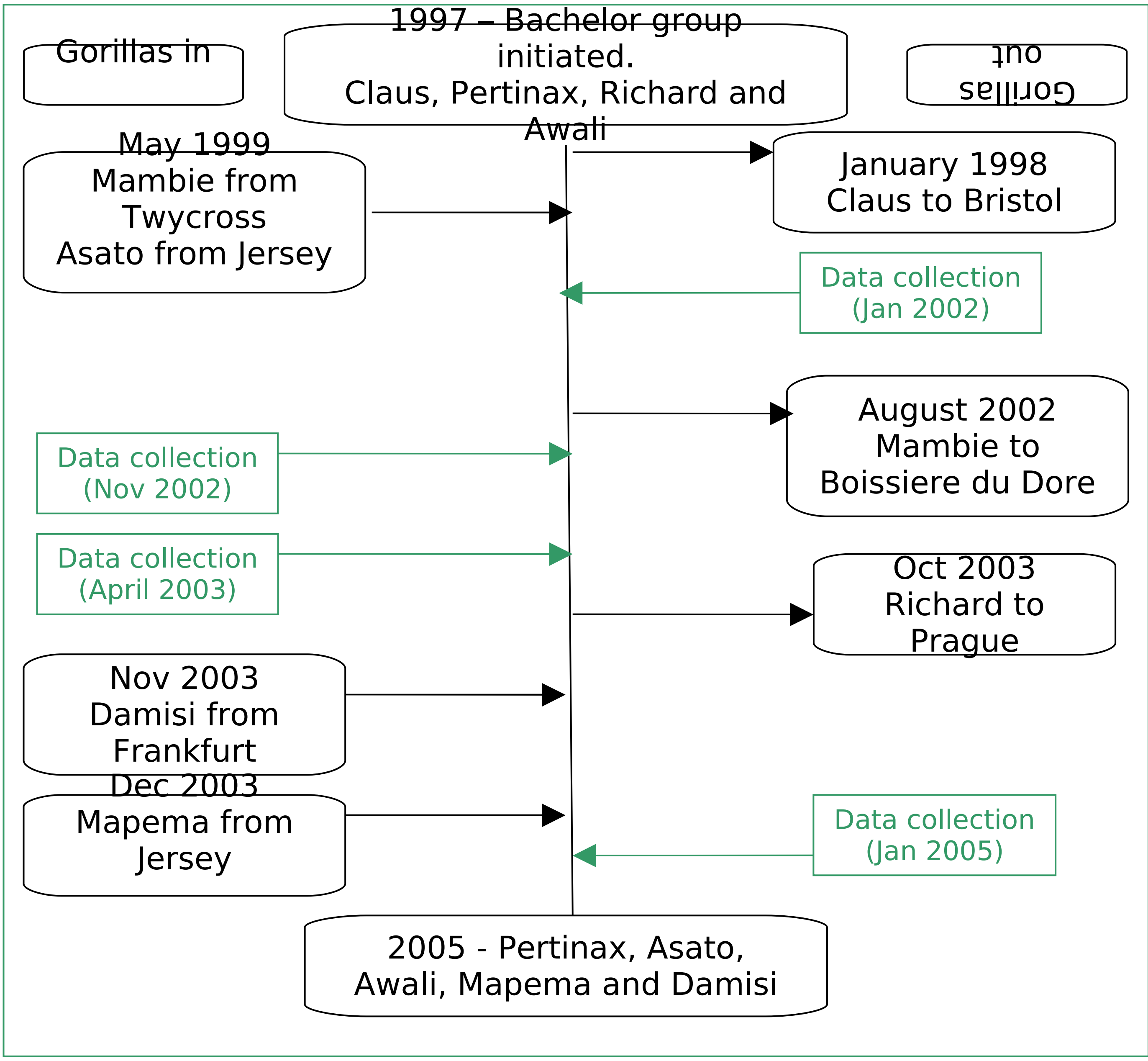
Paignton Zoo Environmental Park (U.K.):

Paignton Zoo's bachelor group was initially established in 1997 with two silverback gorillas (Claus and Pertinax, both aged 16) from Cologne Zoo in Germany. In addition two younger males (Richard, 7 yrs, from Frankfurt Zoo; Awali, 5 yrs, from Wuppertal Zoo) were brought over to form a core group. Despite Pertinax and Claus previously having been housed together at Cologne Zoo, the different situation here at Paignton triggered off a chain of events. Whilst at Cologne, both Claus and Pertinax had been part of a successful breeding group led by an older silverback who had maintained dominance, intervening to prevent any conflict between the two young males. Once housed at Paignton, conflict between the two young silverbacks escalated as they struggled for dominance. The tension between the two silverbacks led to the decision to separate them permanently. Claus was then moved to Bristol Zoo in January 1998 to become part of a breeding group there.

Claus' move from Paignton allowed the introduction of the two younger males to Pertinax to begin. Within a few months the three individuals were spending 24hrs together, with a separation of approximately half an hour in the afternoon for a feed. This social situation continued until two further males were introduced during the year 2000. Both Mambie (from Twycross Zoo) and Asato (from Jersey) were integrated to the group through preliminary introductions to Richard and Awali before being introduced to the silverback Pertinax. Asato had come from a stable group reared situation in Jersey Zoo and settled into the bachelor group with relative ease. However, Mambie had been hand reared at Twycross Zoo and had had little experience of socializing with other gorillas. His introduction to the group was a slower, more demanding, experience both for the keepers and the individual gorillas.

The bachelor group at Paignton has remained flexible, responding to the needs of the EEP, leading to two of the original study group being sent to alternative situations and the introduction of two younger males to the group (Fig. 2.1).

Fig.2.1 Individual gorilla moves in and out of Paignton Zoo and data collection periods



The alteration in the structure of the gorilla group provided the opportunity to extend the research beyond bachelor and breeder group comparisons. Longitudinal research into the group housed at Paignton was carried out, focusing on the progressive hierarchy and social patterns within the group as individuals were removed or added to the group, and individuals remaining in the group aged.

Boissiere du Doré, (France):

The group at Boissiere du Doré was established in 2002 with five unrelated animals, one silverback, two blackbacks and two sub-adults. Out of the five group members only two (one blackback and one sub-adult) had been parent reared. The silverback, Mambie, had previously been a part of the group at Paignton Zoo before being transferred by the EEP to take on a silverback role. Although the group was initiated in 2002, there were a few difficulties in the establishment and this group was still somewhat unsettled when observed in 2006. During 2004 a young hand-reared male had been introduced to bring the numbers up to six animals. Unfortunately, potentially due to the lack of social skills of both the new youngster and the silverback (Mambie), the introduction was unsuccessful and the young male was returned to his natal zoo.

Loro Parque (Tenerife, Spain):

The group at Loro Parque was established in 1992, again to house surplus males from the EEP. As with Paignton, there were some initial changes to group structure. However by the time of my research visit in 2004, the group was established with five individuals (two silverbacks, two blackbacks and one sub-adult). Of these animals only one (the blackback Mayaabu) was parent reared. The two youngest were full siblings. The oldest male, Schorsch, was listed as rearing unknown.

Port Lympne (U.K.):

Port Lympne is part of the privately owned Howletts and Port Lympne Foundation and, between its two zoos, holds the largest number of captive gorillas worldwide (currently listed at over 70 animals). Both zoos have a number of productive breeding families, and surplus males from these were used to form a bachelor group. This was established at Port Lympne in 1995, and at the time of observation in 2006 consisted of five animals. Three were paternal half-siblings (Bonz, Boumi and Ambam) and the other two were paternal half-siblings from another male (Kush and Djimu). There were no dams in common between them. The two half-siblings (Kush and Djimu) were parent reared whereas the other three were all hand reared. At the time of observation the group consisted of three silverbacks and two blackbacks.

Disney (U.S.):

Disney's Animal Kingdom was one of the newest zoos included in this multi-institutional research. The bachelor group housed there was established in 1997 with five animals. After some initial changes the group has been stable since 2001 with four animals, one father / son dyad and two maternal half-siblings. At the time of research in 2006 the group consisted of three silverbacks and one blackback. Only one of the individuals (the son of the father / son dyad) was parent reared.

2.1.3 Breeder groups

Six breeder groups containing a silverback and at least one other male of sub-adult or older age were selected (Table 2.2).

Table 2.2 Males in breeder groups observed during this research (female and juvenile members of these groups are listed in Appendix II; Calculation of mean kinship is described on pg 62)

Institution	Name	Social status (at time of research)	Age months (at time of research)	Stbk No	Mean kinship (with grp)	Rearing	Sire	Dam
Belfast	Boulas	Silverback	189	921	0	parent	458	371
	Kukume	Blackback	149	1089	0	hand	652	760
	Gugas	Sub-adult	84	1397	0	hand	wild	wild
Apenheul	Bongo	Silverback	360	562	0.333	parent	wild	wild
	Uzuri	Blackback	107	1317	0.25	parent	562	595
	M'bewe	Sub-adult	65	1435	0.217	parent	562	575
	Kidogo	Sub-adult	62	1465	0.25	parent	562	595
Calgary	Kakinga	Silverback	306	682	0.25	parent	111	128
	Nsabi	Blackback	107	1366	0.219	parent	682	885
	Jawara	Sub-adult	76	1483	0.25	parent	682	548
Columbus	Macombo	Silverback	249	836	0	parent	342	226
	Nkozi	Blackback	154	1195	0.042	hand	509	432
	Jumoke	Sub-adult	78	1496	0.042	hand	573	1049
Columbus	Mumbah	Silverback	468	379	0	parent	wild	wild
	Jontu	Sub-adult	91	1455	0.167	parent	891	1119
Disney	Gino	Silverback	304	749	0.3	hand	566	530
	Hasani	Blackback	138	1332	0.35	parent	749	413
	Jabari	Sub-adult	103	1645	0.3	parent	749	828

Belfast (U.K.):

The breeding group at Belfast had recently undergone the introduction of two new animals to the group. The young male (Gugas) had been introduced to the existing group of females in order to provide some socialisation experience. Gugas had been wild caught and later confiscated from a circus. Despite being introduced to a captive group of hand-reared gorillas at the Stuttgart Zoo ape nursery, he was still exhibiting deep-seated stereotypic rocking when separated from the rest of the group (a stressful situation) and appeared to have some difficulty in socialising effectively with all the group members (particularly the silverback). Towards the end of 2001 Boulas (the silverback) was introduced to the Belfast group after the death of the previous breeding male. Boulas had good group experience from his natal group but had spent a period of time housed in a bachelor group before being moved to Belfast. Despite the occurrence of matings between Boulas and the females within the group there was no sign of any pregnancy at the time of the research in 2002. The additional male within the group was the blackback (Kukume). Kukume had been born at Apenheul (The Netherlands) and removed for hand-rearing at an early age. Whilst being hand-reared the decision had been made to castrate Kukume and monitor his re-introduction to a family group. Kukume is descended from a genetically well-represented bloodline, so his loss of breeding potential was not a concern. There has been some speculation that castration may be another option for dealing with the number of surplus males in the breeding programme. However without ‘test cases’ no further decision on this is possible. Kukume has integrated well into the family group at Belfast and appears to play a role in the social interactions of the group. The three males within the Belfast group are unrelated, and only one of them is parent reared.

Apenheul (The Netherlands):

The Apenheul group has been long established around a core of wild caught animals in the 1970’s and has been one of the most successful captive breeding groups to date. It has also been one of the largest captive family groups, reaching nineteen individuals at its largest point. During the time of the research the group consisted of sixteen animals – one silverback, one blackback, two sub-adult males, six adult females, five juveniles and one infant. Four of the males (the silverback, the blackback and the two sub-adults) were included in the research. All of these were parent reared animals and the three younger animals were off-spring of the silverback (paternal siblings) and two are full siblings.

Calgary (Canada):

Calgary's breeding group has been prolific in the past, but with three of the four females becoming older, a younger female had recently been introduced to stimulate further breeding success. However with nine animals in the group in total there was still a good age structure for the research purposes. The group contained a silverback, one blackback and one sub-adult male, with the two younger animals both being offspring of the silverback from different females. All three males were parent reared.

Columbus / Mac's group (U.S.):

The group at Columbus, Ohio formed around the young silverback Macombo had yet to experience breeding within the group. However, young animals had been introduced to the group through Columbus Zoo's surrogacy programme. Infant animals that have needed to be hand-reared have been introduced to the group through certain females in order to give them an opportunity to learn group experience. Mac's group contained seven individuals, including a silverback, a blackback and a sub-adult male. There was no direct relationship between these three males and only the silverback had been parent reared.

Columbus / Mumbah's group (U.S.):

Only two males of an age to be included with the research were present in Mumbah's group (the silverback and the sub-adult male). Despite having a number of females within the group no breeding had occurred with Mumbah, and the younger males in the group (the sub-adult and a juvenile male) had both been introduced rather than being the offspring of the adult male. Both the silverback and the sub-adult had been parent reared.

Disney (U.S.):

The breeding gorilla group at Disney's Animal Kingdom had been established at Chicago Zoo before the park had been built. The group was moved to Disney as a silverback, two adult females and a young male in 1997. Since then two animals have been born into the group (a young male and a young female). At the time of study the group contained three males of appropriate age, the silverback, the blackback and the sub-adult. Both the blackback and the sub-adult were offspring of the silverback and were group reared, although the silverback himself was hand reared.

2.2 Enclosure Use and Husbandry

Although multi-institutional research increases sample size, it can lead to additional challenges. Potential confounds through differences between the institutions in enclosure design and husbandry techniques may have been introduced (Melfi, Marples and Ruxton, 2006). In order to try to minimize these issues data were collected at each institution to allow comparison of both general activity patterns and enclosure use. The inclusion of enclosure use in this way allows comment on the provision of necessary enclosure resources as well as suitability of the enclosure environment for the gorillas.

It is very rare in a zoo situation to have animals using all areas of an enclosure equally as most animals will exhibit preferences for various features within a complex and stimulating enclosure. Ogden, Lindburg and Maple (1993) tested six gorilla exhibits in three institutions and found that the 23 gorillas showed a preference for flat versus sloped terrain, areas close to the holding / indoor facility and appeared to prefer close proximity to trees and rocks. Wilson (1982) researched the environmental factors influencing activity in gorillas and orangutans (*Pongo pygmaeus*) in 41 European Zoos. The results suggested that movable objects (or complexity) within the enclosure may be more important than the size of the enclosure for captive apes. Stoinski, Hoff and Maple (2001) also found that complexity of enclosure was of greater importance than quantity of space when investigating habitat use and structural preferences of the captive gorillas at Zoo Atlanta. The gorillas spent 50% of their time in <15% of the exhibits. However, if good enclosure resources have been provided, the animals will be encouraged to use all areas of the enclosure at appropriate times and rates.

2.2.1 Spread of participation index

The use of a spread of participation index (SPI) to assess an animal's enclosure use has been increasing in zoo research. This technique requires the researcher to divide the enclosure into equal-sized measurable zones and observe the frequency of zone use by the animal. The index gives a single figure, between 0 and 1 (0 indicates all areas of the enclosure used equally; 1 indicates a strong bias to just one area of the enclosure), to grade the animal's use of the enclosure. As such, it can be used within and between individual institutions to highlight potential effects of enclosure design on individual gorillas. The spread of participation index was first used to evaluate captive animal enclosure use by Hedeen (1982), and subsequently has been used in a range of captive situations (e.g. Lindberg and Nicol, 1996; Shepherdson, Carlstead, Mellen and Seidensticker, 1993). However theoretical problems have been identified in association with this SPI formula i.e. the value of the SPI was highly influenced by the size of the identified zones. In addition, the allocation of equal sized zones within a zoo enclosure often does not reflect the distribution of resources within that enclosure e.g. resources may be smaller than the zone size, or lie over the boundary between two zones. As such, although useful, the measure did not account for specific resources of non-uniform shape. Plowman (2003) provided an adjusted SPI formula that allowed for the inclusion of unequal areas within the animal's enclosure. Thus the adjusted SPI can now be assessed in a resource-dependant manner.

2.2.2 Activity levels

A wide range of factors including suitability of enclosure and husbandry techniques can influence an animal's level of activity and expression of behaviour. Assessment of the level and diversity of activity between institutions allows identification of potential differences in behaviour due to the effect of institution in multi-institutional research. In orang utans it has been suggested that a combination of the number of animals, the amount of usable surface area, the number of movable objects, and the volume of the enclosure were the best predictors of activity levels (Perkins, 1992). Whereas Hoff, Powell, Lukas and Maple (1997) determined significant differences in the expression of behaviour in captive gorillas housed at Zoo Atlanta dependant on whether they were in the inside or outside enclosure. In particular there were increased levels of aggressive behaviour within the inside enclosure, but also increased levels of spatial proximity. Certainly there is a large volume of research within zoos on environmental enrichment demonstrating how the provision or adjustment of this husbandry technique can influence the activity levels of the target animals.

Although every effort has been made to standardize between exhibits and to conduct research at institutes with similar husbandry practices, some differences between institutions are inevitable (Table 2.3). In order to assess the impact of institutional differences appropriate data on activity levels and enclosure use have been collected and analysed (see chapter 3).

2.2.3 Assessment of social competence

An additional husbandry factor that could be a confound across both the bachelor and the breeder group sample is the level of social competence exhibited by animals within the group. Currently within the captive gorilla population behavioural assessment of social competence is not carried out. There is an assumption that parent (or group) reared animals that have either experienced or have had the opportunity to observe social interactions within the natal group will exhibit a higher level of social competency than those animals that have not been exposed to this environment (Bowen, 1980; Stoinski *et al*, 2004b). Both the EEP and the SSP breeding programmes advocate hand rearing only in circumstances where all other alternatives (i.e. reintroduction to mother / group, surrogacy by another female) have been ruled out. In these circumstances hand rearing will be carried out; however the recommendation is that infants must not be hand reared in isolation from other gorilla infants (Rietkerk, Bemment and Abello, 2006). Within Europe there is a designated hand rearing facility (Wilhelma Zoo, Stuttgart) that will accept infant gorillas from within the EEP community. This allows some exposure to gorilla behaviour before the individual animals can be introduced to suitable breeder or bachelor groups. To date the history of the individual (i.e. whether hand or parent reared) is the only indication of social competency. Rearing style of the individuals within this research will be incorporated to the analysis.

Table 2.3 Summary of enclosure designs and husbandry routines

Zoo	Research Dates	Group type	Husbandry routine	Enclosure Size	Area of enclosure per individual m^2	Indoor area	Outdoor area / Enclosure type
Paignton Zoo, UK	Jan 2002 9 days Nov 2002 9 days April 2003 6 days Jan 2005 7 days	Bachelor	Morning scatterfeed on island then scatterfeed in hall post cleaning. Access to hall and outside until evening feed. Evening – split off for one feed then together with inside access only.	2,385 m^2	596.25 m^2	Main hall – Daily access Back dens – night-time access only	Yes – complex island enclosure with climbing structure
Belfast Zoo, UK	April 2002 9 days	Breeder	Morning scatterfeed outside then scatterfeed inside post cleaning. Access to hall and outside until evening feed. Evening – split off for one feed then together with inside access only.	2,100 m^2	350 m^2	Main hall – Daily access Back dens – night-time access only	Yes – complex walled area with climbing structure
Apenheul Primate Park, The Netherlands	June 2003 9 days	Breeder	Morning scatterfeed on island. Access to island only during day. Four additional keeper thrown feeds during day. Evening feed given inside – inside access only.	10,330 m^2	645.63 m^2	Yes – limited access No back dens available	Yes – large complex island with climbing structure
Loro Parque, Tenerife, Spain	Nov 2003 9 days	Bachelor	Morning scatterfeed outside. Access to outside only during day. One additional keeper thrown feed during day. Split off for one feed then limited night-time contact – inside access only.	@ 9,000 m^2	@ 1800 m^2	No Back dens – night-time access only	Yes – large walled area with very complex design

Zoo	Research Dates	Group type	Husbandry routine	Enclosure size	Area of enclosure per individual m^2	Indoor area	Outdoor area
Calgary Zoo, Canada	June 2004 8 days	Breeder	Morning scatterfeed outside. Access to outside and hall during day. Evening – split off for one feed then together with inside access only.	2,500 m^2	277.78 m^2	Yes Back dens – night – time access only	Yes – large walled enclosure with climbing structure and stream
Columbus 1, Ohio, US	July 2004 5 days	Breeder	Morning scatterfeed outside. Access to outside only. One additional keeper feed during day. Evening – access to inside area only.	2,482 m^2	354.57 m^2	No Back dens – night-time access only	Yes – large meshed enclosure with complex climbing structure
Columbus 2, Ohio, US	July 2004 6 days	Breeder	Morning scatterfeed outside. Access to outside only. One additional keeper feed during day. Evening – access to inside area only.	2,482 m^2	354.57 m^2	No Back dens – night-time access only	Yes – large meshed enclosure with complex climbing structure
Port Lympne, UK	Nov 2005 9 days	Bachelor	Morning scatterfeed outside (meshed enclosure). Two additional keeper thrown feeds during day either in meshed area or walled enclosure. Evening – split of for one feed then together with inside access only.	6,000 m^2	1200 m^2	Yes Back dens – access over 24 hrs	Yes – both meshed enclosure and walled area with climbing structure

Zoo	Research dates	Group type	Husbandry routine	Enclosure size	Area of enclosure per individual m^2	Indoor area	Outdoor area
Boissiere du Dore, France	Feb 2006 8 days	Bachelor	Morning scatterfeed in inside area. Additional keeper feed during day. Evening – Silverback split off overnight (feed) access to back dens only.	375.5 m^2 Indoor access only during data collection	75.1 m^2	Yes Back dens – night-time access only	Yes – island with no access during winter
Disney 1, Florida, US	April 2006 8 days	Breeder	Morning scatterfeed outside. No access to inside until evening. Split off for evening feed then together in the back for night.	@ 8,500 m^2	@ 1416.67 m^2	No Back dens – night-time access only	Yes – large complex walled enclosure
Disney 2, Florida, US	April 2006 8 days	Bachelor	Morning scatterfeed outside. No access to inside until evening. Split off for evening feed then together in the back for night.	@ 9,000 m^2	@ 2250 m^2	No Back dens – night-time access only	Yes – large complex walled enclosure

2.3 Data Collection

When conducting multi-institutional research it should be recognised that there are variables other than enclosure design and husbandry which can introduce confounds e.g. the impact of zoo visitors on the behaviour of the research animals. It has been well documented (e.g. Chamove, Hosey and Schaetzel, 1988; Hosey, 2005; Shepherdson, Carlstead and Wielebnowski, 2004) that visitor numbers and visitor noise levels can have a profound effect on the activity and welfare of a zoo animal. With this research every effort was made for data collection to be carried out in the institution's off-season so that visitor numbers were at a minimum. However for two zoos in particular (Disney Animal Kingdom and Columbus Zoo and Aquarium), the identification of an off-season and the arrangements for carrying out observational research (despite the willing co-operation of the zoos) imposed limitations on the time available for a research visit.

In order to collect sufficient data both to comment on potential discrepancies between institutions and to compare social interaction and conflict resolution between the males, several data collection methodologies were employed.

2.3.1 Instantaneous scan sampling

Instantaneous scan sampling (Altman, 1974; Lehner, 1996; Martin and Bateson, 1996) was carried out at each institution for between 5and 9 days. Data collection was started when the gorilla group was allowed access to the areas for public viewing (between 08.00 and 09.00 depending on the keepers' routine) and was continued throughout the day until the gorillas were removed from public view for an evening feed (again dependant on the keepers' routine, table 2.3). Scans were carried out at each fifteen minute interval recording four types of data for each male: behaviour, location within the enclosure, nearest neighbour and distance, second nearest neighbour and distance.

Behaviour:

Broad behaviour categories were established (see Appendix III for a full ethogram) to enable activity budgets to be calculated for each gorilla. Activity budgets deal purely with state behaviours but can provide a viable method of assessing differences in levels of activity between institutions.

Location within the enclosure:

The enclosure in each institution was visually divided to account for resource types provided. In each case the visual representation of the enclosure was matched to plans to provide an estimate of the resource type's basal surface area. Proportional frequency of each individual's time spent in each area was then used to calculate an SPI (Plowman, 2003).

Nearest neighbour and distance:

At each 15 minute scan the nearest neighbour to each individual and that neighbour's distance was estimated. In order to attempt to standardize the neighbour distances, five categories were established (touching; 0-1metre; >1-5 metres; >5-10 metres; >10 metres). In order to increase validity in the establishment of these categories, an attempt was made to find a balance between categories that would be too small, where accuracy of assessment would be impaired, and categories that would be too large, where relevant information would be lost. To help with the assessment of the distances involved, wherever possible distances between known features within the enclosure (i.e. two identifiable trees) were measured as a means of comparison. In addition identifiable distances along the public barrier (e.g. the width of a viewing window) were also measured to provide an additional aid.

Second nearest neighbour and distance:

The second nearest neighbour and their distance was recorded as described above for nearest neighbour.

2.3.2 All-occurrence data sampling

During the nine days of the instantaneous scan sampling, all-occurrence data (Altman, 1974; Lehner, 1996; Martin and Bateson, 1996), for key dominance behaviours (see Appendix III) of display, supplant, non-contact aggression and contact aggression were also collected. Bouts were defined by a bout criterion interval (BCI) of ten seconds (Lehner, 1996). In addition information on the initiator and the receiver of these behaviours was noted. Where an initiator and receiver could not be identified, the bout was discarded.

2.3.3 Continuous focal follows

For each male subject (as shown in Tables 2.1 and 2.2) within the research group, twenty minute continuous focal follows (Altman, 1974; Lehner, 1996; Martin and Bateson, 1996) were also undertaken during which all behaviour was recorded (see Appendix III for ethogram). At each zoo care was taken to divide the day according to the husbandry routines to allow for potential time of day effects in behaviour levels e.g. at Paignton Zoo continuous follow data were collected in three sessions:

1. During the morning cleaning routine when the gorillas had access to the island area (with scatter feed) and the back dens.
2. After cleaning for the remainder of the morning when the gorillas had access to the island and the indoor area (with scatter feed)
3. During the afternoon when the gorillas had access to the island and the indoor area but the scatter feed was finished.

In each of these sessions a rotation of data collection was established and nine repetitions of the continuous follows were aimed for. If a dominance behaviour (for the all occurrence sampling) occurred within the group whilst a focal follow was in progress the focal follow took priority. The dominance behaviour would be noted if the criteria of identification of initiator and recipient had been met.

2.3.4 Longitudinal Research at Paignton Zoo

The changes in group composition and structure at Paignton Zoo, both due to the removal and addition of gorillas and the changes in social status of the younger males, allowed the opportunity for longitudinal data to be collected. Four data collection periods, representing different group compositions and age-structure (Table 2.4), were completed each using the three methods of data collection described above.

Table 2.4 Age structure of the Paignton Zoo group at differing data collection sessions

	Pertinax (d.o.b. 04/82)	Mambie (03/91)	Richard (11/91)	Asato (10/91)	Awali (04/93)	Mapema (04/96)	Damisi (04/97)
Jan 02	Silverback (19 yrs)	Blackback (10 yrs)	Blackback (10 yrs)	Blackback (10 yrs)	Sub-adult (8 yrs)		
Nov 02	Silverback (20 yrs)		Blackback (11 yrs)	Blackback (11 yrs)	Sub-adult (9 yrs)		
Apr 03	Silverback (21 yrs)		Blackback (11 yrs)	Blackback (11 yrs)	Blackback (10 yrs)		
Jan 05	Silverback (22 yrs)			Silverback (13 yrs)	Blackback/ Silverback (11 yrs)	Sub-adult (8 yrs)	Sub-adult (7 yrs)

2.4 Statistical analysis

Mixed model ANOVAs have been used for the main analysis of the data collected. Mixed models were developed to incorporate fixed and random effects within a set of variables (Crawley, 2007). These data also have a hierarchical design as institution is nested within group type (breeder/bachelor). Full models are presented in Appendix V (p 175).

Within multi-institutional research there are a number of variables that can contribute to any significant effects on the data. Mixed models allow the inclusion of these variables, and the generation of models with the significant effects that account for variation within the data. Within this research the main factors for most of the mixed models performed were group type, institution (nested in group type), rearing style and mean kinship with other group members. Age was added as a covariate. Non-significant factors were sequentially removed from the initial model as analyses were run.

Institution is a complex variable containing confounds. Area of enclosure per individual and season (expressed as average temperature at each institution) were considered for inclusion in the models. However these variables are correlated with that of institution (area of enclosure per institution, Spearman's rho = 0.300, p = 0.05; average temperature per institution, Spearman's rho = -0.485, p = 0.001). The data presented here does not allow for a separation of these factors. For that reason only institution has been included in the analysis. Where there is a significant institutional effect on the data it should be remembered that these correlated factors could be involved. In some cases the graphical results have been presented with institutions ordered by area of enclosure per individual, where this factor seems to give a logical explanation of the data.

Mean kinship with other group members were calculated for each individual. The International Studbook was used to track kinships within the groups (i.e. full siblings or parent / offspring = 0.5; half siblings = 0.25; cousins = 0.125). Therefore one male with 2 full brothers and 2 other unrelated group members will have a mean kinship of 0.25

$$(MK = \frac{0.5 + 0.5 + 0 + 0}{4} = 0.25)$$

Applied results

The establishment of breeder and bachelor groups in captivity can be heavily manipulated when it comes to group composition. Most breeder groups are started with a silverback male and a small number of females. The groups are then allowed to expand as offspring are born and grow into the group so many of the group are closely related and most younger animals are parent-reared. However there are some breeder groups where the group composition is heavily manipulated in order to try to introduce young males to more normal situations (i.e. Belfast where two young males have been introduced to the group before the addition of a new silverback, effectively creating a multi-male group with three males unrelated to any other group members). On the other hand bachelor groups are all heavily manipulated groups, as they are constructed to suit the needs of the breeding programmes (EEP and SSP) at the time. They often consist of unrelated individuals and include a disproportionate number of hand-reared males. Therefore, in this research where significant effects of rearing style or mean kinship have been found an additional analysis has been performed excluding these factors. The results of these additional models will indicate whether male behaviour, and potentially welfare, differs between breeder and bachelor groups (due to differences in these confounding factors) and will therefore be directly relevant to the establishment of gorilla groups as they are currently run by the breeding programmes.

Chapter 3: Comparisons of activity and enclosure use across institutions

3.1 Introduction

In order to provide an adequate sample size for the comparison of the behaviour of males in breeder groups with that of males in bachelor groups multi-institutional research was necessary (see chapter 2) to allow data from a number of institutions to be pooled into the two husbandry types (breeder or bachelor). This chapter examines broad differences between the institutions and provides evidence for the viability of pooling data from different institutions to give robust sample sizes for bachelor and breeder group comparisons.

3.1.1 Multi-institutional research

Multi-institutional research can be used to overcome the issues of small sample size commonly encountered with research carried out in a zoo setting (Hurlbert, 1984; Kuhar, 2006). When increasing the sample size through multi-institutional research, potential confounds can be encountered through differences between institutions in husbandry practices and enclosure design (Melfi, Marples and Ruxton, 2006). Although the groups observed were selected to be as similar as possible in husbandry practices and enclosures, it is inevitable that there will be some institutional differences that could affect the exhibition of behaviours by individuals within the test groups, and this may compromise the use of multi-zoo data. However if it is possible to consistently demonstrate predictable and definable phenomena (e.g. age differences in the exhibition of behaviour) across all groups, irrespective of institution, then it is reasonable to assume that other phenomena (i.e. those of interest to this thesis) will also not be masked or confounded by the variations between institutions.

3.1.2 Behavioural patterns

Effect of age on expression of behaviour

Amongst mammals the great apes have the longest juvenile period (the period between weaning and the emergence of secondary sexual characteristics) relative to body size (Watts and Pusey, 1993). A variety of theories have been proposed to explain the evolution of an extended juvenile period (Pereira, 1993), but with no consensus. However, there are a number of consistent, observable trends within the exhibition of behaviour of juvenile primates which allow us to predict expected differences in behavioural diversity between male gorilla ages. Play behaviour in particular has been observed with greater frequency and longer duration in younger primates than older primates (Lee, 1983). Although there is still discussion over the function of behaviours such as play (Bekoff and Byers, 1998) the juvenile years provide an opportunity for the observation and practice of social behaviour, as well as the potential for the formation of alliances (Pereira, 1993). Patterns of behaviour of juvenile and adolescent gorillas have been documented (Stewart and Harcourt, 1987; Watts and Pusey, 1993). Stewart and Harcourt (1987) in particular note that in gorillas social interactions occur at higher rates amongst immatures than amongst adults. The social behaviour most commonly observed was play behaviour, and rates of play were inversely related to age from two years of age.

It is therefore reasonable to assume that juvenile and adolescent males (subadult and blackback classes respectively) will exhibit higher levels of behavioural diversity and spend longer in some behaviours than adult male gorillas.

Behavioural Diversity

Although activity (or time) budgets have been used as a method for comparing the expression of behaviour in many situations (e.g. between groups, Mitchell, Boinski and van Schaik, 2005; Weller and Bennett, 2001; across conditions, Doran, 2004; and between wild and captive groups, Melfi and Feistner, 2002), rapid assessment of behaviour across zoos in multi-institutional research can be achieved more effectively by the use of an index of behavioural diversity per individual per institution.

Biological diversity indices are a commonly employed measure designed to allow assessment of the character of an ecological community (Begon, Harper and Townsend, 1996). To gain relevant information on the community's character both the proportion of individuals that each species contributes towards the total (the diversity) and the evenness of distribution of species represented (the equitability) must be determined. Simpson's diversity index, weighted to allow for abundance of species, is one of the more commonly used indices of biological diversity (Simpson, 1952). These biological indices can be applied to behavioural data to give a behavioural diversity index for individuals or groups of individuals (Shepherdson, Carlstead, Mellen and Seidensticker, 1993), and can provide an effective means of comparing patterns of behaviour across groups. Simpson's diversity index is based on the proportion of time spent performing each behaviour and the number of behaviours exhibited. Therefore the calculation gives both behavioural diversity (Simpson's D), the higher the number the greater the level of behavioural diversity, and also behavioural equitability (Simpson's E_D), a figure between 0 and 1 (where 0 implies no evenness in the proportion of time spent in behaviours and 1 implies an even proportion of time spent in all behaviours). The measure of behavioural diversity and equitability allows for the identification of differences in behavioural profiles between individuals or groups of individuals but will not illustrate which behaviours show variation.

3.1.3 Enclosure use

Evaluations of enclosure use can provide useful information for researchers and zoo managers on the effectiveness of the design (provision of resources) of an enclosure as well as an indication of preferred sites within the enclosure. The provision of sufficient type and numbers of enclosure resources can have a far reaching impact on the behaviour and social interactions of the animals housed within the enclosure. It is not uncommon for animals to exhibit preference for design features (refer chapter 2; Ogden et al, 1993; Perkins, 1992; Wilson, 1982; Stoinski, Hoff and Maple, 2001) and for individuals within a group to display competition for access to key resources or features. Therefore evaluation of enclosure use across the institutions within this thesis will allow assessment of the potential impacts of enclosure design.

Spread of participation index

In the previous chapter, the relevance of the SPI to assess enclosure use was discussed. It is worth re-iterating that the implementation of SPI to evaluate an animal's enclosure use has been increasing in zoo research, particularly through the adjusted version (Plowman, 2003), which allows resource-dependant determination of enclosure use. The index gives a single figure, between 0 and 1 (0 indicates all areas of the enclosure used equally; 1 indicates a strong bias to just one area of the enclosure), to grade the animal's use of the enclosure, as such it can be used within and between individual institutions to highlight potential confounds between enclosures.

Despite the use of the adjusted SPI and its relevance to the use of resources within the enclosure, there are inherent difficulties in applying a comparison of SPI across a number of institutions. Institutions can vary widely in the design of enclosures and the provision of resources. Zoos have seen a trend in recent years towards enclosures designed to minimise the impact of barriers between the public and the animals, and provide 'naturalistic' environments for the animals (Hancocks, 1996; Hediger, 1950). This has lead to growing numbers of moated or walled enclosures rather than the more traditional bar and mesh enclosures. Selecting zoos for multi-institutional research inevitably crosses a number of enclosure types (see chapter 2; table 2.3) affecting the functionality of the enclosure area. This directly impacts on the assessment of the SPI and indicates that SPI, although extremely useful for assessing enclosure use over time or conditions within one enclosure, cannot be used for direct comparisons across multiple enclosures, but can provide a guide to the amount of enclosure use (i.e. can allow assessment of whether one institution encourages particularly poor enclosure use, an SPI close to 1.0, which could indicate either poor enclosure design or social constraints preventing individuals effectively using the area provided for them).

3.1.4 Aims and hypotheses

This chapter seeks to validate the use of multi-institutional research to increase sample size by demonstrating that a known behavioural phenomenon can be observed within multiple institutions. In addition this chapter seeks to demonstrate that it is acceptable to pool institutions to look for phenomena across group type (i.e. breeder or bachelor groups).

The following hypotheses will be tested:

1. Adult males (>14 yrs or 168 months) will exhibit significantly lower levels of behavioural diversity (Simpson's D) than younger males, indicating fewer behaviours exhibited.
2. Institution will not have a significant effect on behavioural diversity (Simpson's D).
3. Adult males (>14 yrs or 168 months) will exhibit significantly lower levels of behavioural equitability (Simpson's E_D) than younger males, indicating an unequal time spent in behaviours exhibited.
4. Institution will not have a significant effect on behavioural equitability (Simpson's E_D).

In addition the results of the SPI assessment will be reviewed to enable comment on potential confounds due to enclosure design.

3.2 Methods

Data were collected as described in chapter 2 (see Appendix III). The data derived from instantaneous scan sampling (at 15 minute intervals) of behaviour were used to calculate Simpson's behavioural diversity indices. Data from instantaneous scan sampling of location in enclosure were used to calculate the spread of participation index (SPI).

3.2.1 Data manipulation and statistics

Simpson's diversity indices and equitability

The proportion of sample points scored for each behaviour was calculated for each individual gorilla. These proportions were then used to calculate Simpson's index of diversity and equitability as per the following equations:

$$\text{Simpson's diversity } D = \quad {}^{s} \quad 1$$

$$\sum_{j=1} p^2$$

Proportions of behaviours are squared and summed, and the reciprocal is taken. Simpson's D can then be used to determine the equitability (Simpson's E_D):

Simpson's equitability $E_D = D/S$

Where S = the number of behaviours exhibited by an individual.

Simpson's D and Simpson's E_D were calculated for each individual (18 breeder group males, 23 bachelor group males). Mixed model ANOVAs were used to analyse both behavioural diversity and behavioural equitability.

Spread of participation index

The adjusted spread of participation index (SPI) was calculated following the modified formula allowing for unequal zones (Plowman, 2003).

$$\text{spi} = \frac{\Sigma\,[f_o - f_e]}{2\,(N - f_{e\ \min})}$$

Where:

fo = the observed frequency of observations in a zone

fe = the expected frequency of observations in a zone (based on zone size and assuming even use of the whole enclosure)

fe min = the expected frequency of observations in the smallest zone

N = the total number of observations in all zones

An SPI was calculated for each individual gorilla.

3.3 Results

3.3.1 Activity patterns

(Full Mixed Models are given in Appendix V)

Behavioural diversity

There was a significant effect of age in months ($F_{(1, 38)} = 81.665$, $p < 0.001$) and group type ($F_{(1, 38)} = 7.983$, $p = 0.007$) on behavioural diversity. Inspection of the data (Fig. 3.1 below) shows that younger gorillas have a higher behavioural diversity, with levels of diversity falling sharply after approximately 200 months. Males housed in bachelor groups show lower levels of behavioural diversity than those housed in breeder groups. Non significant factors were removed from the model as the analyses were run (as described in chapter 2) however in this case it is worth stating that there was no significant effect of institution on behavioural diversity ($F_{(1,27)} = 0.682$, $p = 0.416$) (fig 3.2).

Fig. 3.1 Behavioural diversity (Simpson's D) of captive male western gorillas housed in breeder and bachelor groups.

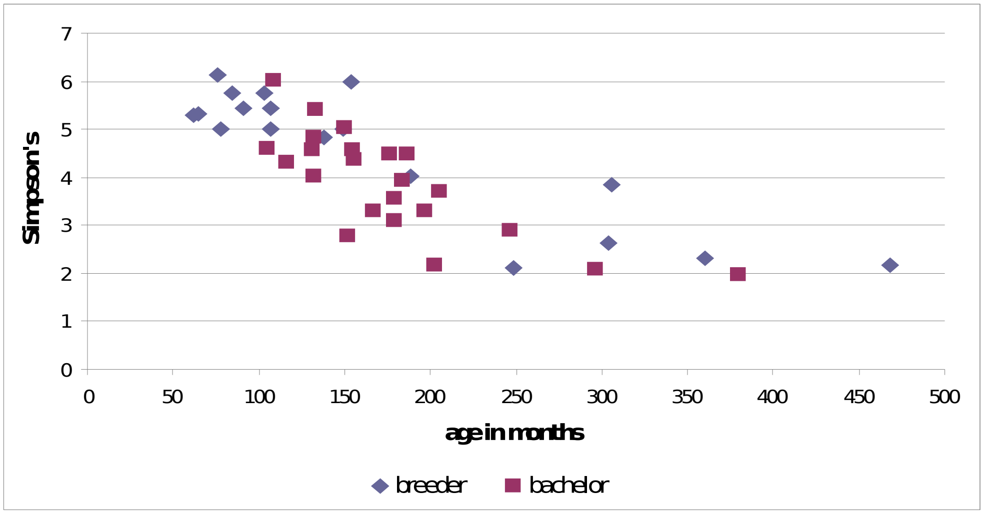
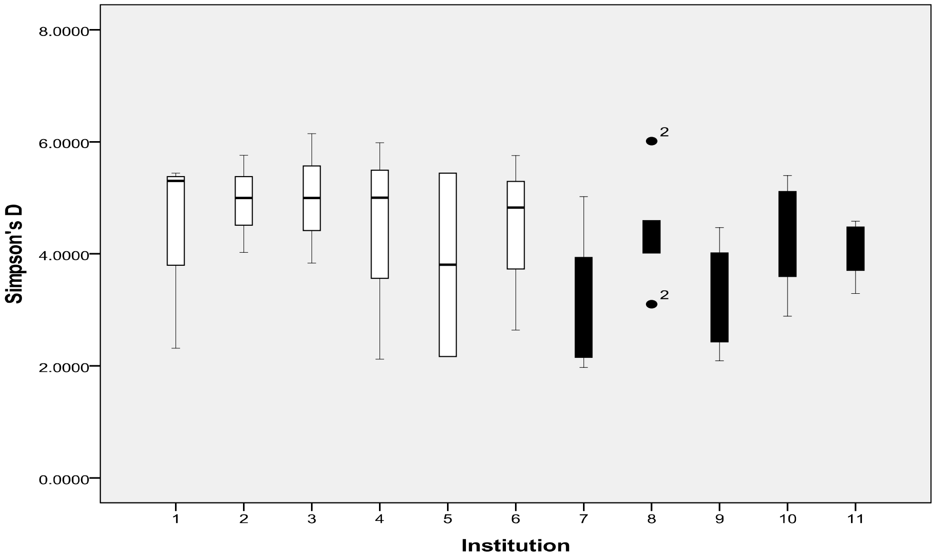


Fig. 3.2 Behavioural diversity (Simpson's D) across institutions. Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes.



Behavioural equitability

There was a significant effect of age in months on behavioural equitability ($F_{(1, 37)} = 33.779$, $p < 0.001$), with younger males showing a higher behavioural equitability (a more even spread of time spent performing a behaviour) than older males (fig. 3.2 below). There was also a significant effect of whether the individuals were hand reared or mother reared on behavioural equitability ($F_{(2, 37)} = 4.130$, $p = 0.024$), with hand reared animals showing lower behavioural equitability (fig 3.3). As previously, non significant results were sequentially removed from the model, but it is worth stating that neither group type (breeder/bachelor) ($F_{(1, 17)} = 0.076$, $p = 0.787$) nor institution ($F_{(6, 17)} = 1.676$, $p = 0.188$) had a significant effect on behavioural equitability.

Fig 3.3 Behavioural equitability (Simpson's E_D) of captive male western gorillas housed in breeder and bachelor groups.

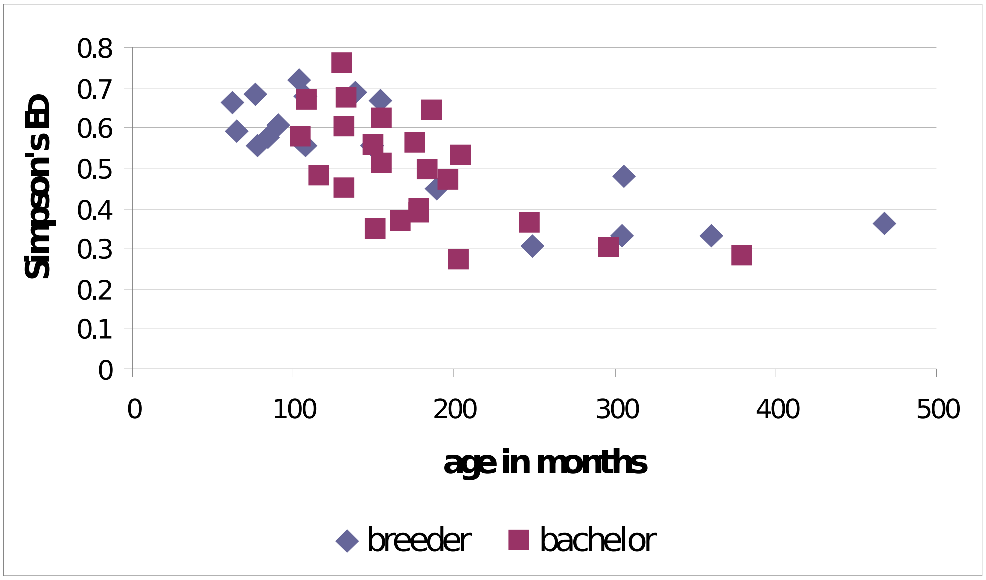


Fig. 3.4 Behavioural equitability (Simpson's E_D) of hand reared or mother reared captive western gorillas.

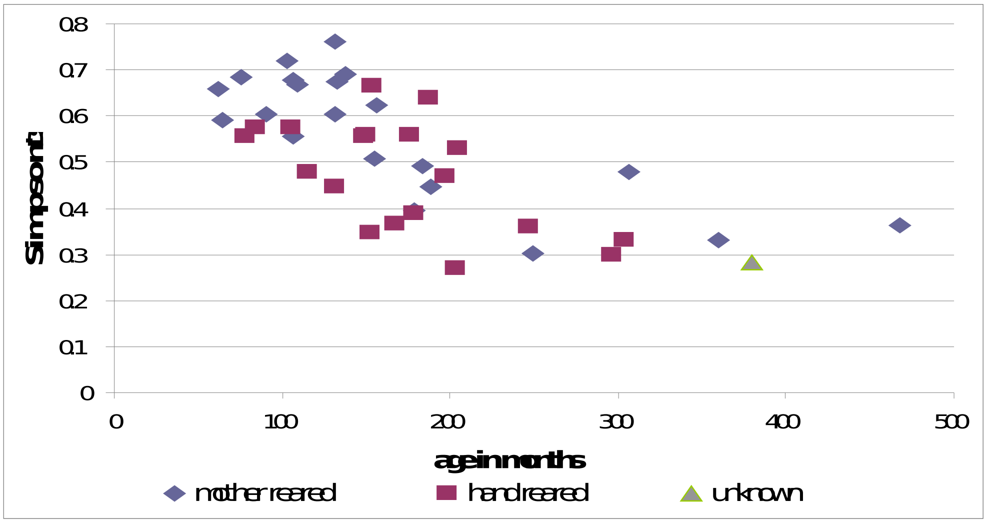
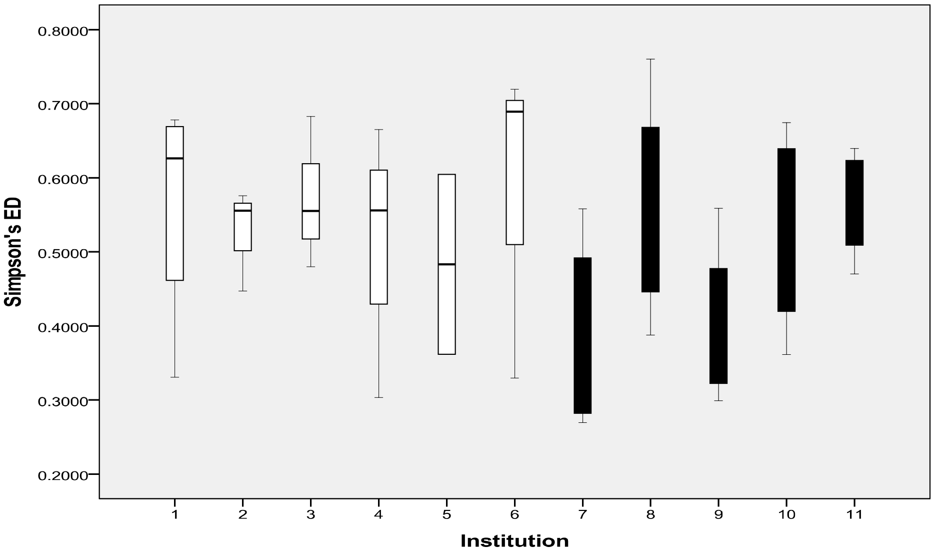


Fig 3.5 Behavioural equitability (Simpson's ED) across institutions. Breeder groups are represented by open boxes, bachelors are represented by closed boxes.



3.3.2 Enclosure use (SPI)

There was a large variation in SPI values across all individuals but a similar range was apparent within bachelor and breeder groups (fig. 3.4 and 3.5). In both group types silverbacks tended to have the highest SPI values i.e. the least even use of the enclosure

Fig 3.6 Enclosure use (SPI) of captive male western gorillas held in bachelor groups (0 = even use of whole enclosure, 1 = use of only one zone).

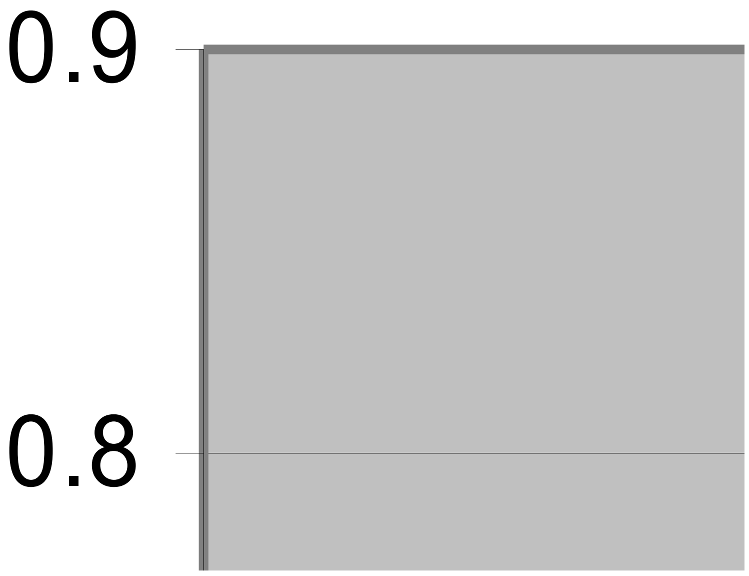
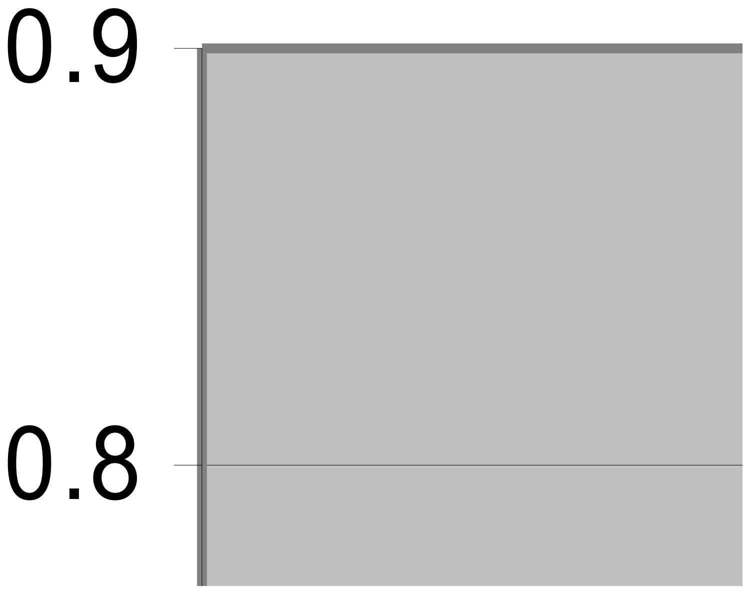


Fig 3.7 Enclosure use (SPI) of captive male western gorillas held in breeder groups (0 = even use of the whole enclosure, 1 = use of only one zone).



3.4 Discussion

3.4.1 Behavioural diversity

Older males (silverbacks) express a significantly lower diversity of behaviour than the younger individuals (blackback and subadult). This corresponds with previous research with juvenile primates indicating that they show greater variety of behaviour, particularly social interactions such as play behaviour (Lee, 1983; Pereira, 1993; Watts and Pusey, 1993), but in particular with Stewart and Harcourt, 1987, who documented a decrease in the levels of social interactions such as play behaviours in gorillas as they matured. Although the use of the behavioural diversity index precludes the identification of which behaviours are decreasing in the repertoire of an adult male, it does clearly demonstrate the effect of age on the expression of behaviour.

The results also indicate, as predicted, that there was no significant effect of institution on the level of behavioural diversity. This indicates that, although there may be differences in enclosure design or husbandry between the institutions, it does not mask the effect of behavioural phenomena. It is therefore acceptable to pool institutions into two groups, breeder or bachelor, to enable comparison of male behaviour between those groups.

Although not the main focus of the analysis in this chapter, there was a significant difference in levels of behavioural diversity between males in breeder and bachelor groups. The males housed in bachelor groups generally demonstrated lower levels of behavioural diversity than those housed in breeder groups. Again, although the behavioural diversity index does not allow identification of which behaviours have decreased within bachelor groups, it does clearly indicate that behavioural differences can be identified through multi-institutional research.

Significant differences were also found for the effect of age on levels of behavioural equitability. These results suggest that the juvenile age-classes (blackback and subadult) show a more even expression of behaviour (more equal times engaging in behaviours) than the silverback age-class. Silverbacks show a bias in the time spent expressing behaviours, with certain behaviours being expressed far more frequently. This result is not unexpected given that adult male mountain gorillas exhibit less diversity of behaviours and more time resting than juveniles (Stewart and Harcourt, 1987). However this again reinforces the use of multi-institutional research to increase sample size by demonstrating a known behavioural phenomenon.

A further reinforcement of the use of multi-institutional research to increase sample size by demonstrating a known phenomenon, is the effect of hand or parent rearing on the behavioural equitability. There has been a large body of work (Capitanio and Reite, 1984;

Ljunberg and Westlund, 2000; Weaver and de Waal, 2002) demonstrating the effect of rearing type, including impoverished behavioural expression in hand reared animals, and it is reasonable to assume that this would be equally applicable to behavioural equitability.

The data used in the calculation of the Simpson's Index were collected using ethogram I (See Appendix III), consisting of broad behavioural categories to give an overview of patterns of behaviour. There is some subjectivity in the estimation of behavioural diversity depending on how broad or detailed the behaviour categories are. However, in this case it is not the absolute diversity but the relative value of different individuals and groups that is of interest. Using broad categories will give a more conservative indication of how much the individuals and groups differ as they will mask more differences in more detailed behaviour types and therefore will have made it more difficult to detect the age-related differences that have been shown here.

3.4.2 Spread of participation index

As has been previously mentioned, there are difficulties in carrying out comparisons of SPI scores across a number of enclosures; however there is still worthwhile information to be gained from the SPI results. It is important to remember that the spread of participation index is counter-intuitive (i.e. 0 indicates even use of the enclosure, 1 indicates that only one area of the enclosure is being used).

The SPI results indicate variation in the use of the enclosures between animals of differing social status. It suggests that silverback use their enclosures far less evenly (have higher SPI scores) than either blackbacks or subadults. This is not necessarily surprising given that juveniles are expected to participate in a wider range of social interactions, including play.

In some instances the SPI scores for the silverbacks rise above the 0.6 level, indicating that there are significant areas of the enclosure that are not or very rarely utilized. However in these cases the SPI scores for the blackbacks and subadults are lower (i.e. enclosure use is more even). Thus, particularly considering the lower level of behavioural expression for silverbacks, it suggests that there may simply be a lack of motivation for the silverbacks to utilize these areas, rather than a social or design implication.

The subadult at Belfast does show a high SPI, suggesting that he does bias his use of enclosure to a small number of zones. As the level of enclosure use for both the blackback and the silverback at Belfast are at lower levels (e.g. showing a more even use of the enclosure), it may suggest that there are other reasons (e.g. social pressure) limiting his use of the enclosure.

In summary, this chapter has demonstrated that, despite the potential for confounds due to differences in enclosure design and husbandry, predictable behavioural phenomena can clearly be identified from multi-institutional data. In addition across the institutions selected there is no detectable effect of institution on gross behavioural expression. Therefore it is reasonable to expect to be able to identify differences in patterns of behaviour of relevance to this thesis within the gorilla groups selected. In addition a difference in the levels of behavioural diversity has also been demonstrated, suggesting that bachelor males have reduced opportunities to express a range of natural behaviours. The following chapters will examine the expression of key behaviours between breeder and bachelor groups in more detail.

Chapter 4: Male social spacing and dominance hierarchies in breeder and bachelor gorilla groups.

4.1 Introduction

Wild gorilla groups have previously been considered to have a one male mating system (Harcourt and Stewart, 1981; Robbins, 1999; Yamagiwa, 1992) with the majority of male-male encounters consisting of encounters between groups, or groups and lone males. These encounters are contests in which males try to attract or retain females, to protect infants from infanticide or, on occasion, to kill the infants of another male (Harcourt, 1978; Sicotte, 1993; Watts, 1988, 1996; Yamagiwa, 1987).

However within mountain gorilla populations, it has been found that approximately 40% of all groups are multi-male (Robbins, 1999; Schaller, 1963). Although dominant males will often interrupt mating attempts by subordinates and may exhibit mate guarding (Robbins, 1999; Watts, 1996), some benefits may occur from tolerating a follower male within the group, such as assistance in female and infant defence in both inter-group and lone male encounters. In co-resident situations natal philopatry is often the mechanism by which the follower remains in the group. This may be useful to the follower as not all dispersing males will gain the opportunity to mate and philopatric males will often start to reproduce at a younger age than dispersing males (Robbins 1995; Watts, 1996).

In wild situations where co-resident males are found, aggression is more common than affiliation whether between adult males, between adult and adolescent males or between adolescent peers (Watts, 1996). It has been seen that maturing natal males spend progressively less time near older males and receive more aggression from them, although it also appears that older males may be more tolerant of close kin than more distant relatives, and of younger males than those closer in age (Harcourt, 1979; Harcourt and Stewart, 1981; Robbins, 1995; Sicotte, 1994; Watts, 1996). Co-resident male gorillas have a clear dominance hierarchy with rank reversals occurring at a low frequency (Watts, 1996).

In a captive situation where there are no inter-group or lone male encounters, the perceived benefits of co-residency of males are not apparent. Traditionally captive gorillas are not kept in co-resident male situations, however with increasing pressure on the captive breeding programmes to house males considered ‘surplus to breeding’ in acceptable situations, it is important to determine the implications of co-residence on captive males.

4.1.1 Dominance hierarchies (despotism and egalitarianism)

The evaluation of dominance hierarchies has become central to many aspects of the study of animal behaviour (Richards, 1974), and have been used to predict the outcome of a variety of social interactions within groups (e.g. access to drinking in *Lemur macaco*, Fornasieri, Caubère and Roeder, 1993; food competition in female chimpanzees, Wittig and Boesch, 2003).

Social competition within groups is reflected by the division of those resources focal to the competition. Access of individuals to those resources (food patches, breeding females) determines the designation of a society along a continuum from despotic to egalitarian. Within a despotic society, access to a resource is dominated disproportionately by a small number of individuals (i.e. the dominance hierarchy will be more transitive, moving towards a linear hierarchy), whereas within an egalitarian society access to resources is more equal across individuals (i.e. the dominance hierarchy will be non-linear) (Vehrencamp, 1983). Therefore in situations where access to a valued resource, such as females, is limited there may be elevated levels of competition between males leading to more despotic hierarchies. Where access to resources becomes limited for subdominant animals, emigration may occur in search of better situations.

4.1.2 Social spacing and the implications of proximity

Breeder groups of gorillas are stable, cohesive units. Gorilla females form strong associations with the males in order to avoid infanticide by extra-group males (Robbins, 2007; Watts, 2000). The high level of association between females and males is emphasized by proximity patterns, with females spending up to 20% of feeding time and more than 50% of resting time within 5 meters of the dominant silverback (Robbins, 2007; Watts, 2000). It has been suggested that in one-male groups females are responsible for maintaining proximity to the dominant male, however in multi-male groups it appears that males are more responsible for maintaining proximity (Robbins, 2007).

Dispersal/ male natal emigration (peripheralization)

Whereas the majority of polygynous primate species will exhibit male-dispersal patterns, gorillas exhibit both male and female dispersal. In polygynous systems male dispersal could be seen to impact on male reproductive success (particularly where male parental care is negligible) and intra-sexual competition for access to mates. In gorilla social groups the blackback males, which have not obtained full silverback size, are likely to benefit from emigration from the natal group in which access to females is limited and likely to be the trigger of male-male competition with a silverback male (Pusey and Packer, 1987).

Proximate causes of dispersal vary and several evolutionary mechanisms may impact on dispersal patterns across primates (Pusey and Packer, 1987), however three explanations have been suggested for primate dispersal: individuals disperse to seek out better resources (Lidicker, 1962), individuals disperse to avoid intra-sexual competition (Moore and Ali, 1984), or individuals disperse to avoid inbreeding depression (Itani, 1972). The existence of female transfer from natal groups suggests that males would not be emigrating to avoid inbreeding depression, but may be emigrating to avoid raised levels of competition with other group males. There is currently a lack of research on male gorilla behaviour prior to emigration to determine whether dominant males exhibit increased levels of aggression and intolerance to blackbacks yet to emigrate from the natal group. However data from the wild indicates that the silverback-blackback relationship is weak, with low rates of proximity or affiliative behaviours, and any aggression that is exhibited is unidirectional, silverback to blackback (Robbins, 2007), suggesting that peripheralization is driven by intra-group competition. In situations where the focus of the competition is removed (bachelor groups) it is reasonable to assume that distances between males in bachelor groups will be shorter.

Tolerance, avoidance and proximity

Although males do emigrate from natal groups, some young males stay within the natal group leading to multi-male groups (Harcourt and Stewart, 1981, 2007). Although there are higher rates of aggression than affiliation between males in multi-male groups (Robbins, 2007), there are also potential benefits both to the dominant silverback (assistance in protection of females and offspring; Harcourt and Stewart, 2007) and to the subordinate (access to females both whilst the dominant is still in the group and after he has left; Bradley *et al*, 2005; Harcourt and Stewart, 2007). However, within multi-male groups distances between older males are known to be greater (Robbins, 2007) and may be an indication of avoidance behaviour.

Watts (1995a) working with mountain gorillas describes individuals avoiding previous opponents directly after an aggressive conflict, suggesting that social distancing and avoidance behaviours have a role in conflict management. In addition Mallavarapu, Stoinski, Bloomsmith and Maple (2006) working with captive western gorillas, described reconciliation between males in a post aggressive situation through maintenance of close proximity (within 1 meter). Proximity between individual gorillas functions to maintain the social group.

Bachelor groups

Yamagiwa (1987) described mountain gorilla bachelor groups as being a cohesive group maintained by the tendency of the sub-adults to stay within 10 meters of the silverback. Stoinski, Kuhar, Lukas and Maple (2004a) saw similar distances maintained by sub-adults in observations of bachelor groups in the U.S. These observations lead to the suggestion that sub-adults play a role in the cohesiveness of bachelor groups (Stoinski, Kuhar, Lukas and Maple, 2004a; Yamagiwa, 1987). Levrero *et al* (2006) and Robbins (1996) have suggested that bachelor groups provide an alternative strategy for young males to gain social experience.

Robbins (1996) comparing bachelor and multi-male groups of mountain gorillas described the bachelor group as staying closer together than males in multi-male groups, who actively avoided close proximity to avoid aggression.

4.1.3 Hypotheses / predictions

The presence of females within the breeder group can be viewed as a resource that may create a need for control. Therefore the presence of females in the group may influence the social spacing and dominance hierarchies of the males. This chapter examines the social spacing of the males, levels of association between individuals and hierarchies within breeder and bachelor groups.

Hypotheses to be tested include

- Younger animals will have shorter distances between themselves and their nearest and second nearest neighbours than older animals, as older males show more tolerance to younger males than to those closer in age.
- Social distances will be shorter in breeder groups as females develop strong associations with dominant males.
- However, social distances between males only will be further, and levels of individual associations between males will be weaker in breeder groups, where access to a resource (females) may be contested, than in bachelor groups,
- Dominance hierarchies may be more linear (despotic) in breeder groups, where access to a resource (females) may be contested.

4.2 Methods

This chapter will examine the social structure exhibited by both bachelor and breeder groups of captive western lowland gorillas by examining a number of social measures including social spacing and measures of hierarchies.

For details on data collection see Chapter 2

4.2.1 Data manipulation and statistics

Nearest and second nearest neighbours:

In order to evaluate social distances data on the distances to an individual's nearest and second nearest neighbour (within defined distance categories) were collected by instantaneous scan sampling (see chapter 2). The proportion of scans that a nearest neighbour was in each of the defined distance categories was calculated for both nearest neighbour and for second nearest neighbour and a mean proportion was obtained. For the breeder groups these data were calculated with the females and juveniles present, and then re-calculated with the data for female and juveniles/infants removed (i.e. the frequency that a male was the nearest or second nearest neighbour of any other male). Therefore the results for the breeder groups are presented as breeder group distances with females (and juveniles/infants) and breeder group distances without females (and juveniles/infants) for both nearest and second nearest neighbours.

In order to run the mixed model, one variable for distance was obtained by weighting the scores for the individual categories (see Table 4.1). Since a gorilla with a bimodal distribution of distances may have the same value of this weighted score as a gorilla with a normal distribution the distance results for each of the individual gorillas were checked for normal distribution. Each of the individual gorillas (both with and without females, juveniles and infants present in the case of the breeder group males) showed a normal distribution in both nearest and second nearest neighbour distances.

Table 4.1 Weighted distance categories used for nearest and second nearest neighbour analysis with an example shown for the Boissiere du Doré silverback nearest neighbour distance data

Distance categories	Weighted values	Proportional frequencies for Boissiere silverback	Corrected values
0 metres (touching)	1	0.007	0.007
>0-1 metre	2	0.036	0.072
>1-5 metres	3	0.652	1.957
>5-10 metres	4	0.254	1.014
>10 metres	5	0.051	0.254
		Sum of corrected values	3.304

Dominance hierarchy calculations:

Data on physical displacement behaviour (also called approach/retreat or supplant behaviour) were collected using all-occurrence sampling (see chapter 2). Physical displacement behaviour can be seen as a reflection of established relationships (Robbins, 1996) with a clear winner or loser of the interaction (Lehner, 1996). The displacement data were entered into a dyadic interaction matrix (dominance matrix) to construct the dominance hierarchies and assess the strength of dominance (or linearity) per group. Within the breeder groups the hierarchies were calculated between the males only.

Dominance hierarchies are considered to be a central theme in animal behaviour research (Hemelrijk, Wantia and Gygax, 2005) and, accordingly, there are several methods for ranking individuals within a dominance hierarchy (e.g. Appleby, 1983; de Vries, 1995, 1998; Jameson, Appleby and Freeman, 1999; de Vries and Appleby, 2000; Singh, Singh, Sharma and Krishna, 2003; Wittemyer and Getz, 2006).

Of this range of papers, many of the differences in methods focus on the problem of dealing with missing data points for interactions between dyads within the group. Within a social group it is possible that some dyads may not engage in pair-wise encounters whether aggressive or displacement). Singh *et al* (2003) reviewed existing methods for calculating hierarchy, and proposed a further method for dealing with missing dyadic interactions. Although it is rare for social groups to have a perfectly linear or transitive hierarchy, they do tend towards linearity. Therefore Singh *et al* (2003) provided a method of estimating the probability of an individual within a missing dyad winning an encounter, based on the proportion of other encounters won within the group. I have adopted this method for calculation of the strength of hierarchies in this thesis.

A t-test was used to compare the strength of dominance hierarchies between the breeder groups and the bachelor groups and an F statistic was calculated to determine any significant difference in the variance of strength of hierarchy within the groups (breeder and bachelor).

Association Indices:

In order to look at patterns of association across all groups a spread of participation index (SPI) per individual was constructed. In chapter 2 the use of an SPI was discussed as a means of assessing enclosure use (Hedeen, 1982; Shepherdson et al, 1993; Lindberg and Nicol, 1996; Plowman, 2003). Within the context of enclosure use, the adjusted version of the SPI (Plowman, 2003) was used to account for unequal sizes of resources within the enclosures. However as the original formula (Hedeen, 1982; Shepherdson et al, 1993; Lindberg and Nicol, 1996) assumes equal association with all areas (or in this case, individuals) it is possible to apply the technique to frequency of nearest neighbour data to assess any bias in associations (White, Beare, Fuller and Houser, 2003) e.g. the output of the formula is again an index from 0 to 1 (where 1 indicates association with just one individual and 0 indicates equal association with all individuals within the group).

In order to achieve the above method a criterion distance between individuals in which their probability of interacting increases, was set (Lehner, 1996). Using the frequencies of distances within the nearest neighbour data it is possible to set a criterion distance as up to and including the >5-10 metre distance category.

Statistical analysis

Four mixed model ANOVAs were carried out on the data for nearest and second nearest neighbour, with and without females for breeder groups (see chapter 2 for details).

4.3 Results

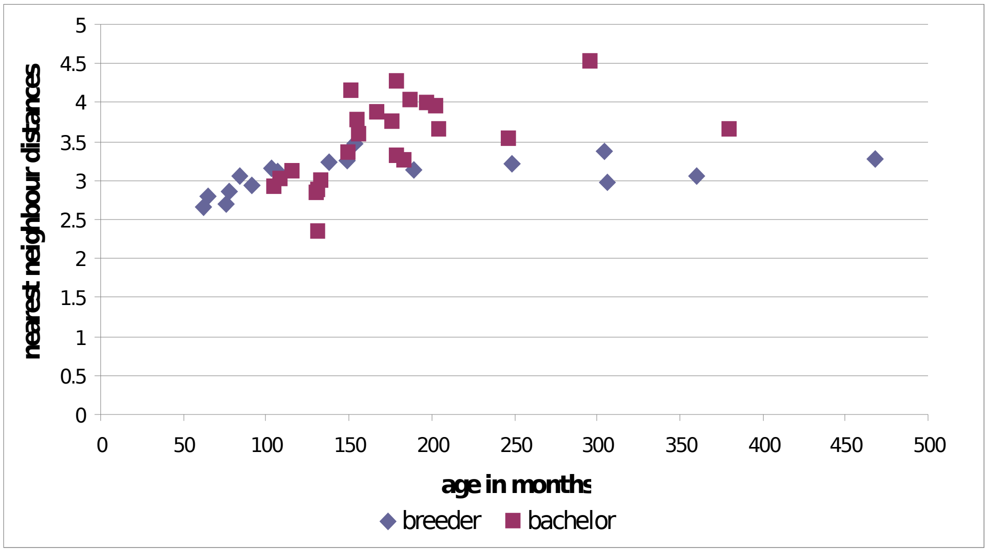
(Full Mixed Models are given in Appendix V)

4.3.1 Social spacing

Nearest neighbours with females

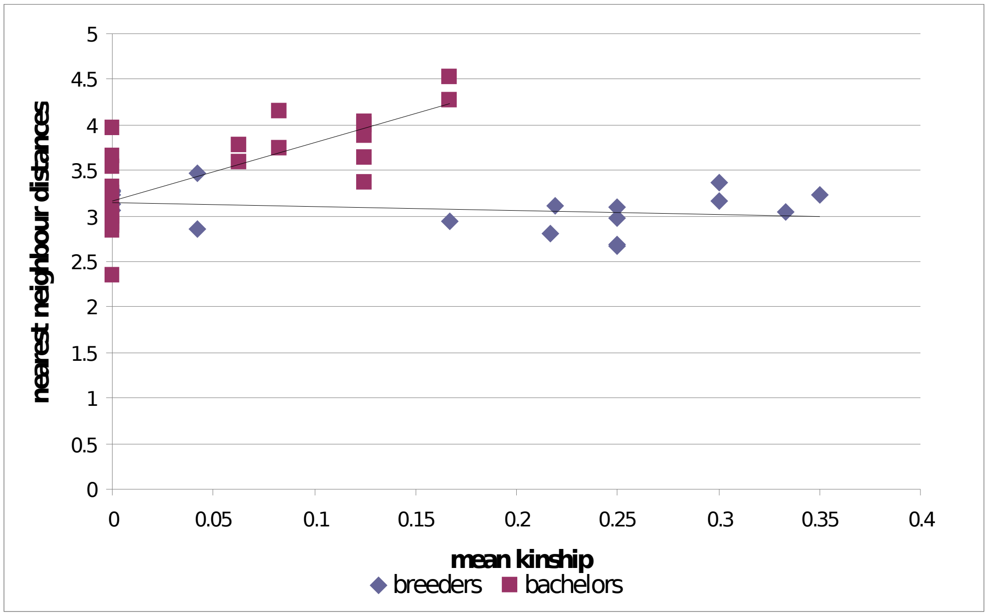
There was a significant effect of both age ($F_{(1, 26)} = 8.397$, $p = 0.008$) and group type ($F_{(1, 26)} = 37.434$, $p < 0.000$) on the distance between an individual and his nearest neighbour (with the data from females, juveniles and infants present). Distances between individuals and their nearest neighbour are further for older individuals (fig 4.1) and further for males in bachelor groups than breeder groups (fig 4.1).

Fig 4.1 Nearest neighbour distances between captive male western gorillas housed in breeder and bachelor groups (data when females, juveniles and infants are the nearest in breeder groups included)



There was also a significant interaction between group type (breeder/bachelor) and the average mean kinship with other group members ($F_{(12, 26)} = 3.995$, $p = 0.002$). Mean kinship seems to have little effect on breeder males but in bachelor groups, males with more relatives in the group (higher average mean kinship scores) are further apart (fig 4.2).

Fig 4.2 Nearest neighbour distances and average mean kinships with group members of captive male western gorillas housed in breeder and bachelor groups (data when females, juveniles and infants are nearest included)



Nearest neighbours without females

Excluding the data when females, juveniles and infants were the nearest neighbours of males in breeder groups, there were significant effects of average mean kinship with other group members ($F_{(9, 21)} = 2.514$, $p = 0.039$), group type (breeder/bachelor) ($F_{(1, 21)} = 8.087$, $p = 0.010$) and institution ($F_{(6, 21)} = 3.539$, $p = 0.014$). In addition there was a significant interaction between group type (breeder/bachelor) and the average mean kinship with other group members ($F_{(9, 21)} =2.514$, $p = 0.039$). However there was no significant effect of age on nearest neighbour distances.

As above (when all the data was included) males in bachelor groups exhibit further distances between their nearest neighbours than those in breeder groups (fig. 4.3). The effect of institution may be due to stocking density since individuals housed in enclosures where there is a greater enclosure area per individual show further distances between individuals and their nearest neighbours (fig 4.4). The overall significant effect of mean kinship suggests that males with more relatives in the group have further distances to nearest neighbours and this is more pronounced for bachelor males hence the significant group type / mean kinship interaction (fig 4.3).

Fig 4.3 Nearest neighbour distances and average mean kinship with other group members of captive male western gorillas housed in breeder or bachelor groups (data when females, juveniles and infants are nearest neighbours excluded)

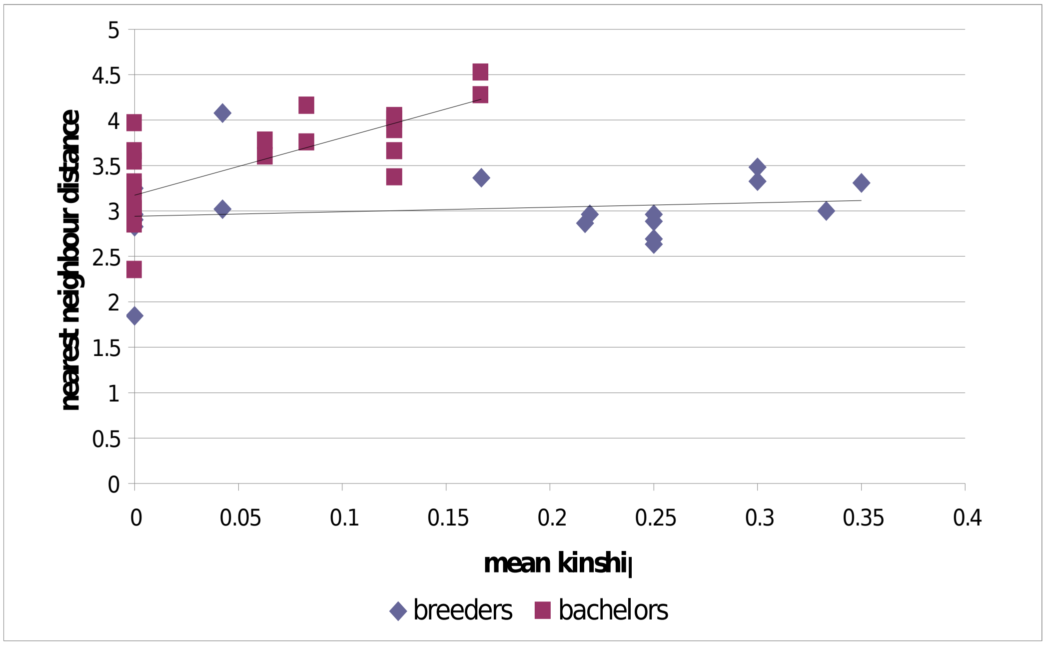
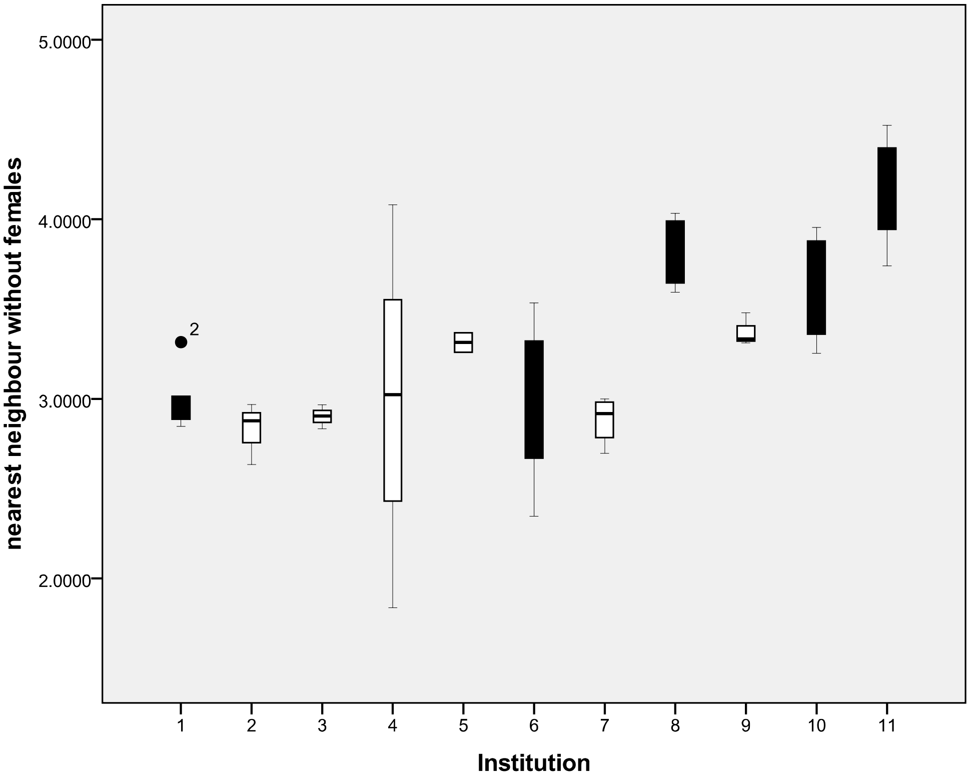


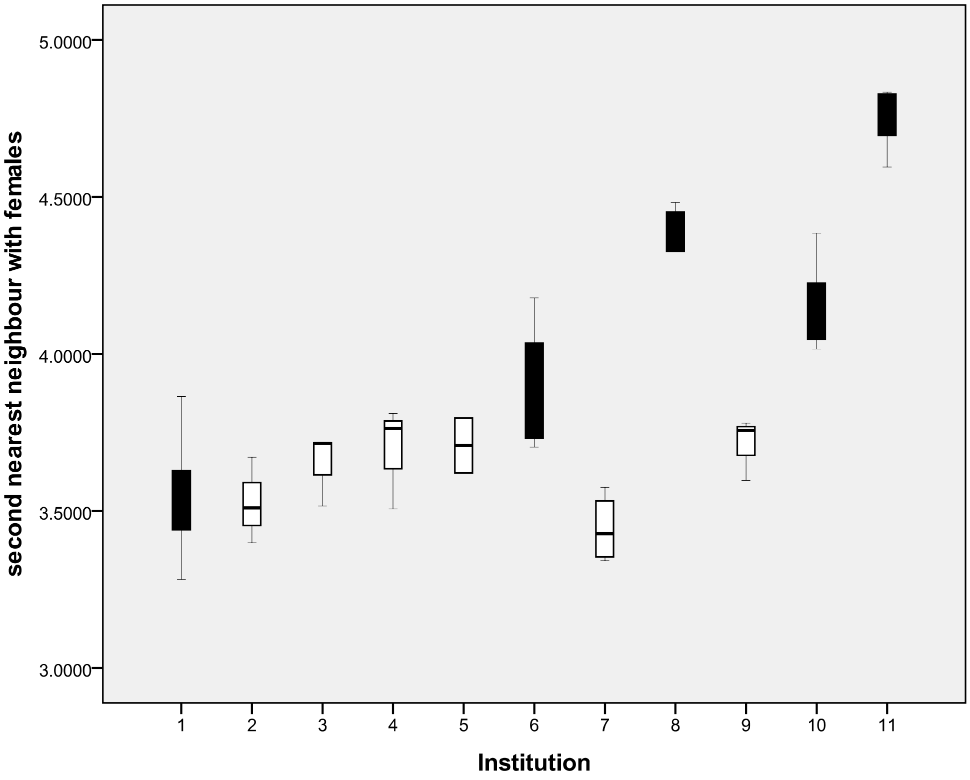
Fig 4.4 Nearest neighbour distances and institutions (data when females, juveniles and infants are nearest neighbours excluded). Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values)



Second nearest neighbours with females

There were significant effects of both group type (breeder/bachelor) ($F_{(1, 30)} = 119.814$, $p < 0.000$) and institution ($F_{(9, 30)} = 20.546$, $p < 0.000$) on the distance between the males and their second nearest neighbour. Bachelor males have further distances between individuals and their second nearest neighbour in comparison to breeder males. In addition institutions with greater area of enclosure per individual also show further distances between individuals and their second nearest neighbour.

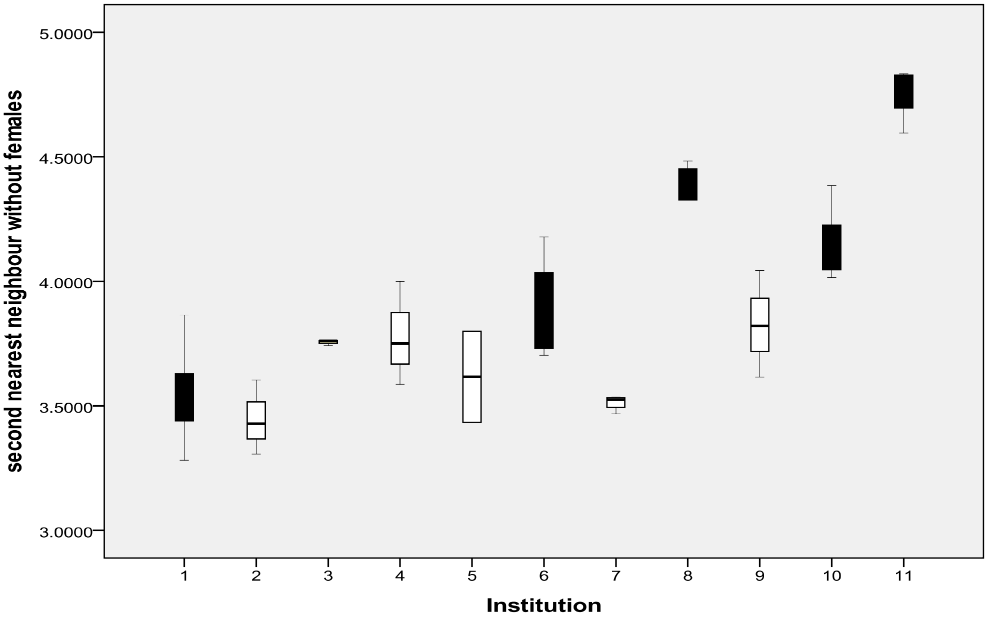
Fig 4.5 Second nearest neighbour distances and institutions (data when females, juveniles and infants are nearest included). Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values)



Second nearest neighbours without females

Excluding the instances when females, juveniles and infants were the second nearest neighbour of breeder group males did not alter the results found above. Again there was a significant effect of group type (breeder/bachelor) ($F_{(1,30)}$= 90.595, p< 0.000) and institution ($F_{(9,30)}$ = 18.505, p < 0.000) on the distance between an individual and his second nearest neighbour. As with the previous result, bachelors have a further distance between males and their second nearest neighbour (fig 4.6), and institutions with greater area of enclosure per individual also have greater distances between males and their second nearest neighbours (fig 4.6)

Fig 4.6 Second nearest neighbour distances and institutions (data from females, juvenile and infants absent). Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes.



Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values)

The significant results of the analyses of the nearest and second nearest neighbour data is summarized in Table 4.2.

Table 4.2 Summary of factors having significant effects on the distance between male gorillas and their nearest and second nearest neighbour.

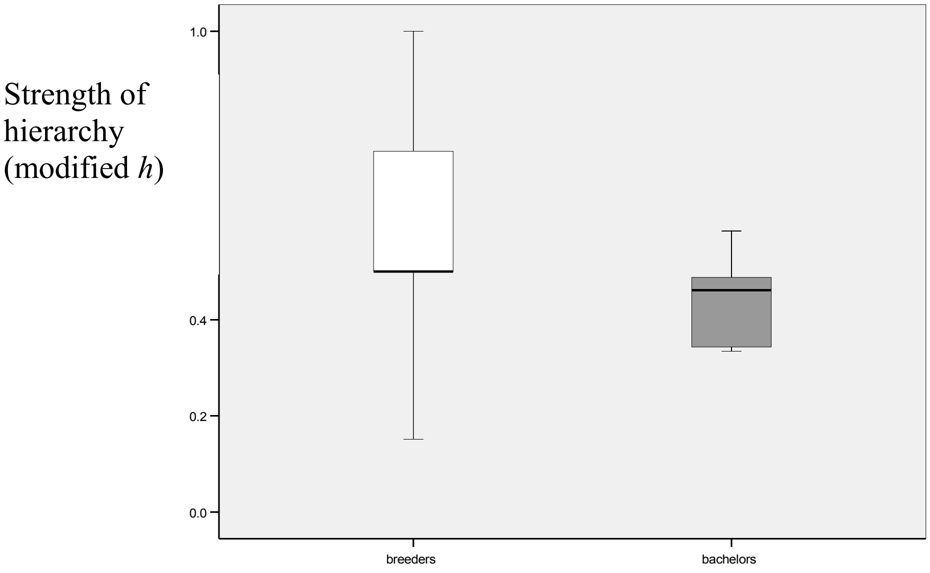
1st neighbour with female data	1st neighbour without female data
Age in months (older males have further distances)	Mean kinship (males with higher mean kinship have further distances)
Group type (bachelor males have further distances)	Group type (bachelor males have further distances)
Breeder bachelor and mean kinship interaction (in bachelor groups males with higher mean kinship have further distances)	Breeder bachelor and mean kinship interaction (in bachelor groups males with higher mean kinship have further distances)
	Institution (further distances in institutions with more area per animal)
2nd neighbour with female data	**2nd neighbour without female data**
Group type (bachelor males have further distances)	Group type (bachelor males have further distances)

Institution (further distances in institutions with more area per animal)	Institution (further distances in institutions with more area per animal)

4.3.2 Dominance hierarchies

Dominance hierarchies for each group were calculated according to the method suggested in Singh *et al* (2003). The strength of hierarchy (or linearity) for males within breeder and bachelor groups was compared (Fig. 4.7).

Fig. 4.7 Strength (linearity) of dominance hierarchies between males in breeder groups and bachelor groups.

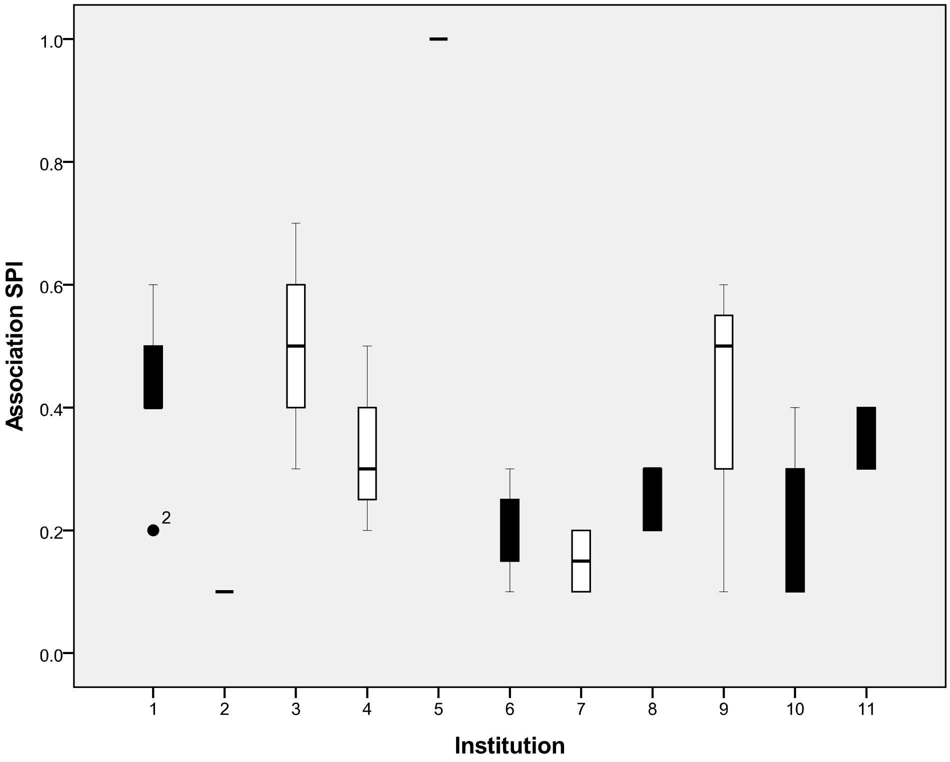


There was no significant difference either in mean hierarchy strength between bachelor and breeder groups, ($T_{(9)} = 0.979$, $p > 0.05$] or between the variance of hierarchy strength ($F_{(5, 4)} = 7.30836$, $p > 0.05$).

4.3.3 Association indices

All the SPI's measured were low (all means are below 0.5) indicating even associations between all dyads. Only institution had a significant effect on the expression of association SPI ($F_{(10, 30)} = 9.36$, $p < 0.000$)

Fig 4.8 Association SPI and institutions. Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values) (0 = even association with group members, 1 = association with just one group member).

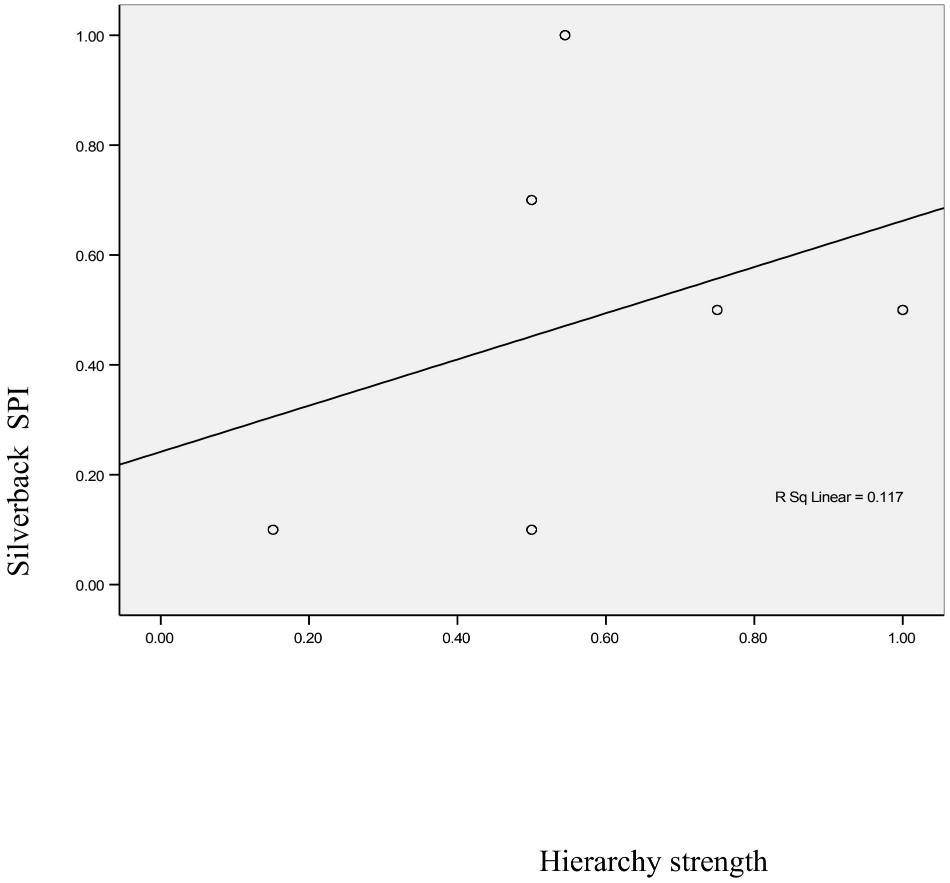


In this case (unlike the nearest neighbor distances) the significant effect of institution on the association SPI does not appear to be due to differences in the area per animal (fig. 4.8).

Relationship between strength of hierarchy and silverback associations

There was a significant correlation between the strength of hierarchy and silverback SPI in breeder groups (Spearman's rho = 0.802, p = 0.05) (fig. 4.9), but not in bachelor groups (Spearman's rho = 0.702, p > 0.05)

Fig 4.9 Correlation between the strength of hierarchy and breeder group silverback SPI



4.4 Discussion

Social distances in breeder and bachelor groups

The distances between males housed in breeder and bachelor groups and their nearest neighbours follow some of the trends predicted. When the data from the females, juveniles and infants is included in the analysis, younger males (subadults) can be seen to have shorter distances between themselves and their nearest neighbours, and this distance increases with age. However, when the instances when females, juveniles and infants were a male's nearest neighbour were excluded, there was no significant effect of age. Therefore we can assume that the younger males within breeder groups are more often closer to the females, juveniles and infants than other males. It is a reasonable assumption in a social animal such as the gorilla that bonds between the younger group members and their mothers is strong, leading to shorter distances to nearest neighbours. In addition, the results of the previous chapter demonstrated that there were behavioural differences with age in the expression of behaviour, and it has been well documented that younger gorillas display higher levels of play and other social behaviours (Pereira and Fairbanks, 1993; Watts and Pusey, 1993). The results of the nearest neighbour analysis seem logical in light of this.

However other effects were not predicted. Bachelor male distances are greater than those seen in the breeder groups despite the reduced competition for resources within the bachelor groups. These results suggest that the bachelor groups observed are avoiding close proximity with each other possibly to reduce aggression. This is contrary to a comparison of multi-male mixed sex and bachelor mountain gorilla groups (Robbins, 1996) where the bachelors were found to spend more time in close proximity. However Robbins (1996) also found that there was a higher incidence of aggression between the bachelors within that comparison suggesting that individuals were not using strategies to avoid aggression.

The effect of kinship on the distance between an individual and his nearest neighbour seems to be far more pronounced in the bachelor groups than in the breeder groups. Those individuals with more close relatives within the group have further distances between themselves and their nearest neighbours. This seems to be somewhat counter-intuitive, as it may be reasonable to assume that males with a higher mean kinship (more relatives) would establish closer bonds and therefore maintain closer proximity, and certainly Robbins (2007) suggests that dominant males are more tolerant of related individuals in multi-male groups. However kinship is not a guarantee of close bonds between males (Van Hooff and Van Schaik, 1994). Equally, this may be an artefact of how we establish bachelor groups in captivity. Although there are closely related animals within the bachelor sample, it is often the case they did not know each other in the natal group before being moved to the bachelor group. Animals will be moved at different times and may have moved to different situations before the bachelor group in question. In addition many of the males within the bachelor groups will have first spent a period of time in the hand raising facility at Stuttgart Zoo before moving to the bachelor situation. This then means that although related, they will not be ‘aware’ that they are and may have developed closer bonds with unrelated individuals that they have been raised with.

There is also an institutional effect on the nearest neighbour distances when the analysis is carried out excluding the data when females, infants and juveniles are the nearest neighbour. As has already been stated (chapter 2) the variable of institution has several confounds including area per individual (m^2) and average temperature per institution. It seems logical to present the data with institutions ordered by area per individual (m^2). Distances between males and their nearest neighbours are further in those institutions with greater area per animal in the enclosure, suggesting that males will increase distance between themselves when given an opportunity to (Judge, 2003; Watts 1995a). The absence of this effect when all the data is included indicates that within the breeder groups the females (and juveniles and infants) are spacing themselves between the males, potentially giving cohesion to the breeder groups (Robbins, 2007). As gorillas are known to be a cross-bonded society (i.e. the females have stronger bonds with the males than with other females within the group; Stewart and Harcourt, 1987; Robbins, 1999) it is likely that the females within the breeder groups will be spacing themselves around the silverback. However the greater male-male distance in larger enclosures may also be indicative of avoidance behaviours to prevent aggression or of peripheralization of blackback males (Robbins, 2007). Blackback male mountain gorillas have been observed to move to the outside of the social group before emigrating, however there is very little information on how this mechanism is driven (Robbins, 2007). This is perhaps not surprising in a species that exhibits male natal emigration in the wild (Harcourt, 1978; Pusey and Packer, 1987; Robbins, 2007). As suggested the benefits of a co-resident male (Robbins, 1995; Watts, 1996) are not obvious within a captive setting (i.e. female and infant defence from intergroup encounters), and so males maybe peripheralizing themselves from the main body of the group (Harcourt and Stewart, 1981; Robbins, 1995; Sicotte, 1994; Watts, 1996). Further investigations into the levels of associations and frequency of behaviours between males within these groups may help to give a clearer indication of why males space themselves out.

Distances between males and their second nearest neighbours consistently showed a significant effect of group type and institution. Bachelor groups consistently show greater distances between males and their second nearest neighbours, regardless of the inclusion of the data from the females within the group. It can also be seen that institution effect, when presented as area of enclosure per individual, also impacts on the second nearest neighbour distances. Where there is more space available gorillas will increase distances between individuals.

Strength of hierarchy

Although there were no significant differences between breeder and bachelor groups in either means of strength of hierarchy or the amount of variance between the two groups, the level of variation within the breeder groups reflects the natural variation in social systems within wild gorilla groups. It's known that in the wild as many as 40% of breeding gorilla groups have co-resident males, assisting in the female and infant defence of the group (Robbins, 1999). In order for this social system to be acceptable, there must be a level of tolerance or avoidance between the males suggesting a more egalitarian hierarchy (Vehrencamp, 1983) to reduced risk of aggression. It seems reasonable to suggest that some captive breeder groups may follow this social system in conditions where competition for resources is not necessary (i.e. several females, plenty of food and space) even when the need for co-resident males to act in defence of females and infants is not necessary; whereas environmental conditions in other captive breeder groups may necessitate the need for a more despotic dominance hierarchy between the males. It appears that dominance hierarchies between males in captive breeder groups are variable and may well be dependant on the resources around them.

In addition, gorillas in the wild are known to exhibit flexibility in social systems, probably dependant on surrounding environmental factors (including the presence of other gorillas) (Weiche, 2006). These results indicate that captive breeder groups are capable of exhibiting variation in social styles which may translate to flexibility if environmental conditions alter.

The bachelor groups show less variation and, although not a significant difference, this may reflect both the lack of need for a strong dominance hierarchy for the control of resources and the lack of need for 'extreme' egalitarian groups to avoid aggression. A lack of both extremes can be said to be due to the same basic cause – they are both mechanisms to minimise outright aggression over females.

Association SPI

The association SPI varied significantly between institutions, but the cause of this was not determined as there was no clear relationship between SPI and area of enclosure per animal. There are other potential variables that may have an impact on the associations within the group, including individual personality. Unfortunately more data will be needed to clarify whether this or some other aspect of the institution is the cause of this result. Despite the prediction there was no effect of group type on association SPI suggesting that males in bachelor groups do not have a more even distribution of association with other members of the group compared with breeder group males.

Correlations between hierarchy strength and silverback SPI

Although there was no evidence of a correlation between bachelor strength of hierarchy and bachelor silverback SPI, there was a significant correlation between breeder group strength of hierarchy and breeder group silverback associations. This suggests that silverback males within the more despotic (linear) hierarchies exhibit associations with fewer co-resident males than silverbacks within the more egalitarian hierarchies. There may be situations, such as control of access to females, where a stronger association with one individual may prove more useful to a silverback in the maintenance of a linear (despotic) hierarchy than several more evenly distributed associations. This does not seem to be the case within a bachelor group system, potentially due to the lack of competition for resources.

In summary, young males have shorter distances between themselves and their nearest neighbours, suggesting that in breeder groups young males are more often in closer proximity to females, juveniles and infants. In bachelor groups, males have further distances to their nearest neighbours and when coupled with the effect of institution, it suggests that bachelor males will utilise available space to decrease proximity and avoid the potential for aggression. The counter-intuitive result for the effect of kinship on the distances between nearest neighbours for bachelor males suggests that when not in the presence of a resource, kinship is not a predictor of strong bonds between related males. However this result may also be an artefact of captivity.

Chapter 5: Social relationships between males in breeder and bachelor groups of gorillas

5.1 Introduction

5.1.1 Social groups

Although there are many potential benefits to living within a social group (e.g. female and infant defence, Robbins 1995; Watts, 1996) there is also the potential for increased conflicts, competition and aggression between group members. These three phenomena can be defined as separate issues within a social situation (Mason, 1993; Bernstein, 2007). A conflict of interest can arise in situations where two individuals may want to engage in differing activities (e.g. one individual may want to play fight, the other doesn't) or in competition over limited resources. This may lead to a range of potential behavioural responses (de Waal, 1996; de Waal, 2000).

Multi-male mixed sex groups of mountain gorillas exhibit higher levels of aggression than affiliation between males, but also maintain greater distances to avoid potential aggression (Robbins, 2007). There was a previous assumption that dominant males would monopolise breeding in groups. However, genetic analysis has indicated that subdominant males in multi-male groups may sire up to 15% of the group offspring (Bradley *et al*, 2005), demonstrating an obvious benefit to remaining within the group. Robbins (1994) found that aggression between males in multi-male mixed sex groups was more frequent when a female was in oestrus, suggesting that males compete over access to females.

Whilst species that vary between one-male and multi-male systems, often exhibit highly agonistic relationships between males, it has been reported in comparison that bachelor groups are characterised by peaceful male-male interactions (Pusey and Packer, 1987). The lack of females within the bachelor group reduces the motivation for male competition.

5.1.2 Aggressive behaviours

Aggression can be seen as a behavioural mechanism necessary to resolve a conflict of interest (Mason, 1993), or alternatively as a means of negotiation between individuals (Aureli and de Waal, 2000).

Traditionally aggression has been viewed as a negative social behaviour leading to the deconstruction of social bonds (Popp and DeVore, 1979). Indications that losers of aggressive conflicts tend to avoid winners led to the assumption that there is a dispersive impact of aggression, and so to the establishment of the dispersal hypothesis (Lorenz, 1963), where aggression works as a spacing mechanism. In this scenario aggressive behaviour causes the loser to avoid the winner and predicts a decreased probability of contact and an increase in distance between the individuals involved. This would obviously have a negative effect on the cohesion of a social grouping, imposing distances upon individuals.

Conversely some studies of aggression in primate groups have often shown that distances between individuals involved in aggressive incidences lessen instead of increase (de Waal and Ren, 1988; de Waal and van Roosmalen, 1979; de Waal and Yoshihara, 1983). This has led to a body of research based on the behaviours of aggressors and victims in post aggressive situations, and the identification of reconciliation or consolation behaviours in a range of primates (e.g. Aureli and van Schaik, 1991; Cheney and Seyfarth, 1989; Cordoni, Palagi and Tarli, 2006; Judge, 1991; Watts, 1995a, 1995b; York and Rowell, 1988).

However aggression can also be viewed as a costly behaviour (expenditure of energy, damage to social bonds, risk of injuries) and therefore may only be an appropriate response to a conflict of interest when the benefits of aggression (i.e. control of resources) outweigh the potential costs. Whilst it is reasonable to expect that social interactions may escalate into aggression in response to competition over a limited food resource, it is far less likely to occur in response to an unwilling play partner (Bernstein, 2007).

Behavioural mechanisms that may work to prevent aggressive escalation may be strongly selected for in social animals; however there has been very little research focussed on this particular area to date (Arnold and Aureli, 2007).

5.1.3 Affiliation in social systems

The evaluation of affiliative behaviours has underpinned a large proportion of the research into the social complexity of many social species, particularly non –human primates. Affiliative behaviours are often termed 'positive interactions' and within the primates can include grooming, social resting and play fighting.

Social rank and dominance hierarchies can be seen to affect the distribution of affiliative behaviour within a group. High ranking individuals generally initiate affiliative interactions (particularly grooming) at a far lower rate and receive affiliative interactions at an increased rate in comparison to lower ranking individuals (de Waal and Luttrell, 1986; Mehlman and Chapais, 1988; Silk, 1982, 1992).

The distribution of affiliative interactions within a primate group can also be strongly influenced by the reproductive status of the females within that group. In this situation it has been suggested that increased grooming behaviour reduces the risk of aggression, allows the increased proximity necessary for mating to occur and can temporarily impact on social status within groups (Mehlman and Chapais, 1988).

It seems likely that the benefit received by the initiator of an affiliative interaction is social tolerance, so that a low ranking animal initiating an affiliative interaction with a higher ranking animal is able to maintain proximity and thereby some level of protection or sharing of resources. However there is a lack of easily interpretable data on a causal relationship between affiliative behaviours and agonistic support, partly because these interactions often occur at a low rate and can be separated by long time intervals. Tolerance may not be the only benefit to establishing an affiliative relationship. Within mountain gorilla groups it appears that male infants who establish a strong bond with the silverback and maintain that through adolescence are more likely to inherit leadership of the group whereas those male infants who do not establish such as strong bond are more likely to emigrate from the group (Harcourt, 1981).

It has been observed that social development is strongly affected by the experiences within a peer group. Therefore the acquisition and development of affiliative behaviours can be paramount to an individual's development. Research has indicated that individuals that are deprived from or not exposed to social interaction with peer groups may exhibit reduced social competence in adult life (de Waal and Johanowicz, 1993; Pereira and Fairbanks, 1993; Roney and Maestripieri, 2003;).

The results from the previous chapter indicate that there was variation in the hierarchy strength of the breeder groups from despotic to more egalitarian situations but far less variation in the hierarchy of bachelor groups. This chapter will explore the social relationships and the expression of conflict and affiliative behaviours within breeder and bachelor groups.

5.1.4 Hypotheses / predictions

- Females can be viewed as a resource where the benefits of maintaining access outweigh the potential costs (injury, damage to social bonds) of aggressive behaviour. Therefore it is predicted that:
    - Males in breeder groups will have higher frequencies of all dominance and aggressive behaviours than males in bachelor groups.
    - Dominance behaviour of males in breeder groups will tend more towards aggression and less towards display i.e. they will have a higher dominance behaviour index (DBI) than males in bachelor groups.
- In the absence of females and assuming less dominance behaviour (see hypotheses above) there will be reduced motivation for affiliative behaviour to maintain social cohesion and encourage tolerance. Therefore it is predicted that:
    - Males in bachelor groups will have a lower frequency of affiliative behaviour than males in breeder groups
    - Males in bachelor groups will have a poorer relationship quality index (ie more dominance behaviour relative to affiliative behaviour) than males in breeder groups.
- Males in groups with a stronger hierarchy will have a poorer relationship quality than males in groups with weaker hierarchy.

5.2 Methods

5.2.1 Data manipulation and statistics

Data were collected through continuous focal follows in twenty minute sessions (see chapter 2). Frequencies of aggression (both contact and non-contact aggression), dominance behaviours (aggression, display and supplant behaviours) and affiliative interactions (grooming, social resting, play fighting) between the focal males in each group were calculated for each individual. In order to compare levels of behaviours across the groups, each individual's score was corrected for the number of potential male partners (e.g. at Apenheul there were four focal males, therefore the total number of behaviours for each focal male was divided by three), and a rate per minute was calculated.

Dominance Behaviour Index (DBI)

In order to evaluate the relative intensity of dominance behaviours, a single weighted variable, the dominance behaviour index (DBI) was calculated where a higher value indicates a higher proportion of escalated aggressive behaviour relative to less aggressive dominance behaviours (display etc). Each behaviour was assigned a value, and the proportional frequency of that behaviour calculated. This was then multiplied by the assigned value and the resultant figures summed to give one representational value per individual gorilla (See chapter 4 for a worked example using the distance categories). Assigned categories were as follows, 1 = supplant, 2 = display (both tense stance and display charge behaviours), 3 = non-contact aggression, 4 = contact aggression.

Relationship Quality Index

The relationship quality index (RQI) was based on a mother-infant relationship quality index developed by de Waal and Weaver (2002) to examine the influence of parenting styles on infant behaviour patterns.

$$\text{RQI} = \frac{\text{affiliative interactions (per min)}}{\text{affiliative interactions + dominance interactions (per min)}}$$

In this situation the rate per minute of affiliative interactions is divided by the total rate per minute of both affiliative and dominance behaviours (corrected for number of potential male partners). This calculation gives a number between 0 and 1, where 0 represents dominance interactions only and 1 represents affiliative interactions only, this allowing an assessment of the ratio of expression of social behaviours.

The effects of group type, institution, age, mean kinship and rearing style on the frequency of all dominance behaviours, the frequency of aggressive behaviour, the DBI, frequency of affiliative behaviour and the RQI were investigated using mixed model ANOVAs. In cases where there was a significant effect of mean kinship or rearing type an “applied” analysis (see chapter 2) was also performed to identify differences between bachelor and breeder groups that might have implications for management and welfare. Correlations were used to investigate the relationship between hierarchy strength and RQI.

5.3 Results

(Full Mixed Models are given in Appendix V)

5.3.1 Frequency of dominance behaviours

The effect of group type on the frequency of dominance behaviours was approaching significance ($F_{(1, 27)} = 4.129$, $p = 0.052$) showing a trend for bachelor males to exhibit lower frequencies of dominance behaviour than breeder group males (Fig 5.1). There was a significant interaction between group type and mean kinship with other group members ($F_{(12, 27)} = 3.361$, $p = 0.004$). In breeder groups individuals with low mean kinship (unrelated to the rest of the group) showed higher frequencies of dominance behaviours than those with higher mean kinship (Fig 5.2), whereas in bachelor groups there was little effect of mean kinship.

Fig 5.1 Frequency of dominance behaviours in captive male western gorillas housed in breeder and bachelor groups.

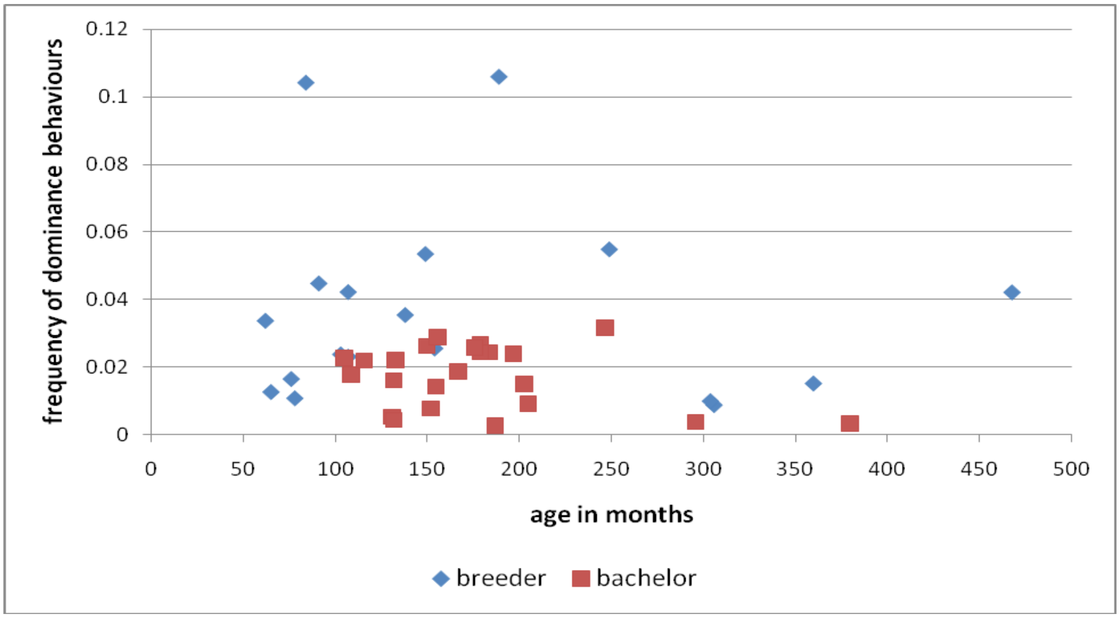
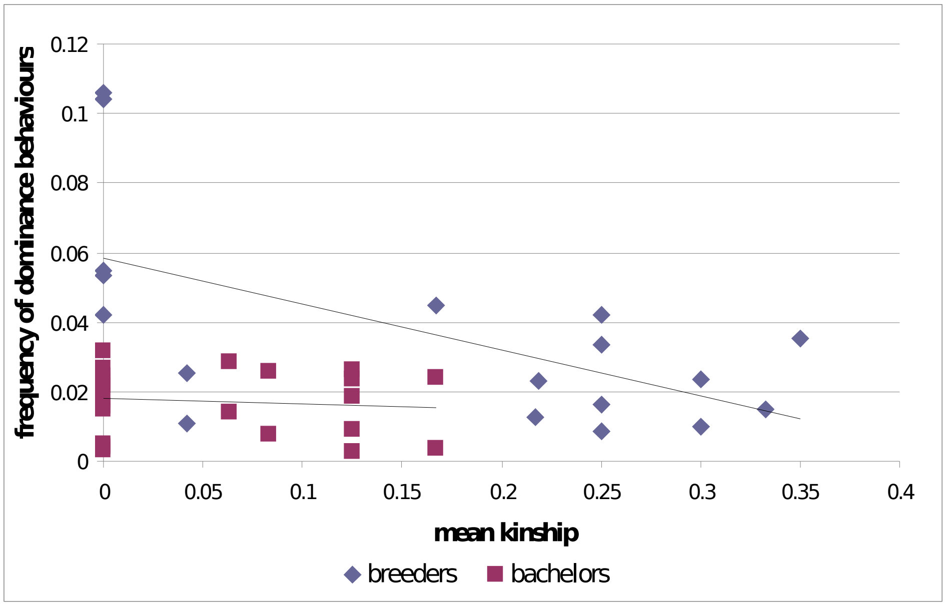


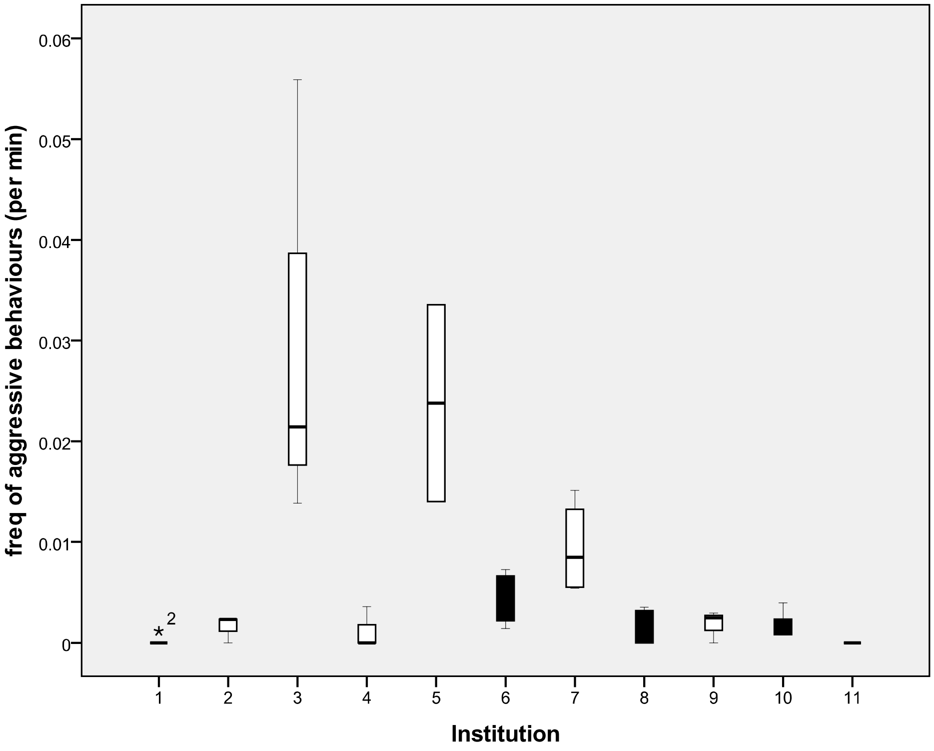
Fig. 5.2 Frequency of dominance behaviours (per min) and mean kinship with other group members in captive male western gorillas housed in breeder and bachelor groups



5.3.2 Frequency of aggressive behaviour

There was a significant effect of group type (breeder/bachelor) ($F(1, 30) = 21.145$, $p < 0.000$) and of institution ($F(9, 30) = 5.863$, $p < 0.000$). Frequency of aggressive behaviours was lower in bachelor groups than breeder groups. The institution effect seems to be related to enclosure size with a tendency for fewer aggressive behaviours as area of enclosure per individual increased (Fig 5.3). Three breeder groups, all formed of unrelated males, with low-medium area per individual had the highest frequencies of aggressive behaviours. However, there was no overall significant effect of mean kinship.

Fig 5.3 Frequency of aggressive behaviour (per min) and institutions. Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values)



5.3.3 Dominance behaviour index (DBI)

There was a significant effect of institution on the index of dominance behaviours ($F_{(6, 21)} = 5.569$, $p = 0.001$). The effect of institution again appears to be due to enclosure size; as the area of enclosure per individual increases, the DBI weighted more towards display behaviour rather than supplant behaviour or aggressive behaviours (Fig 5.4). In addition the effect of mean kinship and the interaction between group type (breeder / bachelor) and mean kinship with other group members was approaching significance ($F_{(9, 21)} = 2.351$, $p = 0.051$).

In breeder groups individuals with higher mean kinships had a lower DBI whereas in bachelor groups mean kinship had little or possibly the opposite effect on DBI (Fig 5.5).

Fig 5.4 Dominance behaviour index and institutions. Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2).

(See chapter 2, table 2.3 for values)

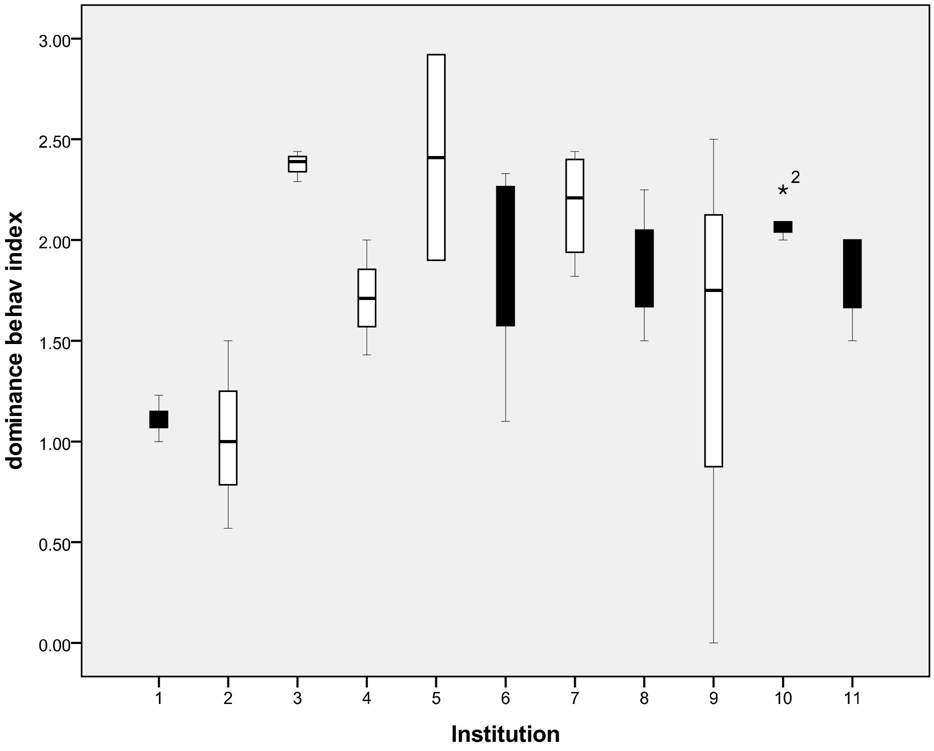
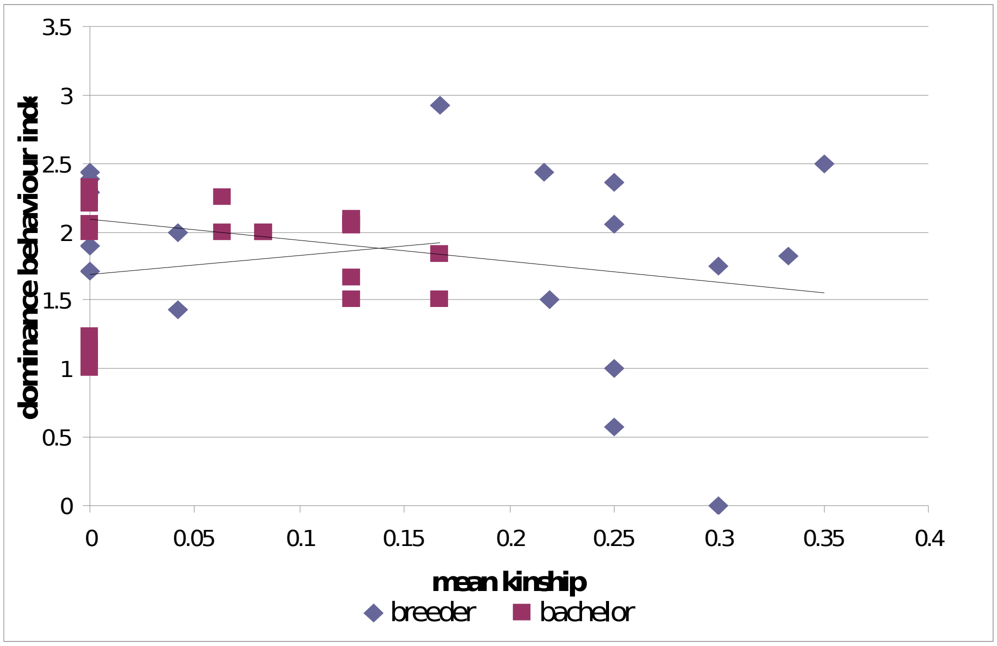


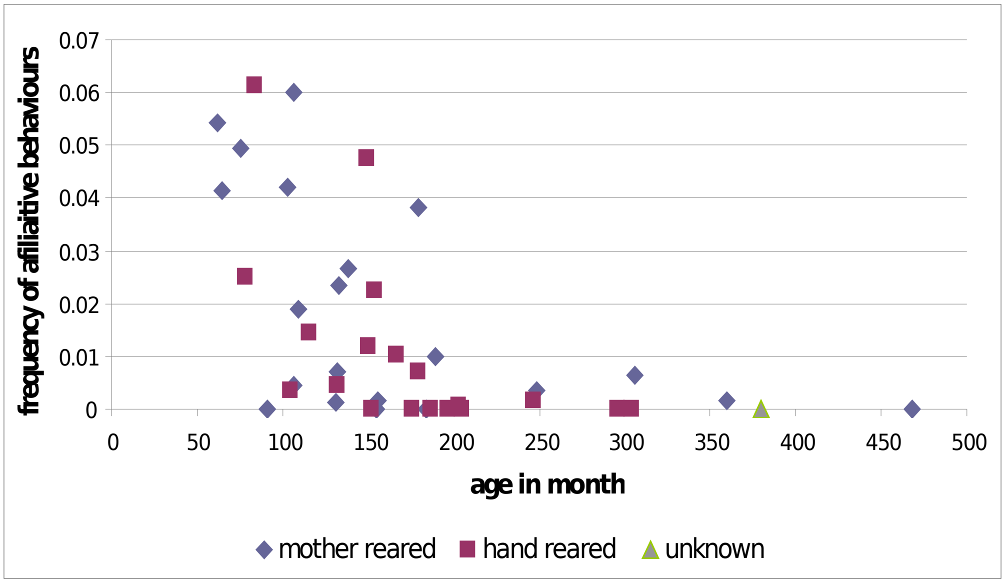
Fig 5.5 Dominance behaviour index and mean kinship with other group members in captive male western gorillas housed in breeder and bachelor groups.



5.3.4 Frequency of affiliative behaviours

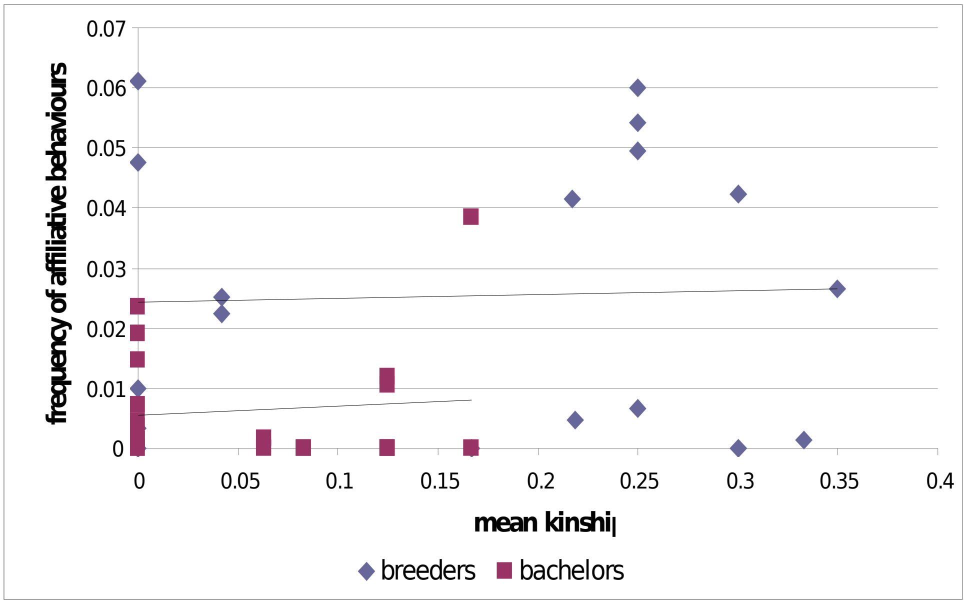
There was a significant effect of age ($F_{(1, 24)} = 50.393$, $p < 0.000$) and rearing style ($F_{(2, 24)} = 3.484$, $p = 0.047$) on the rate of affiliative behavior. Mother reared males showed a greater frequency of affiliative behaviours than hand reared males and young males showed a greater frequency of affiliative behaviours than older males (Fig 5.6).

Fig. 5.6 Frequency of affiliative behaviours in captive male western gorillas that have been hand reared or mother reared.



There was also a significant effect of mean kinship with other group members ($F_{(11, 24)}$ = 4.115, p = 0.002) and a significant interaction between group type and mean kinship with other group members ($F_{(2, 24)}$ = 18.280, p < 0.000). Individuals with a low mean kinship with other group members (fewer related males in the group) showed lower frequencies of affiliative behaviours than males with higher mean kinship with other group members (more related males in the group) and this effect is more pronounced in breeder than bachelor groups (Fig 5.7).

Fig 5.7 Frequency of affiliative behaviours and mean kinship in captive male western gorillas housed in breeder and bachelor groups



5.3.5 Relationship Quality Index (RQI)

There was a significant effect of group type (breeder/bachelor) ($F_{(1, 26)} = 5.099$, $p = 0.033$) and age ($F_{(1, 26)} = 22.721$, $p < 0.000$) on the RQI. Males in breeder groups had higher RQI's (i.e. more affiliative than dominance behaviour) than males in bachelor groups and younger males had higher RQIs than older males (Fig. 5.8).

There was also a significant effect of mean kinship with other group members ($F_{(11, 26)} = 2.928$, $p = 0.012$) and a significant interaction between group type (breeder/bachelor) and mean kinship ($F_{(1, 26)} = 6.674$, $p = 0.016$). Overall males with a higher mean kinship had higher RQIs than those with lower mean kinship (Fig. 5.9). However the interaction between group type and mean kinship shows that this is mainly for males in breeder groups, in bachelor groups the trend may be opposite.

Fig. 5.8 Relationship Quality Index in captive male western gorillas housed in breeder and bachelor groups

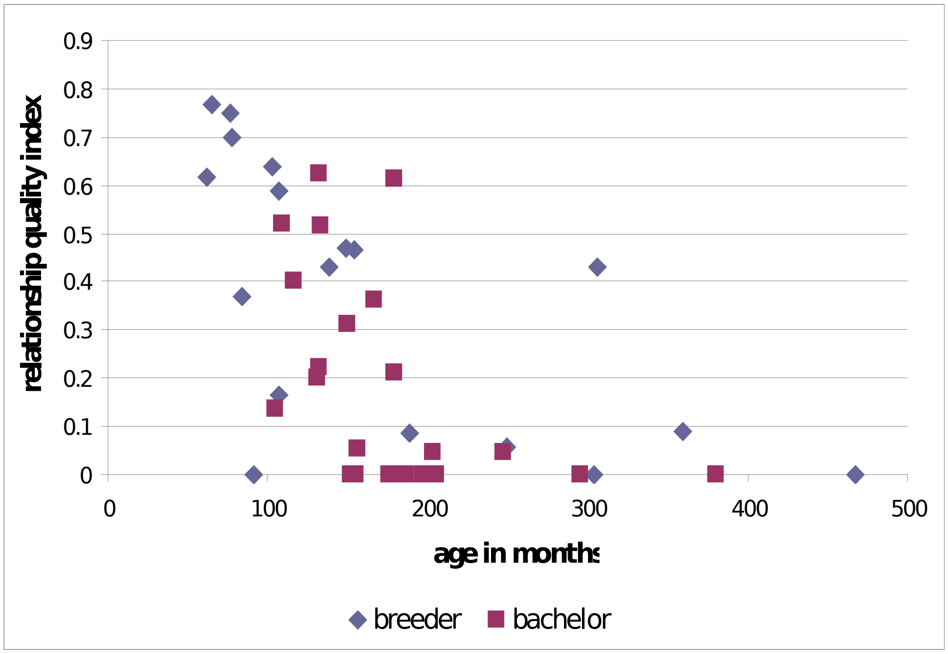
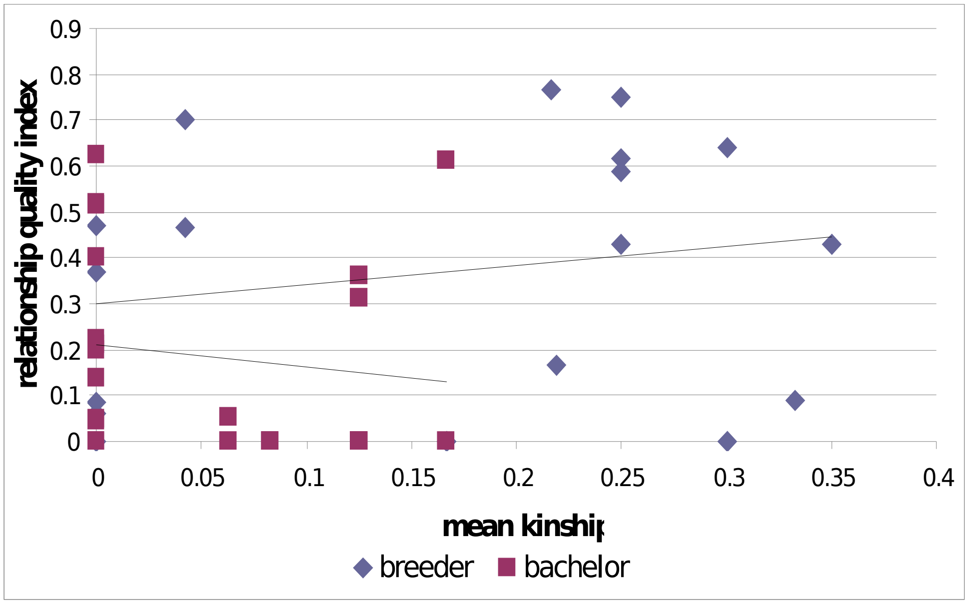


Fig 5.9 Relationship Quality Index and mean kinship in captive male western gorillas housed in breeder and bachelor groups.



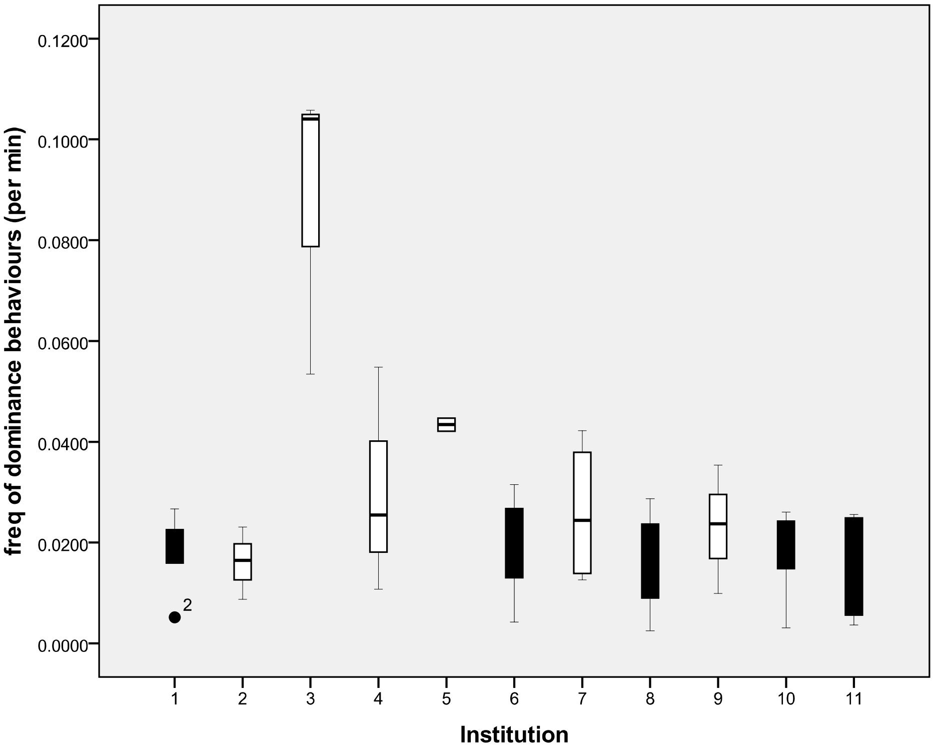
5.3.6 “Applied” Results

These were performed only where there was a significant effect of mean kinship or rearing type and excluded these factors from the model (see chapter 2).

Frequency of dominance behaviours

There was a significant effect of group type (breeder/bachelor) ($F_{(1, 30)} = 22.190$, $p < 0.000$) and institution ($F(9,30) = 6.134$, $p < 0.000$). Bachelor groups exhibited lower frequencies of dominance behaviours than breeder groups, and frequencies of dominance behaviours decreased as the area of enclosure per individual increases (Fig. 5.10).

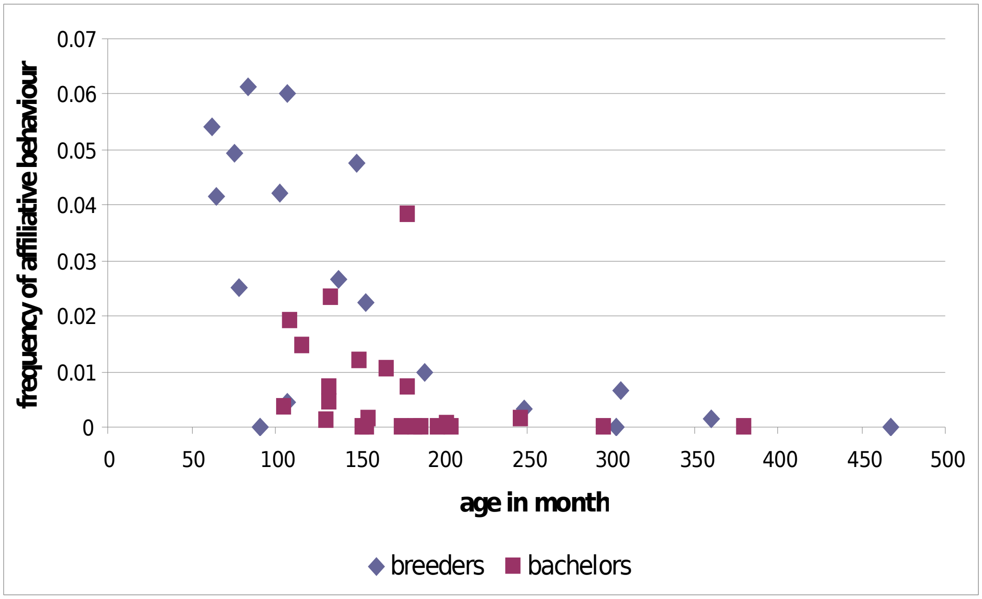
Fig 5.10 Frequency of dominance behaviours and institutions. Breeder groups are represented by open boxes, bachelor groups are represented by closed boxes. Institutions are presented in order of increasing area of enclosure per individual (m^2). (See chapter 2, table 2.3 for values)



Frequency of affiliative behaviours

There was a significant effect of group type (breeder/bachelor) ($F_{(1, 38)} = 18.103$, $p < 0.000$) and age ($F_{(1, 38)} = 19.985$, $p < 0.000$). Breeder group males show higher frequencies of affiliative behaviours than bachelor group males, and younger males show higher frequencies of affiliative behaviours than older males (Fig 5.11).

Fig 5.11 Frequency of affiliative behaviours in captive male western gorillas housed in breeder and bachelor groups.



Relationship Quality Index (RQI)

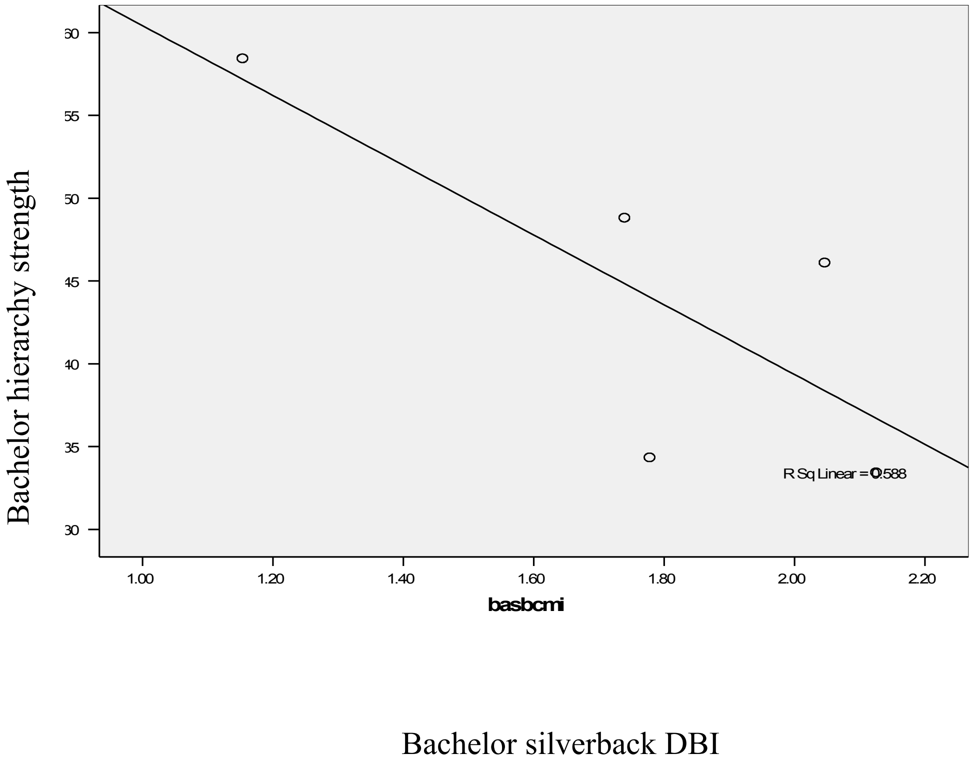
There was a significant effect of group type (breeder/bachelor) ($F_{(1, 38)} = 7.413$, $p = 0.01$) and age ($F_{(1, 38)} = 19.607$, $p < 0.000$) on the relationship quality index. Bachelor males had a lower RQI than breeder males indicating fewer affiliative behaviours relative to dominance behaviours and younger males a higher RQI than older males (see Fig 5.8).

5.3.7 Correlations of strength of hierarchy with DBI, and RQI and behaviours

When including all the males in the group there were no significant correlations between RQI and strength of hierarchy for either the breeder or bachelor groups. However in

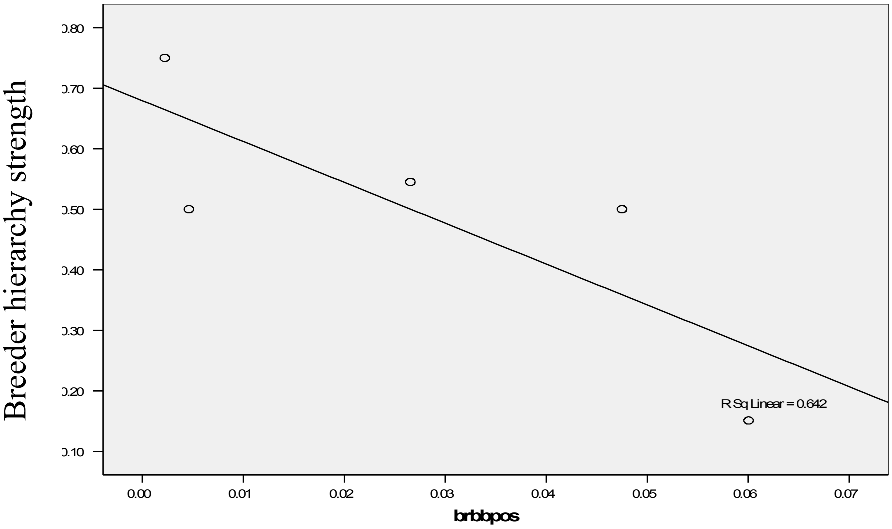
bachelor groups there was a significant negative correlation between bachelor strength of hierarchy and the DBI for adult dominant males only (silverbacks)
(Spearman's rho = -0.90, p = 0.019) (Fig 5.12). However it should be noted that one individual is an outlier, and driving the correlation. Removal of this data point causes the relationship to be lost (Spearman's rho = -0.80, p = 0.20).

Fig. 5.12 Correlation between strength of hierarchy and silverback's DBI in bachelor gorilla groups (averaged per group)



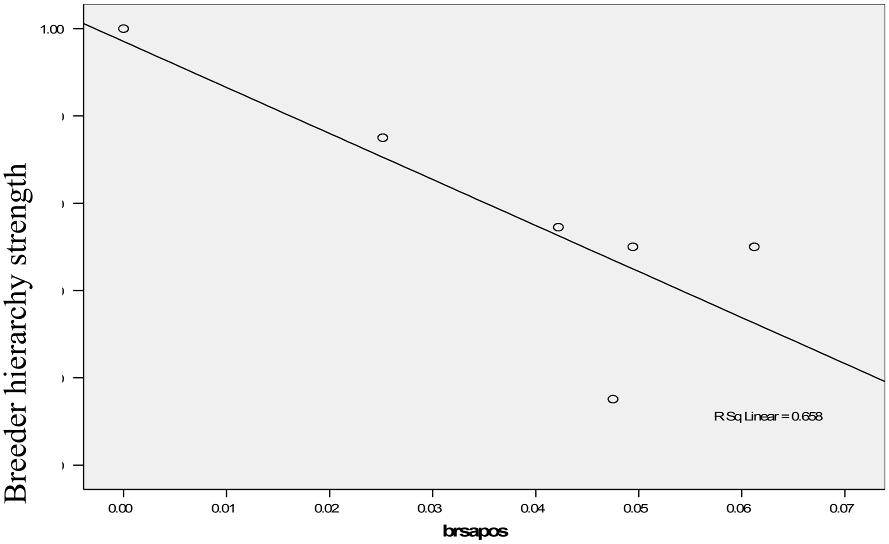
In addition significant negative correlations were found between the strength of hierarchy in breeder groups and the rate of affiliative behaviours in breeder group blackbacks (Spearman's rho = -0.821, p = 0.044), and subadults (Spearman's rho = -0.812, p = 0.025) (Figs 5.13 and 5.14).

Fig 5.13 Correlation strength of hierarchy in breeder groups and the rate of affiliative behaviours of blackbacks (averaged per group)



breeder blackback affiliative rate

Fig 5.14 Correlation between strength of hierarchy in breeder groups and the rate of affiliative behaviours of subadults (averaged per group)



breeder subadult affiliative rate

5.4 Discussion

Dominance and aggressive behaviours and DBI

The frequency of all dominance behaviours (approaching significance) and of aggressive behaviours (significantly) were both found to be greater in breeder groups than in bachelor groups as predicted. This was also true for all dominance behaviours when mean kinship was excluded in the applied model. In addition frequency of aggressive interactions and the Dominance Behaviour Index were both significantly affected by institution with higher frequencies of aggression and higher (more aggressive) DBIs occurring in smaller enclosures. As previously stated (chapter 2), institution is a complex variable, however it seems logical that area of enclosure per individual (m^2) will impact on this result. In breeder groups individuals with more relatives in the group (higher mean kinship) showed less dominance behaviour and had a lower DBI but in bachelor groups mean kinship had little effect on dominance and aggression. Dominance, aggression and DBI were not significantly affected by age or rearing style.

These results support the predictions that breeder groups would have higher levels of dominance and aggression due to the presence of an additional resource – females (Bradley *et al*, 2005). They suggest that the benefits of control of this resource (the females) outweigh the potential costs of dominance behaviours (injury, damage of social bonds) leading to higher levels of dominance encounters and specifically aggressive interactions between males within a breeder group. In addition it has previously been noted that interactions within all-male primate groups are often markedly more peaceful in contrast to the same species when in mixed sex groups (Pusey and Packer, 1987). Since significant effects of group type were detected despite the presence of other significant factors in the model it suggests that this, in part, related directly to the presence of females.

The frequencies of aggressive behaviours and the DBI were significantly affected by institution, with frequencies of aggression and DBI both decreasing in enclosures with a greater area per individual. The variable of institution consists of several potentially confounding influences including area of enclosure per individual, season and number of animals within the group. Although the data within this research does not allow for the analysis of the individual variables which contribute to 'institution', there is a body of literature focussing on the effect of the environment on the activity of captive animals including gorillas. Competition for resources in 'crowded' conditions can lead to high rates of aggression, although the evidence can be conflicting and seems to be confounded by variables that include the surrounding environment (such as level of provisioning) (see review by Judge, 2000). In addition several papers focus on the responses of gorillas to the design and complexity of the enclosures (Wilson, 1982; Ogden, Lindburg and Maple, 1993; Hoff, Powell, Lukas and Maple, 1997; Stoinski, Lukas, Kuhar and Maple, 2004b). It is reasonable to assume that, particularly as institutions have moved towards more 'naturalistic' enclosures, size of enclosure (or area per individual of enclosure) and the enclosure complexity are intrinsically linked and can have a significant effect on the behaviour of captive gorillas.

There was a significant interaction between group type and mean kinship for the frequency of dominance behaviours. The interactions suggests that whilst bachelor groups are not affected by an individual's mean kinship with other group members (a finding mirrored in wild all-male mountain gorilla groups, Robbins, 1996), individuals in breeder groups with a low mean kinship (not related to other group members) exhibit higher frequencies of dominance behaviours. Intuitively this suggests that kinship within the group acts to decrease frequencies of dominance behaviours. Kinship is often used to explain patterns of cooperation or tolerance within many species as well as the formation of strong social bonds (Gouzoules and Gouzoules, 1987; Mitani, Merriwether and Zhang, 2000). Harcourt and Stewart (1981), commenting on the influence of help in contests in gorillas, reported that 94% of incidences of support were to protect vulnerable kin. Despite this rates of aggressive behaviour between male gorillas are known to be dependant on a number of factors including reproductive status of the females, ages of the males (perhaps surprisingly there was no affect of age on dominance of aggressive behaviour in this study) and stability of relationships (Robbins, Sicotte and Stewart, 2001) as well as kinship. There are also reports suggesting that kinship may only be an ancillary factor in relationships (Moore, 1992; Mitani, Merriwether and Zhang, 2000) and that kinship is not a guarantee that strong male-male bonds will form (Van Hoof and Van Schaik, 1994). This may be more relevant in a captive situation, where higher mean kinship usually indicates individuals have been together for a substantial period of time and low mean kinship may also indicate more newly formed groups.

However there has also been a suggestion (Harcourt and Stewart, 1981) that younger (blackback) males with stronger relationships with the silverback were less likely to emigrate and may gain mating rights within the group. Although age did not have a significant effect on the frequency of dominance behaviours within this research, it is feasible that the breeder groups with higher mean kinship values may be indicative of stronger relationships between silverback males and their offspring. Recent findings for wild western gorillas have led to the suggestion of a dispersed male network of related silverbacks with a low level of aggressive intragroup encounters (Bradley *et al*, 2005). This lends further weight to the argument of kin-biased behaviours (although in an intragroup situation).

However, as stated in chapter 4, the absence or reduced effects of kinship in bachelor groups may be an artefact of how they are formed in captivity. It is worth re-iterating here that although there are closely related animals within the bachelor sample, it is often the case they did not know each other in the natal group before being moved to the bachelor group, whether because of interim transfers to other groups or time spent in the Stuttgart nursery. This then means that although related, they will not be 'aware' that they are and may have developed closer bonds with unrelated individuals that they have been raised with.

It is apparent that although the expression of dominance behaviours is influenced by group type, both institution (enclosure size / design) and mean kinship within the group have significant roles.

It is interesting to note the level of variation in expression of dominance behaviours within breeding groups, particularly. Although this seems to mirror the high level of variation observed in the strength of hierarchy for breeder group gorillas (refer chapter 4) there were no significant correlations between either rates of aggression or rates of dominance behaviours and breeder hierarchy strength.

However there was a significant negative correlation between bachelor hierarchy strength and bachelor silverback DBI, showing that as hierarchy strength decreases (i.e. becomes less despotic) the dominance behaviours alter from being weighted towards supplants to being weighted towards display. It seems counterintuitive that a stronger hierarchy will be maintained by a silverback weighting towards supplant behaviours. However it may be that carrying out a supplant has a greater risk for both opponents as the close proximity of the individuals during the behaviour may increase the likelihood of contact aggression.

Affiliative behaviours and Relationship Quality Index

The frequency of affiliative behaviours was not affected by group type when all variables were included in the model, but was significantly affected by age, mean kinship and rearing style in a predictable way (i.e. individuals with a higher mean kinship, younger individuals and mother reared individuals all had higher frequencies of affiliative interactions). When the mean kinship and rearing style were excluded from the model (i.e. the applied model) there was a significant affect of group type; males in breeder groups showed more affiliative behaviour than males in bachelor groups. RQI was significantly greater for younger males, males with higher mean kinship and also for males in breeder groups.

These results support the prediction that within bachelor groups there is less of a need to maintain the level of social bonds that would characterise a breeder group. Certainly in a wild situation, where threats from other gorillas in inter-group encounters or potential predators of youngsters and infants are prevalent, social bonds and the level of social cohesion they encourage will assist in maintaining and protecting a functional group. Although in captivity these pressures are removed, it is clear that males in breeder groups still invest more time and energy into affiliative behaviour (ie social cohesion) than bachelor groups. Within bachelor groups, the need for social cohesion and social bonds may appear to be reduced even further. In the wild, male gorillas (both mountain and lowland) have been known to exist in a solitary situation for periods of time, although there are potential benefits to living within a bachelor group (Yamagiwa, 1987, Levrero et al, 2006).

Levels of positive social interactions between males in bachelor groups are reduced and may potentially affect the levels of social cohesion within the group. Levrero, 2006, describes bachelor (or non breeding) groups of western gorillas as "…temporary and unstable structures that are induced by many migratory events…".

The significant effect of mean kinship (individuals with a high mean kinship weight towards affiliative behaviours, individuals with low mean kinship weight towards dominance behaviours) is intuitive with higher levels of affiliative behaviours than dominance behaviours shown by animals with more relatives in the group. This is particularly true in breeder groups but once again in bachelor groups mean kinship has very little effect or possibly has the opposite effect. . Although this seems to be counter-intuitive, it has been reported that kinship is not a guarantee that strong male-male bonds will form (Kappeler, 2000; Van Hoof and Van Schaik, 1994). In addition, it is possible that those bachelor males with high mean kinship were also the older bachelor males in the sample, therefore may be showing a decrease in the levels of affiliative behaviours.

There is also a significant effect of whether the males were hand reared or parent reared on the frequencies of affiliative behaviours. Mother reared males exhibit higher frequencies of affiliative behaviours, whereas hand reared males exhibit lower frequencies of affiliative behaviours (Capitanio and Reite, 1984; Ljunberg and Westlund, 2000). This result matches research in other primate species where the absence of a mother has been shown to limit social development of the offspring, thereby reducing hand reared animals affiliative capacity.

Applied results

The establishment of breeder and bachelor groups in captivity can be heavily manipulated when it comes to group composition. Many breeder groups are started with a silverback male and a small number of females. The groups are then allowed to expand as offspring are born and grow into the group so breeder groups usually consist of several closely related inidividuals. However there are exceptions where breeder group composition is heavily manipulated in order to try to introduce young males to more normal situations (e.g.. Belfast where two young males have been introduced to the group before the addition of a new silverback, effectively creating a multi-male group with three males unrelated to any other group members). Conversely bachelor groups are usually heavily manipulated groups as they are constructed to suit the needs of the breeding programmes at the time and very often are made up of unrelated and/or hand-reared males. Therefore, when the main effects of rearing style and/or mean were significant an 'applied' model was tested excluding these factors. These results give information directly relevant to the establishment of gorilla groups as they are currently run by the breeding programmes. The applied results for the frequency of dominance behaviours again confirms that there is a greater frequency of dominance behaviours in breeder groups than bachelors but that there is an institutional effect, and potentially large or more complex enclosures will allow a reduction of frequency of all dominance behaviours.

Within the applied model significant effects were found for both age and group type (breeder/bachelor) on frequencies of affiliative behaviours. Again the results of age group were not unexpected given the discussion above. However the results for group type, where bachelor males exhibited lower frequencies of affiliative behaviours (albeit that this is explained in the full models by reduced mean kinship and more hand-reared animals in bachelor groups), have potential significance for the current management of bachelor groups in captivity.

There is literature focusing on the importance of peer orientated behaviours in the social development of primates. The reduced level of affiliative social interaction experienced by subadults and blackbacks in bachelor groups may impact on their social development and therefore on their social competency in later life (de Waal and Johanowicz, 1993; Pereira and Fairbanks, 1993; Roney and Maestriperi, 2003). From the point of view of the European captive breeding programme, this may prove a key issue in the management of the ‘surplus’ male problem. Bachelor groups are often considered a ‘genetic reservoir’ for males until they become old enough or a suitable space becomes available in a breeding situation. However if young males that have spent time housed within a bachelor situation are less socially competent when introduced to a group or breeding situation, the effectiveness of the breeding programme may be compromised.

Chapter 6: Longitudinal changes in hierarchy and social relationships within a bachelor group at Paignton Zoo Environmental Park

6.1 Introduction

6.1.1 Living in bachelor groups

Western gorilla bachelor groups in the wild mainly consist of young (blackback) males that have voluntarily migrated, preferentially joining bachelor groups that include a silverback male (Levrero *et al*, 2006). However these groups could be categorised as temporary and unstable groups with a high number of migratory events, both primary and subsequent transfer (Levrero *et al*, 2006, Robbins, 2007). This high number of migratory events suggests that social bonds between males are weaker in bachelor groups than in breeder groups, and may be facilitated by an absence of clear dominance hierarchies (Levrero *et al*, 2006). Despite this Yamagiwa (1987) and Robbins (1996) reported that males living in bachelor groups had a higher frequency of social interactions and a lower risk of serious wounding than those living in breeder groups, and hypothesized that living in bachelor groups could enhance the development of social skills. In addition it has been suggested that bachelor silverbacks may demonstrate tolerance to younger males, whether related or not, in order to maintain a social life (Levrero *et al*, 2006).

Recent publications on western gorillas in the wild have demonstrated that they show greater variation in social structure with groups ranging from the more traditional one-male units (Magliocca, Querouil and Gautier-Hion, 1999; Parnell, 2002; Tutin, 1996) to multi-male units which show seasonal fission (Olejniczak, 1996), as well as bachelor groups (Levrero *et al*, 2006). This diversity of social structure coupled with the large range of environments inhabited by western gorillas in the wild may have in turn, favoured selection for behavioural flexibility (Weiche, 2006) in response to social and environmental factors.

The unstable group structures, high number of migrations and tolerance between silverbacks and young males exhibited in bachelor groups again suggests that gorillas may exhibit behavioural flexibility (Levrero *et al*, 2006). There has to date been very little published on the flexibility of social behaviour within individual gorillas in these groups, however it is known that gorillas from bachelor groups can transfer between bachelor groups, occasionally into breeding groups and also form new breeding groups (Levrero *et al*, 2006), indicating a range of behavioural responses to a social environment.

Behavioural flexibility is described as reversible, within-individual alternative behavioural phenotypes in response to external stimuli, and can be seen as a 'toolbox' of potential responses (Jones, 2005). As such, the longitudinal observation of a captive bachelor group, cataloguing changes in age of individuals within the group and composition of the group itself can provide valuable information on the occurrence of behavioural flexibility in gorilla social interactions.

This chapter seeks to examine the expression of hierarchies and associations within Paignton Zoo's bachelor gorilla group, to identify potential patterns of behavioural flexibility.

6.1.2 Paignton's bachelor gorilla group

Paignton Zoo Environmental Park's bachelor gorilla group was first established in 1997 in response to the European Breeding Programme's need to find suitable housing for males considered 'surplus' to the breeding programme. At that time there were only two other bachelor groups within the European region and a small handful in the U.S. The establishment of a third bachelor group within the European region was also considered necessary to increase husbandry experience with bachelor gorilla groups. Details of the group's establishment and changes in group membership have been given in chapter 2. It is worth remembering that group membership at Paignton has remained flexible in response to the needs of the European breeding programme, as well as responsive to the group's behaviour.

6.1.3 Hypotheses / predictions

Results from the previous chapters have indicated that the expression of behaviours within a gorilla group may be flexible depending on physical circumstance and the age of the gorilla. Longitudinal research with the bachelor group at Paignton allows examination of the following hypotheses.

- Dominance hierarchy will become less linear (the strength of hierarchy will decrease) as young males begin to mature.
- Levels of association between older males (silverbacks) and young males will decrease as young males begin to mature, reflecting variation in the dominance hierarchy and the strength of hierarchy.
- Levels of association are likely to be weakest between the silverback and blackbacks, particularly the second dominant animal.
- The bachelor males will exhibit a decrease in relationship quality index RQI as they move from subadult and blackback age classes to the silverback age class, reflecting the result of the RQI analysis in the previous chapter.

- The gorillas will show flexibility in the RQI depending on perceived threats and availability of resources. e.g. The RQI scores will decrease both as the age structure in the group changes and as animals become more dominant within the hierarchy.

6.2 Methods

For details on data collection methods see chapter 2. The membership (with social status) of the group at each of the four data collection sessions is given in table 6.1 below

Table 6.1 Age structure of the Paignton Zoo group at differing data collection sessions.

	Pertinax (d.o.b. 04/82)	Mambie (03/91)	Richard (11/91)	Asato (10/91)	Awali (04/93)	Mapema (04/96)	Damisi (04/97)
Jan 02	Silverback (19 yrs)	Blackback (10 yrs)	Blackback (10 yrs)	Blackback (10 yrs)	Sub-adult (8 yrs)		
Nov 02	Silverback (20 yrs)		Blackback (11 yrs)	Blackback (11 yrs)	Sub-adult (9 yrs)		
Apr 03	Silverback (21 yrs)		Blackback (11 yrs)	Blackback (11 yrs)	Blackback (10 yrs)		
Jan 05	Silverback (22 yrs)			Silverback (13 yrs)	Blackback/ Silverback (11 yrs)	Sub-adult (8 yrs)	Sub-adult (7 yrs)

6.2.1 Data manipulation and analysis

Dominance hierarchies

Hierarchies and the strength of hierarchy was calculated for each data collection session according to Singh *et al* (2003), using the supplant frequency data from the all-occurrence sampling. Assessment of the number of supplants per dyad allows the production of d_a, where d_a is the sum of the proportion of supplants between dyads. These values then lead to a calculation of strength of hierarchy (h), modified from Landau's index of linearity (Singh *et al*, 2003), where 1 represents a strong (linear) hierarchy and 0 represents no observable hierarchy.

Association Indices

Association indices have frequently been used to assess spatial relationships between dyads of animals within groups (Collins, 1984; Grant, 1973; Mitani *et al*, 1991). Within Paignton's bachelor group instantaneous scan sampling for nearest neighbours were carried out in four discrete observation periods. This data was then used to determine associations between individuals within the group based on the half weight association index (Lehner, 1996), also known as Cole's, Dice's, Sorenson's and the coherence association index. An association index was calculated for each individual with all other group members.

$$\text{Association Index} = \frac{x}{(n_a+n_b)/2}$$

Where: x = proportion of observations where a and b are nearest neighbours

n_a = total proportion of observations for a

n_b = total proportion of observations for b

Relationship Quality Index

The RQI was calculated for each individual gorilla according to the method stated in chapter 5

Analysis

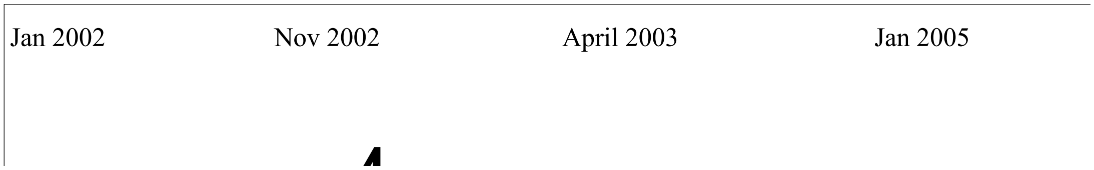
Within this chapter I am using graphical analysis as this is the most appropriate way to handle the data. These data deal with individuals in a longitudinal situation and does not seek to generalise to a larger population. The intensive nature of the observations have not allowed sampling from a population, instead the data are absolute amounts within a discrete time period (true mean) and so there is no way to estimate error. In addition it is unfeasible to look at a group mean in this situation as, although the expectation is for individuals to behave in a similar pattern, the individuals are temporally separated (by membership of different age classes) (Sidman, 1960; Johnston and Pennypacker, 1993).

6.3 Results

6.3.1 Dominance hierarchies

The calculation of d_a for individual gorillas in the group allowed the production of a graph illustrating the hierarchy within the gorilla group (fig 6.1). The greater the value of d_a, the higher the position in the hierarchy. Thus it can be seen that Pertinax remained the dominant silverback within the group for the first three data collection sessions, but Awali had become more dominant than Pertinax by January 2005, despite being a younger animal. It is interesting to note the reversal of hierarchical position between Asato and Awali in November 2002. Despite being the younger animal (a subadult whilst Asato was already a blackback), Awali managed to reach a higher position in the hierarchy.

Fig 6.1 Hierarchy positions for the Paignton bachelor group over the four data collection periods



Strength of hierarchy

The d_a for each individual was used to calculate the strength of hierarchy for the group within each of the data collection sessions (fig. 6.2). Hierarchy strength decreased steadily over the first three of the four data collection sessions, before rising again in the last.

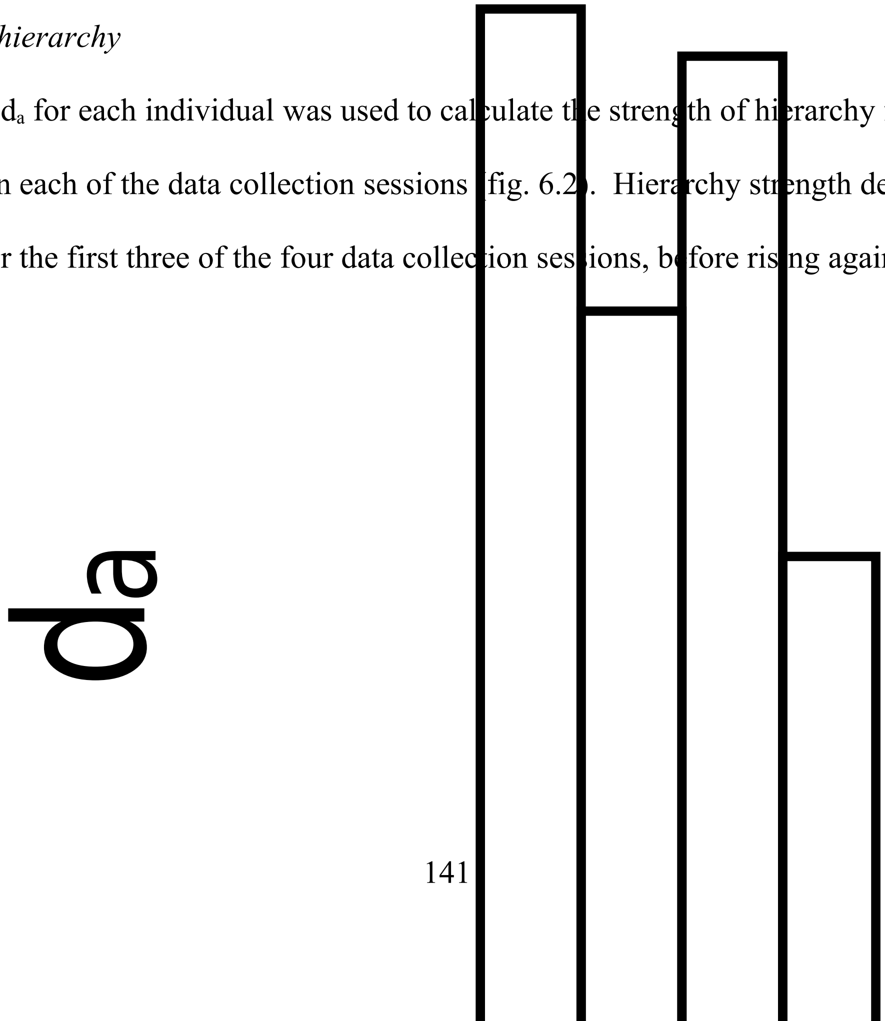


Fig. 6.2 Strength of hierarchy over the four data collection periods

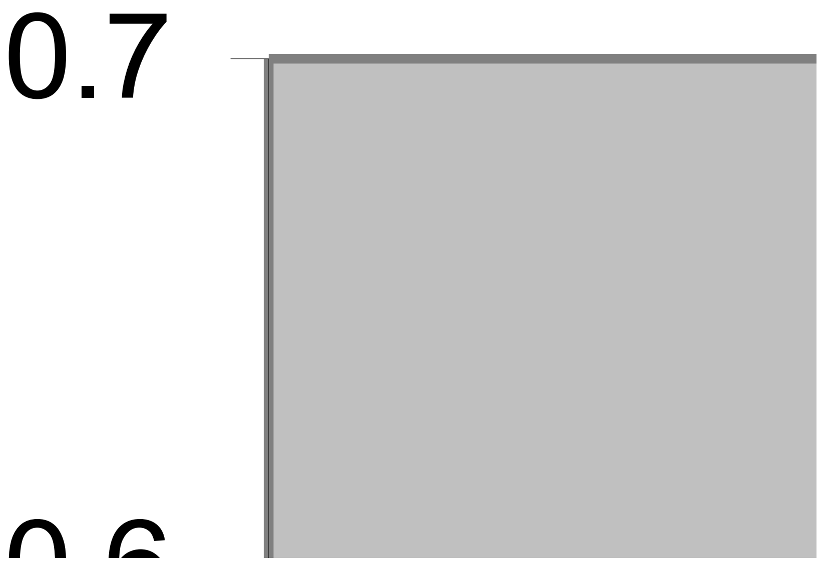
Jan 2002 Nov 2002 April 2003 Jan 2005

6.3.2 Association indices

Association Indices (January 2002)

The association indices for data collection session January 2002 are shown below (fig. 6.3). In all cases individuals exhibited low association indices, however it can be noted that the level of association between the dominant silverback (Pertinax) and the second ranked animal (Mambie) was lowest. Pertinax's strongest associations were with the two lowest ranking animals (Asato and Awali). The lowest ranking animal (Awali) exhibited the most even distribution of associations across the group.

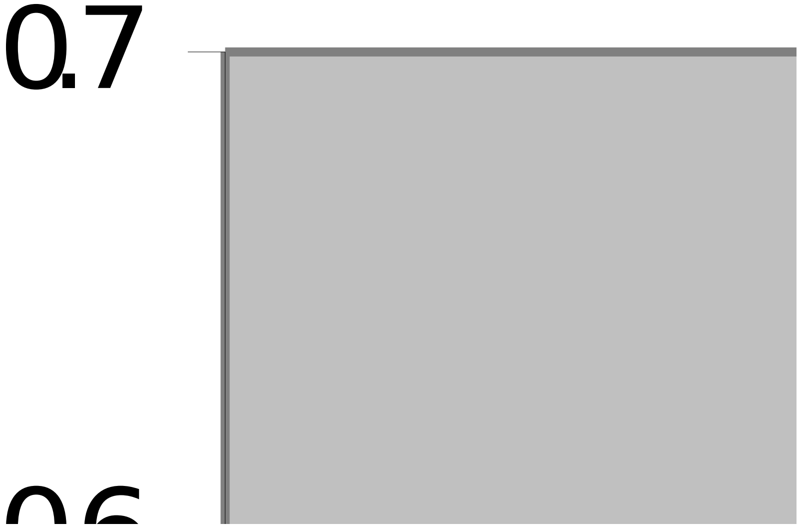
Fig 6.3 Group association indices (January 2002). The figures in brackets refer to hierarchy position.



Association Indices (November 2002)

Between the January 2002 and the November 2002 data collection periods, Mambie was moved to another zoo in response to the recommendations of the European breeding programme. The association indices for the data collection session November 2002 are shown below (fig 6.4). Once again the lowest levels of association were seen between Pertinax (dominant silverback) and Richard (second ranking blackback). In addition the hierarchy had become reversed between Asato and Awali, with the younger Awali reaching a higher hierarchy position. Although there is still a good level of association between Asato and Awali, it appears in this session that Asato is demonstrating a more even spread of association with all group members than Awali.

Fig 6.4 Group association indices (November 2002). The figures in brackets refer to hierarchy position



Association indices (April 2003)

Group membership remained the same for this data collection session, however the reversal of hierarchy between Asato and Awali has now returned to an age graded system, with the older Asato ranking above the younger Awali (fig 6.5). In this session both the second and third ranked animals (Richard and Asato) show the lowest association levels with the dominant silverback (Pertinax) and, once more, the lowest ranking animal (Awali) has the most even spread of associations within the group.

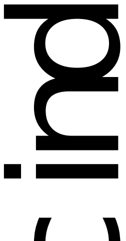
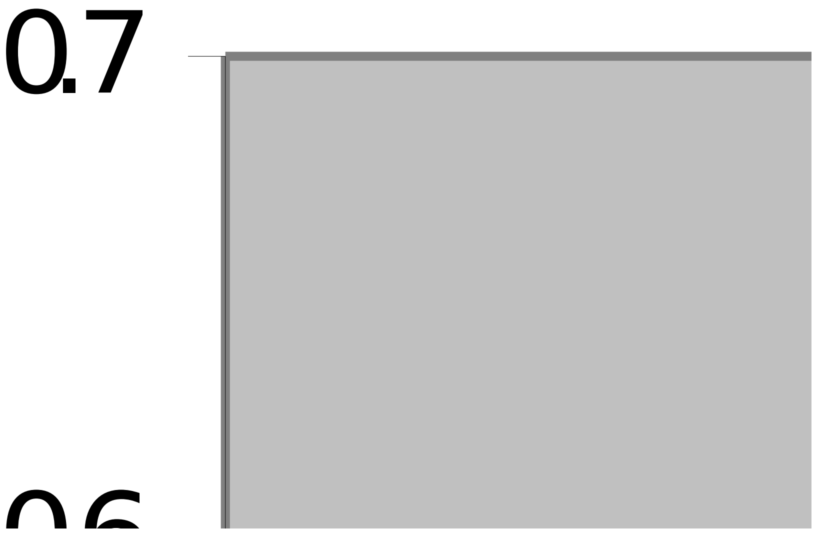


Fig 6.5 Group association indices (April 2003). The figures in brackets refer to hierarchy position



Association indices (January 2005)

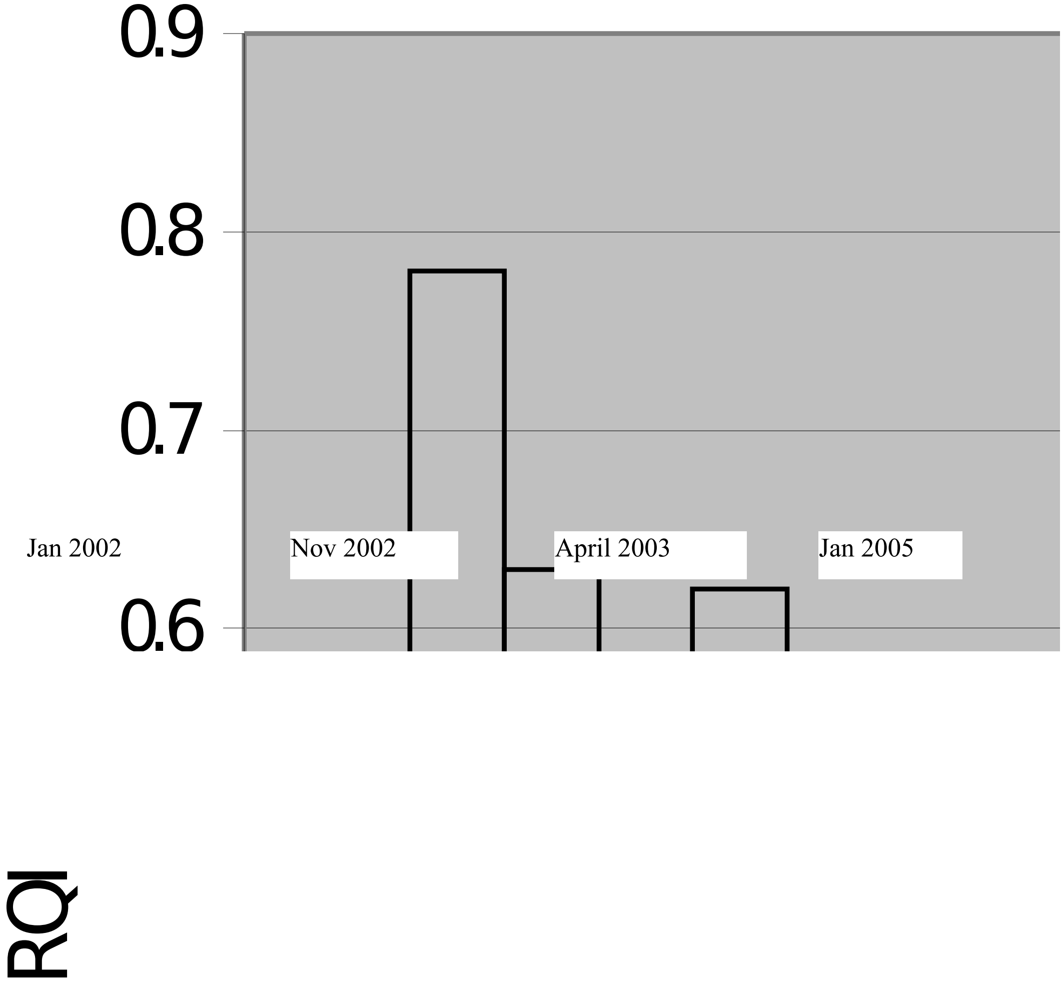
Group membership had once more altered with Richard being transferred out of the group and two younger animals (Mapema and Damisi) being transferred into the group in late 2003 (fig 6.6). In this session Awali had become the dominant male with Pertinax ranking second. The level of associations between the three oldest animals were all low with the strongest associations within the group appearing across the age classes between Awali and Damisi, Pertinax and Mapema, and between the two younger animals Mapema and Damisi.

Fig 6.6 Group association indices (January 2005). The figures in brackets refer to hierarchy position.

6.3.3 Relationship Quality Index

The RQI was calculated for each group member within the four data collection sessions (fig 6.7). Although there appears to be consistently high RQI throughout the first three stages of data collection (indicating a weighting towards affiliative behaviours), this dropped in the last stage where the group consisted of three silverback males and two subadults. In this last session all three silverbacks showed a decrease in RQI score, indicating a stronger weighting of behaviours towards dominance behaviours. Both subadults still showed a strong weighting towards affiliative behaviours.

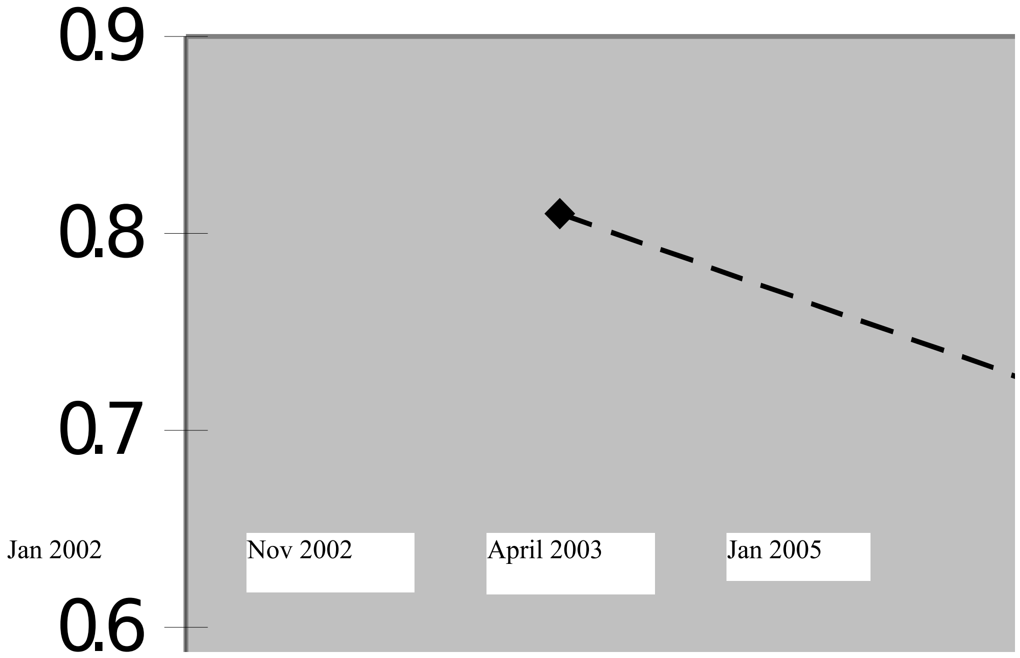
Fig 6.7 RQI scores for the individual gorillas during the four data collection periods



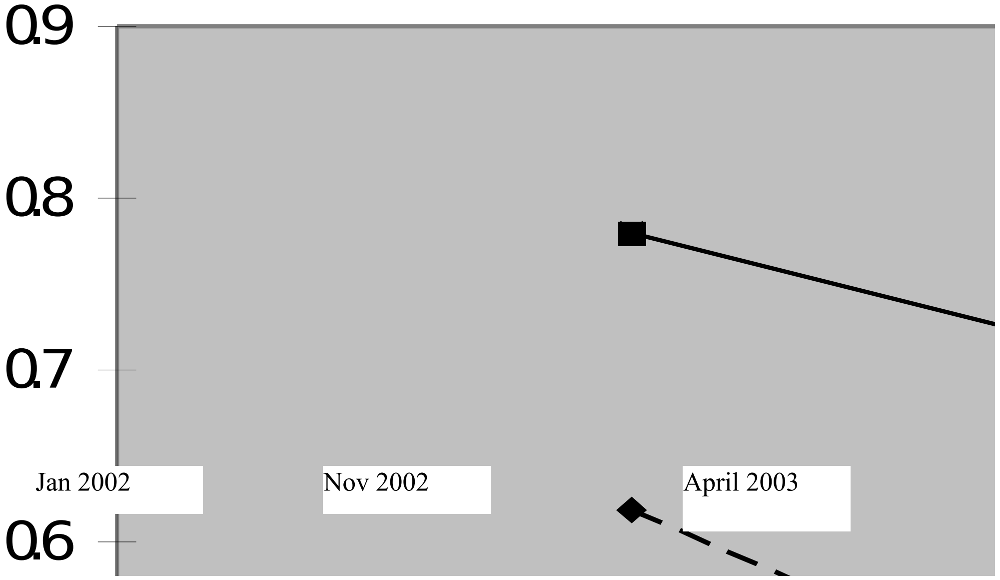
In order to get a clearer view of the potential flexibility in expression of behaviour in response to changes in hierarchy position and age class, graphs of both RQI and d_a were produced for the four animals in multiple data collection sessions (Richard was present for three of the four data sessions; Pertinax, Asato and Awali were present for all four) (figs 6.8a, b, c, d).

Fig 6.8 RQI and d_a (sum of proportion of supplants) values over time for individual gorillas a) Pertinax, b) Richard, c) Asato and d) Awali

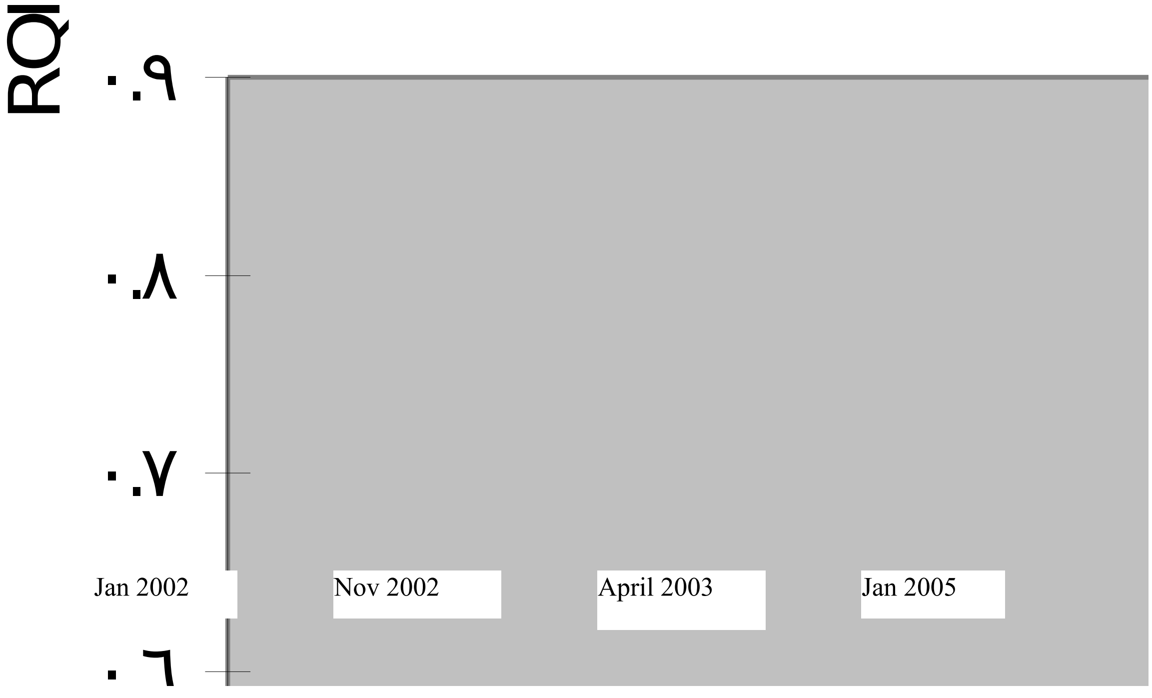
a) Pertinax



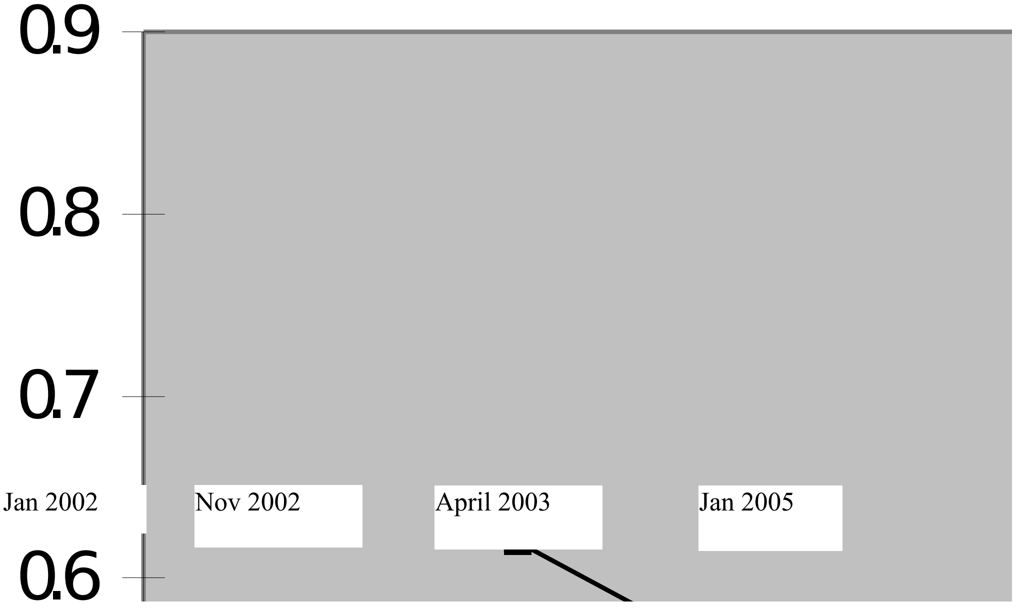
b) Richard



c) Asato



d) Awali



Pertinax's hierarchy strength showed a steady decrease until April 2003 when it once more increased. Conversely his RQI shows marked variation during the period of the study. Richard, Asato and Awali each showed a steady decrease in RQI over the longitudinal study. Although each of the three shows some variation in d_a scores, there was a trend for a rise in d_a at the last data collection period.

Discussion

Dominance hierarchy and strength of dominance

Both the dominance hierarchy and the strength of hierarchy showed variation over the duration of the longitudinal study. Although Pertinax maintained a dominant position during the first three data collection sessions his d_a scores decreased steadily over time, indicating a drop in the strength of his position. During these three data collection times the membership of the group did not markedly alter (except with the removal of Mambie to another zoo), however the age structure of the group did alter with both Richard and Asato growing towards silverback status and Awali becoming blackback. Although in the previous chapter no significant difference was found between age and the rate of aggressive or dominance behaviours, this change in hierarchy indicated that the dominant male (Pertinax) was performing fewer successful supplants as the ages of the other group members increased. In the final data collection session (January 2005) Pertinax's d_a score returned to close to the original level, however at this time it was Awali (the youngest of the three mature gorillas) who held the dominant position in the group.

Awali showed a variation in his hierarchy position over the time of the study. Although the youngest of the four gorillas in the November 2002 session he was more dominant than Asato. This however had reversed for the next data session (April 2003) to a more expected position below Asato, before he became the dominant male in the final data collection session (January 2005).

This fluctuation in individual hierarchy position was matched by changes in hierarchy strength over the period of the research. The strength, or linearity, of hierarchy within the group as a whole decreased steadily during the first three data collection sessions, before rising again slightly in the last. It would appear that during the January 2002 session, the hierarchy was more linear indicating a despotic style within the group (Vehrencamp, 1983). It may be argued that as perceived threats from males rising in hierarchy position increase, a dominant male may attempt to maintain position through an increasing level of despotism. However as the younger males began to mature, the level of linearity of hierarchy decreased, suggesting that a despotic style was not able to be maintained at that time. As the value for the modified h simply dipped below 0.5, it cannot be said that the group achieved an egalitarian style.

Association indices

The levels of association between individuals also showed some variation over the time of the longitudinal study. Whilst all the levels of association within the group are quite low, it appeared that the lowest was consistently found between the dominant and the second dominant animal within the group. It seems intuitive that interactions between the dominant and second dominant animal may easily lead to an aggressive situation if a conflict of interest arose between them. Although the previous chapter did not give any clear indications of differences in behaviour when in a conflict of interest situation either between age or between bachelor or breeder groups, the reduced level of association between the two most dominant animals within this group could indicate avoidance behaviour. Watts (1995a) found that subordinate male mountain gorillas would avoid dominant male opponents in conflict situations. It has also been suggested that for captive western gorillas proximity is an effective indicator of affiliation between individuals and may be used in place of physical contact to restore ‘valuable’ relationships after aggression, as either ‘reconciliation’ or ‘consolation’ mechanisms (Mallavarapu, Stoinski, Bloomsmith and Maple, 2006). The reduced level of association between the two most dominant individuals also supports the prediction that bonds are likely to be weakest between the silverback and the second dominant animal in the group (Robbins, 1999)

Within the final data collection period it is interesting to note that the highest levels of association were between Awali and Damisi, Pertinax and Mapema, and Damisi and Mapema. Whereas it is easy to consider the level of association between Damisi and Mapema to be a direct result of their age (both subadult during this data collection session), the levels of association between the two youngest and the two most dominant individuals may have an impact on the dominance hierarchy. Damisi, although being the youngest animal in the group, had a markedly higher d_a score than Mapema. Damisi's closer association with the dominant animal in the group may have assisted him in moving up the hierarchy.

Relationship Quality Indices

Within the group membership, three animals (Richard, Asato, Awali) grew from subadult or blackback to blackback/silverback status during the longitudinal study. Each of these three animals showed a marked decrease in RQI, with a stronger weighting towards dominance behaviours when in the older age classes. This result reflected the significant difference found in RQI and frequencies of affiliative behaviours between ages in the previous chapter and indicates that male gorillas exhibit flexibility in behavioural expression that is impacted upon by their age. This can be seen clearly in the series of graphs for the four individual animals present in the group for multiple data sessions (fig.6.8). Richard, Asato and to a lesser extent Awali showed a steady decrease in RQI over time.

However fig 6.8 also gives an indication of the potential relationship between individual hierarchy strength and expression of behaviour. Pertinax is the one group member who remained in the same age class throughout the longitudinal study, having already been a fully mature male (a silverback) at the beginning of the study. Pertinax also showed marked variation in RQI. Although initially weighted towards affiliative behaviours (when the other group members were young), the RQI dropped towards dominance behaviours during the second session before rising in the third and subsequently decreasing again in the fourth. It appears that as Pertinax's individual strength of hierarchy began to decrease in the second session, his RQI weighted towards dominance behaviours, suggesting that with other group members still young the risks associated with the expression of dominance behaviours (damage to social bonds, risk of injury) may not outweigh the potential benefits of engaging in those behaviours (maintenance of position).

However, in the subsequent data session (April 2003) Pertinax, whilst still the dominant male (but less clearly so) exhibited an RQI weighted towards affiliative behaviours. This suggests that, with the increasing age of the opponents, the risks associated with dominance behaviours may outweigh the potential benefits, and affiliative behaviours, perhaps for garnering support, may be more beneficial.

Within the final data session, Pertinax's strength of hierarchy had again risen, although he was no longer the dominant animal. However the group structure had altered with the introduction of the two younger animals (Mapema and Damisi), potentially reducing the risks associated with dominance behaviour.

As stated previously the fig 6.8d, detailing Awali's RQI and d_a over time, shows a marked drop in RQI (decrease in the expression of affiliative behaviour) in the last data collection session, coupled with a rise in hierarchy strength when he moved into a blackback / silverback age group. However Awali also exhibited a rise in hierarchy strength during the second data collection session (Nov 2002), where he became more dominant than the older Asato. This rise in hierarchy strength was mirrored by a drop in RQI, leading to weighting towards dominance behaviours.

Although this data cannot be tested for statistical significance, the results indicate that male gorillas exhibit a flexibility in their RQI scores (expression of affiliative and dominance behaviours) dependant on both age class and position within the dominance hierarchy.

Chapter 7: Concluding discussion

Behavioural differences can be identified between captive breeder and bachelor groups of gorillas in multi-institutional studies, without the differences being masked by the potential confounding effect of institution. This was demonstrated through the known behavioural phenomenon of the effect of age on expression of behaviour, with behavioural diversity decreasing as age increased.

7.1 Group type effects

A number of significant differences were found between breeder and bachelor groups. Bachelor males were shown to have lower levels of behavioural diversity than males housed in breeder groups, suggesting that males housed in bachelor groups had either less opportunity or less need for the expression of some behaviours due to the social environment.

Bachelor groups consistently exhibited further distances between themselves and their nearest or second nearest neighbours, regardless of whether the data for females, juveniles and infants were included in the analysis. Although Robbins (1999) in a comparison of an all-male mountain gorilla group to mixed sex mountain gorilla groups, suggests that distances between males within the all male group were shorter, Levrero *et al* (2006) describe bachelor groups as unstable associations with a high level of transfer between groups, suggesting weak bonds between bachelor males. Within this research it appears that bachelor males are increasing distances between themselves, which would tend to support the suggestion of unstable groups. These results suggest that bachelor males, in situations where there is a lack of resources over which to compete (i.e. enough food and space, no females) will form less cohesive groups, exhibiting further distances between themselves and their neighbours. This result is corroborated by the effect of institution on the distances between nearest neighbours and second nearest neighbours (see below).

Increasing distance between individuals and nearest neighbours can be interpreted as an avoidance strategy to reduce the risk of potential conflict. Within this research bachelor males exhibited a lower frequency of both dominance and aggressive behaviours, in comparison to males housed in breeder groups. Within a bachelor group it appears that the potential costs of aggressive or dominance behaviours (i.e. risk of injury) outweigh any potential benefits, making avoidance of conflict through increasing distances a more worthwhile strategy. In addition, the benefits of affiliation are possibly lower in bachelor groups, since there are no females to compete for and food is plentiful, so there is less motivation for alliance formation, and inherently shorter distances.

Despite lack of significant effect of group type (breeder / bachelor) on the frequencies of affiliative behaviours, there was a significant effect of group type on the Relationship Quality Index, with bachelor males exhibiting a significantly lower RQI (i.e. engaging in fewer affiliative behaviours than dominance behaviours). Although it has been suggested that bachelor groups may function as an alternative strategy for young males to gain social experience (Levrero, 2006; Robbins, 2007), the reduced opportunities for affiliative behaviours in bachelor groups may impact on the social development of young male gorillas (Capitanio and Reite, 1984; Ljunberg and Westlund, 2000).

Within this research there were also a number of other factors with significant effects on the data collected.

7.2 Age effects

As has already been stated the effect of age on gorilla behaviour was used to demonstrate the effectiveness of multi – institutional studies, and in line with this, other predictable results were found. Behavioural diversity and behavioural equitability were significantly affected by the age of the males, with younger males demonstrating higher levels of both (i.e. younger males perform more behaviours and are more even in the time spent performing them). This phenomenon has been well documented in primate literature, with observations showing that young primates engage in higher levels of play behaviour (Pereira, 1993; Stewart and Harcourt, 1987; Watts and Pusey, 1993). The results of this thesis corroborate previously published work as young gorillas in both breeder and bachelor groups engage in significantly higher levels of affiliative behaviour, a category including play behaviour, and display a higher RQI level (a greater proportion of affiliative behaviours in comparison to dominance behaviours).

In addition, young males can be seen to have shorter distances between themselves and their nearest neighbours when the data from females, juveniles and infants are included in the analysis. This result was lost on removal of the data from the females, juveniles and infants indicating that young males generally have short distances between themselves and female, juvenile and infant members of breeding groups. It is reasonable in this case to assume that these young males may still have positive relationships to females within the breeder groups (i.e. their mothers) and as a consequence may still be associating with them. The greater distances between older males and their nearest neighbours when the data from females, juveniles and infants are included could be indicative of a changing social relationship between males and females as the males approach maturity. Within gorilla groups both males and females emigrate from their natal groups (Stewart and Harcourt, 1987), however there is still very little known about the behavioural mechanisms underlying the peripheralisation of males leading to emigration (Robbins, 2007).

7.3 Kinship effects

Mean kinship had a significant effect on several of the variables mainly as an interaction with group type. Within breeder groups the effects of mean kinship detected are generally intuitive and concur with the predictions of kin selection models. Breeder males with higher mean kinships showed shorter distances between themselves and their nearest neighbours, a lower frequency of dominance behaviours (weighted more towards supplant behaviours than aggressive behaviours), an increase in the frequency of affiliative behaviours and a relationship quality weighted towards affiliative behaviours. Each of these can be readily explained from the large body of primate literature of positive kin effects (e.g. Gouzoules and Gouzoules, 1987; Harcourt and Stewart, 1981; Mitani, Merriwether and Zang, 2000) and may impact on control of or access to resources such as females.

However within the bachelor groups mean kinship either had very little effect or possibly opposite effects to those seen in breeder groups. Bachelor males with higher mean kinships maintained greater distances between themselves and their nearest neighbours, had DBIs weighted towards displays and, although they exhibited a slight increase in the frequency of affiliative behaviours, their relationship quality was weighted towards dominance behaviours. There has been research suggesting that in some circumstances kinship appears to be an ancillary factor only (Moore, 1992) and does not guarantee strong bonds between related males (Van Hoof and Van Schaik, 1994). Alternatively, it may be that in the relatively competition-free situation of captive bachelor gorilla groups there is no need or advantage in maintaining close bonds with kin.

However it is important to remember that the mean kinship scores for bachelors are clustered at a lower level (there is less relatedness amongst bachelor groups than breeder groups), and this may impact on the results. Also it is possible that this counterintuitive effect of mean kinship is an artefact of bachelor group establishment in captivity, where bachelor groups are often composed of males rejected (for a number of potential reasons) at a very young age from their breeding group. Many of these males are hand reared at the Stuttgart nursery before being placed in bachelor groups. Although the individuals in the bachelor groups may be related, they may not have experienced the usual mechanisms to ‘know’ this i.e. they may not have spent time within the same group at an early age. Indeed they may have spent time at an early age with unrelated males and therefore behave towards them as though they were related. This would result in the opposing effects of kinship that were observed in breeder and bachelor groups and suggests that gorillas ‘recognise’ kin based on early life experiences rather than some mechanism of actually detecting genetic relatedness.

7.4 Rearing style effects

Rearing style had a significant effect on both behavioural equitability and the frequency of affiliative behaviours, with hand reared animals showing less behavioural equitability (spending time unevenly in behaviours) and lower levels of affiliation than mother reared animals. The effects of rearing style follow predictable trends from published literature (Capitanio and Reite, 1984; Stoinski et al, 2004b; reviewed in Weaver and de Waal, 2002). Individuals with a history of social disturbances during development are known to exhibit disturbed social functioning in adult life, which can include a lack of grooming partners (i.e. a reduction in an affiliative behaviour; Ljunberg and Westlund, 2000).

7.5 Effect of institution

Although it was shown that effects of institution did not mask predictable behavioural phenomena, it was also found to be a significant factor on some levels of behavioural expression. Institution had a significant effect on the distances between nearest male neighbours and second nearest neighbours, but also on the frequency of aggression and the dominance behaviour index. The factor of institution in this research can be seen to have several components, including area of enclosure per individual, each of which shows correlation with institution. However, area of enclosure per individual does appear to give a logical explanation for some of the results. When described in this way, it can be seen that males maintained further distances between themselves and their nearest neighbours and lower frequencies of aggression in enclosures with a greater area per individual. These results suggest that where possible, males will increase distances between themselves. This can be seen as an avoidance technique to lessen potential aggression between males (de Waal and Aureli, 2000). Institution also has a significant effect on the frequency of aggression, with less aggression exhibited in enclosures with greater area of enclosure per animal (Judge, 2006).

7.6 Variation and indications of flexibility

Within this research there have been several indications of the variability in behaviours within gorilla groups. Behavioural flexibility has been described as a toolbox of potential responses to situations (Jones, 2005). The variety of responses exhibited by the gorillas in this research to the different factors included in the analysis suggests that behavioural flexibility can be seen in male-male gorilla interactions.

The impact of institution when interpreted as area of enclosure per individual suggests that in enclosures with greater area there are lower frequencies of aggression, indicative of avoidance of potential aggression with other males. Many species develop behavioural mechanisms for dealing with close conditions indicating a flexibility of behaviour in response to the social environment (reviewed in Judge, 2006).

The effect of mean kinship had a significant interaction with group type showing that breeder and bachelor males respond in different ways. Whereas males with high mean kinship in breeder groups will exhibit behavioural responses that could be termed positive, this effect seems to be either not as apparent or not present for males with high mean kinship in bachelor groups (i.e. although both breeder and bachelor males show an increase in the frequency of affiliative behaviours with high mean kinship, the effect is far more pronounced in breeder males). It can be argued that in situations where a resource that may be competed for is present, it may be beneficial to maintain positive relationships with those animals that are closely related. Certainly Harcourt and Stewart (1981) hypothesized that is some circumstances younger male gorillas maintain a closer relationship with the dominant male and remain in the group rather than disperse. These males gain the opportunity for mating with more females (Bradley *et al*, 2005) and may eventually take over control of the group (Harcourt and Stewart, 1981)

Although it is difficult to demonstrate behavioural flexibility within the multi-institutional research presented here, the level of behavioural variation does allow a prediction of flexibility within gorilla behaviour. However the results of the longitudinal study at Paignton gave clear hints of the flexibility of individuals in response to the impact of age class and changes in hierarchy within the group. Expression of affiliative behaviour (measured through the RQI) were seen to decrease in three of the individuals as they reached adulthood, again supported by knowledge of levels of affiliative behaviours in the wild (Stewart and Harcourt, 1987; Watts and Pusey, 1993). In addition, both the silverback (Pertinax) and the subadult (Awali) demonstrate flexibility in the expression of affiliative behaviours in response to individual strength of hierarchy.

7.7 Implications for management of captive gorilla groups

Within this thesis there are a number of significant factors that have an impact on the management of gorillas in captivity. The effect of institution on the distances between males and their nearest neighbours, and on the frequency of aggression clearly lead to the conclusion that recommendations for gorilla enclosures should allow for large areas per individual gorilla. It has already been stated that in many situations the effect of enclosure size can't be separated from the complexity of enclosure (Maple and Perkins, 1996; Wilson, 1982), particularly as many zoos have increased enclosure size and complexity simultaneously. However it is reasonable to suppose that in situations where animals are avoiding potential conflict, large and complex enclosures will be beneficial to the effective management of the animals. The boxplots for the effect of institution on nearest neighbour and second nearest neighbour (figs 4.4 and 4.5) do indicate that gorillas will use the space available to them. The results of the frequency of aggression and the Dominance Behavioural Index (figs 5.3 and 5.4) both suggest that enclosure sizes of greater than 600m^2 per individual (institution 6) allow for a reduction in the expression of these behaviours. The recommendation for institutes developing new gorilla enclosures or those looking to make adjustments to existing enclosures would be to aim for a minimum enclosure size of 600m^2 per individual.

Rearing style has been shown to have an effect on the expression of affiliative behaviour between males, with hand reared males showing a lower frequency of affiliation. Practically, the introduction of a hand reared animal into either a breeder or a bachelor group may reduce the level of positive social interaction within the group, thereby affecting the social competence of other gorillas within the group. Group structure must be carefully considered when groups are manipulated, allowing the integration of hand reared to parent reared animals may increase the social ability of the hand reared animal (Ljunberg and Westlund, 2000), however placing too many hand reared animals within either a bachelor or a breeder group may impair the opportunities for positive social interactions within the groups. It seems logical that new groups need a good balance of parent reared to hand reared. Breeding programme recommendations must aim to achieve that balance in order to provide accommodation for males considered surplus to the breeding programme, many of which will be hand reared. However the silverback of any new bachelor group should be parent reared, or have been integrated to a family group for group experience, in order to maximise opportunities for affiliative social learning. Institution managers need to assess social competence by assessing the interactions, particularly affiliative interactions, between individuals.

The results of the ‘applied’ models show that there is an effect of group type on a number of factors including affiliative behaviours. The reduced affiliative interactions in bachelor groups (probably as a result of a higher proportion of hand reared animals) may impact on the social competence of subadults in later life. Within the gorilla captive population there are gorillas younger than those included in this research being introduced to bachelor situations in captivity, primarily due to a lack of opportunities to introduce them to breeder groups. Gorillas that have spent their juvenile years in a bachelor group may be required to join or lead a breeding group in later life (depending on the requirement of the EEP). As such it is important for the breeding programme to be confident that the animals that they are recommending for group membership are socially competent individuals and the co-ordinators need to be aware of the potential long term consequences of housing subadult gorillas in situations with reduced rates of affiliative contact. Breeding programme recommendations must plan beyond the immediate need to find suitable housing during the pre-adult period, and ensure that potential group silverbacks are allowed to develop appropriate social responses. Institution managers must assess the level of positive social interactions within their groups to increase background knowledge, to enable population managers to make informed decisions regarding an individuals ability to transfer into new situations.

7.8 Critique

The longitudinal data from Paignton Zoo indicates that gorilla groups can show marked variation in hierarchy order and strength over time, and that this may be highly influenced by group composition. This level of variation in hierarchy and its potential impact on observed levels of dominance and affiliative behaviours may cause problems when comparing the frequencies of these behaviours between bachelor and breeder groups. Ideally more groups of each type would have been included and each group would have been observed for more than one period but this was not feasible. However variation within groups over time is likely to obscure real differences between groups rather than create differences where there are none. Therefore where differences have been found between groups these are likely to be genuine.

7.9 Further research

Effect of reduced affiliative interactions

The potential effect of an environment with reduced opportunity for affiliative interactions on the social development of young male gorillas leads to the necessity of further research on these individuals. Although hard to do in a formal, structured way (as the needs of the gorilla EEP are unpredictable from year to year), there is a need to follow individuals that have been housed in a bachelor group (an impoverished affiliative situation) as they move into a breeder situation, in order to determine their social competence in later life and the social impact of early life in a bachelor group.

Kin recognition in gorillas removed at an early age from the natal group

This research has suggested that gorillas may not recognise kin when not allowed the chance of early social bonds and, in fact, may form stronger bonds with non-kin whom they have spent early development time with. The captive gorilla population, where group composition is manipulated to achieve the goals of the captive breeding programme may provide a suitable environment for longitudinal studies into kin recognition.

Longitudinal research

As the breeding programmes in both Europe and North America are still under pressure to place males considered surplus, there is the possibility that some males will need to be housed in bachelor groups permanently. This thesis examined changes in social interactions over time within the Paignton group, however group membership was changing in response to the EEPs needs. Conversely the bachelor group at Disney is likely to remain at the current composition indefinitely. Extending longitudinal research on these groups to assess variations in behaviour as the gorillas mature will provide valuable information on the long term effects of bachelor housing.

Behavioural Flexibility

This thesis presented clear indications of behavioural flexibility in response to the changing social situation within Paignton Zoo Environmental Park. The captive environment gives a range of opportunities to examine behavioural flexibility within species. Longitudinal research with focal individuals can determine the extent of behavioural flexibility in response to changing situations, both social and environmental, within and between institutions.

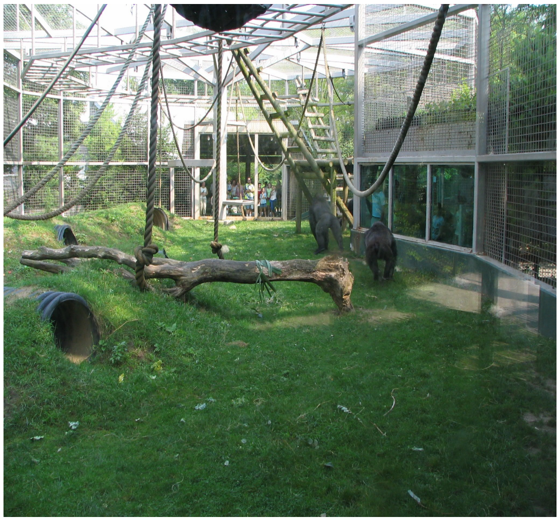
Impact of females and juveniles on the peripheralization of males

The results of the nearest neighbour data presented in this thesis indicate that females and juveniles can be a cohesive feature of breeder groups. Assessing impact of female / male social interactions and how these may alter as young males grow up would provide information on the mechanisms for male peripheralization in natal groups.

Appendix I: Enclosure pictures

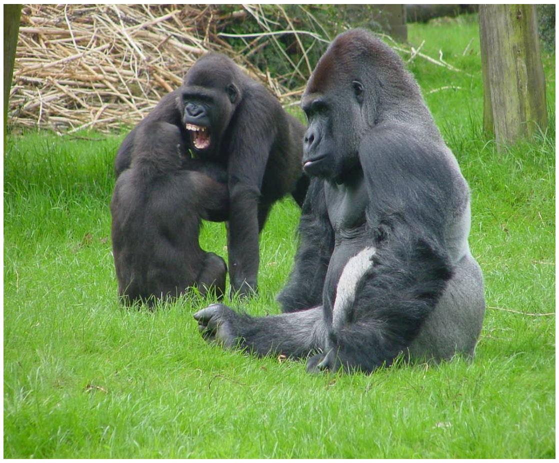
Disney Animal Kingdom

Columbus Zoo



Calgary Zoo

Apenheul



Port Lympne

Paignton

Appendix II: Breeder group membership

Institution	Name	Ageclass / sex (at time of research)	D o b	Stbk No	Rearing	Sire	Dam
Belfast	Boulas	Silverback male	13/07/86	921	parent	458	371
	Kukume	Blackback male	29/09/89	1089	hand	652	760
	Gugas	Sub-adult male	~1995	1397	hand	wild	Wild
	Delilah	Adult female	~1963	264	parent	wild	wild
	Kamili	Adult female	~1987	961	parent	350	557
	Bakira	Adult female	12/08/95	1352	hand	185	972
Apenheul	Bongo	Silverback male	~06/73	562	parent	wild	wild
	Uzuri	Blackback male	19/07/94	1317	parent	562	595
	M'bewe	Sub-adult male	16/11/97	1435	parent	562	575
	Kidogo	Sub-adult male	17/04/98	1465	parent	562	595
	Dalila	Adult female	~1972	567	parent	wild	wild
	Lobo	Adult female	~1973	574	parent	wild	wild
	Mintha	Adult female	~04/74	575	parent	wild	wild
	Mandji	Adult female	~01/75	595	parent	wild	wild
	Irala	Adult female	30/04/85	943	parent	578	589
	Miliki	Adult female	25/12/94	1319	parent	562	567
	Bibi	Juvenile female	25/02/97	1433	parent	562	574
	Kisiwa	Juvenile female	17/05/97	1434	parent	562	567
	M'kono	Juvenile male	28/01/99	1512	parent	562	943
	Zoezi	Juvenile female	14/12/00	1581	parent	562	574
	Nemsi	Juvenile female	23/08/01	1662	parent	562	595
	Gyasi	Infant female	29/04/02	1703	parent	562	567
Calgary	Kakinga	Silverback male	01/12/78	682	parent	111	128
	Nsabi	Blackback male	14/07/95	1366	parent	682	885
	Jawara	Sub-adult male	08/02/98	1483	parent	682	548
	Julia	Adult female	~1970	548	parent	wild	wild

	Tabitha	Adult female	06/11/80	747	hand	515	524
	Donge	Adult female	10/04/85	885	hand	255	477
	Zuri	Adult female	31/12/96	1416	hand	515	745
	Zwalani	Juvenile male	14/01/00	1572	parent	682	747
	Barika	Juvenile female	18/10/00	1573	parent	682	548
Columbus	Macombo	Silverback male	26/10/83	836	parent	342	226
	Nkozi	Blackback male	26/09/91	1195	hand	509	432
	Jumoke /Joe	Sub-adult male	09/01/98	1496	hand	573	1049
	Lulu	Adult female	~1964	262	parent	wild	wild
	Kebi	Adult female	13/01/91	1179	parent	509	262
	Nia	Adult female	21/12/93	1306	hand	573	528
	Kambera	Juvenile female	19/02/99	1543	hand	891	1179
Columbus	Mumbah	Silverback male	~1965	379	parent	wild	wild
	Jontu	Sub-adult male	27/01/97	1455	parent	891	1119
	Pongi	Adult female	~1963	269	parent	wild	wild
	Cassi	Adult female	15/08/93	1303	parent	342	269
	Colo	Adult female	22/12/56	56	hand	22	23
	Jumoke	Adult female	10/11/89	1119	hand	509	432
	Muchana	Juvenile male	23/06/00	1576	parent	891	1119
Disney	Gino	Silverback male	30/12/80	749	hand	566	530
	Hasani	Blackback male	12/10/94	1332	parent	749	413
	Jabari	Sub-adult male	04/11/97	1645	parent	749	828
	Benga	Adult female	21/04/71	413	parent	184	96
	Hope	Adult female	07/09/83	828	parent	599	631
	Makena	Juvenile female	24/01/99	1648	parent	749	413

Appendix III: Ethograms

Although gorilla vocalisations have been well documented both in captivity and the wild they are not always easy to hear in captive settings, and therefore have not been included in the ethograms except in the case of scream vocalisations.

Ethogram I: Instantaneous scan sampling

Behaviour	**Description**
Self directed	Physical contact with self, including scratching, self grooming, and self play (head and limb movements), self inspection. Can be performed when stationary or may involve movement.
Object manipulation	Interacting with object within enclosure, often puzzle feeder or part of enclosure furniture. Can be performed when stationary or may involve movement.
Social interaction	Physical contact with another individual, engaging in social resting, grooming, play fighting. Play fighting may include chase behaviour, and is usually accompanied by a bouncy gait and play face.
Sexual	Sexual behaviour, including genitalia inspect, mounting, thrusting, intromission, solicitation display
Aggressive	Contact and non-contact aggression – chase, bite, slap, tumble, includes threat displays. May include chase, usually accompanied by pursed lip face (aggressor) / fear face (victim) and scream vocalisations
Locomotion	Movement from one are to another either bipedally, quadrupedally or braichiation. Includes walking, running, climbing, swinging
Feeding	Feeding from available food source without having to actively search for it (i.e. keeper's provision of food)
Foraging	Active search for food. Including scanning whilst moving, sorting through substrate, gathering food with hands and arms.
Inactive	Motionless either sitting or lying, no contact with another individual or with an object. Eyes may be open or closed.
Abnormal / undesirable	Includes stereotypic movement, coprophagy, hair plucking and eating (trichophagy), rocking behaviour, regurgitation and re-ingestion
Out of view	Individual is out of sight or identification of behaviour being carried out is obscured

Ethogram II: Continuous focal follows

Behaviour	**Description**
Contact aggression	Physical contact between protagonists, including bite holds, biting, slapping or

	cuffing, tumbling, Usually accompanied by pursed lip face (aggressor) / fear face (victim) and scream vocalisations
Non contact aggression	No physical contact between protagonists, Includes chest beat and charge towards individual (indicating a motivation to engage in aggression), chase. Usually accompanied by pursed lip face (aggressor) / fear face (victim) and scream vocalisations
Display	Tense stance display – lips pursed, fore arms locked, shoulders raised and back legs braced for stability - and display charge – chest beat and charge, but direction of charge oblique to opponent
Play fighting	Physical contact between individuals with rough and tumble, cuffing and mock biting, accompanied by play face, may involve chase with bouncy gait
Supplant	Approach of protagonist towards victim. Can be accompanied by eye contact and vocalisation. Protagonist will sometimes touch or gesture to victim to stimulate movement. Victim moves away.
Sexual solicitation	Inspect or sniff genitalia. Solicit behaviour - strut with cheeks puffed out, arms often extended
Sexual	Mounting, thrusting, intromission
Self directed	Physical contact with self, including scratching, self grooming, and self play (head and limb movements), self inspection. Can be performed when stationary or may involve movement.
Object manipulation	Interacting with object within enclosure, often puzzle feeder or part of enclosure furniture. Can be performed when stationary or may involve movement.
Locomotion	Movement from one are to another either bipedally, quadrupedally or braichiation. Includes walking, running, climbing, swinging
Feeding	Feeding from available food source without having to actively search for it (i.e. keeper's provision of food)
Foraging	Active search for food. Including scanning whilst moving, sorting through substrate, gathering food with hands and arms.
Inactive sit	Motionless. Body posture upright, no contact with individual or object. Eyes may be open or closed
Inactive lying	Motionless. Body posture recumbent, no contact with individual or object. Eyes may be open or closed
Relaxed stance	Motionless, quadrupedal stance. Face relaxed and shoulders down
Nest	Collecting and sorting substrate into nest. Movements often exaggerated, posture relaxed.
Social interaction	Physical contact with another individual, engaging in social resting, grooming, play fighting. Play fighting may include chase behaviour, and is usually accompanied by a bouncy gait and play face.
Scratch	Scratch behaviour, exaggerated movements gaze directed away from body.
Defecation / urination	Expellation of faeces and urine
Out of view	Individual is out of sight or identification of behaviour being carried out is obscured

Ethogram III: All occurrence sampling (conflict resolution behaviours)

Behaviour	Description
Contact aggression	Physical contact between participants, including bite holds, biting, slapping or cuffing, tumbling, Usually accompanied by pursed lip face (aggressor) / fear face (victim) and scream vocalisations
Non-contact aggression	No physical contact between participants, Includes chest beat and charge towards individual (indicating a motivation to engage in aggression), chase. Usually accompanied by pursed lip face (aggressor) / fear face (victim) and scream vocalisations
Display	Tense stance display – lips pursed, fore arms locked, shoulders raised and back legs braced for stability - and display charge – chest beat and charge, but direction of charge oblique to opponent
Supplant	Approach of protagonist towards victim. Can be accompanied by eye contact and vocalisation. Protagonist will sometimes touch or gesture to victim to stimulate movement. Victim moves away.

Appendix IV: Transcript of academic activity

Peer-reviewed articles

Pullen, P.K. (2005). Preliminary comparisons of male/male interactions within bachelor and breeding groups of western lowland gorillas (*Gorilla gorilla gorilla*). *Applied Animal Behaviour Science* 90: 143-153.

Published work

Pullen, P.K. and Bemment, N. (2006). 'Surplus' males and bachelor groups. In: *EEP Gorilla Husbandry Guidelines.* Reitkerk, F. *et al*. (eds). Apenheul Primate Park, Holland.

Conference presentations

Pullen, P.K., Plowman, A.B. and Leaver, L.A. (2006). Comparisons in hierarchical associations and alliances in bachelor and breeding groups of captive western lowland gorillas (*Gorilla gorilla*) 21st International Congress, Entebbe, Uganda

Pullen, P.K., Plowman, A.B. and Leaver, L.A. (2006). Comparisons in hierarchical associations and alliances in bachelor and breeding groups of captive western lowland gorillas (*Gorilla gorilla*) The English Riviera Gorilla Workshop, Torquay June 2006

Pullen, P.K., Plowman, A.B. and Leaver, L.A. (2005). Changes in social interactions within a captive bachelor gorilla group over time and following changes in group composition: indications for the regulation of social relationships. Primate Society of Great Britain, Easter Meeting, Chester, 22nd-23rd March, 2005.

Pullen, P.K. (2004). Conflict management in Western lowland gorillas: comparisons between bachelor and breeding groups. XX International Primatology Congress, Turin, Italy, August 2004.

Conference proceedings

Pullen, P.K., Plowman, A.B. and Leaver, L.A. (2006). Changes in social interactions within a captive bachelor gorilla group over time and following changes in group composition: implications for bachelor group stability. Proceedings of the EAZA Conference, September 2005, Bristol Zoo Gardens. EAZA Executive Office, Amsterdam. pp 273-280.

Pullen, P.K., (2004). *Enclosure use and dyadic interactions of a bachelor group of western lowland gorillas (*Gorilla gorilla gorilla*).* In: Hiddinga, B. (ed.) Proceedings of the EAZA Conference 2003. EAZA, Amsterdam. pp 35-39.

Pullen, P.K. (2003). *Preliminary comparisons of male/male social behaviour within bachelor and breeding groups of Western lowland gorillas (*Gorilla gorilla gorilla*).* In: Dow, S. (ed.) Proceedings of the 4th Annual Symposium on Zoo Research. Federation of Zoological Gardens of Great Britain and Ireland/Bristol Zoo Gardens. ISSN 1479-7100.

Appendix V: Mixed models

Behavioural diversity model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	38	7.983	0.007*
Institution (nested in group type)	1	27	0.682	0.416
Age	1	38	81.665	<0.001*
Rearing style	2	27	0.799	0.460
Mean kinship	9	18	1.384	0.266
Group type * mean kinship	9	20	0.686	0.713
Group type * rearing style	1	17	1.659	0.215

*denotes significant effects

Behavioural equitability model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	17	0.076	0.787
Institution (nested in group type)	6	17	1.676	0.188
Age	1	37	33.779	<0.001*
Rearing style	2	37	4.130	0.024*
Mean kinship	9	17	1.385	0.269
Group type * mean kinship	13	24	0.688	0.756
Group type * rearing style	1	17	1.318	0.267

*denotes significant effects

Nearest neighbour with females model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	26	37.434	<0.001*
Institution (nested in group type)	6	17	1.729	0.175
Age	1	26	8.397	0.008*
Rearing style	2	17	1.192	0.328
Mean kinship	9	17	0.747	0.663
Group type * mean kinship	12	26	3.995	0.002*
Group type * rearing style	1	17	1.096	0.310

*denotes significant effects

Nearest neighbour without females model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	21	8.087	0.010*
Institution (nested in group type)	6	21	3.539	0.014*
Age	1	17	2.466	0.135
Rearing style	2	17	0.966	0.400
Mean kinship	9	21	2.514	0.039*
Group type * mean kinship	9	21	2.514	0.039*
Group type * rearing style	1	17	0.787	0.387

*denotes significant effects

Second nearest neighbour with females model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	30	119.814	>0.001*
Institution (nested in group type)	9	30	20.546	>0.001*
Age	1	17	0.637	0.436
Rearing style	2	17	1.473	0.257
Mean kinship	9	17	0.818	0.608
Group type * mean kinship	9	18	0.828	0.600
Group type * rearing style	1	17	0.027	0.872

*denotes significant effects

Second nearest neighbour without females model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	30	90.595	>0.001*
Institution (nested in group type)	9	30	18.505	>0.001*
Age	1	17	2.287	0.149
Rearing style	2	17	1.202	0.325
Mean kinship	9	17	1.095	0.416
Group type * mean kinship	9	21	0.908	0.537
Group type * rearing style	1	17	0.017	0.898

*denotes significant effects

Association SPI model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	20	1.536	0.230
Institution (nested in group type)	10	30	9.360	>0.001*
Age	1	20	2.939	0.102
Rearing style	2	17	0.448	0.646
Mean kinship	9	17	0.779	0.638
Group type * mean kinship	9	20	1.048	0.439
Group type * rearing style	1	17	0.042	0.841

*denotes significant effects

Frequency of dominance behaviour model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	27	4.129	0.052[1]
Institution (nested in group type)	6	17	1.661	0.191
Age	1	17	0.037	0.849
Rearing style	2	17	0.868	0.438
Mean kinship	9	17	0.571	0.802
Group type * mean kinship	12	27	3.361	0.004*
Group type * rearing style	3	24	0.371	0.775

*denotes significant effects

[1]denotes values approaching significance

Frequency of aggressive behaviours model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	30	21.145	>0.001*
Institution (nested in group type)	9	30	5.863	>0.001*
Age	1	17	3.508	0.078
Rearing style	2	27	2.475	0.103
Mean kinship	9	18	1.769	0.145
Group type * mean kinship	9	18	1.769	0.145
Group type * rearing style	3	27	2.433	0.087

*denotes significant effects

Dominance Behaviour Index model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	21	0.452	0.509
Institution (nested in group type)	6	21	5.569	0.001*
Age	1	17	2.762	0.115
Rearing style	2	17	1.558	0.239
Mean kinship	9	21	2.351	0.051[1]
Group type * mean kinship	9	21	2.351	0.051[1]
Group type * rearing style	1	17	2.783	0.114

*denotes significant effects

[1]denotes values approaching significance

Frequency of affiliative behaviours model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	17	1.126	0.303
Institution (nested in group type)	6	18	2.152	0.097
Age	1	24	50.393	>0.001*
Rearing style	2	24	3.484	0.047*
Mean kinship	11	24	4.115	0.002*
Group type * mean kinship	2	24	18.280	>0.001*
Group type * rearing style	1	17	4.010	0.061

*denotes significant effects

Relationship Quality Index model

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	26	5.099	0.033*
Institution (nested in group type)	6	20	2.336	0.071
Age	1	26	22.721	>0.001*
Rearing style	1	17	0.448	0.674
Mean kinship	11	26	2.928	0.012*
Group type * mean kinship	1	26	6.674	0.016*
Group type * rearing style	1	17	2.061	0.169

*denotes significant effects

Applied models: frequency of dominance behaviours

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	30	22.190	<0.001*
Institution (nested in group type)	9	30	6.134	<0.001*
Age	1	29	0.781	0.384

*denotes significant effects

Applied models: dominance behaviour index

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	29	0.327	0.572
Institution (nested in group type)	9	29	4.021	0.002*
Age	1	29	0.793	0.381

*denotes significant effects

Applied models: frequency of affiliative behaviours

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	38	18.103	<0.001*
Institution (nested in group type)	9	29	1.351	0.255
Age	1	38	19.985	<0.001*

*denotes significant effects

Applied models: Relationship Quality Index

Variable	Numerator df	Denominator df	F	p
Group type (breeder bachelor)	1	38	7.413	0.010*
Institution (nested in group type)	9	29	1.348	0.256
Age	1	38	19.607	<0.001*

*denotes significant effects

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