LIFE HISTORY STRATEGY OF WESTERN GORILLAS (*GORILLA GORILLA GORILLA*): AN INVESTIGATION OF JUVENILE AND ADOLESCENT SOCIAL DEVELOPMENT

Thesis submitted in accordance with the requirements of
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Philosophy

by

Johanna Elizabeth Hutchinson

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For my Nan,

Who believed that I would, but often had to tell me that I could! Without your unconditional love and support throughout my life, none of the adventures would have happened and without such experiences, I would not be submitting a PhD today. I love you, with my deepest thanks. This one is for you.

ABSTRACT

Life history theory seeks to explain how comparative developmental and maturational parameters vary between species and how such differences affect survival and reproductive success. In primates, the immature period is found to be longer than in other relatively sized mammals, delaying sexual maturation but being essential for brain growth and social development. Compared to adulthood, the primate immature period remains understudied, limiting our understanding of how delayed maturation contributes towards species fitness. This thesis investigates social development of western gorillas (*Gorilla gorilla gorilla*), who have a relatively prolonged period of immaturity, and focuses on the pre-reproductive period from weaning until sexual maturity. Behavioural data were collected from 13 male (3-11 years) and 9 female (3-8 years) non-reproductive individual (NRI) western gorillas, housed in 5 family groups in European zoos. Data from a further 9 male and 7 female NRIs housed in 3 peer groups in sanctuaries were collected for comparison. A combination of continuous focal sampling, as well as scan, all occurrence and *ad libitum* sampling was used; 1300 hours of data were collected over 180 days.

Within the thesis, a quantitative method to categorise gorillas into a life-stage was designed, which demonstrated distinct behavioural disparities between immature life-stages and between the sexes, highlighting the problems of life stage categories that are based only on static age classes. A study of social relationship development followed, finding that spatially, NRIs became increasingly peripheralised from the group core with age. Socially, younger NRIs invested in prominent maternal and conspecific relationships, whereas older NRIs did not. Relatedness affected sociality, with full siblings being more interactive than paternal half siblings are. An investigation of alloparenting showed that both male and female NRIs displayed this behaviour, with females continuing infant interactions until adulthood. It was postulated that gorilla alloparental behaviour is driven by the NRI and supports the 'learning to parent' hypothesis. Social play behaviour was also examined and found to be most common between similar-sized peers, with males generally being the preferred play partner. Disparate-sized play partners were more likely to be full siblings than paternal half siblings were. Younger NRIs were found to engage in more predictable play sequences whilst older NRIs engaged in play that was more sporadic. Support for the 'neural' hypothesis of social play was found, with social play having delayed benefits for the individual, although the immediate benefits of play were not dismissed. Finally, family-raised NRI behaviour was compared to peer-raised NRI behaviour. Behavioural trajectories and spatial orientation were comparable between rearing groups. Peer-groups thus enabled the development of species-specific behaviour, although atypical behaviours also developed. In conclusion, the success of novel methods to understand behaviour in the pre-reproductive period and its function in gorilla life history has been demonstrated.

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ACKNOWLEDGMENTS

In general, a PhD requires the committed work of the author and the support of friends and family, however a PhD in primatology often necessitates years of field experience and training prior to the PhD. It is for this reason that the following acknowledgements thank those who supported and encouraged my career preceding as well as during the PhD.

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GLOSSARY

Conspecific. A NRI of the same life stage as the gorilla in question, or two gorillas of same life stage

Full sibling. NRI related through the mother and father

Immature period. Ranging from birth until sexual maturity

NRI. Non-reproductive individual – gorillas from 3 years to 8 years in females and 12 years in males whom reside in their natal groups. NRIs did not include infant (0-3 year old) gorillas.

Older NRI. Adolescent male, adult female or blackback

Paternal half sibling. NRI related through the father with a different mother

Pre-reproductive period. The period of immaturity ranging from the end of infancy until sexual maturity, specifically omitting the infant life stage

SI. Sociality index

Younger NRI. Old infant or juvenile

Chapter 1

1 GENERAL INTRODUCTION

The overall aim of this thesis is to contribute towards the largely understudied discipline of primate ontogeny and to further the understanding of primate life history. Using captive western gorillas as a study species, a focus of the thesis is the divergent trajectories of non-reproductive individuals (NRIs) based on environment, sex and sociality. New methodology and novel research questions are used as appropriate, which expand upon the current understanding of NRI life history in general and western gorilla life history specifically.

1.1 Juvenility and adolescence in primates

1.1.1 Life history strategy and the 'extended juvenile period'

Processes of natural selection acting on a species lead to adaptations suitable for survival in a specific environment (Williams, 1966). Convergent patterns of adaptation in phylogenetically similar species have long been recognised and the formation of models to predict which forces shape life events have been developed (reviewed by Harvey & Purvis, 1999; Leigh, 2001). The study of life events (termed life history strategies) in animals has typically concentrated on the timing of variables such as growth, development, reproduction and mortality (Fleagle, 1999; Hill & Kaplan, 1999; Pereira, 2002). Such ontogenetic models show primate life histories to be unique among mammals, exhibiting a longer juvenile period than predicted by relative body size (Harvey & Clutton-Brock, 1985; Hill & Kaplan, 1999; Janson & van Schaik, 2002; Kaplan *et al.*, 2000). During juvenility and adolescence, changes in physical development and behaviour occur, with behavioural complexity developing in parallel to physiological development (Joffe, 1997). However, studies that investigate the trajectory of behaviour across the juvenile and adolescent period have remained limited throughout primatology (Pereira & Fairbanks, 2002).

The juvenile and adolescent period is defined as beginning at weaning and proceeding until sexual maturity, encompassing pre-pubertal animals that can survive the death of a caretaker and those who are of adult size, but who are not yet sexually competent (Pagel & Harvey, 2002; Pereira, 2002; Pereira & Altmann, 1985). Life history theories predict that large animals will grow slowly due to constraints in body growth and will subsequently display weaning and maturity at a later age (Fleagle, 1999; Purvis *et al.*, 2003). Extended growth and ultimate large size is an adaptation selected for in large primates to reduce predation risk and increase lifespan, which ultimately increases the time available for an individual to reproduce (Hill & Kaplan, 1999). All primates however, delay their maturation for longer than expected by size, further extending the immature period (Bogin, 1999; Fleagle, 1999; Harvey & Purvis, 1999; Hill & Kaplan, 1999; Ross, 2004). Growth rates in juvenile apes are slow and constant (Janson & van Schaik, 2002; Worthman, 2002), often with growth spurts in adolescence to attain full body size before sexual maturity (Bogin, 1990; Leigh, 1996). Selection for slower growth and thus a prolonged pre-reproductive period (defined throughout this thesis as the period of immaturity ranging from the end of infancy until sexual maturity. The aim of using this term is to focus discussion on the juvenile and adolescent period of development. In contrast, the term immaturity is used to discuss development from birth to sexual maturity, incorporating infants, juveniles and adolescents) must therefore be highly adaptive in a species and subsequently lead to an increased chance of survival or greater production of progeny in the future (Pagel & Harvey, 2002; Pereira, 2002).

1.1.2 Development of skill and knowledge in the juvenile and adolescent period

Many life history models in primates (Joffe, 1997; Pagel & Harvey, 2002; Rubenstein, 2002) consider social group living as the factor which promotes the extension of the juvenile period. Group living requires individuals to develop species-specific behaviour and the skills necessary to survive and be reproductively successful within the group (Bock & Sellen, 2002; Bogin, 1999; Joffe, 1997; Kaplan et al., 2000; Leigh, 2001; Rubenstein, 2002). Knowledge, skill and information processing ability, for example, in the development of cognitive mapping, are learned through group living and are essential for securing high energy foods, readily distributed by season and habitat for frugivorous and omnivorous primates (Barton, 1996; Harvey & Clutton-Brock, 1985; Hill & Kaplan, 1999).

Knowledge and skill acquisition must outweigh the costs of remaining in the pre-reproductive period as juveniles suffer increased vulnerability to predation and starvation by remaining smaller and less competitive for longer (Fleagle, 1999; Janson & van Schaik, 2002; Johnson & Bock, 2004; Rubenstein, 2002). This is particularly the case for young juveniles who grow more slowly and are predated upon more than older juveniles and adolescents (Cheney *et al.*, 2004; Harvey & Purvis, 1999; Janson & van Schaik, 2002; Walters, 1987). As juvenility progresses, environmental competence emerges (Janson & van Schaik, 2002) in line with an increased cognitive capacity relative to adults of the species (Russon, 2004b). In chimpanzees for example, the majority of skills needed for adult survival have been learnt by the end of adolescence, with post adolescent learning being greatly reduced and relatively inflexible (Boesch & Boesch-Achermann, 2000).

Evidence for the importance of social development and learning across the pre-reproductive period comes from cross-species comparative studies. The proportion of a primate's lifetime spent in the juvenile period, relative to other orders, is positively correlated with group size, large body size and the relative size of the non-visual neocortex, implicated by cognitive memory and social problem solving behaviour (Barton, 1996; Dunbar, 1998; Joffe, 1997; Kudo & Dunbar, 2001; Ross, 2003). It is predicted that a larger non-visual neocortex is selected for in species where social groups have more individuals than the average primate species, particularly when the species is diurnal and frugivorous since a greater cognitive capacity is needed to maintain multiple social relations and seek food (Barton, 1996; Dunbar, 1998). In addition, the role of individual experience plays an important part in shaping phenotypic expression enabling the individual to learn and benefit from direct experience in its immediate environment (Joffe, 1997; Pereira, 2002; Rosenblum & Andrew, 1994).

The extension of the juvenile period allows the juvenile to acquire a wealth of species-specific social repertoires and to shape each behaviour relatively slowly over time (Pagel & Harvey, 2002; Pereira, 2002; Rubenstein, 2002). Understanding behavioural change and skill acquisition over the juvenile period is important in determining how success in the pre-reproductive period affects adult reproduction and survival as it can highlight the processes occurring during the adult life-stage (Fairbanks & Pereira, 2002).

1.1.3 Western gorillas; a suitable species to study the extended juvenile period?

In line with the factors discussed above that predict the extension of the pre-reproductive period (Dunbar, 1998; Joffe, 1997; Kudo & Dunbar, 2001; Ross, 2003), western gorillas (*Gorilla gorilla gorilla*) provide an exemplary species in which to study social and behavioural development. Gorilla development is dominated by a long pre-reproductive period, lasting up to 14 years in males and 10 years in females (Nowell, 2005; Watts & Pusey, 2002). Additionally gorillas are the largest of the primates weighing up to 170 Kg (Rowe, 1996) with a modal breeding group size of around twelve individuals (van Schaik, 2004), ranging from three to fifteen gorillas (Gatti *et al.*, 2004). Further to group size, gorillas boast a large brain and neocortex relative to body size (Barton, 1996; Dunbar, 1998; Harvey & Clutton-Brock, 1985; Ross, 2003, 2004). Large sexual dimorphism in the species is a cause of physiological sex differences throughout the pre-reproductive period (Rowe, 1996; Watts & Pusey, 2002). Males mature at a slower rate than females (Nowell, 2005), which is adaptive in a polgynous social system where the larger, stronger males often monopolise reproductive efforts (Rubenstein, 2002). Gorilla juvenile growth rate remains slow until the onset of sexual maturity where both sexes exhibit marked increase in growth rates to reach adult size and weight (Leigh, 1996).

Fruit provides an important component of western gorilla diet but availability fluctuates with season (Cipolletta, 2004; Doran & McNeilage, 1999; Kuroda *et al.*, 1996; Williamson, 1988). The availability of fruit patches along with patch size and patch density, can potentially lead to a territory size of between 11-22 Km^2 and a day range of between one and two kilometres which ultimately limits group size in western gorillas (Cipolletta, 2003, 2004; Doran

& McNeilage, 1999; Doran *et al.*, 2002; Goldsmith, 1999; Williamson, 1988). The home range allows ample foraging to secure maximum fruit consumption (Doran-Sheehy *et al.*, 2004; Williamson, 1988) but territories often overlap with other group territories leading to inter-group interactions (Bermejo, 2004; Robbins & McNeilage, 2003).

1.2 Gorilla taxonomy

Two species of gorilla are currently recognised, divided by location. In central and west Africa the western gorilla (*Gorilla gorilla gorilla*) span the forests of Angola, Cameroon, Central African Republic, Democratic Republic of Congo, Equatorial Guinea and Gabon (Rowe, 1996; Tutin *et al.*, 2005). They are estimated to be the most populace of the entire gorilla sub-species, with population estimates ranging from 50,000 to 110,000 (Walsh *et al.*, 2003); no accurate population estimate exists for the species due to the methodological problems of conducting censuses across the large area inhabited (Tutin et al., 2005; Walsh & White, 2005). Western gorillas are highly threatened by the Ebola virus, habitat destruction and the increasing bushmeat trade and are categorised by IUCN (2007) to be critically endangered. Recently categorised as a separate sub species to the western gorillas, the cross river gorilla (*Gorilla gorilla diehli*) is isolated to the Nigerian/Cameroonian border, has received little research/tourism attention and is categorised as critically endangered with approximately 150 individuals remaining (IUCN, 2007).

In the eastern African forests the mountain gorillas (*Gorilla beringei beringei* ssp) of the Virungas National Park (spanning the borders of Uganda, Rwanda and Democratic Republic of Congo) and Bwindi Impenetrable National Park (Uganda) form two distinct populations of approximately 600 individuals and are both categorised as critically endangered (IUCN, 2007). A separate sub-species, situated solely in the Democratic Republic of Congo in lower altitude forest, the Eastern gorilla (*Gorilla beringei graueri*) has been little studied recently due to ongoing political unrest and illegal mining activities, the last population estimate was five thousand individuals and is thus categorised as endangered (IUCN, 2007).

1.3 Gorilla life-stages

1.3.1 Past research

The development of independence and social maturity is still understudied in all African apes. Studies of wild western gorillas (*Gorilla gorilla gorilla*) are limited to a bai environment in Congo (Nowell, 2005), and short term captive studies, (Hoff *et al.*, 1981; Maestripieri & Ross, 2002; Maestripieri *et al.*, 2002; Meder, 1989a, 1990) mountain gorilla (*Gorilla beringei beringei*) research is limited to one population (Fletcher, 1994, 2001; Fossey, 1979; Stewart, 1981). In the other African apes, chimpanzee (*Pan troglodytes*) social development is documented in only two populations (Hayaki, 1985; Pusey, 1983); and bonobo (*Pan paniscus*) social development is documented in one wild study (Enomoto, 1990). Throughout the following discussion of western gorilla social development reference is made to the mountain gorilla, for which more data are available due to the longer length of habituation and continuous research effort.

1.3.2 Developmental stages

Four stages are categorised in the life cycle of an ape; infancy, juvenility, adolescence and adulthood (Schultz, 1963), the duration of each differing between species and between individuals depending upon the physical and social environment (Pereira & Leigh, 2003; Rosenblum & Andrew, 1994). For western gorillas, the transition from infancy to juvenility is considered to occur at the completion of weaning; between 4 and 5.75 years (Nowell, 2005), with variation in parenting strategies between mothers (Lee, 1997) and due to age of the mother (Nowell, 2005) altering the duration of lactation. Independence is usually attained once the individual is no longer dependant upon the mother for either nutrition or transportation, (Rubenstein, 2002; Watts & Pusey, 2002). In mountain gorillas, this occurs at around 3.5 years of age (Fletcher, 1994, 2001).

Testes growth and first documented ejaculation are often determinants of adolescence and the beginnings of sexual maturity in apes (Kuroda, 1989;

Nishida *et al.*, 1990; Pusey, 1990; Watts, 1991). However, gorillas have inconspicuous genitalia and it is often difficult to determine the onset of adolescence using such parameters. Instead, first full copulation is usually taken as a determinant of adolescence in males and is observed between 8 and 10 years with first labial swelling in females at around 6 years of age in mountain gorillas (Watts & Pusey, 2002). Adulthood commences in males with exclusive mating with fertile females, from 14 years and in females at the onset of regular oestrus cycling, between 7 and 9 years in mountain gorillas (Watts & Pusey, 2002). Due to the limited available data on wild western gorillas it is not yet known if the trajectory of western gorilla development mimics that of mountain gorillas or to what extent developmental stages are dependant upon the environment and might change across populations and/or environment, such developmental changes, due to environment are documented in baboons (Altmann & Alberts, 2005). However, in all environments as the individual matures, the onset or reduction of specific behavioural activities occurs which facilitates advancement towards full maturity and the individual's adaptation to its physical and social environment.

Development occurs in a progressive manner from birth to maturity, but the course through the pre-reproductive period is variable between different species, the sexes and indeed between individuals (Lee & Kappeler, 2003; Pereira & Leigh, 2003). Life-stages are used as a classification mechanism to group individuals of a similar developmental stage thus enabling comparisons between individuals within the life-stage and across species. Determining whether an individual fits a particular life-stage in the literature for any given primate species however, is fraught with difficulties and error to date. Classifications are generally age-based with placement into a life-stage dependant upon age of the individual, perhaps with additional non-quantified behavioural traits (such as the cessation of suckling to determine a juvenile) or somatic growth (e.g. development of secondary physical characters to determine adulthood). Age categories, when used to define a life stage provide an inflexible boundary and growth systems are hard to quantify. Further to this, growth systems are based on the assumption that somatic, physiological and behavioural growth is linear and asynchronous across the pre-reproductive period (Pereira & Leigh, 2003). This is not the case (Leigh & Blomquist, 2007). Chapter 3, addresses the problem of categorising NRI western gorillas in the pre-reproductive period, devises a quantifiable system to determine life-stage in an individual, independent of categorical age and assesses error associated with using current age-based classifications which have been published and used with mountain gorillas but have also been regularly used in studies of western gorillas. The categorisation devised is applied to non-reproductive individuals (NRIs) in this study and will then be used for the remainder of the thesis with the aim of demonstrating the usefulness of such a method.

1.4 Social development in gorillas

1.4.1 Group structure

Western gorilla NRI are commonly raised in large family groups comprised of one adult male with multiple females, thus allowing for interactions with a range of adults and conspecifics during much of the pre-reproductive period. Upon adolescence both males and females may emigrate to other breeding groups or become part of a non-breeding group; males may remain solitary (Levrero *et al.*, 2006; Stokes *et al.*, 2003). Factors leading to male and female emigration are unknown for western gorillas but could be a result of large group size or motivation by closer proximity to older males for breeding purposes or to build alliances (Levrero et al., 2006). Non-breeding groups consist predominantly of NRI males, which range from juvenile aged males to silverbacks; NRI females who emigrate to non-breeding groups move into breeding groups upon fertility (Levrero et al., 2006). Bachelor group size remains large and comparable to breeding group size, ranging from 4 to 15 individuals (Levrero et al., 2006), but aggressive interactions are found to be lower than in natal groups with adolescent males sustaining fewer injuries (Levrero et al., 2006), an observation also documented in mountain gorillas bachelor groups (Robbins, 1996).

1.4.2 Changes in association across juvenility and adolescence

Living either in family groups or non-breeding groups requires the constant maintenance of relationships to build alliances, exploit social knowledge and to develop an understanding of the dyadic relations between other group members (Joffe, 1997; Russon, 2003). Living in a large breeding group or moving to another group, whilst still immature, exponentially increases the amount of social experience gained before maturity (Levrero et al., 2006). Both the strength of associations between group members and the number of other individuals available to interact with will affect the social competence of a NRI. For example, adolescent gorillas in non-breeding groups potentially experience a greater social immersion through increased peer interactions. Relationship formation and tolerance of other group members is changeable with age and sex across the pre-reproductive period (Russon, 2003). Associations may be formed within the group for specific daily activities, such as play or travelling, allowing the formation of relationships with a variety of group members (Parker, 2004). These relationships may then diminish as priority of activities and affiliations change towards maturity.

The distribution of social relations across age and activity determines how, when and from whom new skills will be learnt throughout development (Russon, 2003). In gorillas, this is dependant upon demography and ability to transfer into non-breeding groups. Significant relationships are created and maintained by NRI gorillas with their mothers, the group silverback (the presumed father) and with other NRIs. In all primates maternal care is extended beyond infancy and reduces slowly until sexual maturity (Rosenblatt, 2003). In wild mountain and western gorillas regular contact with the mother can be maintained until the end of adolescence, although time in association is driven by the NRI and decreases with age (Fletcher, 1994; Nowell, 2005; Stewart, 1981; Watts & Pusey, 2002). Likewise, relationships between silverbacks and juveniles in gorillas are initiated and maintained by the juvenile (Enciso *et al.*, 1997; Fossey, 1979; Stewart, 2001). In western gorillas, multimale groups are rarely seen (Gatti et al., 2004; Nowell, 2005) but in captive multimale groups the father of the NRI is found to be more responsive and less aggressive than other, unrelated males (Enciso et al., 1997; Hoff et al., 1981). Juvenile and adolescent western gorillas show continued close association with silverbacks, until emigration. In wild mountain and western gorillas juveniles show a propensity to associate with like-aged gorillas (Fletcher, 1994; Nowell, 2005), who exhibit similar levels of socialisation and provide an appropriate point to practise and develop behaviour in a non-confrontational relationship (Fagen, 2002). Peer relationships are highly dependant upon group demography, with smaller groups limiting the extent of relationship formation (Nowell, 2005). In general, male juveniles show little discrepancy in relationship formation between age and sex, maintaining affiliations with infants, juveniles and male adolescents. Female juveniles however, show a preference for associations with female infants and same aged juveniles (Fletcher, 1994; Nowell, 2005).

The study of social relationships in primate NRIs however, remains understudied, with the exception of pertinent dyadic relationships, determined primarily through proximate methods. Although informative, these give little indication as to how the NRI develops the mechanisms to maintain relationships and how the species' social system affects relationship formation. The use of proximity to measure social relationship strength assumes that distance is an accurate indicator of relationship strength, which may limit our understanding of primate relationships. Chapter 4 proposes hypotheses of relationship formation and maintenance across the pre-reproductive period and tests these using a sociality index comprised of affiliative behaviours and proximity. To put these findings in context, a scaling plot is used per gorilla group to assess the spatial relationship of each NRI in relations to all other group members.

1.5 Survival and skill acquisition in juvenility and adolescence gorillas

Changes in behavioural repertoires over the pre-reproductive period signal psychological growth and an increase in the inclusive fitness of the individual as it develops into its environment. Behavioural change and skill acquisition occur slowly, requiring practise through repetition and trial and error and involve social interchange between multiple age and sex partners (Pereira, 2002; Pereira & Altmann, 1985; Russon, 2004a).

1.5.1 Costs of being smaller and less experienced

The extended juvenile period presents significant risk to the survival of the NRI (Janson & van Schaik, 2002; Purvis et al., 2003). Firstly, as a gorilla gets older, the proximity and protective capacity of the mother decreases as she produces her subsequent infant and attends to its survival as a priority (Hoff et al., 1981; Maestripieri et al., 2002; Watts & Pusey, 2002). The juvenile is at this time mostly independent within the social group, but still much smaller than adult group members are. Safety from predation and perhaps infanticide is paramount in younger, smaller juveniles with proximity and play behaviour often taking place in the centre of the group and close to the silverback for protection (Watts & Pusey, 2002). Silverback protection is considered essential, particularly in vulnerable situations; maternally orphaned mountain gorillas for example have a higher rate of survival compared to maternally orphaned chimpanzees, perhaps due to the protective capacity of the silverback (Watts & Pusey, 2002).

Competitive ability to attain highly prized food items improves with increased juvenile size and experience, particularly in larger groups where food competition is often greater (Cipolletta, 2004; Janson & van Schaik, 2002; Kaplan et al., 2000). In addition, abundant food items can require manipulation before consumption, the skills of which are developed over time through the observation of conspecifics and through trial and error learning (Johnson & Bock, 2004). In mountain gorillas 80% of their folivorous diet must be manipulated before consumption (Byrne, 1999; Byrne *et al.*, 2001) and in the bai habitat western gorilla juveniles spend longer processing vegetation than adolescents (Nowell & Fletcher, 2007). This is not atypical for primates, young juvenile baboons and children of hunter gatherer communities also spend longer attaining difficult to manipulate food items and are found to be less efficient foragers than older juveniles (Bock & Sellen, 2002; Johnson & Bock, 2004).

Growth development and subsequent weight increase often leads to new challenges arising in the acquisition of previously accessible food items (Russon, 2003); in orang-utans differing techniques to acquire the same food item at different times over the pre-reproductive period are seen (Russon, 2003). A lack of experience in physical movement with an ever growing body may lead to a reduction in co-ordination and an increase in accidents in younger juveniles (Janson & van Schaik, 2002; Walters, 1987) which can be fatal or lead to physical disabilities, thus necessitating continual skill development.

As gorillas progress through specific development stages, such skills and sex-specific behaviour necessary for survival are observed and practised (Pereira, 2002). What is learned is predicted to be either functional and necessary for the survival of the juvenile period or necessary for the development of a competent adult (Bateson, 2005). Behaviour that is commonly documented in primates is predicted to have evolved in a common ancestor and to have remained in the repertoire of the species as it provides a specific benefit to the individual.

1.5.2 Alloparenting behaviour

A behaviour frequently observed in juvenile primates is alloparenting, described as the carrying, caring, grooming, or babysitting of infants by group members other than the mother. Although widely documented in the monkeys (Clarke *et al.*, 1998; Fairbanks, 2002; Förster & Cords, 2005; Manson, 1999; Silk, 1999) alloparenting is little understood in the apes with few published quantitative data available to determine its evolutionary function.

In western and mountain gorillas the handling and grooming of infants by NRIs of both sexes has been documented *ad hoc* in the wild (Fletcher, 1994; Nowell, 2005; Watts & Pusey, 2002). In western gorillas the alloparent is generally a juvenile of either sex or an adolescent female, and carrying is directed towards infants (Nowell, 2005). In mountain gorillas however, infants are not frequently carried but infant grooming is conducted by juveniles and adolescent gorillas of both sexes, with adolescent females spending a large proportion of their time grooming infants (Fletcher, 1994). Such behaviour has remained undocumented in captive western gorillas.

Relevant theories describing the advantages of alloparenting include the 'learning to mother' hypothesis (Fairbanks, 2002; Lancaster, 1971; Small, 1990) whereby female NRI primates benefit from infant-carrying by increasing the skills that will be essential for the survival of their own first offspring. In male primates, alloparenting is less commonly reported outside the Callitrichids, but the opportunity to handle infants may promote gentle interactions and an affinity to protect infants in the future (Pusey, 1983). The 'inclusive fitness' model assumes that alloparents would care for related infants' more than unrelated infants, promoting common genes into the subsequent generation (Hamilton, 1964). In Chapter 5, the first quantitative data for gorilla alloparenting behaviour is presented and evidence for the function of this behaviour discussed for western gorillas and the apes in general.

1.5.3 Social play

A second, profuse behaviour, documented in all the primates, is that of social play, which, although reasonably well studied compared to other areas of NRI development, has little quantitative evidence in support of its function (Burghardt, 2005; Lewis, 2005). Social play is focused upon in the thesis as it requires interactions with other individuals and thus is predicted to require a greater cognitive understanding of sociality (Lewis, 2005).

Social play behaviour begins in infancy and remains a frequent activity until adolescence across all primates species (Fagen, 2002; Fairbanks, 2002). Described as an 'improvised performance' by Fagen (2002), play in gorillas consists of a variable repertoire of behaviour generally involving one or two mutually participating individuals. Late infancy and juvenility are documented as the most prominent life-stages for play in all primates (Fagen, 2002; Fairbanks, 2002; Ross, 2003), with both rate and duration declining during adolescence (Fagen, 2002; Watts & Pusey, 2002). Play shows prominent sex differences in many species, including gorillas (Fletcher, 1994;

Maestripieri & Ross, 2002; Nowell, 2005) with males out-playing females in juvenility and into adolescence (Fagen, 2002; Fairbanks, 2002; Fletcher, 1994; Nowell, 2005; Watts & Pusey, 2002).

Theories that seek to explain the function of social play behaviour are numerous. The most current assumption is that it is beneficial for adult success through priming the body and brain during development (Fairbanks, 2000; Lewis, 2000; Ross, 2004). Fagen (2002) however, argues that the adaptive significance of play may solely be the promotion of a successful juvenile through cognitive and motor development, thus increasing survival until adulthood by gaining an understanding of its environment. He is supported in this claim by play theorists in child development (reviewed by Pellegrini & Smith, 2005). Finally, play has been proposed as a mechanism of training for the unexpected (Spinka *et al.*, 2001). Although play is predicted to be advantageous to the juvenile period, little evidence as to how it benefits reproductive success in the future has been sought (Byers, 1998).

The significance of play behaviour, documented in most mammal and some other taxa (Bekoff & Byers, 1998), may be in dispute, but the characteristics of play across primate NRIs remain largely comparable in form. Chapter 6 addresses the issue of functionality in social play and contributes to this area of literature by proposing how the benefits of social play may differ across the pre-reproductive period. Further to this, the pattern of social play in older and younger NRIs is investigated to determine if the function of social play changes across the pre-reproductive period in line with the reported frequency of social play.

1.6 The effect of social group structure and welfare on NRI social development

The majority of European zoos house western gorillas in social groups mimicking natural social group structure in the wild where possible, allowing a study of social development, which is predicted to resemble that of wild gorillas. However, the captive environment differs in significant ways from the wild due to being a static environment managed through regular daily routines. Captive gorillas are however, not expected to experience nutritional stress or inter-group aggression, which allows juveniles and adolescents time to build on intra-group associations and to develop social relationships. For example, play in most captive animals is recorded at higher frequencies than in their wild counterparts (Thompson, 1996). However, the captive environment does pose several disadvantages which should be considered in a species known for its sensitivity to environmental stressors (Hill, 2004; Meder, 1992). Limited sized enclosures reduce species typical behaviour documented in the wild and may reduce fertility (Lukas, Hoff *et al.*, 2003). In addition, reduced environmental complexity may lead to boredom, inactivity or stereotyped behaviour in gorillas (Hill, 2004; Lukas, Hoff et al., 2003; Meder, 1989b; Stoinski *et al.*, 2002). Also, adolescent males that are unable to withdraw from the group can become aggressive towards other group members and subsequently receive increased agonistic interactions and injury from the dominant male (Carlstead, 1996; Sannen *et al.*, 2004). Management considerations may alter group composition; often zoos prefer to move males from their natal group during juvenility to reduce the risk of injury and expense of transportation at a later age (Stoinski *et al.*, 2004), thus limiting the exposure of adolescent males to life in the family unit.

The welfare of captive primates by reducing stress, abnormal or stereotypic behaviour and by enriching their lives, has been constitutional in the captive environment and has enabled understanding of the effects of atypical social grouping/rearing strategy on both the developing NRI and the reproductive functioning of adults (Broom & Johnson, 1993; Wolfensohn & Honess, 2005). Many studies demonstrate that maximal competencies in adulthood cannot be reached without individuals being raised by parents in socially and environmentally enriching environments, which allow the development of species-typical behaviour (Bloomsmith *et al.*, 2006; Bloomsmith *et al.*, 2003; Meder, 1989b, 1992). In western gorillas, which account for the vast majority of gorillas kept in captivity (Schmidt, 2005), it has been shown that the hand-rearing of infants impacts the ability of the individual to raise their own offspring, and that living in peer groups affects their ability to engage appropriately in mixed-aged breeding groups (Meder, 1989b, 1994).

Hand-rearing strategies and subsequent re-introduction of NRIs into gorilla groups are issues specifically associated with captive handling and management techniques which can affect the NRI and group dynamics in ways not witnessed in the wild (Hoff *et al.*, 1994; Jendry, 1996; Meder, 1989a, 1989b; Vermeer, 2005). However, the similarity of social experience in parent-raised and hand-raised individuals is often limited, as hand-reared individuals have often been kept solely with a human caregiver, or raised in small peer-groups with other (two or three) hand-reared individuals. Thus not only have they been they raised without parents, but also without adequate models of species-specific behaviour and in limited social group size. The question of how the mother influences NRI social development, compared to conspecifics has long interested researchers of social development (reviewed by, Novak & Sackett, 2006), an understanding of which remains limited in the apes to date (but see, Bloomsmith *et al.*, 1994). The final data chapter in this thesis seeks to compare social development between captive NRIs held in family breeding groups and in large sanctuary peer groups to understand how social deprivation in infancy and hand rearing might affect the subsequent social development of NRIs in large peer groups but in the absence of adult models.

1.7 Aims of the thesis

Although long-term studies concerning the life history of adult primates are numerous (e.g. Boesch & Boesch-Achermann, 2000; Doran-Sheehy et al., 2004; Harris & Monfort, 2006; Johnson, 2003; Nishida *et al.*, 2003; Robbins *et al.*, 2004; van Roosmalen, 1985), an understanding of behavioural development and physiological change during the extended juvenile period is lacking, as is an understanding of how the social environment affects NRI development. Reaching adulthood defines a level of success, having survived the precarious juvenile period and it follows therefore, that understanding how individuals survive the pre-reproductive period is an essential component in understanding the life history of a species. Western gorillas, being large brained, highly social apes with a lengthy developmental period, provide an appropriate subject to study social development in juvenility and adolescence. Relating behaviour change to adult gorilla life history strategy will enable a greater understanding of gorilla adaptation to the environment in which it evolved.

This research aims to expand on previous studies of gorilla social development (Fletcher, 1994; Nowell, 2005; Stewart, 1981). Using the captive environment, a greater understanding of social development in the lesser-studied western gorilla will be attained and used for the following objectives:

- To develop a method of categorising life history stages in western gorillas, using behaviour as a flexible indicator of development change, which can be transferable to other primate studies.

- To determine strategies used by NRIs to develop relationships across the pre-reproductive period, using methods which seek to understand relationships from a social group perspective, as opposed to a dyadic perspective.

- To investigate the evolutionary significance of alloparenting behaviour in western gorillas, with reference to alloparenting in other apes.

- To provide evidence to support or refute commonly proposed theories that aim to explain the function of social play behaviour.

- To assess disparity in social development between NRIs raised in breeding groups and those raised in peer groups and to further understand the role of the social environment in the development of behaviour.

Chapter 2

2 METHODS

2.1 Site choice criteria

2.1.1 European Zoos

To ensure a comparable study of gorilla social development across European zoos it was necessary to choose establishments where the juvenile and adolescent gorillas were housed in family groups, with a similar group composition to those in published accounts of wild western gorillas (such as Gatti et al., 2004; Magliocca, 1999; Parnell, 2002). Such a group structure is predicted to facilitate species-typical relationships and interactions. A minimum restriction of three juvenile or adolescents present per research group was adhered to in order to enable a study of species typical social development, peer relationships and play behaviour. In addition, gorilla groups were not considered if they had suffered a gorilla death, transfer or introduction within six months before data collection commenced. This ensured that not all behaviour documented was a result of recent change in demography or zoo management. Zoos were identified and these criteria met using The International Gorilla Studbook (Schmidt, 2005). Where possible, zoos were visited before data collection to ensure reasonable visibility of the gorillas. Table 2.1 details the zoos included in data collection, gorilla group composition and sampling effort. One group of gorillas was housed by each zoo.

2.1.2 Cameroon Sanctuaries

To allow behavioural comparison with the European zoos it was necessary for each sanctuary to hold several gorillas estimated to be of juvenile or adolescent age. Permission for data collection was thus requested and attained from Limbe Wildlife Centre (furthermore LWC), Cameroon Wildlife Aid Fund (furthermore CWAF), both in Cameroon (Table 2.1), which were chosen due to their relatively close distance to each other and since they are the only long-term sanctuaries in Africa to be raising NRI western gorillas. One group of gorillas was housed at LWC and two groups at CWAF (Table 2.1, Appendix 1). At CWAF group 1 was an established adolescent peer group with six individuals and Group 2, was composed of 7 juvenile/infant peers, into which newly-rescued gorillas were introduced (Table 2.1).

Table 2.1 - Gorilla group composition, location and observation time at each institution

Location	Institute	Country	Total no. of gorillas	No. of immatures[1]	No. of adult females	No. of silverbacks	Group type	Enclosure design	No. of observation hours	Data collection periods
Europe	Apenheul Primate Park	The Netherlands	15	10	4	1	Breeding	Island	288.5	April-Aug 2005
	Burgers' Zoo	The Netherlands	7	5	1	1	Breeding	Island	167	May-Aug 2005
	La Vallée des Singes	France	9	5	3	1	Breeding	Island	136	Sept 2005
	Basel Zoo	Switzerland	11	4	5	1	Breeding	Inside	120	April 2006
	Zurich Zoo	Switzerland	9	5	3	1	Breeding	Inside	125.5	May 2006
Africa	LWC	Cameroon	11	7	4	0	Peer	Fenced	203	Nov-Dec 2006
	CWAF (Group 1)	Cameroon	6	5	1	0	Peer	Fenced	141.5	Jan-Feb 2006
	CWAF (Group 2)	Cameroon	7	7	0	0	Peer	Fenced	118.5	Jan-Mar 2006

[1] Incorporates gorillas from birth to 8 years in females and 12 years in males.

2.2 Data collection periods

Data collection began in May 2005 and continued until June 2006. In Europe, data were collected across the spring and summer months when the gorillas often had access to larger outdoor enclosures. In Cameroon, data were collected over the dry season, when rain was rare and the temperature remained largely constant.

2.2.1 European zoos

Enclosure size and design differed between zoos from a 2.5 acre island at Apenheul Primate Park, 4000m^2 islands at Burgers' Zoo and La Vallée des Singes to indoor enclosures of 139m^2 and 105m^2 at Basel and Zurich Zoo respectively. Mixed species exhibits were found at Apenheul Primate Park, where the gorillas shared the island with four Patas monkeys (*Erythrocebus patas*) and at La Vallée des Singes, with two red tailed monkeys (*Cercopithecus ascanius*) and six black and white colobus monkeys (*Colobus guereza*). All gorillas were provisioned with enrichment material often this was not scheduled and was noted upon occurrence.

All gorillas followed a static feeding regime throughout data collection (Table 2.2.), often being fed different food items across the day. Water was available in all enclosures *ad libitum*. Talks to the public were conducted daily by Keepers at Apenheul Primate Park and La Vallée des Singes. At these times, the gorillas were encouraged to assemble at a feeding station to be thrown desirable food items.

2.2.2 Cameroonian sanctuaries

All the gorillas were fed fruit and vegetables throughout the day (Table 2.2) with water available *ad libitum*. The LWC outdoor enclosure was 2500m^2, and incorporated a grass field with several mature trees which the gorillas had access to the lower branches. The LWC gorillas received a variety of food enrichment daily, such as scatter fed popcorn and fruit frozen in ice to encourage foraging.

The CWAF group 1 enclosure was 120,000m^2, in logged, degraded native forest habitat; the gorillas were fed twice during the day, although the lunchtime feed was kept at a minimum to encourage the gorillas into the night time holding enclosure. The CWAF group 2 enclosure was approximately 200m^2 of degraded, logged native forest habitat, divided into two areas to separate the juvenile and infant gorillas if the Keeper left the enclosure. This group had constant access to human contact through a known Keeper inside the enclosure to reduce group aggression focused towards the infants and to help build group cohesion. Group 2 were fed in the presence of a Keeper twice a day (Table 2.2.). The Keeper entered the enclosure with a basket of food and passed pieces of food or vegetable to each group member to ensure a fair distribution.

Table 2.2 - Gorilla feeding regime at each institute during data collection

Location	Zoo	Feeding Times						
Europe	Apenheul Primate Park (Apr-Jun)	▒ 9.00	░ 12.00	░ 13.45	░ 15.45			
	Apenheul Primate Park (Jul-Aug)	▒ 9.00	░ 11.30	░ 13.15	░ 14.45	░ 16.15		
	Basel Zoo	▓ 8.00	▒ 9.15	░ 11.00	░ 12.00	▓ 14.30	░ 15.30	░ 16.30
	Burgers' Zoo	▒ 8.00	░ 13.30	░ 15.30				
	La Vallée des Singes	▒ 9.00	░ 11.45	░ 14.00	░ 15.00	░ 16.00	░ 17.00	
	Zurich Zoo	▒ 10.00	▓ 11.30	░ 13.30	▓ 14.30	░ 15.30	▒ 16.30	
Africa	CWAF (Group 1)	░ 8.30	░ 12.00					
	CWAF (Group 2)	░ 8.30	░ 14.30					
	LWC	░ 8.45	░ 11.00	░ 13.00				

░ Fruit or vegetable feed ▒ Tree bark feed ▓ Forage feed (seeds/primate pellets)

2.3 Subject choice criteria

2.3.1 European zoos

NRI (non-reproductive individuals) included in the study ranged from 3-8 years for females and 3-11 years for males, which encompasses the age range of juvenility and adolescence used in other gorilla studies (Fletcher, 1994; Nowell, 2005; Watts & Pusey, 2002). To document social development in social situations comparable to wild gorillas, all NRIs raised in their natal group with at least the father present were included in the study. Age appropriate gorillas were excluded from the study if they were either hand reared; living in a non-natal group or if (in the case of females) they had /or have had suckling offspring and thus were considered sexually mature.

2.3.2 Cameroonian sanctuaries

The exact age of the sanctuary gorillas was unknown but an approximate age had been determined through dental examination by veterinarians when each gorilla arrived at the sanctuary. Following the constraints placed on data collection in Europe, all females with an approximate age between 3 years and 8 years and all males between 3 years and 11 years were included to allow for comparison with similar-aged family-raised gorillas. For data collection purposes, all sanctuary gorillas were living in peer groups, with other like-aged gorillas, where interactions with other gorillas could be observed.

2.3.3 Study individuals

A total of 38 gorillas (Table 2.3, Appendix 1), 22 held in five European zoos and 16 held in two Cameroonian sanctuaries were observed for between four and eight full days each. Thirteen males and 9 females were studied in Europe, whilst in Cameroon, 9 males and 7 females were observed (Table 2.3)

Table 2.3 - Focal subject characteristics

Location	Subject	Institute[1]	Age (yrs)	Sex[2]	Hours[3]
Europe	Uz	Ap	11	M	35
	Bi	Ap	8	F	33
	Ki	Ap	8	F	34
	Mb	Ap	8	M	25
	Kd	Ap	7	M	28
	Mk	Ap	6	M	32
	Zo	Ap	5	F	36
	Ne	Ap	4	F	27.5
	Gy	Ap	3	F	38
	Vz	Ba	9	M	39
	Vi	Ba	8	M	40
	Zu	Ba	3	M	41
	Sh	Bu	8	F	42
	Ny	Bu	4	F	40
	Si	Bu	3	F	42.5
	Li	Bu	3	M	42.5
	Bd	La	6	M	46.5
	Kb	La	4	M	45
	Kw	La	3	F	44.5
	Az	Zu	6	M	42.5
	Bs	Zu	4	M	41
	Bg	Zu	4	M	42
Africa	Ja	CWAF$_{\text{group1}}$	8	F	29
	Av	CWAF$_{\text{group1}}$	8	F	27
	Bo	CWAF$_{\text{group1}}$	7	M	28
	Nk	CWAF$_{\text{group1}}$	7	M	29
	Kb	CWAF$_{\text{group1}}$	7	M	28.5
	Nk	CWAF$_{\text{group2}}$	5	M	29.5
	Ss	CWAF$_{\text{group2}}$	4	M	29
	Mv	CWAF$_{\text{group2}}$	3	F	30.5
	Nu	CWAF$_{\text{group2}}$	3	F	29.5
	Ch	LWC	11	M	28
	Be	LWC	8	M	31
	Pi	LWC	8	F	30
	Tw	LWC	8	F	30
	Ar	LWC	6	M	28
	Bt	LWC	6	M	28
	Ak	LWC	5	F	28

[1] Ap = Apenheul Primate Park, Ba = Basel Zoo, Bu = Burgers' Zoo, La = La Vallee des Singes, Zu = Zurich Zoo, CWAFgroup 1 = Cameroon Wildlife Aid Fund adolescent group, CWAFgroup 2 = Cameroon Wildlife Aid Fund juvenile and infant group, LWC = Limbe Wildlife Centre. [2] M = male, F = female. [3]Hours of observation

2.4 Procedures

2.4.1 Pilot study

A pilot study was conducted at Apenheul Primate Park in April 2005. The behavioural codes for data collection were established, and gorilla behaviour monitored to ensure the inclusion of all necessary behavioural categories in the Ethogram. Through watching the gorillas, a correct identification of each group member was attained as well as the chance to practise estimation of distance for proximity measurements. These parameters were checked by the gorilla keepers and by Alison Fletcher during a supervisory visit. Before collecting data at each additional institute, a smaller pilot study was conducted for 2 hours on each gorilla to practice gorilla identification and to ensure the compatibility of the group behaviour to the Ethogram. No pilot data were used for analysis in this thesis, as the accuracy and speed of data collection were often considered unreliable.

2.4.2 The Ethogram

The Ethogram (Table 2.4) was designed by the researcher, in line with previous data collected on gorilla social development (Fletcher, 1994; Nowell, 2005) and previous captive gorilla studies where abnormal and stereotypic behaviour were recorded (Gold, 1992; Hill, 2004; Meder, 1989a).

Table 2.4 - Ethogram of behaviour recorded

Behaviour	Behavioural definition
Feeding and Grooming	
Suckling	Focal consumes milk from the mothers breast
Feeding on vegetation	Focal consumes vegetation
Feeding on bark	Focal consumes tree bark
Feeding on grass	Focal consumes grass
Drinking water	Focal consumes water
Feeding on vegetables	Focal consumes vegetables
Food transfer	Food taken from within 1metre of another
Food snatch	Food snatched from another's hand
Food manipulation	Focal handles or processes an item of food
Self grooming	Focal tends to its own coat to remove dirt or matter
Receiving grooming	Another tends to the focal's coat to remove dirt or matter
Grooming another	Focal tends to another's coat to remove dirt or matter
Genital touch	Focal touches another gorilla's genitals
Receive genital touch	Another touches focal's genitals
Movement	
Lying down	Focal takes a horizontal position on the ground or on enclosure furniture
Sitting	Focal is stationary and supported by the buttocks
Locomotion	Focal is moving
Climbing	Focal ascends or descends an object using hands and feet
Rump cling	Focal holds onto another's hind during locomotion
Focal is carried dorsally	Focal travels on the back of another
Focal carries another ventrally	Another clings to the front of the focal during locomotion
Focal carries another dorsally	Another travels on the focal's back
Interactions	
Focal approaches another gorilla	Focal moves towards another
Another gorilla approaches focal	Another moves towards the focal
Focal leaves another gorilla	Focal moves away from another
Another gorilla leaves focal	Another leaves the focal
Another gorilla follows focal	Another moves directly behind the focal
Focal follows another gorilla	Focal moves directly behind another
Focal displaces another gorilla	Focal supplants another and takes the location
Another gorilla displaces focal	Another supplants focal and takes the location
Focal retrieved by another	Focal is collected by another

Behaviour	Behavioural definition
Focal looking at another gorilla	Focal gazes and attends to another
Focal interacts with another gorilla	Focal initiates an action with another
Another gorilla interacts with focal	Another initiates an action with the focal
Self or human directed behaviour	
Rocking	Repetitive movements back and forth
Hair plucking using hand	Focal pulls out hair using its hand
Hair plucking using teeth	Focal pulls out hair using its teeth
Clasping	Focal embraces itself with its arms
Regurgitation	Focal vomits undigested food or liquid
Re-ingestion	Focal re-consumes vomit
Coprophagia	Focal consumes own or another's faeces
Interacting with the public	Focal initiates involvement with the public
Watching the public	Focal pays attention to activities of the public
Masturbation	Focal stimulates its own genitals
Finger sucking	Focal places a finger in its mouth and creates suction by pulling in the finger
Play	
Chase	One gorilla follows in pursuit of another
Gentle play	Slow, largely inactive contact engagement by two gorillas
Wrestle	Fast, active contact engagement between two gorillas
Spar	Grapple between two gorillas using elaborate arm action
Chest beat	Slapping the chest with the hands
Body beat	Slapping the stomach, groin or legs with the hands
Solicit play	Focal initiates play with another
Foliage in mouth display	Holding foliage in the mouth to signal the intention of play
Rest play	Stationary, non-contact respite occurring for short periods in the middle of bouts of active contact play
Socio-sexual play	One gorilla mounting another in a ventral or dorsal position often with the mounting gorilla thrusting against the other
Play face	An open mouth display, used during play
Object play	Focal engages with an available inanimate object
Self play	Focal spins or tumbles alone
Object used in display	An object is used by the focal to make noise or to throw as a display to another gorilla.
Strut stance	Standing in a stiff stance, with narrow front legs, wide back legs and the chest thrown out
Handclap display	Focal repeatedly strikes its hand palms against each other
Charge	Bipedal running to create a display

2.4.3 Psion Workabout

Using the Ethogram, a data configuration programme was designed using The *Observer* software and transferred onto a hand held Psion Workabout using PsiWin. All behavioural patterns were given two letter codes for efficient data entry. In addition, each behaviour could be programmed with one or two modifiers that allowed additional specific information to be collected (Appendix 2, 3, 4). Chasing behaviour for example was recorded along with the play partner (modifier 1) and the initiator of play (modifier 2). The Psion Workabout prompted the researcher to enter the programmed modifiers where applicable. Each behaviour was programmed as either a state, (recording the duration and frequency of the behaviour occurrence e.g. wrestling behaviour; Appendix 2) or as an event, (whereby only the frequency of the behaviour was recorded, e.g. a slap; Appendix 2). Events were predetermined in the Ethogram as behaviour that only takes an instant of time and thus where only the occurrence of the behaviour was useful (Noldus, 2003). Data were then downloaded onto the laptop for storage and analysis.

2.4.4 Focal sampling

Each day one focal gorilla (Table 2.3) was observed and continuous data collection was employed following Altman (1974). This is considered the ideal choice of data recording for subjects living in social groups (Martin & Bateson, 2002) and particularly where activity patterns of the animals in question fluctuate across the day (Fletcher pers comm.). For example in gorillas, due to their highly fibrous diet is it regular for the group to be active in the morning hours and spend multiple hours resting across the afternoon (pers. obs). Continuous focal observations ensure that complete patterns of daily behaviour are collected for each focal NRI and subsequently that data are comparable between NRIs. If the subject moved out of sight an ‘out’ category was used to stop data collection, following the criteria for focal sampling (Altmann, 1974), until the individual re-appeared. One day of data collection was attained for every focal gorilla before subsequent days of observation on a particular subject were collected to keep sampling effort similar across subjects. The behaviour documented is specified in Appendix 2. A bout of behaviour for this study was determined as a period whereby the individual engaged solely in a particular behaviour, e.g. if a focal NRI engaged in spinning behaviour (solo play) and spun around in a circle twice or five times both would be considered as 1 bout. However, if the NRI spun once, then ate a piece of browse, then spun again this would be recorded as two separate bouts of spinning behaviour, separated by a feeding behaviour. This applied to all behaviours regardless of whether they were programmed as states or as events.

2.4.5 Scan sampling

At 20-minute intervals, the group were scanned to determine activity and proximity of the focal to other group members (details in Appendix 3). Twenty minutes was deemed long enough to attain independence between scans and to record changing group activity and proximity, without hindering the focal sampling data collection. Data were collected on the Psion Workabout. Proximity scanning began with the nearest individual to the focal and continued in a concentric manner to the furthest away to ensure all gorillas in view were sampled. The focal was recorded to be either in contact, within 2 metres, between 2 and 5 metres, between 5 and 10 metres or over 10 metres from each other group member every 20 minutes.

2.4.6 All occurrence sampling

2.4.6.1 For all study subjects

Behavioural patterns, such as alloparenting (Appendix 4) were recorded onto a dictaphone whenever it was seen to occur by any of the subjects. This method allowed a greater amount of frequency data to be collected for behaviour that occurred rarely, but was of interest to the study.

2.4.6.2 *For all gorillas in observed groups*

Behaviour that occurred rarely within a group (e.g. fights between adult group members, change in enclosure design and illness of group members) was recorded on the dictaphone opportunistically and daily transcribed into field notes.

2.4.7 Exceptions during data collection

- Data were not collected during 'Keeper feeding' sessions (Table 2.2) when the attraction to food led to an artificial spatial arrangement of the gorillas and a focus on the Keeper rather than conspecifics.

- During periods of heavy rain the gorillas on islands were allowed access to the indoor enclosures for the remainder of the day and were often off show, thus data were not collected during these periods.

- Focal gorillas were not studied if they or their mothers were deemed ill by the Keepers. After an aggressive encounter a gorilla was not observed for 2 days or until the agonistic behaviour dispersed.

- On 14th August 2005 the group silverback at Apenheul Primate Park died unexpectedly. The death created a change in the behaviour of the NRI gorillas and the adult females. Without the silverback, NRI gorillas no longer met the research criteria and data collection ceased. A lower than anticipated number of observation hours was attained from Apenheul Primate Park for this reason.

2.4.8 Position of observer during data collection

Data collection was conducted from the public viewing area at Apenheul Primate Park, La Vallée des Singes, Basel Zoo and Zurich Zoo. At Burgers' Zoo data were collected from the Keeper feeding station above the public viewing area. At LWC and CWAF data were collected from the periphery of the enclosures, in areas away from the visiting public.

2.4.9 Duration of observations

A total of 1300 observation hours were accumulated for this study. Observation hours were calculated daily by the number of hours the researcher was present with the gorillas. Number of days spent in each zoo was dependant upon the number of subjects in the group and ranged from 15 days (Basel Zoo) to 60 days (Apenheul Primate Park and Burgers' Zoo collectively). In the European zoos a mean of 38.0 hours of data were accumulated for each gorilla, ranging from 25 hours to 45 hours (Appendix 1, a-e, Table 2.3). In the Cameroonian sanctuaries, mean data collection accumulated per gorilla was 28.9 hours, ranging from 27 to 31 hours (Appendix1, f-h, Table 2.3).

In the European zoos, data were collected from the gorillas on their emergence onto the island (at Apenheul Primate Park, Burgers' Zoo and La Vallée des Singes), or upon opening of the public viewing area (Basel Zoo and Zurich Zoo), at approximately 9am until the end of the public visiting hours, around 5pm. In the Cameroonian sanctuaries data collection commenced upon release from the night holding cages into the outdoor enclosures at approximately 8.30am and was terminated as the gorillas were taken back inside at approximately 4.30pm.

2.5 Data handling

These data were downloaded from the Observer software, version 5, licensed by Noldus Information Technology, 2003 into Microsoft Excel 2003 and analysed in SPSS version 14.0. Behaviour that were programmed into the Observer software as events were downloaded as frequency of occurrence, whereas behaviour recorded as states in the Observer software were downloaded as both frequency and duration of occurrence. Thus, the frequency and duration of all state behaviours were available for analysis, a common method used in behavioural data collection (Martin & Bateson, 2002), allowing the proportion, amount of time spent in an activity, and frequency of occurrence to be analysed as necessary. All data were standardised to frequency or duration per hour (for each focal NRI, the total value of each behaviour was divided by the total number of hours of observation for that NRI, see Table 2.3) before being used in analysis to ensure that the behaviour were comparable between individuals and across observation days. Time calculated for the observation of each focal gorilla does not take into consideration time spent out of sight of the researcher. This is largely because from where data were collected by the researcher the gorillas were in full view when in their daytime enclosures. Considering all 38 NRI gorillas, living in either European zoos or Cameroonian sanctuaries the median time spent out of sight was calculated to be 0.05 minutes/hour, with a range of 0.02 minutes/hour to 5.82minutes/hour.

2.6 Statistical analysis

The gorilla groups in Europe were held in family breeding groups, which were as comparable in demography to wild western gorilla groups (Nowell, 2005) as the captive environment allows. For this reason, the analysis in chapters 3-6, which focuses on the behavioural development of NRI's, incorporate only the 22 NRI's from the 5 European Zoos. Chapter 7 then provides a comparative analysis of behavioural development of the 16 NRI's raised in sanctuary peer groups (without parents) to those in European family breeding groups. The nature of statistical analysis conducted was dependant upon the question being answered and the amount of data available to answer it. In each chapter, the most appropriate analysis was chosen and is explained in detail in the individual chapter methods section.

Chapter 3

3 USING BEHAVIOUR TO DETERMINE IMMATURE LIFE-STAGE IN WESTERN GORILLAS

This chapter provides a method of categorising life history stages in a primate species using behaviour as a flexible indicator of developmental change. It provides the first life-stage classification specific to western gorillas and illustrates error caused by using life-stage classifications devised for a different species.

3.1 Introduction

3.1.1 Life history strategy and modularity in primate development

Selection pressures in the environment of a given species lead to adaptation over time. These adaptations maximise the survival and reproductive potential of a species (Hamilton, 1964). The common events that occur within the life of any given individual can be recorded and used to understand the evolutionary selection pressures that led to adaptive divergence between species. Such factors, including growth, development, reproduction and mortality (Fleagle, 1999; Hill & Kaplan, 1999; Pereira, 2002; Ross, 1998) together form an interpretation of the life history strategy for a species. A common understanding of life history in mammalian ontogeny is that the length of the growth and development period is largely dependant upon body size. Larger mammals are slower to reach maximum body size than smaller mammals due to the energetic constraints of body growth, with larger bodies taking longer to grow (Harvey & Clutton-Brock, 1985). In line with this, weaning and sexual maturity occur at a later age for large-bodied species compared to smaller bodies species (Harvey & Clutton-Brock, 1985).

The brain, being the central arena for co-ordinating behaviour and functioning is proposed to be energetically expensive to grow (Dunbar, 1998). Due to the metabolic expense of creating brain tissue; its formation is slow and often assumed to restrict somatic and physiological growth and behavioural maturation during ontogeny (Deaner *et al.*, 2003; Dunbar, 2003). Primates are unique compared to the other mammalian orders, as they have a larger brain (relative neocortex) size and longer growth period (juvenile period) than can be predicted by body size (Dunbar, 1998; Janson & van Schaik, 2002). Within the primates, and in line with Harvey & Clutton-Brock (1985), large bodied species still grow more slowly than small-bodied species, which may be due to the energetic demands of growing a relatively larger brain; this may contribute towards the extended juvenile period in the apes (Ross, 2004; Ross & Jones, 1999).

The evolutionary factors that have led to the selection for ontogenetic differences within life history strategies, and which can explain the extended primate juvenile period have been the subject of much empirical and theoretical research over the past few decades (Harvey & Purvis, 1999; Janson & van Schaik, 2002; Leigh & Blomquist, 2007; Pagel & Harvey, 2002). In general, support is found for the theory that the juvenile period developed as a result of a trade off between delayed reproduction to increase body size and the rate of mortality through the juvenile period (Charnov, 1993; Janson & van Schaik, 2002). An indirect effect of growing a large brain may be related to body growth and maturational timing (Leigh & Blomquist, 2007).

Recognised models of life history strategy in mammals (Charnov, 1993; Janson & van Schaik, 2002; Kozlowski & Weiner, 1996; Stears, 1992) use phylogenetic contrasts to correlate allometric aspects of life history across species, for example body and brain growth (Harvey & Clutton-Brock, 1985; Leigh, 2001; Leigh & Blomquist, 2007). Life history theories provide exceptional insight into divergence in ontogeny between species and indicate potential extrinsic factors that drive these evolutionary disparities (Harvey & Purvis, 1999). However, they are limited by portraying development in an individual as uni-dimensional; where all bodily systems are developing together over time and all structures cease growth synchronously at reproductive maturation (Leigh & Blomquist, 2007). However, development within an individual is presumed to be multidimensional, such that body systems develop asynchronously and that correlated growth between systems is highly variable by stage of development and between species (Leigh & Blomquist, 2007; Pereira & Leigh, 2003): i.e. that ontogeny is modular.

A ontogenetic mode is defined as a pattern of development which depicts the rate and schedule of growth for an organ or organ system (Leigh & Blomquist, 2007). Developmental trajectories therefore consist of a combination of timings and rates of co-development between integrated systems such as the brain, somatic size, organs and behaviour (play, dispersal, agonism, aggression) (Pereira & Leigh, 2003). Modal development is highly advantageous in mediating the growth of expensive metabolic tissue (the brain): it minimises the risk of metabolic competition between growing structures and limits offspring production until after growth cessation. In primates, with an extended juvenile period, this dissociation of development structures is highly important to enable growth flexibility, keeping the energetic costs of ontogeny low, without limiting development or further extending the juvenile period (Leigh & Blomquist, 2007).

Modularity in development is not a new concept, regardless of its omission from currently accepted life history models. Gould (1977) discusses the dissociation of ontogenetic systems, which recombine over evolution to express alternative modes of development between species. Additionally Stears (1992) determines modularity as an ontogenetic reaction norm, which combines a range of possible phenotypic expression for particular genotypes. However, empirical evidence to support ontogenetic modularity is limited due to inadequate ontogenetic knowledge of many primate species (Pereira & Leigh, 2003). Empirical evidence shows that different developing systems (found in different environments, belonging to different species or of different sexes) have asynchronous growth patterns and indicate independent growth patterns across multiple systems within the same body. For example, Leigh (1996) found body mass growth rates of African ape species to be highly variable with fluctuations in growth rate apparent between similar sized species: i.e. both fast and slow phases of somatic growth occur across development, but these are not necessarily similar between species. In a similar comparative analysis, Godfrey, Samonds, Jungers, & Sutherland (2003) found large inter-specific ontogenetic differences in dental development in the timing of weaning across primate species. Dental emergence was largely not dependant upon age at weaning.

Being energetically expensive to grow, the brain is partly responsive to selection on metabolic performance. However, brain growth trajectories for a number of New World monkeys are similar (with a similar relationship occurring between chimpanzees and humans), despite disparity in their age at reproductive maturity and somatic growth completion. This indicates that the brain and somatic growth are for the most part independent of each other in these primate species (Leigh & Blomquist, 2007). Similarly, within-species differences in development trajectory can occur, for example between males and females of the same species (Leigh, 1995).

Evolutionary extrinsic factors select for particular traits or timings of system growth within a species. One extrinsic factor is that of environmental risk. Janson and van Schaik (2002) provide a model which explains the extended juvenile period in primates as a risk aversion tactic, whereby slow growth reduces the ecological risk of death, by predation and starvation. The extended juvenile period therefore allows extra time for the development of adult specific behaviour, which increases reproductive success. Modularity extends this theory by assuming that juveniles will respond to risk in the environment by changing the rate and shape of their development trajectory to reduce risks. For example, by reducing body growth rate and remaining smaller, they receive greater protection from the natal group and reduce the risk of predation whilst developing other essential systems, e.g. the brain (Pereira & Leigh, 2003).

3.1.2 Life-stages – a classification to document ontogeny

The pre-reproductive period in primates is split traditionally into distinct ontogenetic phases. These are usually defined through physiological or physical development or through un-quantified behavioural development to enable the understanding of each distinct phase of development and subsequently allow cross-species comparisons. The framework defining the life-stages of primates was first described by Adolph Schultz (1963) based on a comparative study of deciduous and permanent tooth eruption sought from captive primate NRIs and from taxidermic specimens. In this original classification, infancy was determined by the presence of the deciduous teeth alone, with juvenility split into the eruption of permanent teeth alongside the deciduous teeth (juvenile stage 1) and the loss of the deciduous teeth (juvenile stage 2). Adulthood was assumed when all permanent teeth were fully grown (Schultz, 1963). It is from this research that the modern theory of life history has stemmed (Bolter & Zihlman, 2007), with current primate life-stages termed infancy, juvenility/juvenescence, adolescence/sub-adulthood and adulthood (Altmann & Alberts, 2005; Fairbanks, 2002; Fletcher, 1994; Watts & Pusey, 2002).

With an advancement in the understanding of primate behaviour and ecology, and increasing interest in the study of life history strategy over the past two decades (Charnov, 1993; Janson & van Schaik, 2002; Kappeler & Pereira, 2003; Kozlowski & Weiner, 1996; Leigh & Blomquist, 2007; Stears, 1992), a variety of markers to ascertain comparable development between and across taxa have accumulated. These include: behavioural indicators (Altmann & Alberts, 2005; Bolter & Zihlman, 2003; Janson & van Schaik, 2002; Robbins, 2007; Setchell, 2003), allometric patterns (Deaner et al., 2003; Dunbar, 2003; Leigh, 1996; Ross, 2003, 2004; Taylor, 1997; Walker *et al.*, 2006) and physical maturation (Bolter & Zihlman, 2003; Czekala & Sicotte, 2000; Lee, 1997). Determinants of life-stages have moved on from Schultz's early work on dental emergence to become largely based on categorical age along with a combination of behavioural, physical or physiological traits.

However, ontogenetic trajectories, and life-stages are not static entities as appears to be assumed across the literature through the determination of life-stage by categorical age, independent of sex, environment or species (Janson & van Schaik, 2002; Kappeler & Pereira, 2003). Even physical, physiological or behavioural ontogenetic development is largely undescribed within species making cross species comparisons difficult. Studies of life history strategy must ascribe to classifications comparable across species, where flexibility in the development trajectory brought about by phenotypic plasticity can be detected and therefore allow considered comparisons between phylogenetically similar species. The development of ontogenetic markers is one way is which researchers can document transition through the life-stages. However, as will be demonstrated, the markers currently used are highly variable between studies and thus are hard to quantify and compare between species or across sexes.

3.1.3 Life-stage markers

A life-stage marker is a physical, physiological or behavioural change that signals the transfer of the individual into the subsequent ontogenetic stage. The current use of life-stage markers is typically species-specific, but often not sex-specific. Markers provide an overall framework from which to determine who fits within a life-stage, a step forward from using biological age alone as a determinant, but largely ignoring phenotypic plasticity or environmental variation (Lee & Kappeler, 2003). Markers can be used in conjunction with categorical age, physical or behavioural observable traits used to correlate with age, but studies are few (Altmann *et al.*, 1981; Bolter & Zihlman, 2003; Deputte, 1992). This combination of life-stage markers may be sufficient in studies of physical or physiological growth, which are more comparable between similar individuals of a species, or in studies using fossils to extricate phylogenetically comparable information (Flinn *et al.*, 2005; Zihlman *et al.*, 2004). However, in studies of natural living populations, physical and physiological growth are difficult to measure and individual development trajectories are of as much importance in understanding the species as species-typical traits (Pereira & Leigh, 2003). Such markers, limited by categorical age, may pose limits to the understanding of for example, the 'extended juvenile period' within a species, and subsequently limit the understanding of the life history strategies for a species. The following section seeks to emphasis the disparity in life-stage markers across studies and between species.

3.1.3.1 Determinants of infancy and transition to juvenility

The earliest stage of postnatal life is termed infancy and as such commences at birth. The determinants of the passage from infancy to juvenility remain obscure and typically un-standardised even within research on the same species (Bolter & Zihlman, 2003; Deputte, 1992). In general, infancy is considered to be the period where the offspring is dependant upon the mother for survival (Pereira & Altmann, 1985), through her protection and by the provision of travel and nurturance needs (Pereira & Fairbanks, 2002). Often weaning is associated with the transition to juvenility, as the infant is refused maternal milk with the mother resuming oestrus cycling (Barrett *et al.*, 1995; Lee, 1997). Cross-species definitions of becoming a juvenile are unavailable (e.g. for gorillas see Fletcher, 1994; Nowell, 2005) and the timing of weaning is shown to be highly variable within and between a species (Nowell & Fletcher, 2007; Pereira & Altmann, 1985; Pusey, 1983). In addition, the timing of weaning may be affected by other factors such as the availability of food suitable for a weanling to eat as well as maternal restrictiveness (Barrett *et al.*, 2006).

Across the literature, infancy and the transition to juvenility is frequently determined solely by an existing categorical age range (Bastian *et al.*, 2003; Brent *et al.*, 1997; Carpenter *et al.*, 1998; Hoff et al., 1994; Huck *et al.*, 2004; Maestripieri & Ross, 2002; Maestripieri et al., 2002; McCann & Rothman, 1999; Pika *et al.*, 2003; Range & Noe, 2005; Schino *et al.*, 2000; Tomasello *et al.*, 1990). The exclusion or inclusion of subjects in a study of a particular life-stage is often based solely on this age range (Bastian et al., 2003; Pika et al., 2003). The results are often averaged by median age of individuals, further reducing variability between individuals. On occasion, other behavioural variables related to the specific study are used as a guide, for example infancy is determined to be when the individual nurses regularly and stays in close proximity to the mother in mangabeys (Range & Noe, 2005). Whether un-quantified behavioural variables alone are sufficient to determine infancy in a species, or how such age range classifications are justified within a study and between subjects are rarely substantiated in the literature.

3.1.3.2 Determinants of juvenility

A general behavioural description pertaining to juvenile primates is that of a prepubertal individual who can survive the death of its caretaker, usually the mother (Pereira & Altmann, 1985). Therefore the individual is expected to travel and forage independently (Boesch & Boesch-Achermann, 2000; Doran, 1997; Pereira & Fairbanks, 2002; Range & Noe, 2005), but will spend the majority of its time in close proximity to immediate family members (Boesch & Boesch-Achermann, 2000; Fletcher, 1994; Nowell, 2005). Typically behavioural markers of this life-stages are descriptive and lack quantitative assessment i.e. a male gorilla NRI is considered an immature until the first full copulation is witnessed (Watts & Pusey, 2002), which is highly dependant upon observer effort and juvenile opportunity. Quantified physical development includes the emergence of incisors and first molars upon independent feeding and can be used to categorise juvenility in chimpanzees (Zihlman et al., 2004). The current un-quantified classification of juvenility makes the transition from infancy into adolescence hard to ascertain.

However, the majority of recent primate literature uses age classification to define juvenility, with for example, the macaque juvenile period ranging from 1-3 years of age (Bastian et al., 2003; Maestripieri, 2005) and gorillas from 3.5-5years (Pika et al., 2003) in one study or 3.5-6 years in another (Watts & Pusey, 2002). Definitions between the sexes are often lacking, with some exceptions such as juvenile mangabeys, baboons, chimpanzees and gorillas (Fletcher, 1994; Johnson & Bock, 2004; Nowell, 2005; Range & Noe, 2005; Watts & Pusey, 2002). This is despite multiple references in the literature to the emergence of physical and behavioural differences between the sexes during the juvenile period (Bolter & Zihlman, 2007; Clarke et al., 1998; Förster & Cords, 2005; Nowell, 2005; Small, 1990; van Noordwijk *et al.*, 2002; Watts & Pusey, 2002).

3.1.3.3 Determinants of adolescence

An adolescent or subadult primate is described as being post-pubertal, yet not fertile (Pereira & Altmann, 1985). Largely, adolescent primates are defined by the secondary physical characters displayed, relating to sexual development. For males this is most likely to be the enlargement of the testes (Altmann & Alberts, 2005; Anestis, 2006; Boesch & Boesch-Achermann, 2000; Charpentier *et al.*, 2004; Setchell & Dixson, 2002; Watts & Pusey, 2002) and signs of menarche (i.e. labial swellings) in females (Altmann & Alberts, 2005; Boesch & Boesch-Achermann, 2000; Czekala & Sicotte, 2000; Watts & Pusey, 2002). As sexual maturity is reached, the growth rate of the individual is shown to slow (Leigh, 1996). However the relationship between sexual maturity and growth cessation differs between species and is currently little understood (Janson & van Schaik, 2002) and hard to quantify.

Rarely are behavioural characteristics used to define adolescence, perhaps due to limited studies pertaining specifically to this age group, and due to the relative ease of categorising physical change, as sexual development promotes observable differences. From a behavioural perspective, relationship change also signals adolescence across the literature. For example, mandrill males are shown to increase their proximity from other group members during adolescence, and reduce proximity again upon sexual maturity, with increased dominance assertion towards other group members (Setchell & Dixson, 2002). Chimpanzees and gorillas of both sexes spend even less time in close proximity to their mother, instead developing relationships necessary to increase their future breeding success (Fletcher, 1994; Pusey, 1990). Males are more regularly involved in aggressive encounters with older males and with females associating with potential breeding partners as opposed to same-aged or adult females (Boesch & Boesch-Achermann, 2000; Fletcher, 1994; Nishida et al., 1990; Nowell, 2005; Watts & Pusey, 2002).

Categorical age is also a less commonly used marker in adolescence, particularly in the apes who exhibit profound secondary physical characteristics. However, use of age in monkey species to define sub-adulthood is more common (for a review see Bolter & Zihlman, 2003). The move away from use of age classifications in younger life-stages to the use of mainly physical attributes in adolescence reflects the nature of adolescence as a period of great variability between individuals, which as of yet is not quantified.

3.1.3.4 Determinants of adulthood

The end of the growth period and attainment of full body weight often marks adulthood across primate species (Anestis, 2006; Janson & van Schaik, 2002; Leigh, 1996; Walker et al., 2006), the timing of which is difficult to pin point. Likewise, pregnancy in female non-human primates is used to signal adulthood (Boesch & Boesch-Achermann, 2000; Nishida et al., 2003; Walker et al., 2006) but pregnancy is often not detectable for several months. Adulthood as defined by puberty maturation in female humans, can occur between 12 years and 18.5 years and is influenced by multiple environmental and cultural factors (Ellis, 2004). Behaviour is often used to characterise adulthood in males, the pursuit of dominance in chimpanzees, mandrills and baboons (Altmann & Alberts, 2005; Boesch & Boesch-Achermann, 2000; Nishida et al., 1990; Setchell & Dixson, 2002). However in cooperative breeding groups of callitrichids, males reach physical and physiological maturation but suppress social signals of competition until leaving the natal group (Ginther *et al.*, 2002). In female migrating species, sexual maturity may be determined by entry into non-natal breeding groups (Boesch & Boesch-Achermann, 2000; Levrero et al., 2006; van Roosmalen, 1985), but this may depend on opportunity which leads to difficulties in classification.

Physical colouration such as the facial colours of the male mandrill and silvering of the male gorilla back, also signal adulthood. (Robbins, 2007), ontogenetically these are highly variable between individuals, due to environmental and individual development pressures (Breuer *et al.*, 2007).

Difficulties in determining maturity are expressed richly in the discussion of human teenage pregnancies, where the individual may be physically and physiologically mature, but exhibits behaviour typical of the adolescent stage (Macleod, 2003), defined as risk taking, succumbing to peer pressure, reproductive ignorance, emotional turmoil and at times insufficient care of the offspring.

Defining adulthood in humans pertains to cultural norms as opposed to behavioural, physical or physiological attributes and is flexible across cultures (Ellis, 2004). Categorical age changes from a specific to a ranged variable when defining adulthood in human and non-human primates, often linked with physical signs of sexual maturation (Pusey, 1990; Watts & Pusey, 2002). Comparatively, in published research using only 'adult' subjects, classification is often absent, or based on age, physical size or position held in a social group, e.g. mother, which removes the possibility that there might be important stages to adulthood that can be judged by both physical and behavioural attributes.

3.1.4 Justification for the formation of a quantitative system to determine life-stage using behaviour

In essence, infancy and juvenility in primates are currently determined largely by categorical age and un-quantified behavioural attributes, whereas adolescence and adulthood are categorised more by categorical age, residence in a social group, cultural norms and observable physical development. Determining the ontogenetic trajectory of just one sex in one species is therefore problematic and non-comparable to the opposite sex or to other species. This can be hindered further in situations where a life-stage classification already exists for a species. At times, these can be non-quantitative and so it is difficult to determine if they fit the species well. In addition, they are sometimes adopted for a similar species, without understanding the life history strategy differences between the two species. Pertaining to the current literature the main question to be dealt within this Chapter is:

Is it possible to develop a quantifiable system to determine life history stages in a species?

The development of such a quantified system whose method can be adapted to other species, or used to compare between the sexes is a necessary development if scientists are to further understand primate life history strategies (Pereira & Leigh, 2003). To do this the following advances must be achieved. Firstly, in line with current understanding of mammalian development (Harvey & Purvis, 1999) each system within an individual is predicted to develop asynchronously with variable correlation between systems throughout development (Leigh & Blomquist, 2007; Pereira & Leigh, 2003). Thus, the interchangeable use of multiple systems to monitor ontogeny (e.g. somatic growth and behaviour change) is not justified if comparison between other species is the aim. Secondly, and again for comparative purposes, the system chosen to monitor ontogeny needs to be quantifiable from the individual's birth to its death. Thirdly, data for the chosen system should ideally be collected from populations living in natural habitat, where the species develops in its evolved manner and where the effect of the natural habitat can be considered to further understand how environmental risks to immatures affect development (Janson & van Schaik, 2002; Pereira & Leigh, 2003). Considering these factors, the ontogeny of species and sex-specific behaviour is the obvious choice to document primate development. Behavioural data can be collected in a quantitative and non-invasive manner, in the natural habitat and thus, in habituated populations, will alter the animal's behaviour minimally.

In developing this quantifiable classification of ontogeny, observations of captive western gorillas will be used. Gorillas are ideal subjects as they exhibit a long pre-reproductive period (Leigh, 1995; Ross, 2004), which is already classified in the literature into infant, juvenility, adolescence and adulthood. Through living in large polgynous groups, often with multiple offspring, data can be collected from several immature individuals easily. Finally, being highly sexually dimorphic (Taylor, 1997), male and female NRIs are expected to exhibit a different schedule of development, which should be detectable through behavioural observations. Once a quantifiable classification has been developed, data collection from NRIs in wild western and mountain gorilla populations will be used to support the classification produced.

3.2 Aims

- To determine the relationship between behavioural variables and NRI (non-reproductive individual) age;
- To explore the success of the published mountain gorilla classifications in explaining captive western gorilla behaviour;
- To form a life history classification specific to captive western gorillas using quantitative behavioural data;
- To assess the use of behaviour within a life-stage classification with regards to explaining sex differences and progression through the pre-reproductive period.

3.3 Methods

In this chapter, all behaviour recorded during focal and scan observations were subjected to a correlation with gorilla age (months, Appendix 5). Behavioural groups can act as markers and allow a determination of life-stage if relationships exist between behaviour and gorilla age. Groups of similar behaviour, for example, chasing, wrestle and spar behaviour were also combined as social play, giving a more substantial data set and enabling visibility of relationships where they emerged.. Behaviour that did not significantly correlate with gorilla age due to insufficient data across the study subjects was omitted from further analysis. All other behaviours were incorporated into the analysis until they were statistically shown not to determine life-stage in NRI western gorillas. Considering the overlap between some of the behavioural groups in Appendix 5, e.g. proximity to the mother is measured by contact, 0-2metres and 0-5 metres, where significance is gained for all similar behavioural groups the group with the largest amount of data is used for analysis, e.g. in the example above proximity to the mother 0-5 metres would be used.

The nine groups incorporated into subsequent analysis are listed in Table 3.1 were either activity based or social based behaviour and were measured by either frequency per hour (freq/hr) and/or duration per hour (dur/hr). Behaviours were deemed independent as no single behaviour was used in more than one category. Non-normally distributed groups were transformed using SQRT, Log10 or inverse methods as appropriate, depending upon the distribution of the original data (Tabachnick & Fidell, 2007); the mean was used as the central tendency.

Four published life history classifications for mountain gorillas were taken from the literature, each varied in its classification of NRI life-stages (Table 3.2). In this chapter, each classification is named after the first author and date of first publication. Classifications by Harcourt *et al.* (1980), Schaller (1963), Watts & Pusey (2002) have been used in other mountain gorilla studies (Fletcher, 1994, 2001; Fossey, 1982; Stewart, 1981; Watts, 1990), and in behavioural research on wild and captive western gorillas (Levrero et al., 2006; Lukas, Stoinski *et al.*, 2003; Nowell, 2005), for which no specific life history classification currently exists.

The Schaller (1963) classification for mountain gorillas is categorised in the following way (Table 3.2). A *juvenile* is described as being an animal larger than an infant is and smaller than an adult, who lacks prolonged contact with an adult female, and weighs between 60-120 pounds. A *subadult female* is a female over 6 years of age who is advanced beyond the juvenile stage, whereas an *adult female* is one who transports an infant and/or with round body, smooth curves and sagging breasts with nipples up to an inch long. A *blackback* is an animal of between 6 -10 years and is described as being female-sized, but with a more angular and muscular body and without prominent nipples. Finally, a *silverback* is defined as being over 10 years in age and over 300 pounds in weight, with a large sagital crest with pelage on the saddle, legs, neck and sides being grey or silver in colour.

The Harcourt *et al.* (1980) classification (Table 3.2) is largely based on age classifications, whereby a *juvenile* is aged from 3-6 years and a *subadult* from 6-8 years, with no differentiation between males and females. Since males mature later than females they are given an additional category of *blackback* before reaching adulthood, which lasts up to 12/13 years of age. The term blackback is used to distinguish young males from fully mature *silverback* males, who turn silver on the lumbar region.

The Watts & Pusey (1993) classification (Table 3.2) is categorised using the following parameters; a *young juvenile* is a male or female in the fourth year of life, whereas an *old juvenile* is a male between four years and age at first copulation and a female is an *old juvenile* between four years and first labial swelling. A male *young adolescent* is categorised as an individual who has been seen to copulate until he receives he first wounds from the silverback, between 8-10 years, and an *old adolescent* is between 11-13 years of age. Males are fully grown from 15 or 16 years of age, but if they dominate females from before this age, they should then be labelled a *silverback.* Females between the first labial swelling and fertility (7-9 years) are termed *adolescent females.*

The Doran (1997) life-stages for mountain gorilla NRIs were determined by significant quantitative differences in locomotion style between age classes, whereby each year group was found to locomote in a significantly different way compared to the former and latter year group, this is proposed to be due to changing body size. No significant difference was found between males and females of the same age (Table 2.3). Age groups were determined by the percentage of quadrapudalism, climbing, suspensory behaviour, leaping, bipedalism and somersaulting of individuals.

Table 3.1 - Behavioural groups, measurement and transformation used in analysis.

Behavioural group	Behaviour	Transformation
Approach *F*	Focal approaches the mother	Logarithm
Chest beat *F*	Slapping the chest with the hands	Square Root
Feeding *F & D*	Consuming food	Logarithm
Grooming *F & D*	Receiving & accepting grooming	Inverse
Lying *F & D*	Resting whole body on the ground	No transformation
Locomotion *F & D*	Climbing & travelling	Square Root
Play (social) *F & D*	Wresting, chasing, gentle, spar	Square Root
Play (solo) *F*	Spin, tumble	Square Root
Proximity to the mother (Contact -5 metres) *F & D*	Sitting/resting with the mother as the nearest neighbour	Square Root

F = Frequency/hour, D = Duration/hour

In addition to previous published classifications, an age classification (Hutchinson & Fletcher) for specific use with captive western gorillas is proposed here through consideration of the current western gorilla literature, particularly NRIs. Firstly, in agreement with current western gorilla NRI life history studies, adolescent males were ascribed as 6-8 years old (Levrero et al., 2006), and blackbacks proposed as being in this life-stage from 8 years until sexually mature at around 15 years of age (Levrero et al., 2006; Nowell, 2005; Watts & Pusey, 2002). Secondly, gorillas under 4 years old who continue to suckle from the mother (Nowell, 2005) are classified as old infants, due to their continued nutritional dependence on the mother, used extensively in the current literature to determine infancy (Pereira & Altmann, 1985). Finally, the juvenile category is split into male or female to illustrate any sex related differences, due to recent understanding of gorilla sex differences beginning in the juvenile period (Nowell, 2005). The Hutchinson & Fletcher proposed classification (Table 3.2) thus has sufficient categories to differentiate between gorillas of different life-stage and sex, without overly limiting available sample size.

To test the success of each of the available classifications in explaining western gorilla behavioural data, in a way that will allow subsequent manipulation of life-stage group for each gorilla, a multivariate analysis of variance (MANOVA) and a direct discriminative analysis were conducted. Both are multivariate tests which examine differences between groups using several dependant variables, taking into consideration any relationships between the behaviour (Field, 2005). Using several dependant variables in this way leads to greater power to differentiate life-stage groups (Field, 2005) In the initial test, a MANOVA, all behavioural groups were included along with each classification. The MANOVA model was accepted when a) the behavioural groups significantly co-varied (determined using Pillais Trace), b) when the variance-co-variance matrices were the same for all behavioural variables incorporated, determined using Box's Test and c) if the assumption of homogeneity of variance was met, using Levene's Test. For this to occur, several behavioural groups were eliminated from the model. The following discriminative analysis used the mean value of each significant behavioural group to distinguish life-stage per gorilla. This was then used to classify individuals based on similarity in behaviour variables. This can be achieved using canonical correlation which allows the factoring of behaviour simultaneously to extract uncorrelated factors and to identify which two variants provide maximum correlation of behaviour across the life-stage groups (Lee & Gilchrist, 1985). The discriminative analysis converts the dependant variables accepted into the MANOVA (i.e., those that significantly co-vary) to underlying dimensions or factors (Tabachnick & Fidell, 2007). By using Wilik's Lambda it is possible to determine how many of these underlying factors significantly discriminate between groups and thus differentiate between the life-stages for each of the classifications (Field, 2005). The individual effect of each dependant variable on the underlying function can then be assessed through determining the loadings of each behaviour in the standardised canonical discriminative function co-efficients and these represent the relative contribution of each dependant variable to the group separation. Together this enables an understanding of how the life-stages in each classification are discriminated.

Within the new Hutchinson & Fletcher classification, gorillas that were flagged up in the discriminative analysis for being in an incorrect life-stage group were then re-assessed and if necessary reallocated, dependant upon the behavioural variants as opposed to categorical age. The relationship between the variants and the classification was illustrated using a combined-group plot, which spatially arranges the variant scores for each gorilla grouped by life-stage. A group centroid indicates the average variant score for each life-stage. The underlying factors differentiating between the life-stages are then determined and an understanding gained of how the dependant variables affect the differentiation of the life-stages is gained using canonical discriminate function coefficients. Subsequently, the discriminative values for each gorilla determined by the discriminative analysis were used to determine the effect of sex on NRI gorilla development, using independent t-tests and one way ANOVA.

Table 3.2 - Published life-stage classifications for mountain gorillas and proposed classification for western gorillas, where age range is stated in years

1. Schaller (1963)		2. Harcourt *et al*. (1980)		3. Watts and Pusey (1992)		4. Doran (1997)		5. Hutchinson & Fletcher	
Classification	**Age range**	**Classification**	**Age range**	**Classification**	**Age range**	**Classification**	**Age range**	**Classification**	**Age range**
Infant	0-3	Infant	0-3	Infant	0-3	Under 10 months	Under 10 months	Infant	0-3
Juvenile	3-6	Juvenile	3-6	Young juveniles	3-4	10-15 months	10-15 months	Old infant	3-4 & suckling
Adult ♀	6 years +	Sub-adult	6-8	Old juveniles ♀	4-6	17-21 months	17-21 months	Juvenile ♂	4-6
Blackback ♂	6 – 10	Adult ♀	> 8	Old juveniles ♂	4-7	2 years	2	Juvenile ♀	4-6
Silverback ♂	10 years +	Blackback	8-12	Young adolescents ♀	7-9	3 years	3	Adolescent ♂	6-8
				Young adolescents ♂	8-10	4 years	4	Adolescent ♀	6-8
				Old adolescents ♂	11-13	5 years	5	Blackback ♂	8-12
				Adult ♀	> 9	6 years	6	Adult ♀	8 +
						7 years	7		
						8 years	8		
						Adult ♀	> 9		
						Adult ♂	> 9		

3.4 Results

3.4.1 Determining the effectiveness of the life-stage classifications.

A MANOVA was conducted to determine the effectiveness of each life-stage classification in explaining the co-variance of the significantly correlated behavioural groups. For each life-stage classification, the mean value for each gorilla in each behavioural group was analysed. Table 3.3 lists the behavioural groups that significantly co-varied with each life-stage classification and the significance value of the MANOVA (Pillai's trace). The Schaller (1963), Hutchinson & Fletcher and the Watts and Pusey (1992) classifications were all found to have four behavioural groups (frequency and durations of a behaviour were considered as separate variables), which significantly co-varied. The Doran (1997) classification was least successful with only two behavioural groups co-varying.

For the four published mountain gorilla classifications each accepts one function to significantly determine life-stage in the captive western gorillas. In these classifications this one underlying function (Function 1, Figure 3.1a-d) is able to significantly determine life-stage, Function 2 (Figure 3.1a-d), does not significantly determine life-stage in these four classifications (i.e. Wilik's Lambda = $P > 0.05$). The Hutchinson and Fletcher classification is significant in determining life-stage in both Function 1 and Function 2 (Figure 3.1e), indicating that two underlying functions can explain the variance in the dependant variables accepted into the classification.

The one underlying factor, which explains the behavioural variance in the published mountain gorilla classifications, can be explained in terms of activity pattern in the NRI gorillas. In the Schaller (1963), classification feeding and social play have a strong positive contribution to the underlying function, whereas lying has a strong negative contribution (Figure 3.4). In terms of life-stages, juveniles, who feed, and play more frequently and rest less than older NRIs load higher on Function 1 compared to older NRIs. The highest loading on Funtion 1 is for juveniles, whereas the lowest is for the silverbacks. A similar pattern is documented for the Harcourt *et al.* (1980) classification, where lying has a strong negative loading on Function 1, whereas a medium positive loading is attained for locomotion and social play (Table 3.4). In Figure 3.1b, the life stages are again differentiated by activity pattern, whereby younger NRIs load higher on Function 1 than older NRI life stages. In a similar way in the Watts & Pusey (1992) classification lying once again has a high negative contribution to Function 1, with medium positive loadings from feeding and social play behaviour (Table 3.4). Younger NRIs (young and old juvenile male and females) who feed and play more frequently than older NRIs load higher on Function 1, whereas the old adolescent male life stage, with males who play less and rest more loads very low on Function 1. The Doran (1997) classification only accepts two behaviours to determine its underlying function, once again with lying behaviour having a high negative contribution on Function 1 and social play having a high positive contribution (Table 3.4). NRIs loading higher on Function 1 (3 and 4 year olds) play more and spend less time lying than those who load lower (8 year olds, Figure 3.1).

The Hutchinson & Fletcher classification differs in accepting two underlying functions to explain the data set and significantly differentiate between the life-stages of NRI captive western gorillas. Function 1 has a high negative loading from lying and a high positive loading from social play, whereas Function 2 has a high loading contribution from locomotion and a lower contribution from social play (Table 3.4). In this classification Function 1 is described as a measure of maturation, whereby older NRI life-stages load lower than younger life stages, whereas Function 2 portrays a measure of activity, where high loading NRIs (juvenile males) are found be more active than those with lower loadings (e.g. adolescent males).

The four published life stage classifications for mountain gorillas explain between 88-90% of the behavioural variance in the data set using one underlying function. Although able to differentiate between life-stages, the variance of individual behaviour in each life-stage is large, with individuals of different life-stages often overlapping in range (Figure 3.1a-d). This is particularly the case in the Schaller (1960) classification, which has fewer life stages and thus has a larger age and sex range of NRIs in each life-stage. This leads to greater behavioural disparity, the exact cause of which cannot be discerned. The Hutchinson & Fletcher classification explains 95.1% of the behavioural variance in the data set, in two underlying functions and has less variability between individuals in the same life-stage group, as life-stage groups categorise NRIs of smaller age ranges and from juvenility of one sex.

To determine classification effectiveness, the amount of variance that each life-stage classification explained was calculated. Using a discriminate analysis, (to determine individual effect and combined effect of the behavioural groups), the percent of NRI gorillas who were correctly classified into their life-stage group was determined for each classification (Table 3.4, Figure 3.1). Once again the Schaller (1963) and the Hutchinson & Fletcher classification were found to explain more variance in the behavioural data sets and correctly classify more NRI gorillas into life-stages than the other classifications. The least successful was the Doran (1997) classification, although with only the variance of two behavioural groups to explain, a high r^2 value was attained.

Table 3.3 - Results of the MANOVA showing significant co-variance of behavioural groups

Classifications	Co-varying behavioural variables	Pillai's Trace		
		F	d.f.	P
Schaller (1963)	Feeding *F* Lying *D* Social play *F & D*	2.37	12	0.02
Harcourt *et. al* (1980)	Locomotion *D* Lying *D* Social play *F*	3.33	9	0.003
Watts & Pusey (1992)	Feeding *F* Lying *D* Social play *F & D*	1.91	20	0.03
Doran (1997)	Lying *D* Social play *F*	4.45	24	0.001
Hutchinson & Fletcher	Feeding *F* Lying *D* Locomotion *D* Social play *F*	2.33	20	0.01

F = frequency/hour, *D* = duration/hour

Table 3.4 - Structure matrixes of pooled within-group correlations between discriminating variables and standardised canonical discriminative functions for all classifications.

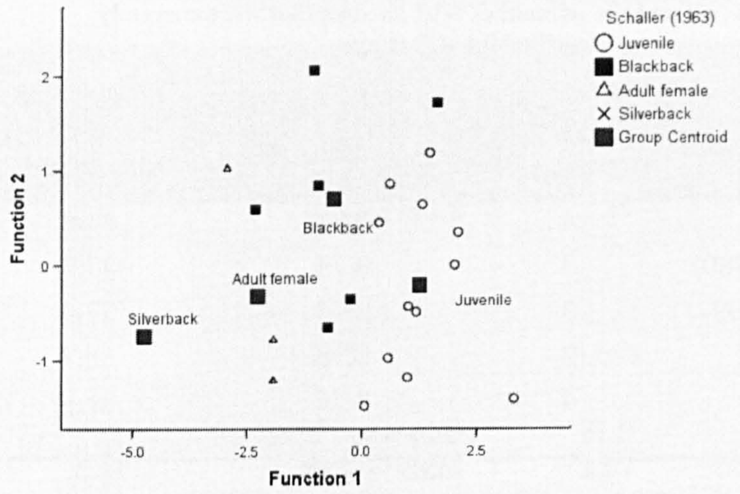
Classification		Factor loadings, eigenvalues & % variance explained	
Schaller (1963)		**1.**	
	Variance explained	**89.9%**	
	Eigenvalues	**3.29**	
	Feeding *F*	0.783	
	Lying *D*	-0.641	
	Social Play *F*	-0.26	
	Social Play *D*	0.658	
Harcourt *et al.* (1980)		**1.**	
	Variance explained	**87.9**	
	Eigenvalues	**2.67**	
	Locomotion *D*	0.482	
	Lying *D*	-0.796	
	Social Play *F*	0.321	
Watts & Pusey (1992)		**1.**	
	Variance explained	**88.8**	
	Eigenvalues	**5.25**	
	Feeding *F*	0.445	
	Lying *D*	-0.924	
	Social Play *F*	0.508	
Doran (1997)		**1.**	
	Variance explained	**87.9**	
	Eigenvalues	**3.84**	
	Lying *D*	-0.750	
	Social Play *F*	0.969	
Hutchinson & Fletcher		**1.**	**2.**
	Variance explained	**58.3**	**36.8**
	Eigenvalues	**3.39**	**2.13**
	Feeding *F*	0.336	0.316
	Lying *D*	-0.852	0.492
	Locomotion *D*	0.029	1.067
	Social Play *F*	0.589	-0.438

F = frequency/hour, *D* = duration/hour

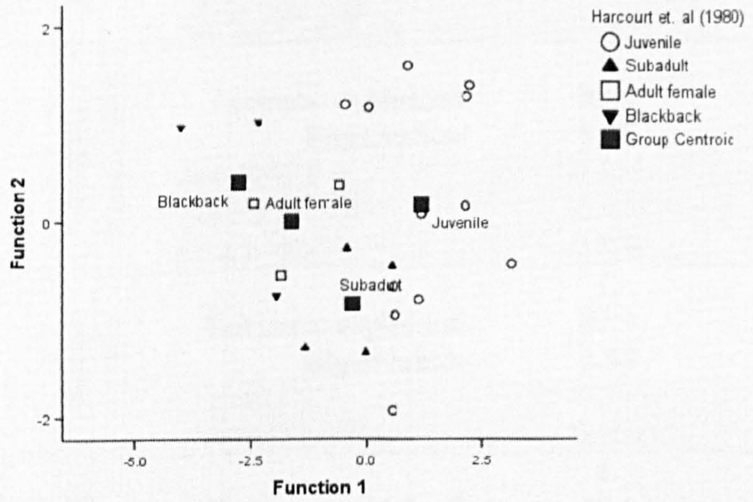
Table 3.5 - Comparison of the effectiveness of classifications, by the numbers of behaviour groups that co-varied, the amount of variance explained (r2) and the percent of NRI gorillas that were correctly classified into life-stage.

Classification	No. of co-varying behaviour	r^2	% classification predicts life-stage
Schaller (1963)	4	0.74	81.8
Harcourt *et. al* (1980)	3	0.73	77.3
Watts & Pusey (1992)	3	0.70	77.3
Doran (1997)	2	0.78	66.7
Hutchinson & Fletcher	4	0.74	81.8

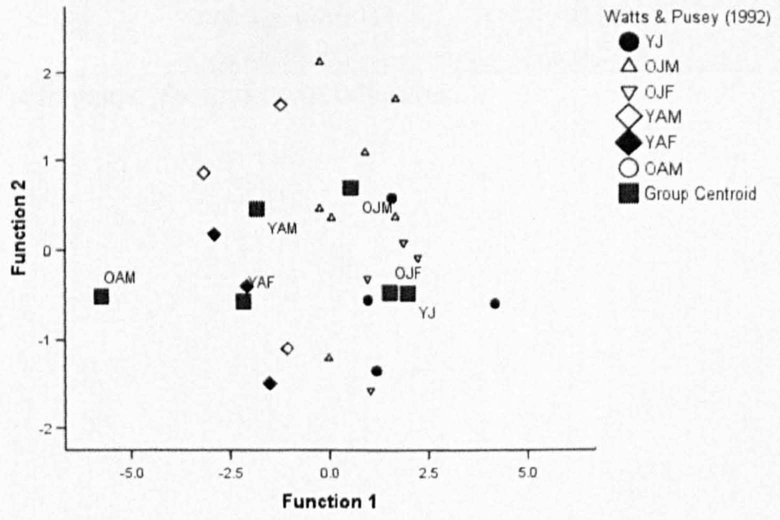
a) Schaller (1963)



b) Harcourt *et. al* (1980)



c) Watts and Pusey (1992): YJ – Young juvenile; OJM – Old juvenile male; OJF – Old juvenile female; YAM – Young adolescent male; YAF – Young adolescent female; OAM – Old adolescent male



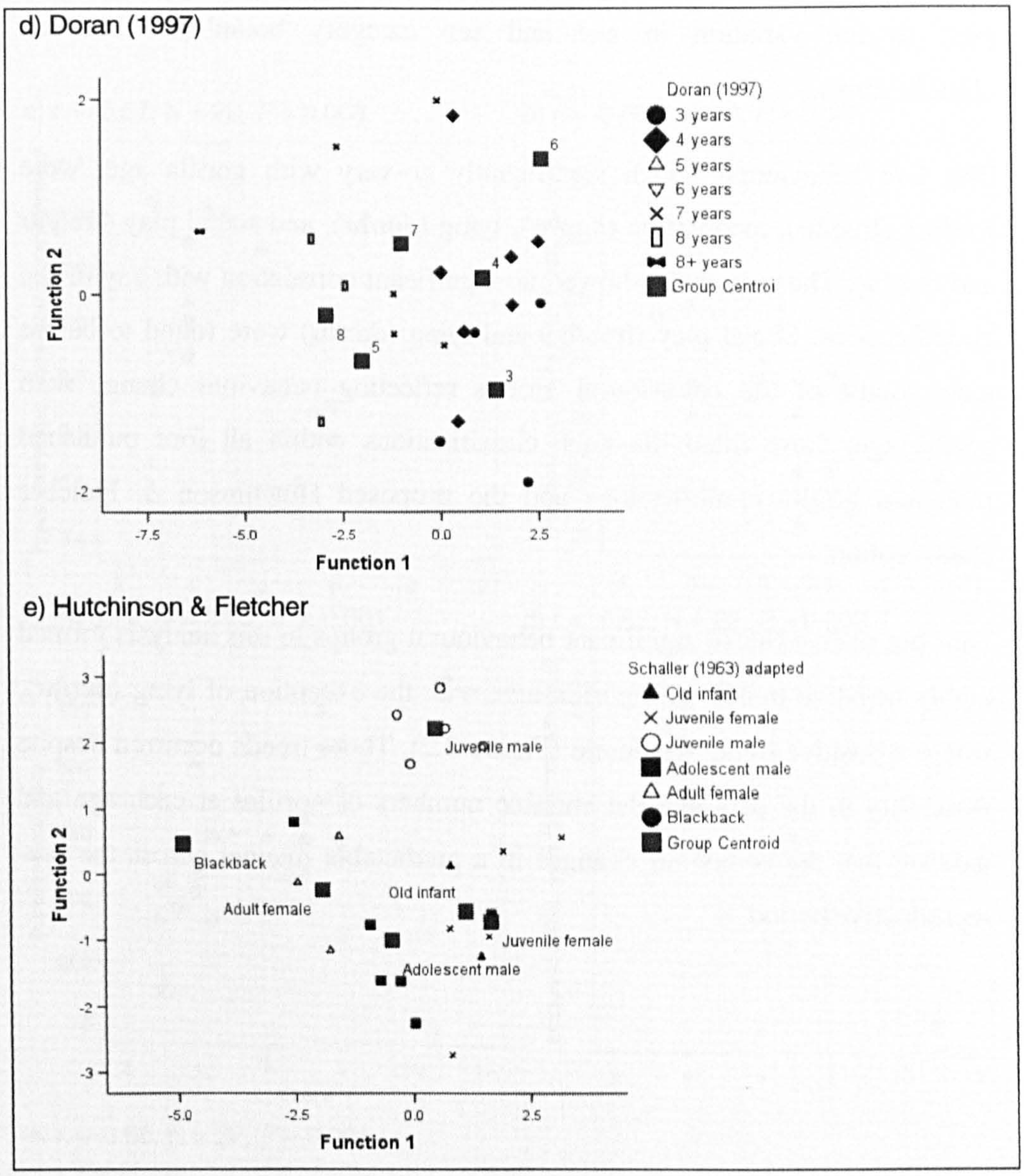


Figure 3.1a-e - Spatial representations of life-stage classifications based on significant co-varying behavioural groups, where the group centroid represents the central spatial region of the life-stage category, based on the mean attributes of the NRIs

The Schaller (1963) and the Hutchinson & Fletcher classifications (Table 3.3) co-varied with four behavioural groups each and were thus proposed as reasonable classifications to explain captive western gorilla behaviour. The three other published classifications (Table 3.3) co-varied with 2 or 3 behavioural groups and were thus considered less able to represent the captive western gorilla data. Clearly then, disparity exists between published life-stage classifications when mountain gorilla classifications are tested using captive western gorilla behavioural data; this appears to be due, at least in part, to the variation in age and sex category boundaries between classifications.

The five behaviours, which significantly co-vary with gorilla age, were feeding (freq/hr), locomotion (dur/hr), lying (dur/hr), and social play (freq/hr and dur/hr). The remainder showed no significant correlation with any of the classifications. Social play (freq/hr) and lying (dur/hr) were found to be the most robust of the behavioural groups reflecting behaviour change with gorilla age; these fitted life-stage classifications within all four published mountain gorilla classifications and the proposed Hutchinson & Fletcher classification.

Four out of five (80%) significant behavioural groups in this analysis formed highly negative trends with gorilla age, with the exception of lying (dur/hr), where a positive trend was found (Figure 3.2). These trends occurred despite variability in the data and the variable numbers of gorillas at each age and indicate that the behaviour changes in a predictable manner across the pre-reproductive period.

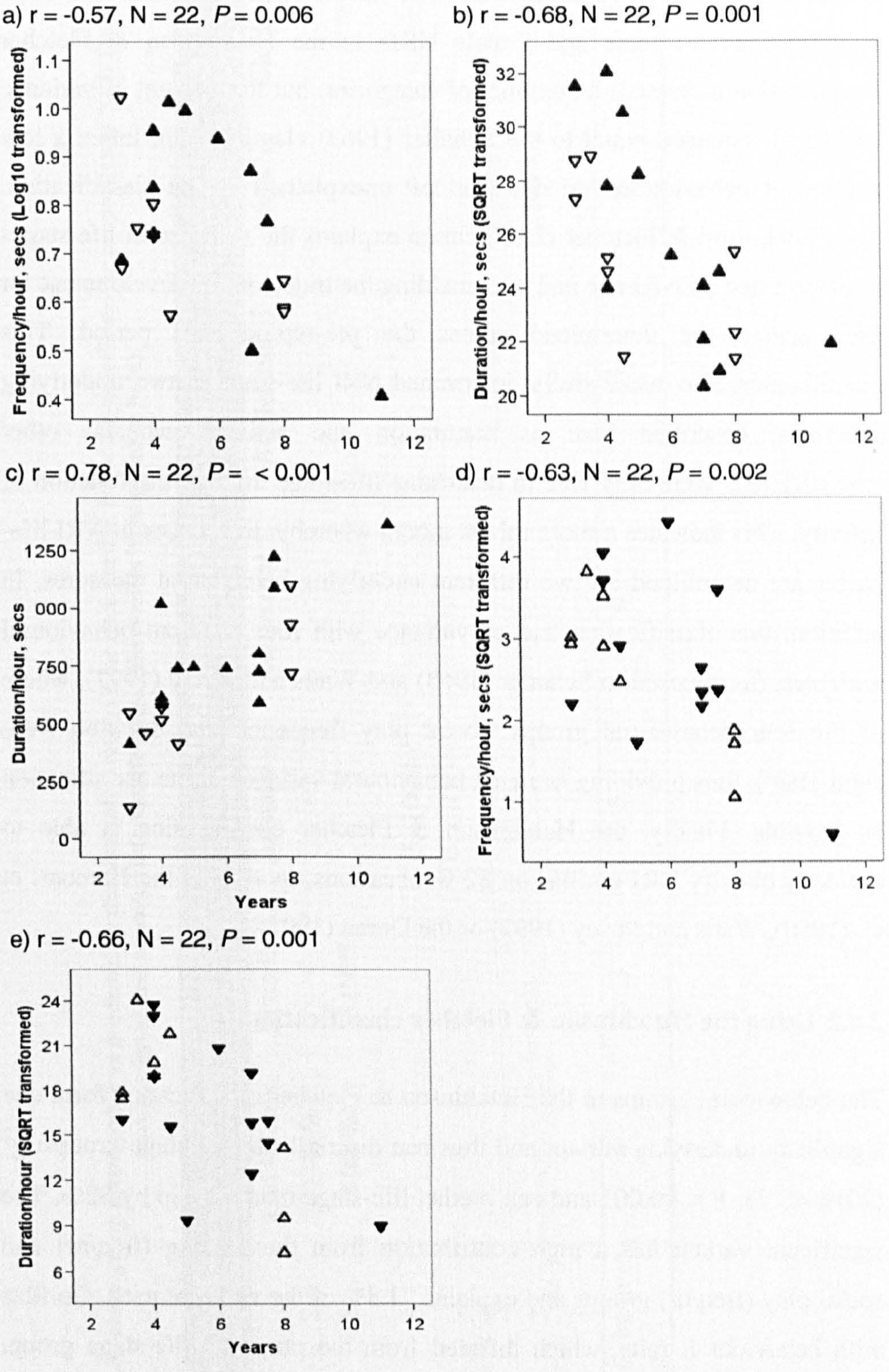


Figure 3.2 - Correlations (Pearson's) between significant co-varying behaviour and NRI age. Mean a) Feeding (freq/hr), b) Locomotion (dur/hr), c) Lying (dur/hr), d) Social play (freq/hr), e) Social play (dur/hr). Open triangles represent females; filled triangles, males.

Of all five life-stage classifications, the Hutchinson & Fletcher model was found to be the most successful. The inclusion of separate life-stage classifications for male and female NRIs in the Hutchinson & Fletcher classification increased the number of categories, but the amount of variance explained remained equal to the Schaller (1963) classification, infact a low amount of behavioural variance was left unexplained by the classification. The Hutchinson & Fletcher classification explains the variance in life-stages as determined by NRI age and sex, enabling the trajectory of development for each sex to be determined across the pre-reproductive period. This classification also successfully determined NRI life-stage in two underlying functions, described here as maturation and activity, whereas other classifications were only able to determine life-stage through the function of activity. This indicates a more robust model whereby differences in NRI life-stages are determined on two different underlying behavioural measures. In addition, this classification had co-variance with four different behavioural variables, (as opposed to Schaller (1963) and Watts and Pusey (1992), where of the four behavioural groups, social play frequency and duration were significant), thus providing as much behavioural variance to the classification as possible. Finally, the Hutchinson & Fletcher classification is able to correctly classify NRI gorillas on 82 % occasions, more than the Harcourt et al. (1980), Watts and Pusey (1992) or the Doran (1997).

3.4.2 Using the Hutchinson & Fletcher classification.

The behavioural groups in the Hutchinson & Fletcher classification form one significant underlying variant and thus can discriminate life-stage groups; χ^2 (20) = 48.73, P = <0.001 and can predict life-stage membership by 82%. The significant variant has a high contribution from the feeding (freq/hr) and social play (freq/hr) groups and explains 71.3% of the variance used. Gorillas with behavioural traits, which differed from the proposed life-stage group, were predicted by the discriminative analysis to belong to other life-stages. *Wrongly* categorised gorillas were those predicted by their behaviour group scores to belong to other life-stage groups, shown in Table 3.6 along with correctly predicted life-stage group.

Table 3.6 - Life-stage group membership as predicted by discriminative analysis for each gorilla. Percentages indicate the proportion of NRIs that were predicted and accepted into the life-stage. (Disparities highlighted in bold).

Age based category	No. of gorillas	Predicted group membership						
		Old infants	**Juvenile ♀**	**Juvenile ♂**	**Adolescent ♀**	**Adolescent ♂**	**Adult ♀**	**Blackback ♂**
Old infants	2	**2 (100%)**	-	-	-	-	-	-
Juvenile females	5	**2 (40%)**	3 (60%)	-	-	-	-	-
Juvenile males	5	-	-	5 (100%)	-	-	-	-
Adolescent ♀	-	-	-	-	-	-	-	-
Adolescent ♂	5	-	-	-	-	4 (80%)	**1 (20%)**	-
Adult ♀	3	-	-	-	-	-	**3 (100%)**	-
Blackback	1	-	-	-	-	-	-	1 (100%)
Total predicted to be in each group		**4**	**3**	**5**	**0**	**4**	**4**	**1**

Only two gorillas were classified by the Hutchinson and Fletcher classification as old infants, however the discriminative analysis predicted that two juvenile females also belong in this category: juvenile females, Kw (mean age = 41 months) and Si (mean age = 44 months). It was indeed appropriate that these gorillas were reclassified into the Hutchinson & Fletcher classification as old infants, due to the similarity in age with the other old infant gorillas, and since both were in a social situation, where suckling was not possible, thus the criterion for older infant as a suckling infant was not fitting to them. The other re-classification ascribed by the discriminative analysis was of an individual firstly classified as an adolescent male, but predicted by the discriminative analysis of being in the adult female group. This however, would be counter to this classification method and thus the gorilla (Mb, mean age 91 months) was re-categorised into the next life-stage category for males, termed here as blackback.

3.4.3 The final model

The discriminative analysis was re-run after re-classification of the three gorillas. The discrimination using the same four behaviour groups was significant in discriminating two variants to determine life-stage groups (Variant 1: χ^2 (20) = 60.72, $P = < 0.001$, Variant 2: χ^2 (12) = 29.23, $P = 0.004$), explaining 57.4% and 41.6 % variance respectively (Table 3.7). The Hutchinson & Fletcher classification now discriminates life-stage with 90.5% accuracy. The first factor (Function 1 – Table 3.4) has major contributions from lying (dur/hr) and social play (freq/hr) and discriminated old infant, juvenile female and adolescent male from juvenile male, adult female and blackback and formed a significant positive correlation with gorilla age (months), Pearson $r = 0.556$, $N = 21$, $P = 0.01$. The second factor (Factor 2 – Table 3.7) had high contributions from locomotion (dur/hr) and feeding (freq/hr) (Table 3.8) and discriminates old infant and juvenile male from adult female, juvenile female, adolescent male and blackback and formed a significant negative correlation with gorilla age (months) $r = -0.748$, $N = 21$, $P = <0.001$. Figure 3.3 shows the canonical discrimination with all life-stage groups spatially distinct. Juvenile male and female life-stages were clearly spatially separate using two variants of the four behavioural groups. The spatial distribution of the life-stages was determined by likeness. Canonical spatial maps position life-stages of similar ages close together with the largest distance falling between the youngest life-stage (old infants) and the oldest life-stages (blackback male and adult female). Juvenile males were thus the most distinct life-stage whereas, although separated into distinct groups, the adolescence males, adult females and blackbacks showed more similarity to one another. The discriminative analysis suggested that captive western gorillas of the same life-stage and sex were distinct from other life-stages and showed little overlap with other life-stage groups. One outlying individual remained (Figure 3.3), Zu (male, mean age 46 months) was predicted to belong to the juvenile female category, but since he was male, and still suckling he remained categorised as an old infant.

Table 3.7 - Structure matrix of pooled within-group correlations between discriminating variables and standardised canonical discriminative functions in the Hutchinson & Fletcher classification.

	Factor loadings, eigenvalues & % variance explained	
	1.	**2.**
Variance explained	**57.4%**	**41.6%**
Eigenvalues	**5.800**	**2.120**
Locomotion (dur/hr)	0.091	0.814
Social play (freq/hr)	-0.289	0.291
Lying (dur/hr)	0.473	-0.333
Feeding (freq/hr)	-0.101	0.398

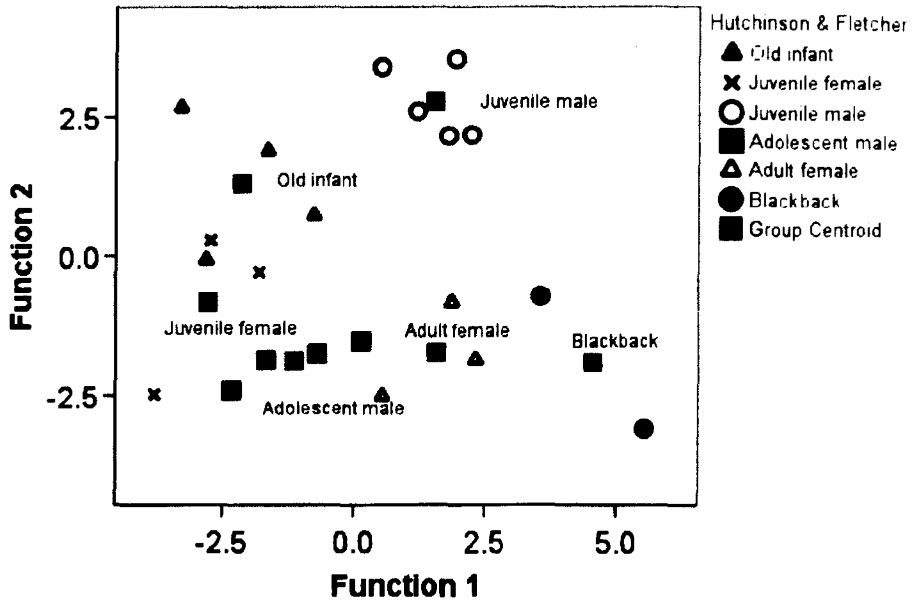


Figure 3.3 - Scatter diagram of individual gorillas discrimination function scores based on behaviour groups (Feeding (freq/hr), Locomotion (dur/hr), Lying (dur/hr), Social play (freq/hr).

3.4.4 Ontogenetic and sex differences in development

The two significant factors derived from the discriminative analysis (Table 3.7) assumed from the Hutchinson & Fletcher classification were used to analyse differences across development and between the sexes. The juvenile group contains both male and female gorillas with the same age range; with both factors a significant difference was found between the sexes (Independent t-test, Factor 1; $t_{(6)} = -7.38$, $P = <0.001$: Factor 2; $t_{(6)} = -4.96$, $P = 0.003$). Unfortunately, there were no adolescent females, thus a comparison between adolescent males and females was not possible. However, a significant difference was found between adolescent males and adult females (all 8 years old) on Factor 1 ($t_{(5)} = 4.33$, $P = 0.01$) and a tendency for a difference between the two life-stages was found on Factor 2 ($t_{(5)} = -2.38$, $P = 0.06$).

Behaviour change across the pre-reproductive period was found for male gorillas (Factor 1: $F_{(3,7)} = 19.15$, $P = 0.001$: Factor 2: $F_{(3,7)} = 25.44$, $P < 0.001$), and for females (Factor 1: $F_{(2,6)} = 13.61$, $P = 0.01$. Bonferroni *Post Hoc* comparisons; adult female vs. old infant and adult female vs. juvenile female: Factor 2: $F_{(2,6)} = 7.83$, $P = 0.02$; Bonferroni *Post Hoc* comparisons; $P = < 0.05$, adult female vs. old infant). This illustrates that behavioural difference is found between the sexes and across development for each sex with disparity beginning in the older infant life-stage.

3.5 Discussion

3.5.1 Using behaviour to determine life-stage classifications

Behaviour can be used to determine life-stage in NRI captive western gorillas. Further to this, quantitative behavioural data can be used to illustrate developmental differences between individuals, to provide a flexible understanding of a species life history trajectory and to understand the disparity in development between the sexes.

A quantitative classification of life history is advantageous when compared to other life history models. Phylogenetic models of mammalian life history (Charnov, 1993; Janson & van Schaik, 2002; Stears, 1992) compare many species using a range of allometric developmental variables, but are criticised for assuming that all developmental systems within a species emerge in a synchronous, linear manner (Leigh & Blomquist, 2007). Linearity has been shown through empirical developmental studies not to occur (Bolter & Zihlman, 2003; Leigh, 1996) with variable synchrony found between variable systems across the pre-reproductive period and between species. Such variability is largely unquantified at present, even at the species level, making cross species comparisons difficult. The method constructed in this chapter accepts individuals into a life-stage through measurement of one developmental system (behaviour), without incorporating development from somatic or physiological systems. Since multiple developmental systems are not used to determine life-stage, there is no such assumption of synchrony between developmental systems.

Individual variation in behavioural development is brought about through phenotypic plasticity (Stears, 1992). Such flexibility is advantageous for studies that use or compare primates by a specified life-stage and to understand how individual experience affects the phenotypic expression of behavioural traits (Stears, 1992). It is expected that to minimise the risks associated with immaturity, individuals should change the rate and shape of development in ways to maximise the chances of survival (Janson & van Schaik, 2002; Pereira & Leigh, 2003) and this leads to variable rates of development between individuals of the same sex and species. A lack of flexibility in life-stage classification, brought about using categorical age alone to determine membership, likely leads to the classification of individuals into a life-stage, when they are significantly different in their behaviour from others in that life-stage, thus increasing variance in the data set. Throughout analyses, such variance can reduce statistical power and increase the chance of type 2 errors.

Widespread use of the methodology proposed here, across primate species, would allow the construction of models and would allow the comparison of developmental periods between multiple species without the effect of linearity and synchrony, but incorporating individual flexibility. This would enable further intricate understanding of evolutionary adaptation to the environment at the species level, and an understanding of which developmental factors are species-specific and which are found more widely across species (Bolter & Zihlman, 2003). This information, which is currently missing from the literature, limits our understanding of both NRI development and also adult reproductive success, which is based on the success of surviving the pre-reproductive period (Pereira & Leigh, 2003).

Behaviour is determined as the mediating factor between an animal and its environment and thus is predicted to be species-specific (Pereira, 2002). Additionally, across the pre-reproductive period, behavioural change may be linked to the energetic constraints of growing a large brain (Ross, 2004) and further influenced by developments in somatic and physiological systems (e.g. Anestis, 2006; Setchell & Dixson, 2002; Setchell & Wickings, 2004). Using behaviour to document life-stage is therefore predicted to encompass changes in the individuals from all developmental systems reflected through behavioural expression. In this chapter, social and activity based behaviour were demonstrated to enable determination of distinct developmental phases that were quantified and independent of interactions with other group members, for example, weaning which may be dependant upon the mother's condition and differ by infant sex (Lee, 1997; Setchell *et al.*, 2001). Likewise, behaviour is used extensively across the primate literature to determine social aspects of adult life history (e.g. dominance, social systems, parental care), which can be used comparatively or longitudinally to monitor individuals fitness or success.

Considering the potential comparative advantages of this methodology and that observational studies are a non-invasive, well-documented method of data collection, behaviour is promoted here as being the most effective measure to represent change in the whole individual, and to enable determination of quantifiable life-stages in a species. In many primate studies, the number of individuals in a social group and the time available for data collection are limited and thus a further aim of this methodology was to provide a method that was easy to replicate with relatively limited behavioural data and/or small sample size. This was achieved using four behaviours, which correlate with a life-stage classification proposed for captive western gorillas. Together these behaviours co-varied to form a measure robust to fluctuations in a specific behaviour within an individual.

3.5.2 Species-specific life-stage classifications

Natural selection results in the adaptation of a species to a particular environment over time, which maximises individual survival and reproduction (Hamilton, 1964). Therefore, similar species living in divergent habitats are expected to demonstrate divergent life history strategies (Kappeler & Pereira, 2003) and be reflected through their behaviour. This has been demonstrated, for example, in recent comparative studies of different conflict resolution strategies in nine macaque species (Thierry *et al.*, 2007) and different maternal styles between chimpanzees and bonobos (Lathouwers & Elsacker, 2004). Due to species-specific adaptations in their behavioural repertoire, it is predicted that life-stage classifications need to be species-specific and further to this, that using a life-stage classification formulated for another species would be less effective in determining an individual's life-stage.

In the case of *Gorilla*; mountain gorillas and western gorillas, although closely related live in extremely different environments in terms of altitude and forest ecology. Current comparative research finds stark differences between the two species in terms of diet (Doran et al., 2002; Ganas *et al.*, 2004), development (Nowell & Fletcher, 2007) and social behaviour (Doran & McNeilage, 2001) indicating divergent life history strategy between the two species. Current research on western gorillas in captivity and in the wild (Levrero et al., 2006; Lukas, Hoff et al., 2003; Maestripieri et al., 2002; Nowell, 2005; Pika et al., 2003; Watts & Pusey, 2002) however, uses age classes published for mountain gorillas, due to the absence of a classification specifically for western gorillas. This method is the first to show that using non-quantified, age-based life-stage classifications designed for a similar species leads to an increased variability between individuals in a life-stage and explains less variability in behavioural data, compared to a classification intended specifically for the species. Such use of a related species' life history classifications thus masks intricate species-specific differences and limits our understanding of the species life history strategies.

The four published mountain gorilla classifications considered here (Doran, 1997; Harcourt & Stewart, 1981; Schaller, 1963; Watts & Pusey, 2002) differ in the number of life-stage categories (ranging from 4-8 categories for NRIs) and the age range in each life-stage (ranging from 1-4 years). The variation between published classifications arises through treating life-stages as static age-based categories, which have been adapted, as the understanding of mountain gorilla life history has progressed over the last 40 years of research. How the various classifications fit behavioural data for NRI mountain gorillas themselves will be presented elsewhere, but variable success was found using mountain gorilla classifications for captive western gorilla data. In this study, disparities between published mountain gorilla classifications were illustrated through the number of captive western gorilla behaviours which significantly co-varied within the classification (ranging from 2 – 4 per classification), and the range of behavioural variability explained by the classifications.

The most successful mountain gorilla life-stage classification to represent the behaviour of western gorillas was the Schaller (1963) classification, presumably due to its limited number of NRI life-stage categories (4) and lack of distinction between males and females until sexual maturity. Spatially, life-stage groups formed loose aggregations, demonstrating large variability between individuals categorised in the same life-stage. Similar was found in the Harcourt & Fossey (1981) classification, also with four NRI life-stage categories, although it was found to be less successful than the Schaller (1963) classification, an effect due to the change of age boundaries depicting acceptance into life-stage. Sex discrimination was incorporated from juvenility and thus more life-stages were defined (7) in the Watts & Pusey (1993) classification. The success of explaining behavioural variation was reduced compared to Schaller (1963). This indicates an inaccuracy in life-stage age boundaries of mountain gorilla classifications when used for captive western gorillas, which are therefore less able to explain behavioural variance in western gorilla data.

The Doran (1997) classification differs from other mountain gorilla classifications in that it determines life-stage by significant changes in NRI physical locomotion, which increases the number of NRI life-stages to 8 by age group. In this case, physical development co-varied significantly less with behaviour (2) than the other mountain gorilla classifications (3, 4) and had the lowest proportion of correct classification into the prescribed life-stage. This classification thus appears to highlight the non-linear development between behavioural and physical systems (Leigh & Blomquist, 2007) and indicates that life-stage classifications formed using indicators of physical development are likely to be less effective than a classification determined using behaviour, in explaining behavioural development in a species.

The proposed Hutchinson & Fletcher classification is to date the only life history classification specifically for western gorillas. The Hutchinson & Fletcher life-stages were proposed using a detailed quantitative study of NRI western gorillas (Nowell, 2005). The effect is a classification, which was more successful than mountain gorilla classifications in terms of the number of behaviours that significantly co-varied with the life-stage (4), the amount of behavioural variance explained (99%), accuracy of predicting life-stage (90.5%) and similar behavioural variability between individuals of the same life-stage. However, this data set does not represent adolescent females and is limited by having no older blackback gorillas. Although here life-stage categorisation is possible to a high degree of accuracy, replicating the method with increased sampling effort and subject size is predicted to lead to increased accuracy, dependant on the behaviour found to co-vary and for the species in question. The data set used represents behaviour in captive individuals and although more likely to represent wild western gorilla life-stages than mountain gorilla life-stages, it is suggested that using this method to determine mountain gorilla classifications using mountain gorilla data would lead to a greater understanding of diversity between the species.

Categorical age is widely used in the classification of primate life histories to determine life-stage (Janson & van Schaik, 2002; Kappeler & Pereira, 2003). The discriminative analysis of the Hutchinson & Fletcher classification significantly correlated with NRI age, showed that age is indeed a useful indicator of life-stage, therefore supporting its use in life-stage categorisation. However, age boundaries are static and inflexible to individual differences. The process of re-classification of NRIs through the discriminative analysis is an important step to increase the flexibility of individual acceptance into a life-stage based on variations in behavioural development. The following discussion of NRIs who were re-classified based on behavioural disparity from others in the life-stage illustrates this point.

Being nutritionally dependent from the mother is a well known, often un-quantified marker separating the infant and juvenile life-stages (Barrett et al., 1995; Lee, 1997; Pereira & Altmann, 1985), but it has been demonstrated in the reclassification process in this method is that the absence of suckling alone does not necessarily determine juvenility. Two gorillas were re-classified from the juvenile female life-stage into the older infant group, although neither was recorded to suckle (suckling is a pre-requisite of belonging to the old infant life-stage, based on field observations (Nowell, 2005)). Both the individuals concerned were unable to suckle, one due to the death of her mother, the other due to the mother having ceased lactation during her infancy (see Vermeer, 2005). However, the behavioural variants of these two gorillas were similar to other old infants and significantly different from the juvenile females thus warranting their reclassification. Conversely, a male and female juvenile of similar mean age to the two female older infants (all ranging from 41 and 46 months) were both significantly different in behaviour from the older infants and therefore categorised as juvenile male and female respectively. Thus, age alone, or clear-cut definitions of life-stage, such as those based on weaning is not always sufficient to determine life-stage in NRI primates.

3.5.3 NRI life-stages as distinct ontogenetic phases

The concept of a life-stage is that of a distinct ontogenetic phase, which each individual of a species must pass through between birth and death. From the initial work of Schultz (1963), a life-stage was uniquely defined and not overlapping in its distinction. More recent life history classifications however, use age-based classifications and a mixture of other behavioural, physical or physiological indicators to signify life-stage change. Although the use of age-based classifications keeps each life-stage unique, the non-quantitative nature of the system makes assigning life-stage subject to error as discussed above. The distinction shown between each life-stage in the Hutchinson & Fletcher classification (with the exception of 1 individual) demonstrates the behavioural uniqueness of western gorillas in each life-stage across the pre-reproductive period and supports the use of quantitative life-stage classifications in the following ways:

Firstly, support is provided for a classification, which encapsulates individuals who are between the infant and juvenile periods; the 'old infant' life-stage was spatially separated from both juvenile males and juvenile females. Western gorilla NRIs have been shown to suckle for approximately a year longer than mountain gorillas (Nowell & Fletcher, 2007; Nowell & Fletcher, In Press), indicating a different strategy of feeding development and weaning in western gorillas (Nowell & Fletcher, 2007). However, from the current analysis it is shown that not only do western gorilla NRIs suckle until much older than mountain gorillas, but they remain behaviourally distinct from juvenile male and females. From this, it is proposed that the juvenile life-stage is behaviourally distinct from the old infant and adolescence life-stages in both males and females and that the reduction or cessation of suckling alone is insufficient to determine life-stage advancement in an individual. However, little variation was found between the old infant male and females in this study, although the sample size was small. The strength of the behavioural variation between juvenile males and females and the continued divergence in behaviour between the sexes across subsequent life-stage demonstrates the importance of incorporating a sex specific classification in sexually dimorphic primates, which thus leads to an understanding of divergent life history strategies between the sexes as they grow into sex-specific roles. Failure to categorise males and females separately will lead to high behavioural variability in life-stage groups, particularly in the juvenile period.

Secondly, sequential life-stages were found to be statistically different for each sex, indicating orderly, linear development. The co-varying behaviours in this method were sufficient to represent distinct ontogenetic differences in each sex over the pre-reproductive period. It is proposed that similar co-varying behaviour would show such distinctions in other primate species. Distinction between ontogenetic phases is advantageous in studies of similarity/disparity between similar age/sex groups (Pereira & Leigh, 2003) or to allow classification of unknown individuals into a life-stage; this is particularly useful in field situations where it is often not the case that all individuals are known from birth

3.6 Conclusion

For the progressive understanding of primate life history, it is proposed that a robust classification method should be used to enable the comparison of allometric life history traits within and between species, from birth to death. This chapter presents one such method using western gorillas. This method uses behaviour to determine NRI life-stage, and allows flexibility in life-stage acceptance based on behavioural variance between other similar-aged gorillas. In using behaviour to determine life-stage, this chapter provides evidence for disparity in developmental trajectory between the sexes, from at least the juvenile period, and ascertains that each NRI life-stage is a distinct ontogenetic phase. Classifications need to be specific to the species in question to encompass adaptation to the environment and quantitative to ascertain acceptance into a life-stage group.

Chapter 4

4 RELATIONSHIP DEVELOPMENT ACROSS THE PRE-REPRODUCTIVE PERIOD

Through a study of group social proximity and dyadic relationships, this chapter proposes strategies for social relationship development in male and female NRIs across the pre-reproductive period.

4.1 Introduction

4.1.1.1 Life history strategy

Dyadic relationships are formed and maintained for one individual to gain an advantage over another, or for mutual gain (Cords, 1997; Russon, 1997). The study of these relationships is a useful method by which to understand the behavioural mechanisms involved in development, maintenance and the adaptive expression of social relationships (Kummer, 1978).

The social system of a species is determined by its ecology and reproductive strategy (Kappeler & Pereira, 2003), which in turn determine which affiliative relationships are beneficial to the individual. In NRIs (non-reproductive individuals), behavioural expression is documented to be the mediator between the individual's physiological development and the environment (Deaner et al., 2003). Studying how relationships change across development allows an understanding of the canalised mechanisms of development in a species (Pereira & Altmann, 1985), the relationships necessary (Russon, 1997) and the skills and knowledge that can be extracted from others at each stage of development (Russon, 2003).

The development and composition of relationships across the pre-reproductive period are less studied than adult relationships. Unlike adult relationships, which are often prolonged across adulthood (Schino et al., 2000; Silk, Alberts *et al.*, 2006; Silk, Altmann *et al.*, 2006), NRI (non-reproductive individual) relationships are theorised to differ by sex and by life-stage, dependant upon the advantage to the individuals (Russon, 1997). Since no immediate reproductive advantage exists in NRI relationships, dyadic relationships in the pre-reproductive period are proposed to be formed for other social benefits (Russon, 2003). An understanding of such NRI relationships is lacking in terms of investment of sociality across the pre-reproductive period and differences due to NRI sex and relatedness.

4.1.2 Why do relationships change across the pre-reproductive period?

For social primates in the pre-reproductive period (from the end of infancy, until sexual maturity), prolonged, prominent relationships across the period are few and gradual changes in the formation and maintenance of relationships occur (Russon, 2003). Typical changes in association between individuals, and the tolerance of other group members to form affiliative bonds are dependant upon the species' socio-ecology, age and sex of the NRI. The development of relationships with specific age/sex groups is reportedly consistent across the pre-reproductive period for a species (Pereira & Altmann, 1985), but variable in its timing between individuals (Lee & Kappeler, 2003).

Relationship change reflects the developing needs of the individual. For example, a newly weaned individual depends less on the mother for nutritional input, and thus spends less time in close proximity to her (Janson & van Schaik, 2002). Changes in relationships across the pre-reproductive period allow the individual to learn skills specific for the future from a range of peers and older group members (Janson & van Schaik, 2002). Such skills are often sex specific due to the disparity in the roles of adult males and females of the same species (Pereira, 1995). Females must ultimately develop skills to adequately provide for and rear their young, whilst males must develop skills, secure mates, and protect an immature family from predators or potential competitors. A reproductive advantage may occur by forming relationships with unrelated members of the opposite sex towards adulthood (Fairbanks, 2002; Pusey, 1990).

The acquisitions of species- and sex-specific skills is limited by the development of the neocortex in the brain (Joffe, 1997; Russon, 2004a). Simple cognitive structures from which to perceive the world are laid down early in development. These are then developed into more complex structures through individual experience during social and environmental interactions (Joffe, 1997; Pereira, 1995; Pereira & Leigh, 2003; Russon, 2004a). The more complex the species' social structure, the longer it takes for the brain to grow to adult size, and the more skills and social knowledge an NRI needs before adulthood (Dunbar, 2003; Joffe, 1997). In complex social systems, as found in higher primates, this slow accumulation of skill and knowledge is theorised to be the factor which has led to an extended juvenile period, compared to other mammalian orders (Dunbar, 1998; Joffe, 1997).

Skill and knowledge acquisition are not linear across the pre-reproductive period (Pereira & Leigh, 2003). The neocortex growth rate peaks in juvenility and declines across adolescence. In accordance with this, a peak in the receptivity to learning is found in juvenility, which then declines towards sexual maturity (Russon, 2004a). Skills necessary for success in adulthood are learnt over the pre-reproductive period, before the end of adolescence and the commencement of reproduction. By adulthood, the ability to learn new skills is greatly reduced and learning becomes less flexible (Boesch & Boesch-Achermann, 2000; Russon, 2004a).

The extension of the pre-reproductive period in primates, where the individual remains relatively smaller (Janson & van Schaik, 2002) for longer than mammals of a similar size, is costly to a species, who must continue to provide protection to the immature individuals for longer than would be necessary in faster growing species. This must be outweighed by the benefits of gaining skills and social knowledge. The incorporation of knowledge and skill learning in the pre-reproductive period must significantly increase the individual's future survival and breeding success (Fleagle, 1999; Janson & van Schaik, 2002; Rubenstein, 2002). Skills are learnt through observational learning and enhanced by practising behaviour regularly over the pre-reproductive period (Janson & van Schaik, 2002). An example of learnt skills in the apes is the use of tools, the adaptation and use of which are learnt through observation and imitation over the juvenile period (Lonsdorf *et al.*, 2004; Russon, 2006). Success of tool use increases with age and thus amount of practice (Byrne et al., 2001; Lonsdorf et al., 2004; Russon, 2006). The increase in social knowledge or expertise, such as sexual techniques and age appropriate behaviour are much harder to document, but are likely shaped by social learning from those with whom the individual has a relationship (Russon, 1997). Thus, relationships at each life-stage determine what expertise could be exploited.

Relationship formation and maintenance are documented to change across the pre-reproductive period (Russon & Begun, 2004), reflecting changing partner preferences for knowledge gain and skill acquisition. Understanding when and how relationships change across the pre-reproductive period in a species provides an understanding of what skills can be learnt through relationships with other group members. This gives an indication of the underlying cognitive development and its associated effect on the behaviour of each sex. To develop an understanding of NRI relationships across the pre-reproductive period, three hypotheses of social relationship formation or maintenance are proposed here for gorilla NRIs. The first hypothesis; the *Selective Investment Hypothesis*, proposes that NRIs may form prominent, highly social relationships with a few specific group members, through which distinct advantages are expected with this partner over other dyadic relationships. Relationships with other group members are presumed to be non-existent or very small and hold no associated benefit to the NRI. The second hypothesis; the *Variable Investment Hypothesis*, proposes that NRIs will maintain relationships with all in the social group, to assume the benefits of group living and only invest in prominent relationships with a specific few during which specific skills can be learnt and practised. A third and final hypothesis; the *Equal Investment Hypothesis* is that NRI gorillas could sustain relationships equally with all group members, to maximise learning opportunities and assume the benefits of group living.

Closer social relationships are expected between those who are more closely related (Hamilton, 1964), particularly in the sex which remains in the natal breeding group (Pereira & Altmann, 1985; Schino et al., 2000; Silk, Alberts et al., 2006; Silk, Altmann et al., 2006). Aiding the survival or breeding success of a relative through affiliation and coalitionary support is documented for adults in multiple species, e.g. female baboons and Japanese macaques (Schino et al., 2000; Silk *et al.*, 2003) male chimpanzees (Vigilant *et al.*, 2001). Building such affiliations across the pre-reproductive period is assumed necessary for social relationships to continue into adulthood. Between NRIs, kin relationships are studied between NRIs and adults (e.g. Govindarajulu *et al.*, 1993; O'Brien & Robinson, 1993) with fewer studies of those between maternal or paternal half siblings, due to uncertain paternities and often long inter-birth intervals, where older siblings may have emigrated from the group before a sibling is born. The following section reviews relationship formation and maintenance in juvenile and adolescent, male and female, sexually dimorphic NRIs.

4.1.2.1 Juvenile relationships

Juvenility is described as being when the individual is nutritionally independent from the mother (Pereira, 2002). Juvenility in both sexes reflects a period of slow growth and therefore precarious, prolonged small size (Janson & van Schaik, 2002). In juvenility, the threat of predation and competition for food is greater than in any other life-stage (Janson & van Schaik, 2002; Rubenstein, 2002). In line with this, the maintenance of the relationship with the mother declines (MacKinnon, 2007). Forming other relationships which will provide protection and develop understanding of dyadic relationships becomes essential (Joffe, 1997; Russon, 2003). Alliances for protection often include, primarily the dominant male (Arroyo-Rodriguez *et al.*, 2007), who is the likely father in most sexually dimorphic primates and also the older related individuals (Levrero et al., 2006). Other related older males and females may also protect juveniles and increase their own inclusive fitness by propagating common genes within the population (Hamilton, 1964).

To develop dyadic relations and skills, non-aggressive relationships with similar-aged peers of either sex are formed (Russon, 2003). In commonly exhibited behaviour such as play (Fagen, 2002) relationships with similar-sized peers reduce the risk of injury (Pereira, 1995). As juvenility progresses, reduced proximity from the mother and increased association with peers are commonly documented across sexually dimorphic primate species (Fairbanks, 2002; Fletcher, 1994; Johnson & Bock, 2004; Nowell, 2005; Pusey, 1990).

4.1.2.2 Adolescent Relationships

The period of adolescence in sexually dimorphic species is represented by the onset of growth spurts (Leigh, 1996) and increased hormone secretion which leads to sexual maturation (Anestis, 2006; Kraemer *et al.*, 1982; Pusey, 1990). Hormone change significantly alters behaviour in both male and female NRIs (Anestis, 2006). The onset of growth spurts is correlated with increased testosterone secretion and an increase in dominance related behaviour in males (Leigh, 1995; Pereira, 1995; Pusey, 1990). In humans, this is found to coincide with an increase in 'risky behaviour', particularly if the behaviour is perceived as having a positive consequence or reward (Galvan *et al.*, 2007). In both sexes, an increase in hormone secretion leads to the development of adult sex-specific behaviour and therefore relationship formation, with reproductive aged members of the opposite sex (Pusey, 1990).

Adolescents must build relationships which allow the accumulation of social knowledge and which enable the development of appropriate, adult-like behaviour. These are necessary for independent living outside of the natal group or to assume the best possible position in the group hierarchy, both of which will influence reproductive success upon sexual maturity (Charpentier et al., 2004).

Relationship development during adolescence differs for males and females (Pereira & Altmann, 1985; Russon, 2003), although during this life stage both sexes, receive less protection from related adult males and the mother (Janson & van Schaik, 2002). An increase in size, subsequently leads to a decrease in association with these individuals (Fletcher, 1994; Nowell, 2005; Pusey, 1990). Conversely, an increased interest in potential mating partners occurs, particularly during periods of female oestrus, which attracts male attention (Harcourt et al., 1980; Pusey, 1990).

In males, an increase in association with older males from whom dominance related skills may be learned is found (Levrero et al., 2006; Pusey, 1990; Setchell, 2003). Towards late adolescence, sexually dimorphic males peripheralise themselves in the social group, specifically during the growth spurts in species such as western gorillas (Nakamichi & Kato, 2001); mandrills (Setchell, 2003); long tailed macaques (van Noordwijk et al., 2002); chimpanzee; (Kraemer et al., 1982). Female adolescent relationships are less commonly documented; perhaps relationship maintenance and development are less obvious to observers or more difficult to observe. In female chimpanzees, continued associations with the mother are seen but are highly variable, with a decline in the relationship presumably linked to pubertal events (Pusey, 1990). In other sexually dimorphic primates, such as Japanese macaques where the female remains in the natal group, associations with the mother and other related females remain into adulthood and determine the NRI's position in the matrilineal dominance hierarchy (Chapais & Gauthier, 1993). In gorillas, where females migrate upon sexual maturity, less association is seen with the mother and other adult females with increasing age (Fletcher, 1994). Adolescent females may also show continued relationships and attraction to infants, which typically ends upon sexual maturity and presumed conception (Lancaster, 1971; Manson, 1999; Schino *et al.*, 2003) .

4.1.2.3 Maturity in western gorillas

In the wild, male and female NRI western gorillas disperse from their natal group around sexual maturity. They either join established breeding groups, form new breeding groups or join non-breeding groups of like-aged males and sometimes sexually immature females (Bradley *et al.*, 2004; Levrero et al., 2006; Robbins et al., 2004). Association with the parents, younger siblings and other NRIs after sexual maturity are often non-existent (Levrero et al., 2006), with the exception of younger males who join non-breeding groups where older male siblings reside (Bradley et al., 2004; Levrero et al., 2006). Relationship change from the end of infancy to sexual maturity is therefore based on a decreasing dependency on parental resources and protection (Janson & van Schaik, 2002) and an increasing necessity to associate with individuals who facilitate the development of skills which enhance survival and reproductive potential (Russon, 2003).

4.1.3 Measurements of social relationship change in NRI gorillas.

The study of interactions between individuals in primate social groups has the potential to develop our understanding of complex primate social relationships (Cords, 1997). Social relationships are necessary in group living primates to co-ordinate the individual's behaviour with the group, to reduce intra-group competition through co-operation (Cords, 1997), to form male and female alliances, attract mating partners or reduce directed aggression (Pereira, 1995).

Typically, researchers seek to understand individual dyadic relationships pertinent to their research questions (e.g. mother-infant relationships, Arroyo-Rodriguez et al., 2007; Brown, 2001; Fletcher, 2001), using dyadic proximity measures calculated between the individuals of interest (Brown, 2001; Kato, 1999; Nowell, 2005; Setchell & Dixson, 2002; Stoinski, Hoff, Lukas *et al.*, 2001). However, within such studies, the proximity relationship between two individuals is measured independently of the dynamics of the social group. Considering that primate social groups are a mesh of interacting complex relationships and that individual behaviour may deviate from expected norms under certain conditions, such a narrow view of a relationship can be misleading.

A better-suited method to the study of relationships using proximity data is that of multidimensional scaling (Corradino, 1990; Nakamichi & Kato, 2001), in which the proximity of all individuals in a social group can be spatially represented in a graphical form. Advantages of using this method include being able to understand the differences in spatial relationships between different social groups of the same population as well as developing a valid understanding of multi-faceted relationships between multiple partners within the social group. Measures of proximity or spatial data have been regularly used in the literature to represent social relationships between individuals (Chalmeau & Peignot, 1998; Corradino, 1990; Fletcher, 1994; Nakamichi & Kato, 2001; Nowell, 2005; Pusey, 1990; Stoinski, Hoff, & Maple, 2001). However the use of MDS has rarely been applied in studies of primate spatial relationships (but see Corradino, 1990; Nakamichi & Kato, 2001), although is used frequently across the social sciences to test structured hypotheses (Borg & Groenen, 2005).

MDS is a collection of geometric models that are used to represent data in two or more dimensions. The aim of an MDS application is to find a low dimensional space in which the points in space represent the gorillas being studied and represent the space and relationship among the gorilla group as a geometric configuration (Beckstead & Beckstead, 2006).

From such an understanding of spatial relationships within a social group, it is then possible to develop and use a sociality index (SI), which specifically seeks to understand the relationship strength between two individuals. Relationships are made up of multiple factors, which need to be considered to give a valid judgement on the strength of relationships. Proximity is a suitable indicator of relationships between individuals in studies that span the sexes and multiple life-stage groups, as it is a continual behavioural state (Cords, 1997) and thus data can be collected with ease across a individual's lifetime.

However, other displayed behaviour also demonstrates relationships between dyads, for example grooming (Sapolsky *et al.*, 1997; Silk et al., 2003; Silk, Alberts et al., 2006; Silk, Altmann et al., 2006), affiliative gestures (Lane & Bard, 2007; Sapolsky et al., 1997), frequency of agonism and consortships (Sapolsky et al., 1997). However, such behaviour may not be displayed by all species (Cords, 1997), all age groups or both sexes, for example, consortships are male-only behaviour directed towards females in oestrus (Sapolsky et al., 1997), whereas grooming behaviour is initiated less by NRI apes compared to adult apes (Watts & Pusey, 2002). Thus, an in-depth analysis of dyadic relationships in a primate species requires an initial understanding of behaviour that is likely to occur between the particular affiliative dyads in question (Cords, 1997). The significance of much of this dyadic behaviour is not fully understood. For example, grooming another individual may have a number of connotations: it may confirm the partners readiness to act; be the benefit of a direct relationship; be the groomer attempting to develop a closer relationship with the recipient or be an attempt to repair a former relationship (Cords, 1997). Thus, a sociality index (SI) gives an indication of relationship strength but does not consider any intentionality in social situation between individuals in a dyad. Building an index of sociality by incorporating several behavioural measures specific to the species, enables a robust measure of the social relationship to be determined within a dyad and reduces the risk that the behaviour measures anything other than the level of sociality (Sapolsky et al., 1997). In this way, it is possible to build a SI specific to the research questions under examination, considering dyadic relationships in the context of the social group.

4.2 Aims

- To investigate the spatial organisation of NRI gorillas, considering life-stage and sex, within the context of the family group.

- To develop a SI for NRI gorillas and to use this to understand dyadic social relationships across the pre-reproductive period.

- To use the findings from above to test three hypotheses of relationship development and maintenance, for each life-stage, sex and between siblings across the pre-reproductive period.

4.3 Methods

4.3.1 Spatial distribution of NRIs in natal gorilla groups.

In this chapter, the MDS attempts to construct a configuration in which gorillas that spend more time in close proximity are represented as being closer in space; the MDS makes the data accessible to visual inspection and exploration (Borg & Groenen, 2005). The success of the configuration is determined through a general measure of stress in the system (defined as the lack of fit between actual proximities and the proximities that arise from the analysis); and the amount of variability in proximity that is accounted for by the model (defined as the dispersion accounted for). The stress measure is calculated by square rooting the normalised residual sum of squares, which amounts to a value ranging from 0 to -1. Smaller values indicate less stress and a better solution, whereby a value of 0.1 is presumed fair and 0.05 or less is good (Kruskal, 1964). Stress is affected by a number of factors including the number of data points, the number of dimensions used, the amount of error and the amount of missing data, all of which should be considered before accepting a stress value (Borg & Groenen, 2005). The dispersion accounted for (DAF; equivalent of the coefficient of determination), is calculated by squaring the coefficient; the closer to a value of one the score is, the greater the amount of variability is accounted for in the configuration. Thus, the higher the DAF value the better the fit of the MDS to the data.

Proximity scores (mean percentage of scans within 5 metres per hour, using proximity scan data ((0-5m), for each NRI, Appendix 3) between dyads were used to form a similarity matrix between all possible pairings of gorillas in each gorilla group. Five metres is considered a reasonable distance in which contact can be made quickly if a gorilla chooses to and is a value used in other similar studies (Brown, 2001; Hoff *et al.*, 1997; Nakamichi & Kato, 2001). The percentage of scans within 5-metres (Equation 4.1) was calculated following the method following Nakamichi and Kato (2001).

$$\boxed{\%scans_{5m} = \frac{N_x(A < B)}{N_t(A + B)} \times 100}$$

Equation 4.1 – Calculating the percentage of scans in which a dyad are within 5 metres. Where A = Gorilla 1; B = Gorilla 2; N_x = total number of scans where A within 5 metres of B; and N_t = total number of scans involving both A & B.

All gorillas were included in the proximity MDS configuration with the exception of infants under one year in age, (whose spatial proximity is assumed to be highly correlated with the mother (Fletcher, 2001)); and two female gorillas, over 45 years of age (Kati and Goma) at Basel Zoo. These elderly females were separated regularly from the group, by the Keepers, during data collection.

The proximity matrices were analysed used Proxscal, designed by the Data Theory Scaling Systems Group of Leiden University, The Netherlands and available on SPSS V.14. Proxscal is an extremely flexible programme and can accommodate data that are ordinal, interval or ratio; with missing values, replicated or non-replicated; similar or dissimilar. This analysis used a non-metric, full matrix analysis, with ratio data using the Simplex model.

4.3.2 Using an index of sociality to determine prominent relationships and relationship change in NRI gorillas

A SI was calculated from a combination of behaviour in which the study population regularly engaged. This provided a meaningful measure of social relationships in primates, where a high SI for a dyad indicates a better-maintained or stronger relationship than a low SI. Such indices have been used to investigate social relationships among adult female baboons (Silk et al., 2003; Silk, Altmann et al., 2006), male and females baboons (Sapolsky et al., 1997) and adult ring-tailed lemurs (Lane & Bard, 2007). Adult primate relationships are typically characterised by frequent grooming, close proximity and occasional acts of coalitionary support (Cords, 1997; Silk, Altmann et al., 2006), whereas NRI relationships regularly incorporate social play as a social behaviour (Fagen, 2002; Lewis, 2000).

In this study of sociality in NRI gorillas, a composite of affiliation behaviour (hug, touch, peer and reciprocal grooming, from NRI focal sampling, Table 2.4), close proximity (0-2 metres, from NRI scan samples, Appendix 3) and social play (frequency; from NRI focal sampling, Table 2.4) were used to calculate the SI. The three behaviour measures were combined into a single composite measure after determining a high level of inter-correlation between them (For all possible dyads; social play x proximity; Spearman's Rho, $\rho = 0.344$, $N = 171$, $P = < 0.001$; social play x affiliation; $\rho = 0.395$, $N = 171$, $P = < 0.001$; affiliation x proximity, $\rho = 0.734$, $N = 171$, $P = < 0.001$). To calculate the SI, the standardised frequency per hour of affiliation proximity and social play behaviour were used. To control for the different composition of gorilla groups in each zoo and the effect of the different captive environments each NRI SI was calculated by dividing each dyadic relationship percentage by the mean sociality score for all dyads in the same social group, following Silk (2006), see Equation 4.2. A SI was determined for each possible NRI dyadic relationship. A total of 171 dyads were available, which incorporated 17 NRI-mother dyads, 22 NRI-silverback dyads, 91 NRI-NRI dyads, 22 NRI-infant dyads and 19 NRI-unrelated adult female dyads.

$$\boxed{SI = \frac{\left[\frac{A_{dyad}}{A_{mean}} + \frac{P_{dyad}}{P_{mean}} + \frac{S_{dyad}}{S_{mean}}\right]}{3}}$$

Equation 4.2 - Sociality index calculation. Where; A = Affiliation $_{(freq/hr)}$; P = Proximity $_{(0\text{-}2\ metres)}$; and S = Social play $_{(freq/hr)}$

4.3.3 Statistical analysis of NRI sociality

The data were negatively skewed and thus non-parametric analyses were employed. A median value was used to determine the mid-point of the index from all dyadic relationships (N = 171). Analyses of relationship change with age were conducted using Spearman's Rho correlation. To determine prominent relationships, one-way ANOVAs were used, which are robust to violations of distributional assumptions (Field, 2005). Where violations in the homogeneity of variance were found (using Levene's test), a Welch correction was employed and reported; this controlled the Type 1 error rate (Field, 2005). Subsequent differences in relationships for each life-stage were detected using Games-Howell *Post Hoc* comparisons, this is a powerful *Post Hoc* test to be used with unequal sample sizes and where population variances differ (Field, 2005). For juvenile female gorillas, where population variances were equal, a Bonferroni *Post Hoc* comparison was conducted. To enable the calculation of *Post Hoc* comparisons, life-stages that were represented by only one gorilla were removed from analysis. Prominent relationships were determined as being those within the top 10% of the SI, which equated to the mean SI value being greater than 2.0. A value of 10% was used, as it was high enough to differentiate relationships with a high SI from the majority of relationships, following Silk (2006). To distinguish between siblings, full siblings are those that share the same mother and father, and paternal half siblings are those that share only a father. A Wilcoxon's related samples test was used with the exact method to determine differences in the social relationships of full and paternal half siblings.

4.4 Results

4.4.1 Spatial distribution of NRIs in captive gorilla groups.

MDS was successfully applied to a proximity matrix, relating gorillas within each group in terms of their proximity. Gorillas are symbolised by their life-stage categorisation as presented in Table 4.1. The resulting co-ordinates are presented in Tables 4.2-4.6, arranged alphabetically by gorilla group. Two-dimensional configurations per gorilla group, which give the nature of epistemic space, are presented in Figures 4.1-4.5. These are easier to interpret than three-dimensional representations, particularly in groups with a large number of gorillas. A criterion using a stress value of less than 0.05 and DAF of above 0.98 was adopted to ensure a high degree of accuracy, in line with Kruskal (1964).

Table 4.1 - Abbreviations used in the MDS analysis.

Life-stage Categorisation	Abbreviation in MDS	Symbol used in MDS
Silverback	SB	■
Adult female (multiparous)	AF (AF1, AF2 etc)	○
Adult female (nulliparous)	F (F1, F2 etc)	★
Blackback	BB (BB1, BB2 etc)	✖
Adolescent male	AM (AM1, AM2 etc)	◆
Juvenile male	JM (JM1, JM2 etc)	▽
Juvenile females	JF (JF1, JF2 etc)	▲
Old infant	OI (OI1, OI2 etc)	▶◀
Infant	I (I1, I2 etc)	●

4.4.1.1 Apenheul Primate Park

The Apenheul Primate Park gorilla group associated around the silverback male (SB) (Figure 4.1). The adult females (AF) formed a loose semi circle around the silverback, which encapsulated the two juvenile females (JF). Likewise the older infant (OI) remained in close proximity to both her mother (AF1) and the silverback. Older NRIs increased their distance from the central core of the group (with the exception of F1); adolescent males (AM) showed some distance from the central core with blackback males (BB) and an adult nulliparous female (F2) being most dispersed.

Table 4.2 - MDS co-ordinates of gorilla group proximity at Apenheul Primate Park.

Gorilla	Life-stage Categorisation	Offspring	Co-ordinates	
			Dimension 1	**Dimension 2**
Bo	SB	-	-.140	.270
Bi	F1	-	-.076	.293
Da	AF1	Ki, Gy	-.580	.004
Gy	OI	-	-.404	.287
Kd	AM1	-	.395	-.380
Ki	F2	-	.381	1.145
Lo	AF2	Bi, Zo	-.431	-.101
Ma	AF3	Uz, Ki, Ne	-.208	-.590
Mb	BB1	-	.566	-.085
Mi	AF 4	Mb	-.534	-.691
Mk	AM 2	-	.333	.491
Ne	JF 1	-	-.261	-.177
Uz	BB 2	-	1.237	-.617
Zo	JF 2	-	-.279	.149

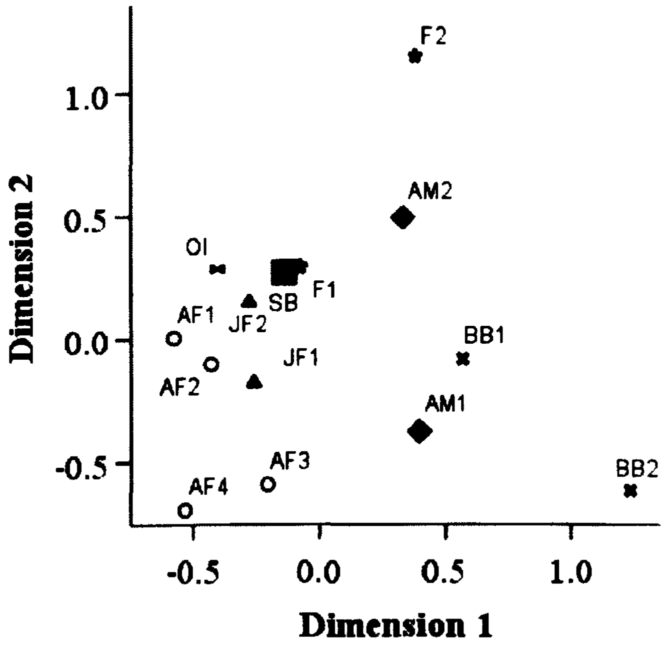


Figure 4.1 - A two-dimensional MDS configuration for proximity values (0-5m) among gorillas at Apenheul Primate Park. S-Stress = 0.05, DAF = 0.98

4.4.1.2 Basel Zoo

The gorillas at Basel Zoo were distributed in a similar format to the gorillas at Apenheul Primate Park. Two adult females (AF) were in close proximity to the silverback (SB) and showed a distinct preference to be in close association, whereas two other adult females in the group were more dispersed (Figure 4.2). The adolescent males (AM) were spatially separated from the rest of the group and were found on the periphery of the group, though AF3 was found in close proximity to her son (AM2). The older infant (OI) was found in close proximity to an adult female (AF), his full sister.

Table 4.3 - MDS co-ordinates of gorilla group proximity at Basel Zoo.

Gorilla	Life-stage Categorisation	Offspring	Co-ordinates	
			Dimension 1	Dimension 2
Fa	AF 1	Vi	.634	-.071
Jo	AF 2	Wi, Zu	.538	-.209
Ks	SB	-	.719	-.025
Qu	AF 3	Vz	-.185	-.681
Vi	AM 1	-	-.826	-.096
Vz	AM 2	-	-.543	-.406
Wi	AF 4	-	-.169	.748
Zu	OI	-	-.167	.740

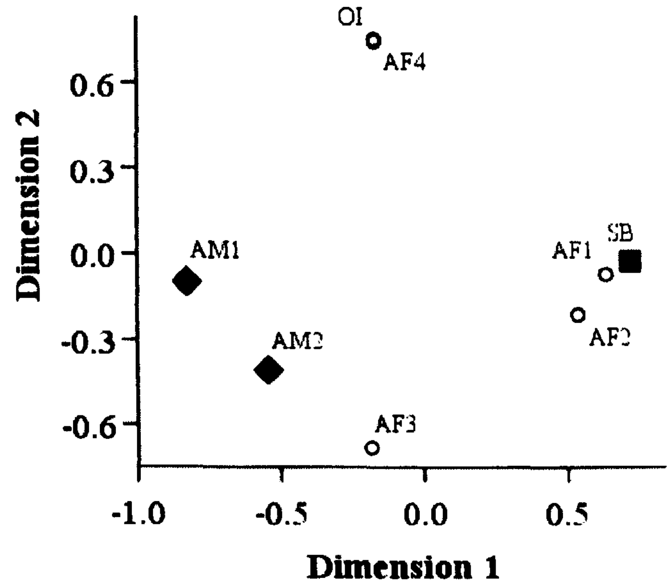


Figure 4.2 - A two-dimensional MDS configuration for proximity (0-5m) among gorillas at Basel Zoo. S-Stress = 0.05, DAF = 0.99

4.4.1.3 Burgers' Zoo

The gorillas in this zoo displayed an unusual social grouping as two of the adult females, who were mothers to two NRIs died a year before this study took place. The NRIs who were both orphaned during infancy included the juvenile male (JM) who had a close association with the silverback (SB), and the older infant (OI) who was spatially separate from the group, despite having an older sister (F) in the group (Figure 4.3). The nulliparous adult female (F) showed a close association to the adult female (AF) and her infant (see Chapter 5 for analysis on this relationship), whereas the juvenile female (JF), who had a mother in the group (AF), was spatially separate from her.

Table 4.4 - MDS co-ordinates of gorilla group proximity at Burgers' Zoo.

Gorilla	Life-stage Categorisation	Offspring	Co-ordinates	
			Dimension 1	**Dimension 2**
Ba	SB	-	-.767	-.040
Li	JM	-	-.508	-.112
Ng	AF	Ny	.186	-.415
N	JF	-	1.092	.121
Sh	F	-	.224	-.092
Si	OI	-	-.227	.538

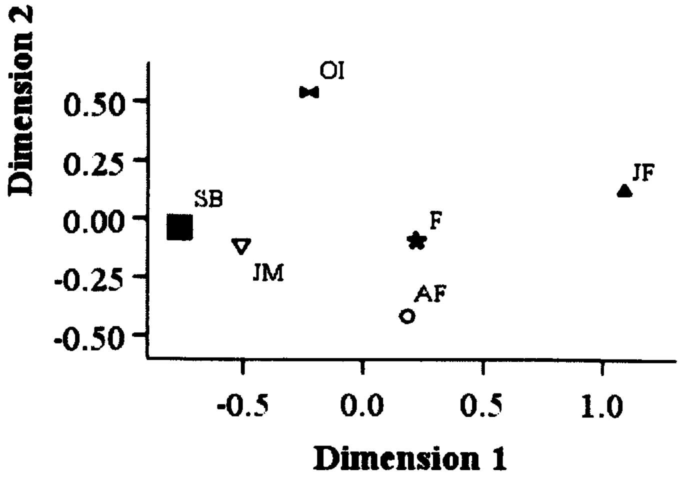


Figure 4.3 - Two-dimensional MDS configuration for proximity (0-5m) values among gorillas at Burgers' Zoo. S-Stress = <0.000, DAF = 0.99

4.4.1.4 La Vallée des Singes

The three adult females (AF) at La Vallée des Singes formed a clear spatial unit with the silverback male (SB), which did not incorporate the NRIs

(Figure 4.4). The juvenile male (JM) and older infant (OI) formed another clear unit away from the adult gorillas and separated from all other group members was the adolescent male (AM).

Table 4.5 - MDS co-ordinates of gorilla group proximity at La Vallée des Singes.

Gorilla	Life-stage Categorisation	Offspring	Co-ordinates	
			Dimension 1	Dimension 2
Bd	AM	-	.323	.906
Ga	AF 1	Kw	-.467	-.123
Kb	JM	-	.775	-.309
Kw	OI	-	.788	-.265
Mo	AF 2	Kb	-.472	-.076
Vi	AF 3	Bd	-.475	-.048
Ya	SB	-	-.472	-.085

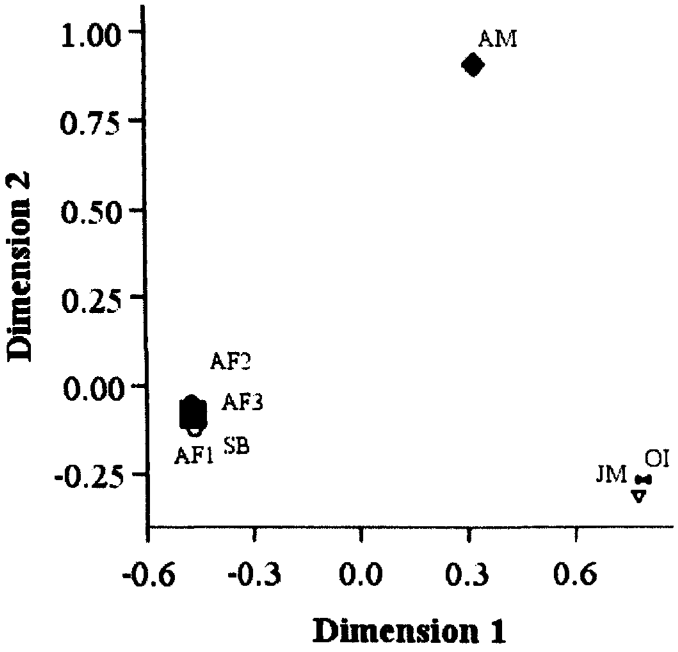


Figure 4.4 - A two-dimensional MDS configuration for proximity values among gorillas at La Vallée des Singes. S-Stress = < 0.000, DAF => 0.99

4.4.1.5 Zurich Zoo

Two adult females (AF1, AF2) formed a close association with the silverback (SB), along with their infants. The third adult female (AF 3) was a new gorilla introduced to the group six months before data collection commenced and showed some distance from the core group (Figure 4.5). The adolescent male (AM), the only NRI without a mother in the group, had a closer spatial relationship to the silverback than the juvenile males (JM), who were spatially distinct to each other as well as to the rest of the group.

Table 4.6 - MDS co-ordinates of gorilla group proximity at Zurich Zoo.

Gorilla	Life-stage Categorisation	Offspring	Co-ordinates	
			Dimension 1	**Dimension 2**
Az	AM	-	-.168	-.731
Bg	JM1	-	1.071	-.565
Bs	JM2	-	1.022	.658
En	I1	-	-.326	.027
Ey	I2	-	-.325	-.010
Ma	AF 1	Bs, Ey	-.326	.027
Na	AF 2	Bg, Bs	-.325	-.010
Ng	SB	-	-.326	.036
Ny	AF 3	-	-.296	.567

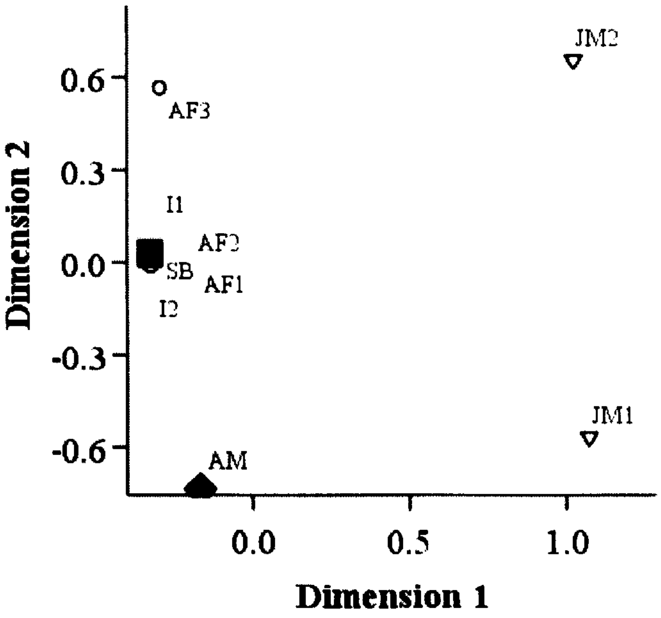


Figure 4.5 - A two-dimensional MDS configuration for proximity values among gorillas at Zurich Zoo. S-Stress = 0.051, DAF = 0.99

4.4.2 Variation in sociality across NRIs.

The distribution of the SI scores (Figure 4.6) provides a measure of the strength of relationships between the NRI gorillas and other gorillas in their social groups. The distribution of scores was negatively skewed, with a mean value of 0.90 and a median value of 0.70, both of which indicate that the majority of NRI-gorilla dyads had weak social bonds, with few strong social bonds.

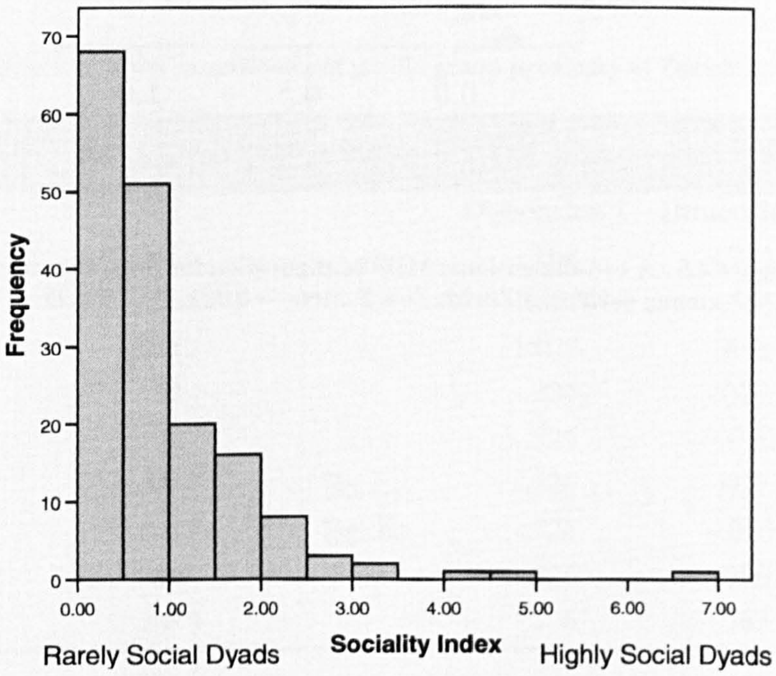


Figure 4.6 - Distribution of SI for all NRI-gorilla dyads (N = 171)

4.4.3 Relationship change with NRI age

Since age and sex of a NRI both affect relationship formation and maintenance (Russon, 2004a), the life-stage of the NRI is predicted to affect its propensity to associate with certain gorillas. Here it is investigated how relationships with related individuals and peers differ with sex and across life-stage categories.

4.4.3.1 Relationship with the mother

The social relationship between a NRI and his/her mother decreased as NRIs increased in age (Figure 4.7, Spearman's Rho $r_s = -0.58$, $N = 17$, $P = 0.01$). For female NRI gorillas there was a tendency for the level of sociality with the mother to decline as the NRI passed into older life-stages ($F_{(2,4)} = 5.94$, $P = 0.06$), although there was no significant difference in sociality between male NRI life-stages ($F_{(2,6)} = 0.82$, $P = 0.48$). The mean SI for juvenile males was slightly higher (but not significantly so) than for juvenile females but by later in the pre-reproductive period less of a difference in the mean SI was found between blackbacks and adult females with their mothers (Figure 4.8).

4.4.3.2 Relationship with the silverback

The social relationship between NRIs and the silverback did not significantly change with NRI age (Figure 4.7, $\rho = - 0.16$, N = 22, $P = 0.47$). With female NRI gorillas, no significant change in sociality occurred with the silverback across the pre-reproductive period ($F_{(2,6)} = 0.27$, $P = 0.77$), although old infants had a higher mean SI than either juvenile females or adult females (Figure 4.8). In a similar way male NRI gorillas did not significantly alter their social relationship with the silverback across the pre-reproductive period ($F_{(2,9)} = 0.90$, $P = 0.44$), although the blackback NRIs had a lower mean SI than either the juvenile males or the adolescent males. Again, the mean SI for the juvenile males was slightly greater than for juvenile females, but by later in the pre-reproductive period primiparous adult females had a greater SI with the silverback than blackbacks NRIs (Figure 4.8).

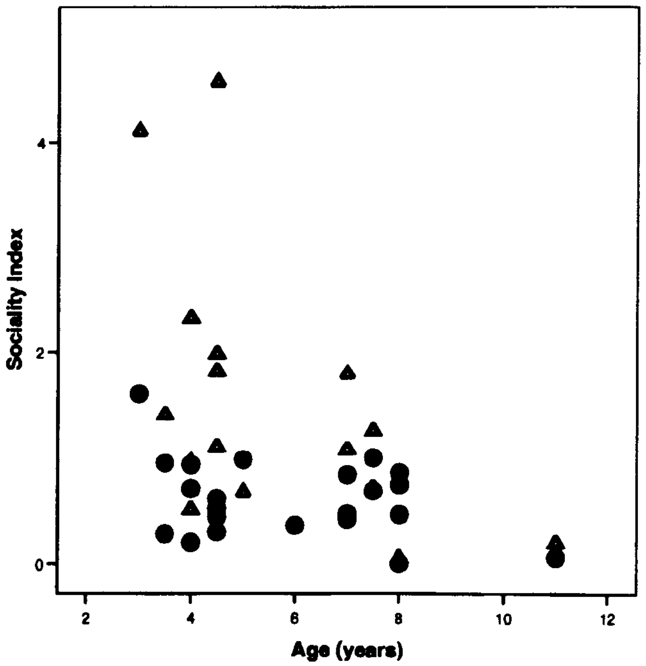


Figure 4.7 - Frequency of social bonds between NRI-mother and NRI-silverback (presumed father). Filled circles represent silverback; triangles represent mother.

4.4.3.3 Other non-NRI relationships

Female NRI gorillas did not show a decrease in sociality with age with non-related breeding adult females (Spearman's Rho $\rho = -0.26$, N = 18, $P = 0.30$), with the highest mean SI being between juvenile females and unrelated adult females. Whereas, a decrease in the social relationship with age occurs between NRI males and non-related adult breeding females ($\rho = -0.55$, N = 37, $P = <0.001$). The social relationship between NRI female gorillas and infants did not significantly change across the pre-reproductive period ($\rho = -0.18$, N = 9, $P = 0.65$). The highest SI was recorded for juvenile females and infants whereas, male NRI gorillas significantly reduce their social relationship with infants as they became older ($\rho = -0.61$, N = 15, $P = 0.02$) (see Chapter 6, Figure 4.8).

4.4.4 Prominent relationships

Prominent relationships are considered those in which a dyad has a high SI, indicating that it engages in social contact and close proximity more than other dyads. In the following analysis, it was investigated which relationships were prominent for each NRI life-stage, for the purpose of these analyses, a prominent relationship was considered when the mean SI value was two or above. This was determined using the SI, where a high value indicates a high level of sociality within the dyads. This value was based on Figure 4.6 in which a SI score of two or more represents the strongest 10 % of social relationships documented in this study.

4.4.4.1 Old infants

Old infant gorillas formed prominent social relationships with three other life-stages, their mothers, juvenile females, and juvenile males, (Figure 4.8a). A one-way ANOVA analysis revealed no significant difference in the social relationships maintained with gorillas of other life-stages (Welch $F_{(8,6.6)}$ = 2.21, $P = 0.16$).

4.4.4.2 Juvenile males

Prominent relationships were found between juvenile male gorillas with three other life-stages (their mothers, juvenile females, and juvenile males,). Strong social relationships were also documented with adolescent males (Figure 4.8b). A significant difference was found between the social relationships of juvenile males with other life-stages (Welch $F(_{7,6.49})$= 20.61, P = 0.001). Juvenile males had a significantly stronger social relationship with other juvenile males and females than with the silverback (juvenile male, 1.6, P = 0.001; juvenile female, 1.35, P = 0.001), infants (juvenile male, 1.85, P = <0.001; juvenile female, 1.60, P = <0.001) and unrelated adult females (juvenile male, 1.58, P = <0.001; juvenile female, 1.33, P = 0.001).

4.4.4.3 Juvenile females

Juvenile females formed prominent relationships with two other life-stage categories (Figure 4.8c, old infants, juvenile females,). A significant difference was found in the level of social relationships that juvenile females engaged in with other life-stages ($F_{(9,18)} = 3.31$, $P = 0.019$), with juvenile females being significantly more social with other juvenile females than with blackbacks (2.13, $P = 0.04$).

4.4.4.4 *Adolescent males*

Adolescent males formed no prominent relationships, but did form stronger than average relationships with three other life-stage groups (Figure 4.8d, old infants, juvenile females, adolescent males,). These relationships were not considered prominent in level of sociality for this analysis. Again a significant difference was found between adolescent male sociality documented between life-stages (Welch $F_{(9,\ 8.06)} = 3.70$, $P = < 0.04$). No significant differences between life-stages were found.

4.4.4.5 *Blackbacks*

No prominent social relationships were found between blackbacks and other life-stages (Figure 4.8f). The strongest social relationship was found between blackback NRIs with adolescent males. A significant difference was found with the social relationships with gorillas from different life-stage groups (Welch $F_{(7,4.04)} = 10.49$, $P = 0.02$). Significantly, stronger social relationships were found with other blackback gorillas as opposed to unrelated adult female gorillas (0.93, $P = 0.003$)

4.4.4.6 *Adult females*

Adult females had no prominent relationships with other life-stage categories (Figure 4.8e), although most social relationship were formed with juvenile males and juvenile females. No significant differences were found for adult female sociality between different life-stage groups ($F_{(9,22)} = 0.71$, $P = 0.70$).

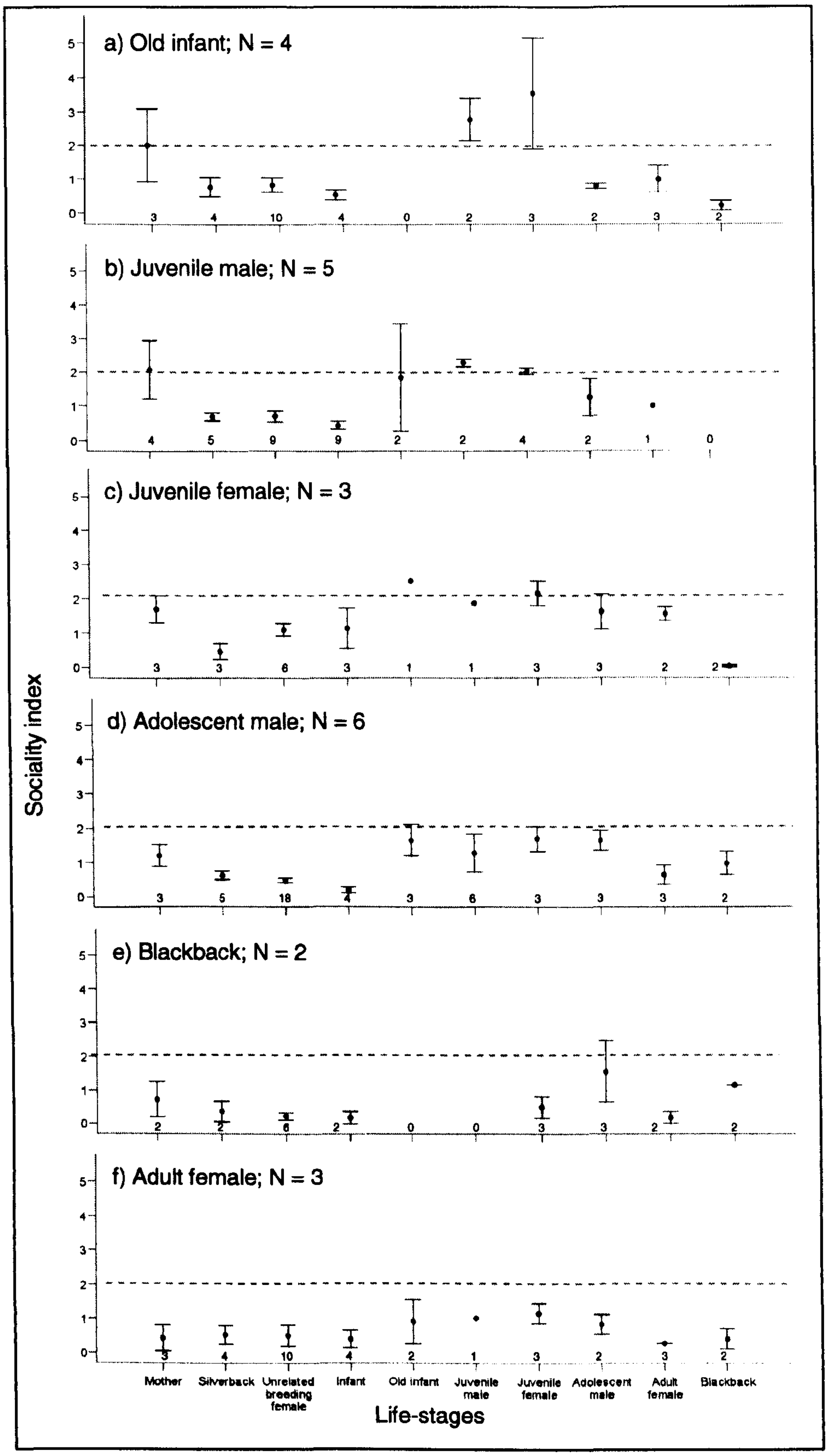


Figure 4.8 – Level of sociality (Mean (+/- 1 standard error) between NRI gorillas. Numbers above x-axis = no. dyads.

4.4.5 Change in sociality across the pre-reproductive period

NRI sociality changed across the pre-reproductive period (Figure 4.9). There was a tendency for SI value to differ by life-stage ($F_{(5)}$= 2.07, P = 0.07). Younger NRI life-stages (old infancy, juvenile males and females) had a significantly higher SI than those in the NRI older life-stages (adolescent males, blackbacks and adult females, t $_{(21)}$= -2.79, P = 0.01, Figure 4.9).

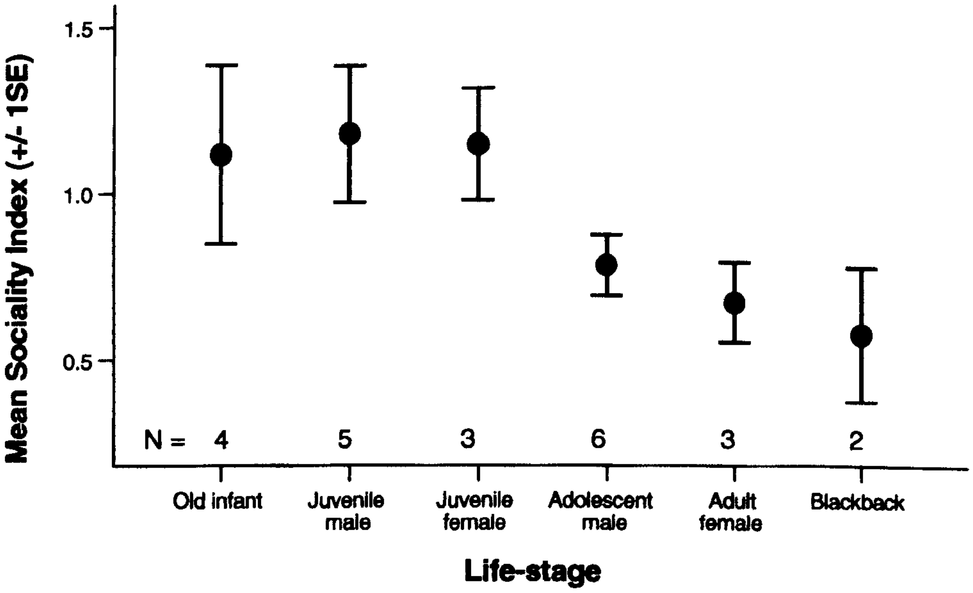


Figure 4.9 - Mean sociality index (+/- 1SE) for NRIs of each life-stage. Numbers above x-axis = no. of gorillas in each life-stage.

4.4.6 Social relationships with full siblings and paternal half siblings

Social relationships between NRI gorillas differed depending on whether they were associating with full siblings or paternal half siblings (Figure 4.10). There was no significant change in relationships with full siblings over the pre-reproductive period (ρ = 0.001, N = 18, P = 0.98), whereas social relationships with paternal half siblings significantly declined with NRI age (ρ = -0.33, N = 94, P = 0.001). The relationship between NRI gorillas with full and paternal half siblings differed by life-stage (Figure 4.10). For old infants and juvenile females, there was no significant difference in the social relationship between full and paternal half siblings, whereas juvenile males had a higher SI with paternal half siblings. Adolescent males, blackbacks and adult females had a significantly higher SI with full siblings compared to paternal half siblings.

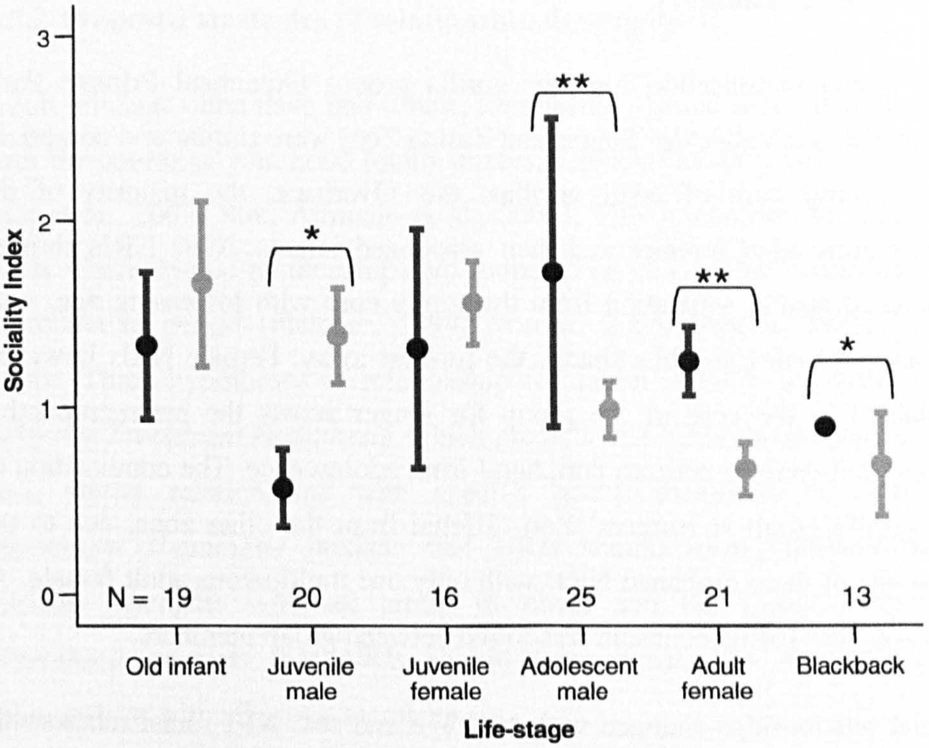


Figure 4.10 - Mean sociality index (+/- 1SE) for each life-stage with full and paternal half siblings. Black bars represent full siblings; grey bars represent paternal half siblings. Numbers above x-axis = no. dyads. Using a Wilcoxon's Ranked Sum; * *P* = 0.05, ** *P* = 0.001.

4.5 Discussion

4.5.1 Results summary

The spatial organisation for four gorilla groups (Apenheul Primate Park, Basel Zoo, La Vallée des Singes and Zurich Zoo) were similar and comprised of a central core of adult gorillas: the silverback, the majority of the multiparous adult females and their associated infants. Male NRIs showed graduated spatial separation from the group core with increasing age, with adolescent males and blackbacks the furthest away. Female NRIs however, remained in the core of the group for longer across the pre-reproductive period, but were sometimes peripheral from adolescence. The composition of the gorilla group at Burgers' Zoo differed from the other zoos, due to the presence of three orphaned NRIs with only one multiparous adult female. At this zoo, less spatial cohesion was found between group members.

Social relationships changed with NRI age and sex. NRI social relationship with the mother declined with age for both males and females, but relationships with the group silverback remained stable across the pre-reproductive period. Male NRI social relationships with infants and unrelated breeding females declined with age, whereas female NRI relationships with these classes were maintained across the pre-reproductive period. Few prominent NRI relationships (those with a high sociality score) were documented. Prominent social relationships were only found in old infants and juvenile life-stages; these were formed between the younger NRI with the mother or with conspecifics. Older infant and juvenile NRIs tended to have a higher SI than adolescent males, blackbacks and adult females

The degree of relatedness influenced NRI relationships with full and paternal half siblings. Relationships with full siblings were maintained across the pre-reproductive period by both male and female NRIs, whereas relationships with paternal half siblings declined with NRI age. Juveniles were found to be more social with paternal half siblings than with full siblings, but from adolescence onwards, stronger social relationships were found between NRIs and full siblings than between NRIs and paternal half siblings.

4.5.2 Proposed strategies of relationship development

Adult primates often have few robust, long-lasting dyadic social relationships over the course of adulthood (chimpanzees, Lawick-Goodall, 1971; baboons, Silk et al., 2003; Silk, Altmann et al., 2006). This is contrary to studies of NRIs where dyadic relationships are found to be changeable across the pre-reproductive period (Fletcher, 1994; Nowell, 2005; Pereira, 1995; Pusey, 1990). Three hypotheses of relationship formation in NRIs are tested. The *Selective Investment Hypothesis*, which predicts that NRIs should form only a few, strong relationships with specific group members; the *Variable Investment Hypothesis* predicts that NRIs should form relationships of variable strengths with all group members and the *Equal Investment Hypothesis* predicts that NRIs should form equal, low strength social relationships with all group members.

The formation of dyadic relationships is presumably beneficial to both partners, or carries a specific advantage to each individual (Cords, 1997). Among adult primates, dyadic relationships vary in strength within a social group, often reflecting relatedness, social structure and individual position in the group hierarchy, which determine the advantages, assumed from the relationship (Silk, Altmann et al., 2006). In a similar manner, NRI-gorilla relationships were shown to be highly variable in strength, ranging from *prominent* to infrequently maintained relationships. (Although this was due to the arbitrary value of the top 10% of social relationships being described as prominent in the methods, this did not constrain the variation, as over half of dyads had a SI value of less than one). The factors affecting social relationships in NRI primates have received little attention in the literature, (but see, Berman, 2004; Pereira, 1995). Thus, it is investigated here how relationships and sociality change with group members across the pre-reproductive period.

Using a sociality index and spatial proximity method has allowed the development of the analysis of NRI social relationships. This was achieved through providing a spatial understanding of the NRI in the context of the social group and by creating an index of sociality built on actual social interactions within dyads, instead of proximity alone, as is often used in similar studies (reviewed by, Berman, 2004). Together, these analyses bring about a more comprehensive assessment of social relationships, which here lead the discussion on relationship development and change over the pre-reproductive period.

Dyadic relationships can be formed with different individuals across the pre-reproductive period, or altered in their intensity through maintaining relationships more or less. In this study, higher levels of sociality and closer spatial orientation to the adult central core were found in the old infant and juvenile life-stages, compared to the older life-stages. The greater sociality in younger NRI gorillas coincides with reported developing independence from the mother (Fletcher, 1994; Nowell & Fletcher, 2007), which likely reflects the greater necessity for strong social relationships with other group members. Such changes are presumed to afford an advantage to the individual, in terms of flexibility in the range of skills and knowledge available for learning (Russon, 2004b).

The *Selective Investment Hypothesis* of forming a few prominent relationships within a social group without forming relationships with all other group members would only be feasible if the group were composed of more individuals than it would be possible in terms of time and energy, to maintain relationships with, or be in close proximity to. For example hamadryas baboon troops, where up to 750 individuals belong to one troop (Rowe, 1996). In the majority of primate social groups however, adult relationships are formed with the majority of group members, but differ in relationship strength which depends primarily on the interaction between feeding competition and the degree of relatedness (Kappeler, 1999). In wild mountain and western gorillas, variable strength social relationships are maintained with the majority of group members (Doran-Sheehy & Lodwick, 2005; Stewart, 2001; Stewart *et al.*, 2001; Watts, 2001). This can perhaps be explained through the strong silverback – adult female bonds and therefore close proximity of adult females in the group along with low feeding competition both in the captive environment, and in the wild, where observations have been conducted to date (Stokes et al., 2003). The strategy of *Variable Investment* in social relationships with all group members may be a necessary strategy for adult gorillas to assume the benefits of living in a group and for specific functional dyadic relationships. Adult gorillas are therefore predicted to support the *Variable Investment Hypothesis*.

The hypothesis of *Variable Investment* proposes that NRIs should invest in a few prominent relationships with specific group members, but maintain variable levels of relationships with all other group members. Stronger relationships are expected to exist between individuals where there is a strong fitness advantage of maintaining the social relationship to both individuals through attaining essential resources or the survival of progeny. Prominent social relationships (the top 10% of social relationships recorded) however, were formed in this study between younger NRIs (old infants and juvenile gorillas), with their mothers or other old infant and juvenile NRIs. It is therefore assumed that these relationships, although not offering the same fitness benefits as adult dyadic relationships are specifically invested in, and are similar to adult social relationships in that they are advantageous to both dyadic partners. How long these relationships remain prominent in younger NRIs is not possible to determine in this study due to the cross-sectional data collection methods, but a future longitudinal study would answer such questions.

The need for prominent relationships in NRI gorillas would be predicted to occur at a time of increasing independence from the mother, which is proposed as a period where allies and skill development are highly important (Russon, 1997). The beginning of juvenility also correlates with growth in the neocortex, which in turn leads to an increased receptiveness in learning species-specific motor and social skills (Russon & Begun, 2004). This learning can either occur alone through practise, or through observational learning, or imitation of others (Cords, 1997; Russon, 1997). Given that old infants and juveniles support this hypothesis of relationship formation, it is suggested that prominent social relationships are allowing the learning of essential skills and enable the NRI to practise and develop skills with the mother and similar-aged peers. These skills are likely to be assimilated faster than would be expected at other life-stages due this neocortical expansion (Russon, 2004a). This might be particularly pertinent at the beginning of independence to reduce the risks involved in play behaviour through accident or injury (Fagen, 2002), or risks of starvation through inadequate attainment of food resources (Janson & van Schaik, 2002). The development of skills in the pre-reproductive period is supported by other NRI social development studies, where preferred play partners for example, are often similar in age, and proximity to the mother remains high during juvenility, despite attaining nutritional independence (Fletcher, 1994, 2001; MacKinnon, 2007; Nowell, 2005; Watts & Pusey, 2002)

The *Equal Investment Hypothesis* proposes that social relationships with all other group members are invested in equally. It would be presumed therefore, that dyadic relationships between group members would differ little in the advantages assumed. This is not found to be the case in adult primates who, as discussed, vary in their sociality between dyads. However, in this study, support for the *Equal Investment Hypothesis* was found in blackback and adult female NRI gorillas and to a lesser extent with adolescent males, who generally maintained social relations with all group members equally, regardless of relatedness. Considering that, adult gorillas and young NRIs are discussed to invest in some prominent relationships, equally maintaining all relationships is an interesting strategy manifested in gorillas potentially only in older NRIs. Older NRIs in these life-stages continued to maintain relationships with all available group members and thus assumed the benefits of group living. A lack of prominent relationships indicates a lack of benefit in dyadic relationships with natal group members. This may be explained by the neocortex growth rate decline along with learning receptivity from adolescence, as the development of social and motor skills is expected to be complete (Russon, 2004a). Thus, the advantage of maintaining prominent relationships seen in younger NRIs is reduced, particularly in a species in which both sexes emigrate from the natal group.

This supports that the development of prominent relationships are strategies within primates, which are functional and have advantages to each dyadic partner. Without any advantages, prominent relationships are not likely to be found. To test this strategy further it would be necessary to compare results from the current captive study to like aged gorillas in the wild living in natal groups, where the choice of being in the natal group and timing of emigration remains with the individual and may lead to variation in relationship maintenance with other group members. The captive environment may limit the study of social development through restricting when females breed within the group thus limiting the number of other NRIs available to interact with and at times increasing the interbirth interval between siblings. A larger wild study of NRIs is large social groups may develop the understanding of sociality in NRIs further.

4.5.3 Sex differences in sociality

Dyadic social relationships are influenced by the sex, dimorphism and age of the NRI (Pereira, 1995). In gorillas, females reach sexual maturity up to eight years earlier than males (Taylor, 1997). The developmental schedule of males and females differs in its trajectory but also in the functional roles between the sexes in adulthood, with males characterised as protectors and females as caregivers. The behaviour exhibited and relationships formed are expected to differ between the sexes in order to assume the greatest advantage for the individual in developing into these future roles (Cords, 1997). It is expected therefore, that male and female NRIs would differ in the sex-specific skills and knowledge that need to be learnt before assuming adult roles at maturation, which is predicted also to affect relationship maintenance (Russon, 2003) and spatial orientation within the social group. In the current study, across all life-stages NRI gorillas were found to socialise with both male and female NRI gorillas, again supporting findings from wild gorilla populations (Nowell, 2005). This is a likely reflection of the necessity to build experience of relationships with the same and opposite sex individuals to build alliances, or to compete for access to the opposite sex (Pusey, 1990).

In this study, the majority of female NRI gorillas remained close to the central core of the group from juvenility into adulthood. In a similar way, chimpanzee adolescent females remained in closer proximity to the mother, where it is presumed that they learn skills such as foraging, tool use and mothering skills in which males show less interest in (Lonsdorf et al., 2004; Pusey, 1983, 1990). However, in this study, females showed a decline in sociality with the mother with age, but not with other individuals in the central core of the group. Since protection from the dominant male is no longer warranted by fully grown individuals without infants (Janson & van Schaik, 2002), the attraction of remaining in the central core is likely to be the association with other group members. Attraction to infants for instance, by female NRI primates is a common phenomenon (MacKinnon, 2007) and has been observed in wild and captive western gorillas (Nowell, 2005, this study) and in chimpanzees (Pusey, 1990).

Gorilla male NRIs, showed disparity in spatial proximity within the natal group compared to female NRI. Males gradually migrated out from the central core, until at the blackback life-stage they had peripheralised themselves to the group's edge (Nakamichi & Kato, 2001; Nowell, 2005; Watts & Pusey, 2002, this study). In the case of wild gorillas, the subsequent decision after peripheralisation would be one of three options, migration into breeding or non-breeding groups (Bradley et al., 2004; Levrero et al., 2006; Watts & Pusey, 2002), or living as a lone silverback, which can not be assessed in the captive environment due to management techniques. Similar proximity patterns of male NRIs are documented for other sexually dimorphic species with increasing age, including mountain gorillas, mandrills and baboons (Alberts & Altmann, 1995; Setchell, 2003; Watt, 1994).

Peripheralisation in male mandrills is proposed as a method of conflict reduction in adolescence (Setchell, 2003); as male mandrills moved back into the centre of the group at maturation, this may be a similar mechanism for adolescent gorillas. From adolescence onwards, ape males engage in growth spurts (Leigh, 1996), which correlate with surges of testosterone (Anestis, 2006; Robbins & Czekala, 1997), and in turn lead to increased risky behaviour (Galvan et al., 2007) and aggression (Pusey, 1990). Aggressive behaviour in a gorilla group may lead to counter aggression from the dominant male and occurs more as NRI males increase in age (Watts & Pusey, 2002). Thus for gorillas, peripheralisation at this life-stage, like in the mandrills, is predicted to reduce agonism and injury, which could otherwise constrain growth and development, allowing maximum body growth prior to dispersal (van Noordwijk & van Schaik, 1985). Mandrill male peripheralisation occurs voluntarily and more readily at times of a growth spurt with males not actively evicted by dominant males (Setchell, 2003). Likewise, in this study and for wild western and mountain gorillas, males from six years of age, showed a propensity to peripheralise (Fletcher, 1994, this study; Nowell, 2005) resulting in decreased association with adult gorillas.

A relationship with the mother and silverback (presumed father) across the pre-reproductive period would be expected to follow the same pattern for males and females, unless the relationship between NRI and the mother or father assumes different benefits for each sex, which in this study there is no support for. Across the pre-reproductive period, the relationship between the mother and both male and female NRIs declined with age as the NRIs invested in relationships and activities that are considered to prepare them better for adulthood. Other similar mother-infant ape studies show the same pattern of relationship change with both sexes (Fletcher, 1994; Lawick-Goodall, 1971; Nowell, 2005; Pusey, 1990; Watts & Pusey, 2002).

Relationships with the silverback however, did not significantly decline over the pre-reproductive period for male or female NRIs. This is similar to other studies of proximate relationship in mountain gorillas, which showed continued proximity to the silverback over time (Fletcher, 1994; Stewart, 2001). Assumed advantages of having a constant relationship with the silverback may include using him as a spatial focus, an attachment figure and a buffer from inter-group aggression (Stewart, 2001), and perhaps also as a role model for appropriate adult male behaviour. Continued relations with the silverback occurred, regardless of the finding that NRI males became spatially separated from the silverback. This indicates that factors other than proximity are used in relationship maintenance in gorillas, supporting the use of a SI in understanding such relationships. In wild multi-male groups, males are also seen to continue their relationship with the silverback, the presumed father, often into adulthood, whereas females maintain social relationships with other less dominant males, who are potential breeding partners (Fletcher, 1994; Stewart, 2001). No such comparison can be made in this study as only one adult male (the presumed father) resided in each group .

4.5.4 Sibling relationships across the pre-reproductive period

The inclusive fitness hypothesis predicts that there is an additional fitness benefit of maintaining relationships with those that are more closely related, particularly if the relationship increases the chance of one individual surviving or producing more progeny (Hamilton, 1964). This has been documented in a number of primate species where the offspring assume the dominance position of the parent at maturation (Schino et al., 2003; Silk, Alberts et al., 2006), or where increasing the maternal provisioning of males before independence can lead to a fitter, more competitive male growing into the population (Boesch, 1997). However, such theories do not take into consideration that relationships between most full siblings may be maintained due simply to sharing a mother, thus they spend more time in close proximity compared to paternal half siblings (Chapais, 2001). Interactions forged through attraction to the mother however, may simply be a by-product of this mutual relationship where the relationship benefits are based on familiarity not on relatedness.

From either perspective, it seems likely that NRIs should have a stronger social relationship with full siblings compared to paternal half siblings. This is particularly so if the relationship provides additional care or protection of infant or juvenile siblings (MacKinnon, 2007), or provides the sibling with a distinct advantage, such as the development of motor skills through play behaviour (Fagen, 2002). Therefore, findings from this study are not surprising in that higher sociality index scores are found for full, compared to paternal half siblings, in all life-stages, except juvenile males.

The benefits of gorilla sibling relationships continuing into adulthood as was found in this study, may also be important for male NRI survival and breeding success (Bradley et al., 2004). NRI western gorillas migrating into non-breeding groups have been found to receive coalitionary support from related silverbacks (Levrero et al., 2006), whilst mountain gorillas in non-breeding groups, with a related male, benefit from fewer wounds and aggression compared to un-related adolescent and blackback males in breeding groups (Robbins, 1996). Overall, in this study, full siblings were more social than paternal half siblings were, with the exception of juvenile males, although the level of sociality with paternal half siblings was similar for both male and female juveniles. This further highlights the proposed benefit for juvenile males to be with like-aged NRIs as opposed to those who are older or younger by three or four years, regardless of relatedness, which is discussed in more detail in Chapter 6 in relation to social play

It is predicted that female gorillas with different adult roles and developmental trajectories assume different benefits from relationships than do males. Where long-term studies of female mountain gorilla emigration have been conducted, females rarely emigrate into groups with relatives (Watts, 2001). Females therefore, are less likely to benefit in adulthood from maintaining sibling relationships into the pre-reproductive period, although a study of the few related mountain gorilla females in the same breeding group did indicate greater affiliation between related females, in particular with maternal relations (Watts, 2001). In this study however, there was some evidence that female relatedness led to increased access to infant full sibling (see Chapter 6 for related discussion) as is also documented for Japanese macaques (Schino et al., 2003), where kin showed increased positive affiliation to infants and were tolerated by the mother more than non-kin. This maximises the necessary skills and knowledge attained (Russon, 2003) specific to females, such as providing high quality of care to infants to enable high offspring survival (Hrdy, 1999), for which strong social relationships are essential. It is thus predicted that, relationships with younger NRI siblings will be more profuse in NRI females compared to relationships with older NRI siblings. Future, in-depth studies would be needed to indicate if this does occur.

4.6 Conclusion

Different strategies of dyadic relationships formation, maintenance and spatial orientation were found for captive western gorillas across the pre-reproductive period. Younger NRIs were found to support the *Variable Investment Hypothesis*, forming more prominent relationships with gorillas with whom there would be a specific benefit. Older NRIs equally maintained all relationships, thus it was assumed that no specific relationships provided them with any greater benefits, this supported the *Equal Investment Hypothesis*. No support was found for the *Selective Investment Hypothesis*, where prominent relationships were invested in, in the absence of maintaining relationships with the remainder of the social group. Relationships with full siblings continue with both sexes across the pre-reproductive period, compared to paternal half sibling relationships, which decline with NRI age and may be found due either to an inclusive fitness advantage or due to the sharing of the same mother, which likely increases familiarity between full siblings. The chapter illustrates the advantages of using a spatial representation of the social group and a sociality index in assessing relationship development strategy in the pre-reproductive period.

Chapter 5

5 ALLOPARENTAL INTERACTIONS WITH INFANTS

This chapter provides the first quantitative assessment of alloparenting behaviour in western gorillas. The data investigates NRI-infant interactions and examines the effect of maternal style upon the occurrence of infant interactions. Finally, an assessment of the evolutionary significance of alloparenting behaviour in the apes is discussed.

5.1 Introduction

5.1.1 Life history

Alloparenting, defined as care (carrying, protection and nurturance) given to an infant by an individual other than the mother. Its occurrence across a range of mammals indicates that alloparenting maximises survival or increases reproductive potential (Hamilton, 1964) in the infant, the infant's mother, the alloparent or a combination of the three individuals. Species which are found to alloparent grow slowly and have a prolonged period of parental dependency, compared to similar sized non-alloparenting species (Mitani & Watts, 1997; Riedman, 1982). Therefore, additional infant care received from other group members releases the mother from non-essential components of care, which are necessary for the socialisation and survival of the infant (Jolly, 1985). In the evolutionary sense, alloparenting is proposed to have evolved as a mechanism to aid in the survival of early weanlings whose mothers have died, where survival with alloparental care from another individual is dependant upon the age of the infant and the availability of suitable weanling foods (Kennedy, 2005). Such adoptions in primates are reportedly common in Cercopithecines (Fairbanks, 1996) and have been reported on occasion in gorillas (Fossey, 1979) orang-utans (Becker, 1982) and habitually across cultures in humans (Kennedy, 2005; Pope Edwards, 1993)

5.1.2 Alloparenting in the monkeys

The mother is generally the infant's primary caregivers in primate species. Mothers invest highly in infant nutrition and transportation over the long infant period until weaning (Lee, 1997; Ross, 2003). This high investment seeks to benefit the mother through the passing of her genes into subsequent generations, the success of which, over multiple offspring illustrates her reproductive fitness (Hamilton, 1964). It is clear therefore; that infants are costly to their mothers and that their survival is paramount to her fitness. Maternal protectiveness over the course of infancy should be paramount and be greater when the infant is younger and more vulnerable to risk and injury. As the infant increases in age, it gains more independence from the mother and shows increasing interest in the surrounding environment and social group (Pereira & Altmann, 1985). Contact between infants and other group members increases as the infant becomes more independent and maternal protectiveness decreases (reviewed by Mitani & Watts, 1997). However, this is not the case in langurs and capuchins, where other group members make contact with infants sometimes a few hours after birth and the rate of infant contact declines with infant age (Kumar *et al.*, 2005; Manson, 1999). The timing and amount of infant contact by alloparents is highly variable and bound by the restrictiveness of the mother, the social group of the primate (Paul, 1999) and the interest in infants by other group members (Silk, 1999).

Despite the potential risks to the mother in terms of inclusive fitness through allowing another group member to have contact with an infant, interactions between infants and other members are common, particularly across the Cercopithecinae, Colobinae and Callitrichidae taxa (reviewed by McKenna, 1979; Mitani & Watts, 1997). Infant handling is commonly initiated by fathers in Callitrichidae and by related and non-related females in Cercophithecines and Colobinae (Bentley-Condit *et al.*, 2001; Brent *et al.*, 2008; Lancaster, 1971; Manson, 1999; Ross, 2003; Schino et al., 2003).

Adult interactions with infants can be described as either agonistic or affiliative in nature. Agonistic interactions have the aim of gaining a reproductive advantage or reducing the pressure on nutritional resources within a social group e.g. infanticide and infant abuse are documented in some primate social groups (van Schaik & Janson, 2000). Evidence of such motivated behaviour occurs in langurs, rhesus monkeys and bonnet macaques (Maestripieri, 1999; Silk, 1999; Sommer, 1989). Affiliative interactions, have no negative effect on infant survival and may even increase infant survival through the provision of an additional carer, which may allow the mother to increase her nutritional input (Ross, 2003). Affiliative interactions are described as the touching, grooming, sniffing, handling and social play with infants (Silk, 1999), where infant contact can be initiated by the infant or by another group member. Alloparental behaviour towards an infant may entail either the infant being in sole contact with the alloparent such as during infant handling (Kumar et al., 2005; Lancaster, 1971; Manson, 1999), or by touching the infant when the infant is being held by the mother (Silk, 1999).

Although alloparenting is widespread across the primates, it does not occur with every infant in a primate group and a great variability in alloparenting is documented within species. The likelihood of alloparenting occurring probably depends on the primate social system, the size and demography of the group, the restrictiveness and parity of the mother and the motivation of potential alloparents to assume contact with the infant.

The mother is the primary agent in allowing access to the infant (Schino et al., 2003); her temperament, maternal experience and position in the social hierarchy affect alloparenting interactions (Fairbanks, 1996). The mother herself is thus an important determinant of the occurrence of alloparenting (Brent et al., 2008), with primiparous mothers in general being more restrictive of infants than multiparous mothers (Hooley & Simpson, 1981). In addition, the style of maternal care differs greatly between mothers of the same species: in Japanese macaques for example, maternal experience and mothers' social rank had little relation to the frequency of permitted infant interactions with others (Schino et al., 2003).

In the most part, maternal reaction to alloparents is found to be dependant upon the infant's age and relatedness of the alloparent (Manson, 1999; Schino et al., 2003), where older infants are less restricted, particularly when the alloparent is related. Maestripieri (1994) argues however, that tolerance of infant handling is determined by the level of agonistic interaction the infant is likely to receive from potential alloparents, which is related to the social structure and relationships between females. In nepotistic or despotic species infant harassment is likely to be more common and therefore maternal restrictiveness greater (Maestripieri, 1994). Along with maternal restrictiveness, the number of adult females and therefore potential alloparents in a social group will affect the frequency of infant interactions as found with infant blue monkey socialisation (Förster & Cords, 2005). Finally, the level of feeding pressure on the social group is also relevant (Maestripieri, 1994; McKenna, 1979). With reduced intragroup feeding competition, the strength of the female dominance hierarchies declines, thus the risk of abuse during infant handling is reduced, such as is found in the Colobine and Cercopithecine social systems (McKenna, 1979).

5.1.3 Theories of alloparenting.

Theories as to why alloparenting occurs in some species and not others have been examined in a cross species comparison, which controls for phylogeny and allometry; Mitani and Watts (1997) found that alloparenting behaviour was most common in primate species with fast infant growth and short inter-birth intervals such as smaller Callitrichid species. In these species, alloparenting increases the reproductive success of the infant's mother, by allowing her extra time to feed or reduce energy expenditure through not carrying the infant (Mitani & Watts, 1997; Ross, 2003; Wright, 1990). In a further comparison of colobines and cercopithecines, Paul (1999) found that the carrying of young infants was common in egalitarian female dominance hierarchies as opposed to nepotistic or despotic hierarchies, where dominance is used to gain access to infants.

Alloparenting must have a beneficial effect on the alloparent, infant, or the mother to occur consistently within a species (Paul, 1999). The following discussion is limited to the motivation of non-reproductive immatures (NRIs) to interact with infants as opposed to adults; these NRIs are likely to have less infant knowledge and thus have more to gain in terms of experience through infant contact. The '*learning to mother hypothesis*' assumes that alloparents are generally of pre-reproductive age and typically nulliparous females, this is found in a number of species (vervet monkeys (Fairbanks, 2002; Lancaster, 1971); yellow baboons (Bentley-Condit et al., 2001); mantled howler monkeys (Clarke et al., 1998); black and white colobus (Brent et al., 2008); capped langurs (Kumar et al., 2005); white-faced capuchins (Manson, 1999); barbary macaques (Small, 1990) and Japanese macaques (Schino et al., 2003). Nulliparous female alloparents are found to be less likely to behave abusively towards infants compared to multiparous females (Maestripieri, 1994), but risks of infant injury are incurred by a mother who allows a inexperienced individual to have access to an infant (Maestripieri, 1999).

Much alloparental literature is focused upon the NRI as an instigator and/or a benefactor of infant interactions. The direct advantages of NRI-infant contact, in line with the *learning to mother hypothesis* are in broadening the NRI's innate motor skills specific for infant care and to practise maternal behaviour under the supervision of the infant's mother (Lancaster, 1971). A female with infant interaction experience is proposed to be more likely to care sufficiently for her own first offspring, heightening its chance of survival (Fairbanks, 2002; Förster & Cords, 2005; Lancaster, 1971; Small, 1990). Little research has found convincing evidence for the *learning to mother hypothesis* as NRI females must be monitored until the survival or death of their first offspring to determine its success. Infants, of course may survive or die for reasons than maternal care alone (e.g. infanticide, maternal physiological deficiencies or infant illness), making such assumptions difficult to interpret. However, where NRI females have been followed to adulthood in bonnet macaques (Paul, 1999) and howler monkeys, (Clarke et al., 1998), no evidence for increased survival of infants to alloparenting mothers was found. Infant handling during the pre-reproductive period had no effect on survival of first offspring. For example, in bonnet macaques where three out of ten primiparous mothers raised their first offspring, these three mothers had lower frequencies of infant handling during the pre-reproductive period compared to those whose first infants did not survive (Silk, 1999).

An alternative indirect alloparenting theory is the *inclusive fitness hypothesis*: an NRI who aids in the survival of an infant through alloparental interactions is predicted to be related to that infant, as aiding a close relative is beneficial to the NRI by promoting common genes into subsequent generations (Hamilton, 1964). This theory is supported by studies of howler monkeys (Clarke et al., 1998) and Japanese macaques (Schino et al., 2003.), where related alloparents were more common than non-related alloparents.

A third final theory is the *non-adaptive hypothesis*, which states that females are predominantly interested in infants as a by-product of being predisposed to care for infants (Manson, 1999). NRI females with a strong attraction to infants are perhaps more responsive to their needs from a young age and make better mothers (Silk, 1999). All infant interactions before parturition would, following this theory, be considered non-adaptive as they have no evolutionary function and no benefit is assumed by the alloparent (Manson, 1999; Silk, 1999).

Aside from the benefits accrued to the NRI as an alloparent, the costs and benefits of alloparenting to the infant are important considerations. The costs to the infant of infant handling may be considerable if abuse and negligence occur (Maestripieri, 1999), but alternatively, increased social stimulation and socialisation from a young age are likely to be beneficial for the development of infant social fitness and subsequent breeding success (Brent et al., 1997; Förster & Cords, 2005; Small, 1990). In species where infants receive regular alloparental care by other group members, empirical evidence shows that alloparental care in early infancy is positively correlated to postnatal growth rate, (Ross, 2003). Infant handling by other group members thus enables the infant to develop faster and allows the mother to resume oestrus cycling quicker.

For the potential alloparents, sex, age and relationship to the infant may have important consequences for the frequency and type of infant interactions. Nulliparous females' predominate alloparenting attempts in most primate species, but in Lemurid species primiparous female interact with infants, whereas in baboons and vervet monkeys, multiparous females alloparent (MacKinnon, 2007). Finally, in some cases pre-reproductive and adult males are also documented to alloparent, particularly co-operatively breeding primates, where the father has a high parental responsibility e.g. Goeldis monkeys (Porter, 2001). Infant interactions by males and specifically male NRIs are rare in the monkeys, but are documented to occur in adult male spider monkeys (Watt, 1994) and male NRI vervet monkeys (Fairbanks, 2002) but always to a lesser extent than females of comparable age and relationship. Species by species, alloparenting requires substantively more attention to understand the divergence of selection pressures that have led to varying patterns of non-parental infant care across the primate order

5.1.4 Alloparenting apes

Although a wealth of literature and theories exist, explaining alloparenting in monkeys, quantitative assessment of alloparenting in the apes is currently missing (except Nishida, 1983). Published studies of alloparenting apes are largely limited to anecdotal evidence, which, although informative is not conducive to understanding the evolutionary pressures determining the form and function of this behaviour across the ape species. Considering that the apes are closely related to humans, where alloparenting across cultures is profuse (Kennedy, 2005; Pope Edwards, 1993), understanding the occurrence and form of such behaviour has an important consideration for understanding the motivation of human alloparenting and its evolutionary origins (if any) from monkey alloparenting behaviour. The following section discusses what is known about alloparenting in the apes and the theories of alloparenting promoted from monkey studies.

The fact that the social living great apes (chimpanzees, bonobos and gorillas, with the exception of orang-utans (C. van Schaik, S. Cheney pers.comm.)) are documented to alloparent is contrary to the proposed models of alloparenting in the literature. Apes are not fast growing species, nor do they have short inter-birth intervals as is theorised to be a requirement of alloparenting species by Watts and Mitani (1997). In addition, apes are not purely egalitarian in their female relationships as is proposed by Paul (1999) to be necessary for alloparenting. However, from the limited reported evidence it seems that all apes are capable of alloparenting, or adopting another's young in exceptional circumstances. To date, quantified infant contact, comparable to the monkey literature is only apparent for two populations of wild chimpanzees (Nishida, 1983; Pusey, 1990) and two captive groups (Markus & Croft, 1995; Sommerfeld *et al.*, 1998), for one population of wild western gorillas (Nowell 2005), a population of wild mountain gorillas (A.W. Fletcher, unpubl data) and a population of wild bonobos (Enomoto, 1990). Although the behavioural understanding of orang-utans remains limited due to the smaller daily group sizes and less data collection effort in captivity and in the wild, alloparenting seems absent from this species to date (S. Cheney & C. van Schaik pers. comm.).

Chimpanzees in the wild live in a fission-fusion society, where the females migrate upon sexual maturity and males remain in their natal group (Rowe, 1996). Adult females within a social group are generally unrelated and may spend a substantial amount of time alone, foraging away from the social group, with their associated offspring (Otali & Gilchrist, 2006). Opportunities for alloparenting in the wild, by individuals other than full sibling are therefore limited to periods of social cohesion. Despite this, alloparenting interaction in captive and wild studies consisted of related and unrelated, male and female NRIs (Markus & Croft, 1995; Nishida, 1983; Sommerfeld et al., 1998). Nulliparous females were the most profuse alloparents in the wild (Pusey, 1990) and in captivity (Sommerfeld et al., 1998), which is proposed to support the 'learning to mother' hypothesis (Nishida, 1983). However, in captive studies access to infants was determined more by relatedness. Related alloparents gained more infant contact than non-relatives, and in the wild populations unrelated alloparents were more profuse in infant handling (Nishida, 1983; Sommerfeld et al., 1998). In both wild studies, attention towards infants by female alloparents waned towards adolescence (Nishida, 1983; Pusey, 1990), indicating an optimum period of infant attraction and associated learning. That juvenile male NRIs alloparent at all is contrary to the majority of monkey studies, where only females show interest in infants (Mitani & Watts, 1997). Potential paternal benefits for the male are considered an explanation for alloparenting; however, typically ape fathers have little infant contact and contribute only indirectly to their survival. Pusey (1990) however, predicts that building relationships with infants and their mothers is beneficial for young males who will remain in the natal group and seek breeding opportunities and alliances in the future.

A study of wild bonobos in a similar fission-fusion, female-migrating society found stark differences from that of the chimpanzee. Care was directed to infants by only adult and adolescent males and only recorded on twenty-eight occasions in a five month study (Enomoto, 1990). Alloparenting incorporated similar caring behaviour to that documented in chimpanzees, but also incorporated a sexual element, in which the infant participated positively. In captivity, bonobo affiliative and carrying behaviour were documented towards infants. Alloparenting occurred on a regular basis by male and female NRIs, towards half and full siblings across four captive groups, although quantitative data are not available (J. Stevens pers comm.).

Gorillas differ from both the *Pan* species and from the orang-utan in that they live in a polygynous social system, where both males and females may emigrate upon sexual maturity. Although only one small quantitative study of alloparenting exists for wild western gorillas (Nowell, 2005), alloparenting is also reported to occur in the mountain gorilla population (A. Fletcher pers. comm., Warren & Williamson, 2004; Watts & Pusey, 2002), but reports remain anecdotal at best. Within both species of gorilla, alloparenting occurs within the family group, where NRIs are likely to be at least paternal half siblings to the infant and of either sex. In the wild, western gorilla group, alloparenting occurred predominantly by nulliparous females although males were recorded to carry infants on occasion (Nowell, 2005). In the bai habitat, infants were more likely to initiate carrying by an NRI than the NRI initiating infant contact (Nowell, 2005), which may reflect the difficult bai environment that the infants are in whilst the adults feed.

Although data on alloparenting in the apes are limited, it is evident that alloparenting occurs where individuals other than the mother are in close proximity to infants, despite the species' social system. This may explain why orang-utans, who often live highly dispersed across the forest, are, so far, undocumented to alloparent in the wild, but may adopt infants in the captive environment (Becker, 1982). However, if proximity were a factor in alloparenting occurrence, it would be expected that the behaviour would be more commonly documented in captivity, where individuals are in closer proximity for longer than in the wild; so far this is inconclusive due to a lack of quantitative data. The specific motivation for alloparenting in ape species is likewise inconclusive; the studies reported here allude to the theories specific to explaining alloparenting in monkeys. However, whether these are acceptable for ape species that would be expected by phylogenetic analysis not to alloparent (Mitani & Watts, 1997; Paul, 1999) raises the question of whether the selection pressures and exhibited behaviour of ape and monkey alloparenting are comparable.

For an initial study of alloparenting behaviour, the captive environment allows the opportunity to quantify NRI interactions with infants in western gorillas, and to consider the effect of NRI age and sex. Zoos are advantageous for this study of behaviour as they constrain the physical environment, which limits the divergence of environmental stressors that could alter parenting of the infant (Rosenblum & Andrew, 1994).

The following chapter provides the first quantitative data on NRI-infant interactions for western gorillas and uses these data to discuss why alloparenting occurs in the apes.

5.2 Aims

- To investigate the social dynamics of infant interactions in NRI western gorillas.
- To investigate how maternal restrictiveness of the infant might affect infant interactions with NRIs.
- To consider current monkey alloparenting theories and their relevance to alloparenting in the apes.

5.3 Methods

NRI interactions with infants were collected by all occurrence sampling during regular focal sampling periods, the specific behavioural variables are listed in Appendix 4. Data were collected upon occurrence within a study subject regardless of the daily focal gorilla. For ease, all data were collected on a Dictaphone and transcribed into Microsoft Excel. Social play data referred to in the forthcoming analysis were taken from focal observations of the NRIs and were stated as median percentage of social play with infant(s) per NRI.

The data were analysed using non-parametric exact statistics as they were highly negatively skewed, non-normally distributed and sample size was small (Field, 2005), with median central tendencies reported throughout. Where statistical analyses were not possible due to limited data, descriptions of trends or percentage inferences were made. No extra consideration during analysis was made for Zurich Zoo where two infants were alloparented in the social group (c.f. one infant resided in each of the other groups). This decision was made based on the low frequency of interaction with either infant during data collection by any of the NRIs, but should be considered when interpreting the results.

Results

The frequency of NRI interactions with an infant is ultimately dependant upon three factors: - the motivation of the NRIs in the group, the restrictiveness of the mother and the willingness of the infant to engage with others. In this section it is addressed how NRI interactions differed between infants due to maternal protectiveness and varying motivation from the NRIs. The small number of infants in this study led to insufficient data to explore infant participation in alloparenting.

5.3.1 Maternal restrictiveness

At least one infant (under 3 years) was found in each of the five European zoos; in La Vallée des Singes and Zurich Zoo two infants were present (Table 5.1). Of these infants, 5/7 (71%) were carried or played with by NRIs. The infant at Basel Zoo and the infants from La Vallée des Singes were not carried by NRIs due to the mother restraining the infant from engagement, and thus analyses were conducted on the remaining five infants. All five infants had different mothers and all mothers were multiparous. Frequency of NRI-infant handling and NRI-infant play differed between NRIs, (handling; Kruskal Wallis; freq/hr $\chi^2 = 68.28$, d.f. = 3, $P < 0.001$; dur/hr $\chi^2 = 91.80$, d.f. = 3, $P < 0.001$; social play; freq/hr = $\chi^2 = 40.08$, d.f. = 4, $P < 0.001$; dur/hr $\chi^2 = 26.61$, d.f. = 4, $P < 0.001$).

Table 5.1 - Demographic information for each infant gorilla.

Infant name	Zoo	Mean age in months	Infant Sex	Interactions permitted by mother?	No. of NRIs in group	No. of full siblings
La	Apenheul Primate Park	7	♂	Yes	9	2
Ch	Basel Zoo	4	♀	No	3	0
Na	Burgers' Zoo	5	♀	Yes	4	1
Lm	La Vallée des Singes	10	♂	No	3	1
Sa	La Vallée des Singes	13	♂	Yes	3	1
En	Zurich Zoo	19	♀	Yes	3	1
Ey	Zurich Zoo	22	♂	Yes	3	1

Four out of five infants were carried by gorillas other than the mother. The behaviour of the infant's mother as the infant is carried away is a likely determinant the mother's tolerance and restrictiveness. La and Na were of a similar mean age (seven and five months respectively) during data collection and spent the majority of time in close proximity to their mothers. Na was taken directly from the mother more frequently than La, who was collected most frequently from the ground (Figure 5.1a). When a NRI approached the mother for access to the infant, the mother could refuse; Na was refused contact with NRIs on 16% of occasions, La on 21% of occasions. At Zurich Zoo, where both infants were over 18 months and thus more independent of the mother, they were always picked up from the ground (100%). In these cases, access to the infant from the mother was not maintained by NRIs and thus refusal of access to the infants did not occur.

Mothers retrieved their infant from the NRIs regularly (Figure 5.1b). The most frequent retrieval was observed from La's mother who retrieved him on 72% of occasions. The retrieval of La was immediate, from all NRIs and within a minute of contact initiation (median length = 0.12 seconds).

Conversely, Na's mother allowed her to be carried by NRIs, for variable periods, with bouts ranging from one minute to 39 minutes (median length = 3.43 seconds), but also retrieved on 37% occasions. At Zurich Zoo, infant retrieval rate was less than at other zoos (Ey 0%, En 6%), bouts range from 1-5 minutes (median length, En, 0.24, Ey, 0.11 seconds; Figure 5.2).

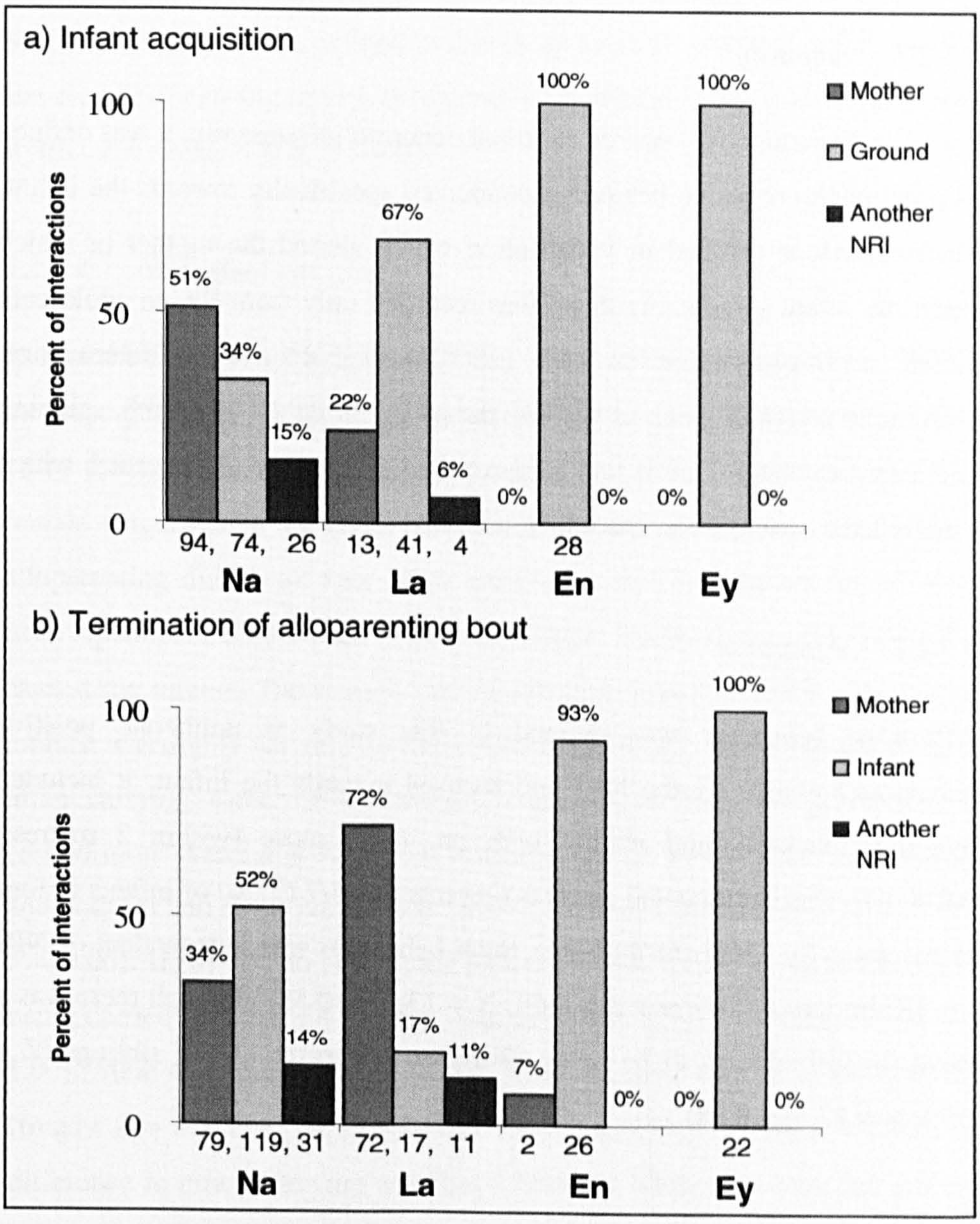


Figure 5.1 - Factors of infant carrying behaviour: a) Where the infant was acquired from and b) which gorilla terminated the alloparenting bout. Infants in descending age order. Numbers below x-axis = no. of bouts.

5.3.2 Infant interactions- affiliation, agonism, social play and carrying behaviour.

To discuss the relationship between NRIs and infants an investigation of agonistic and affiliative actions, play and infant carrying follows.

5.3.2.1 Agonism

Agonism from an NRI towards an infant occurred infrequently, it was defined as a deliberate negative behaviour conducted specifically towards the infant. Such behaviour resulted in vocalisation which alerted the mother or which made the infant scream. Agonism was recorded only from Sh, an adolescent female at Burgers' Zoo on 16% (20/123) of NRI - infant interactions. Unsuitable activities, such as holding the infant in the air by a limb, spinning and carrying the infant in an inappropriate manner were recorded which usually led to a scream by the infant and retrieval by the mother.

5.3.2.2 Affiliation

Affiliative behaviour was defined in this study as deliberate positive behaviour initiated by the NRI and focused towards the infant. It included hugging, touching, and resting with an infant close (within 2 metres). Affiliation was documented as occurring towards 5/7 (71%) of infants in four of the zoos, by 13/19 (68%) NRIs. Such behaviour was independent of NRI sex (Kolmogorov-Smirnov $Z = 0.68$, $N = 13$, $P = 0.53$) although there was a trend for full siblings to be more affiliative than paternal half siblings ($Z = 0.73$, $N = 13$, $P = 0.48$).

5.3.2.3 Social play

In four of the European zoos, social play between NRI gorillas and infants occurred; incorporating the same 5/7 (71%) infants. Ten out of 22, (45%) of the NRIs participated in social play with infants, ranging from 2 – 15% of the total social play recorded for a NRI. Social play with an infant was independent of NRI sex (play freq/hr, Z = -0.69, N = 19, *P* = 0.67), and relatedness (full siblings vs. paternal half siblings: play freq/hr, Z = -1.44, N = 19, *P* = 0.12). However, play initiation tended to be led by the NRIs as opposed to infants (Wilcoxon's Signed Ranks; Z = -2.93, N =11, *P* = <0.001), with the exception of the male infant Sa who initiated 68% social play bouts with NRIs. In addition, a gentle style of social play significantly dominated NRI - infant play bouts, defined in this study as being less energetic and with less chance of causing injury, as opposed to energetic (wrestle and chase) play styles (Z = -2.02, N = 5, *P* = 0.04).

5.3.2.4 NRI infant carrying

Across the five European groups, 11/22 (50%) NRIs carried infants. Within the three groups in which alloparenting by NRI was permitted by the mother, 11/16 (69%) NRIs carried infants, of which four NRIs were male and seven female (Figure 5.2). Of those who did not carry infants, in groups where alloparenting did occur, four NRIs were male and one female and all were from Apenheul Primate Park. All seven NRIs at Burgers' Zoo and Zurich Zoo carried the infants. The overall rate of carrying, based on NRIs who carried infants, was highly variable between NRIs (Figure 5.2). Comparing the rate of infant carrying; there was a non-significant trend for Na at Burgers Zoo to be carried more than La at Apenheul Primate Park (Z = -1.73, N = 8, *P* = 0.06) and both En and Ey at Zurich Zoo (Z = -2.14, N = 7, *P* = 0.06, Z -2.14, N = 7, *P* = 0.06). However, no significant difference was found in the frequency of being carried between En and Ey, both of Zurich Zoo (Z = -0.23, N = 6, *P* = 1.00). Male and female NRIs did not differ in their rate of infant carrying, (freq/hr Z = 0.5, N = 16, *P* = 0.96, dur/hr Z = 0.75, N = 16, *P* = 0.63). No difference in infant carrying was found between NRIs who were full siblings and paternal half siblings (freq/hr Z = 0.61, N = 16, *P* = 0.86, dur/hr Z = 0.607, N = 16, *P* = 0.86, Figure 5.2).

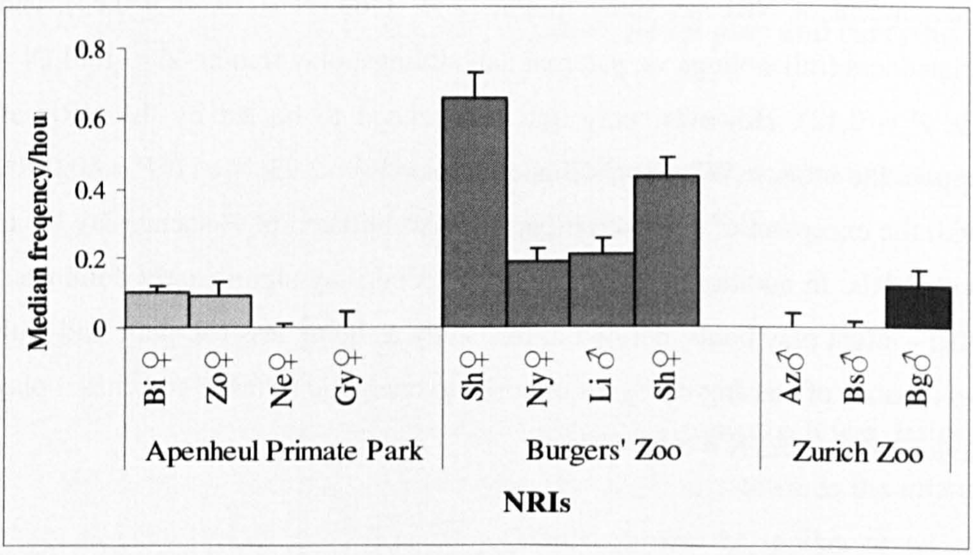


Figure 5.2 - Rate of infant carrying by NRIs at each zoo. NRIs in each zoo arranged in age descending order.

Age was also considered, for male NRI gorillas in the groups where alloparenting was permitted by the mother a significant decrease in alloparenting was found with NRI age (Spearman's Rho freq/hr, $\rho = -0.80$, N = 8, $P = 0.02$, dur/hr $\rho = -0.72$, N = 8, $P = 0.05$, Figure 5.3). For female NRI gorillas no significant decrease in infant carrying behaviour was found, even with the elimination of Sh (freq/hr $\rho = -0.68$, N = 7, $P = 0.09$, dur/hr -0.15, N = 7, $P = 0.75$, Figure 5.3). Of the five NRIs that did not carry, infants all were over six years of age and four out of five were males. The only frequent NRI carried over 6 years was Sh at Burgers' Zoo, who was eight years of age and who gave birth to a stillborn infant on 23rd December 2004.

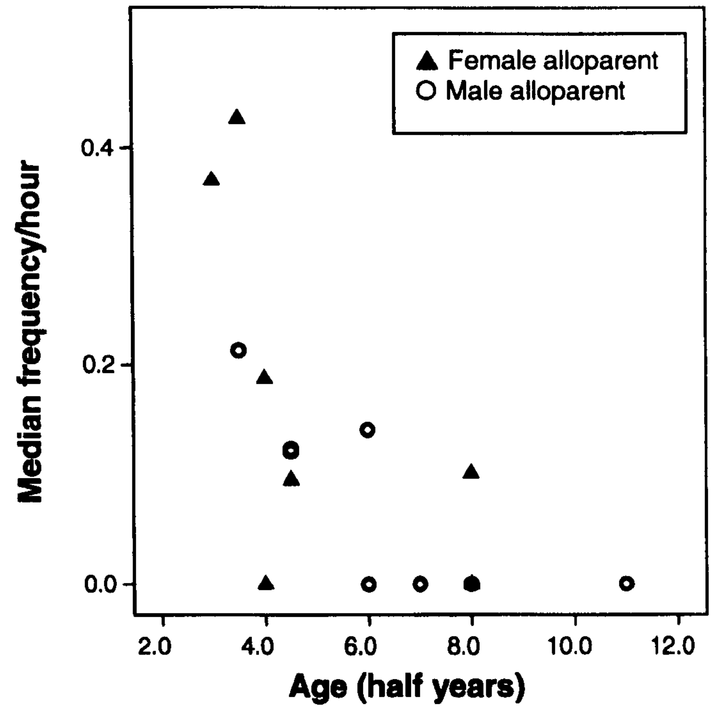


Figure 5.3 - The effect of alloparent age and sex on the frequency of infant carrying behaviour.

NRIs carried infants in either a ventral or a dorsal position. Of those who carried infants there was no significant difference in the median frequency or duration of carrying position (freq/hr $Z = -0.27$, $N = 11$, $P = 0.79$, dur/hr $Z = -0.45$, $N = 11$, $P = 0.66$. The method of infant carrying was not determined by NRI sex (males vs. females: dorsal; $Z = 0.97$, $N = 11$, $P = 0.31$, ventral; $Z = 1.20$, $N = 11$, $P = 0.11$ and was not related to NRI age (dorsal; $\rho = 0.19$, $N = 11$, $P = 0.57$, ventral; $\rho = -0.37$, $N = 11$, $P = 0.26$). The carrying method adopted by a NRI did not significantly differ between infants (dorsal; $\chi^2 = 5.80$, d.f. = 3, $P = 0.12$, ventral; $\chi^2 = 6.88$, d.f. = 3, $P = 0.76$, Figure 5.4), and the percentage of infant carrying with the infant in a dorsal position was not found to significantly increase with infant age ($\rho = 0.53$, $N = 11$, $P = 0.10$).

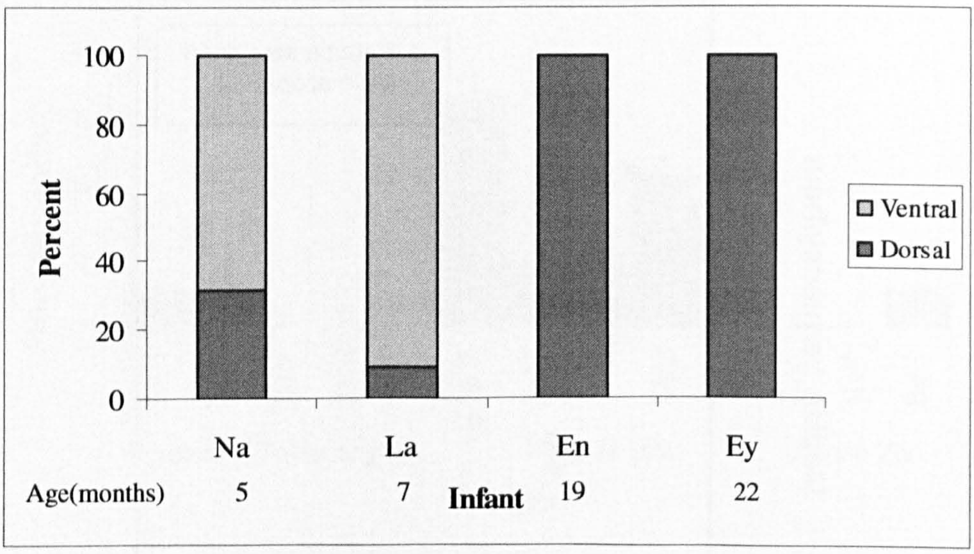


Figure 5.4 - Position of infant during transportation by NRI alloparents (freq/hr) for each infant by age.

Initiation to carry an infant came mainly from the NRI and not from the infant ($Z = -2.93$, $N = 11$, $P = 0.003$). In contrast, the termination of an alloparenting bout was determined by the infant or the infant's mother as opposed to the NRI (Friedman's Test $\chi^2 = 7.94$, d.f. = 2, $P = 0.02$). No significant difference in the frequency of infant-terminated bouts occurred between male and female alloparents ($Z = 1.20$, $N = 11$, $P = 0.11$), whereas a sex difference was found in the frequency of mother intervention, where female alloparents had the infant taken away more than males ($Z = 1.37$, $N = 11$, $P = 0.05$). The age of the alloparent did not significantly affect the rate of initiating infant contact ($\rho = -1.4$, $N = 11$, $P = 0.55$).

The type of interaction between NRI and infant during an infant carrying bout differed between infants. For each NRI the frequency of travelling, being stationary and social play with the infant during infant carrying was dependant upon the mother's restrictiveness. Travelling was the predominant behaviour of most NRIs, which moved the infant away from the mother. In this there was a significant difference in the frequency of NRI travelling during alloparenting between infants ($\chi^2 = 6.75$, d.f. = 2, $P = 0.03$). However, there was not a significant correlation between travel during alloparenting and rate of maternal retrieval ($\rho = 0.16$, $N = 11$, $P = 0.64$). Resting whilst holding the infant occurred only at Burgers Zoo, where the NRIs were mostly female; play behaviour occurred predominantly at Zurich Zoo, where the NRIs were all male and the infants older and more independent of the mother.

The relationship between NRIs and infants differed between the zoos (Figure 5.5). Play with the infant was the predominant behaviour of NRIs at Apenheul Primate Park and Bs at Zurich Zoo, whereas infant carrying predominated at Burgers' Zoo. At both La Vallée des Singes and Zurich Zoo affiliative behaviour towards infants occurred more than play or infant carrying behaviour.

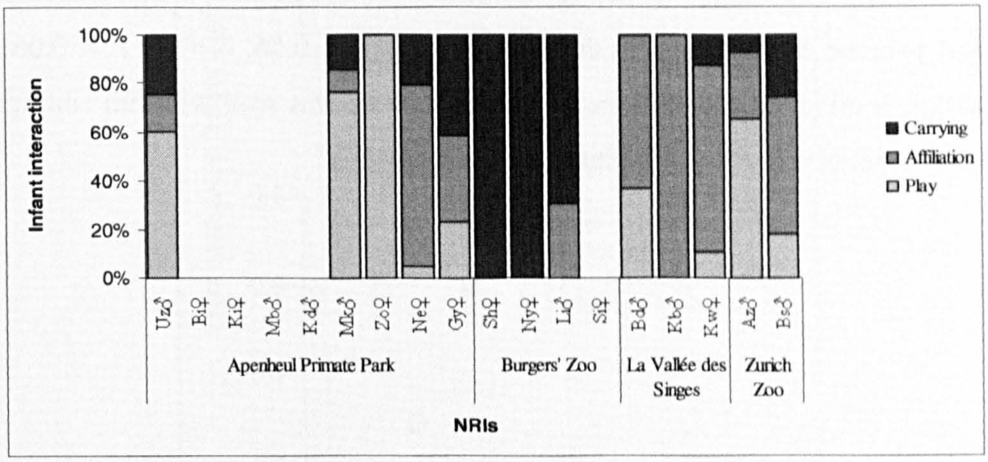


Figure 5.5 - Types of interactions (percent) with infants by each NRI, arranged by descending NRI age and by zoo.

5.3.3 Infant interactions – a synthesis

Finally, all infant interactions (social play, infant carrying, resting within two metres of an infant, hugging and touching an infant) recorded from NRIs towards infants were combined to calculate a median frequency of affiliative interactions/hour to gain an understanding of interaction and relationship change across pre-reproductive period. Of the 19 out of 22 NRIs living in groups where contact with infants was permitted, five (26%) had no recorded affiliative interaction with an infant. These five comprised of three adolescent males, a blackback male and a primiparous adult female, all from Apenheul Primate Park. All other NRIs had variable contact with the infant (Figure 5.5) although no significant difference between NRI - infant contact was found (χ^2 = 13, d.f. = 13, P = 0.48).

The relationship between infants and NRIs changed with age. Although no significant difference was found between male and female NRI in the frequency of affiliative interactions (Z = 0.62, N = 14, P = 0.84), the frequency of affiliation with infants showed a tendency to decline with NRI age (ρ = -0.47, N = 18, P = 0.05), a relationship found only with the exclusion of Sh (Figure 5.6a). With this exclusion, no NRI over seven years of age frequently interacted with an infant. In a similar way, paternal half sibling interaction with infants tended to decrease with age in infants with both full and paternal half siblings in the same group (ρ = -0.56, N= 12, P = 0.06), although no significant decline in infant relations was seen with full siblings (ρ = -0.36, N = 6, P = 0.48, Figure 5.6b).

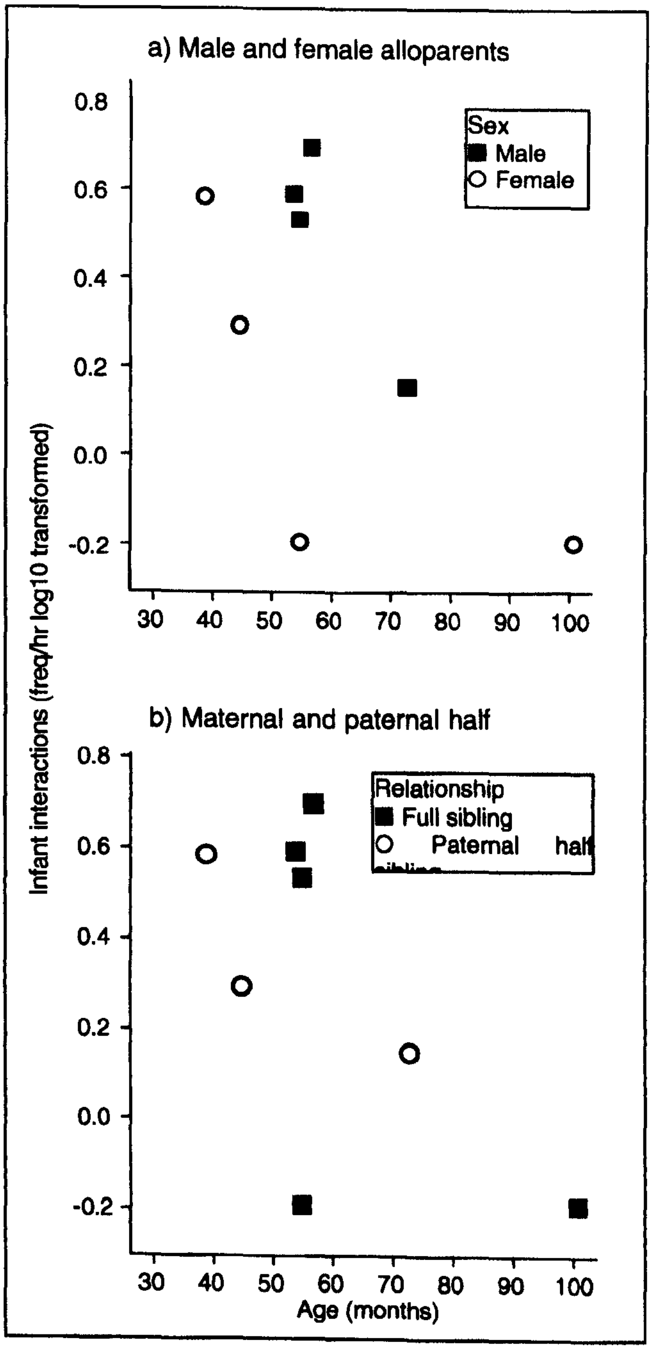


Figure 5.6 - A correlation between frequency of infant interactions and age with a) male and female alloparents, b) full sibling and paternal half sibling NRIs.

5.4 Discussion

5.4.1 Results summary

Interactions between NRIs and infants occurred in 5 out of 7 available infants. Mothers showed distinct variability in their restrictiveness (of their infants); in general, mothers retrieved infants from female NRIs more than male NRIs. Full siblings displayed no greater infant contact than paternal half siblings, regardless of their increased proximity to the infant through attachment to their mother. However, full siblings did retain contact with infants until later in maturity compared to paternal half siblings. Male NRIs exhibited less infant carrying behaviour with increasing age, whereas NRI females did not. NRI gorillas made contact with infants through affiliative interactions, including social play and infant carrying, the occurrence of which declined as NRI age increased. There was a tendency for adolescents and specifically adolescent males to have no infant contact. Agonism towards an infant was reported in only one NRI (Sh, Burgers' Zoo). Initiation of contact with an infant was generally NRI-led. Finally, in groups where more than one infant resided, no infant age or sex preference was found.

5.4.2 Assumed benefits of ape alloparenting to the NRI, the mother and the infant

NRIs drive alloparental interactions in the apes through their attraction and regular affiliative interactions with infants (Nishida, 1983; Nowell, 2005; Pusey, 1990; Sommerfeld et al., 1998, this study). In contrast, infants rarely initiate contact with NRIs (Nishida, 1983, this study), whereas ape mothers often permit alloparenting, but they do not actively pass the infant to the NRI (Enomoto, 1990; Nishida, 1983; Sommerfeld et al., 1998, this study). Since NRI primates predominantly engage in behaviour to promote their own development and survival (Janson & van Schaik, 2002; Rubenstein, 2002) the consistent attempts of NRIs to engage with infants in the apes encourages the assumption that there should be a benefit for NRI apes who alloparent, regardless of any additional benefits assumed by the mother or infant.

If ape alloparental behaviour occurs to benefit the infant, alloparental interactions would be predicted to be limited to the youngest infant in the group, or to infants under a year, who require more intensive care to survive. However, in chimpanzees and gorillas, it has been found that alloparental behaviour was not permitted by mothers until the infant was a minimum of four months in age and that alloparental behaviour did not in general occur for long periods of time (Nishida, 1983, this study). Thus, based on ape studies to date, there was no evidence for alloparenting occurring in such a way as to increase the chance of young infants surviving. If the sole purpose of ape alloparenting behaviour were to increase the socialisation of the infant, infant contact would be assumed to occur when the infants were developed sufficiently to benefit from conspecific interactions, which it is assumed an infant is after 4 months and begins leaving the mother (Nowell & Fletcher, 2007). In chimpanzees and gorillas, alloparenting occurred with all infants permitted to leave the mother, regardless of the infant's age (Nishida, 1983; Nowell, 2005; Sommerfeld et al., 1998, this study). Thus it cannot be dismissed that alloparenting aids the infant in socialisation with conspecifics.

Considering the large disparity in body size between mother and infant apes, the cost to the mother of carrying and providing nutrients for an infant is much lower than for smaller primate species, where paternal or conspecific infant carrying is presumed to reduce the energy requirement to raise the infant for the mother (Lee, 1997; Porter, 2001). It would not be expected therefore, that ape alloparents provide an essential benefit to the infant's mother, as was proposed in a comparative analysis of alloparenting in monkeys (Mitani & Watts, 1997). In line with this, infant interactions in wild chimpanzees generally occur during resting periods, where carrying and caring for the infant do not relieve the mother of the energetic costs of locomotion (Nishida, 1983), nor allow the mother to increase her time feeding, although equally, alloparenting may increase time available for her to rest. However, the infant being away from the mother may indeed increase the mother's costs if she is required to be extra vigilant or to retrieve the infants from alloparental interventions. Further studies of the role of the mother are necessary to understand the motivation of some mothers to allow alloparenting to occur in the apes. Considering that alloparenting must be beneficial to occur regularly within a species (Paul, 1999) and having found little evidence that NRI ape alloparenting provides a benefit to the mother or infant, the following discussion relates directly to the potential advantages assumed by NRI apes who alloparent.

5.4.3 Trends in ape alloparenting behaviour by NRI age, sex and relatedness

The benefits gained by alloparenting NRI apes can be understood by assessing the differences in infant care between NRIs. Male and female NRIs are expected to differ in the amount and type of care and contact with infants, reflecting divergent benefits of alloparenting for each sex. Since adult male apes engage in little direct care of infants (MacKinnon, 2007) they potentially require less skill development in carrying infants, but would benefit indirectly by being reactive to infant needs within the social group. Thus, interacting with infants, but not necessarily carrying infants is expected to be beneficial to males. Studies of chimpanzees, gorillas and anecdotal bonobo evidence support this, in that both males and females interacted with infants through affiliative gesture, carrying and social play (A.W. Fletcher, pers. comm., J. Stevens, pers. comm. Nishida, 1983; Nowell, 2005; Pusey, 1990; Sommerfeld et al., 1998). In chimpanzees however, females were found to transport infants significantly more than males (Nishida, 1983; Sommerfeld et al., 1998), whereas male chimpanzees more commonly engaged in hugging, pulling and wrestling behaviour (Nishida, 1983). Although in gorillas, no differences in carrying behaviour has been found between the sexes (Watts & Pusey, 2002, this study), the majority of NRI gorillas who did not handle infants were male in this study, which supports a disparity in the motivation to carry infants between the sexes in gorillas also. Since both sexes in the apes engaged in infant care and yet some evidence exists for disparity in infant interactions between the sexes, it is proposed that NRI apes develop skills necessary for their future disparate parenting roles, where for females; a more important skill is infant carrying.

In the apes, (except in wild orang-utans to date, where alloparenting is yet to be observed), NRI alloparental behaviour has been recorded from late infancy onwards, and found to be most profuse in juvenility and least in adolescence (Nishida, 1983; Nowell, 2005; Sommerfeld et al., 1998, this study). Juvenility is reported to be the period in which the NRI assimilates the effects of experience and generates expertise (Janson & van Schaik, 2002; Russon, 2003). During juvenility, whilst the individual remains small in size, experience-based learning, such as tool use and social play occur, in a non-competitive environment, where support from parents and allies is forthcoming (Janson & van Schaik, 2002). Infant care can also be classified as an experienced-based activity, where the practise of caring for infants has been proposed to lead to increased competency in both handling and infant association (Fairbanks, 2002) and occurs when the NRI is young. Adolescence however, is portrayed as a developmental period in which the NRI must consolidate previous learning to increase competence and develop sex-specific traits (Russon, 2003). Males, therefore, with little future parental responsibility would be expected to engage in behaviour that would be more useful for future agonistic contests and securing female consorts, whereas females may consolidate experiences that enable them to raise their offspring successfully. Indeed in the apes, this seems to be the case, as adolescent female chimpanzee and gorillas continue to engage with infants in adolescence (Nishida, 1983; Nowell, 2005; Pusey, 1990, this study) to an extent, whereas adolescent male-infant contact becomes highly irregular.

Finally, differences in alloparenting behaviour between full siblings and non-full siblings are proposed to reflect a propensity to either increase own inclusive fitness through aiding the survival of an infant who shares common genes (Hamilton, 1964), or through association with the mother, which leads to increased time in contact with maternal compared to non-maternal infants (Chapais, 2001). In the apes, alloparenting has been reported to occur in full and paternal half siblings, and in chimpanzees by unrelated NRI conspecifics (Nishida, 1983; Nowell, 2005; Pusey, 1990; Sommerfeld et al., 1998). In chimpanzees however, full siblings spent more time in contact with infants than paternal half siblings (Nishida, 1983; Pusey, 1990; Sommerfeld et al., 1998), which has not been supported by gorilla or bonobo studies to date. It is proposed that in the apes, NRI-infant interactions occur when the opportunity arises and full siblings have more opportunity to make contact with infants due to their close proximity to the mother than non-siblings do.

Infant contact and specifically infant handling behaviour can only be engaged in with younger infants regularly or for prolonged periods with younger and older infants when the infant's mothers allows. Although the amount of non-essential care by alloparents is hard to determine, mothers have been seen in this study to actively engage in how, when and with whom infant contact occurs. Gorilla mothers prevented infants from being carried away by some alloparents more than other alloparents and retrieved infants from female more than from male NRIs. Although further studies would be necessary to show why this is, it may be interpreted as an effect of female NRIs taking further away from the mother more frequently, whereas male NRIs often remained close to the mother with the infant. In chimpanzees however, NRI alloparents returned the infant to the mother for suckling when the infant cried (Nishida, 1983) and through this behaviour likely reinforced the mother and increased the likelihood of future alloparenting interactions. In other primate species, maternal restrictiveness of infants was related to the mothers' temperament, social rank and parity (Fairbanks, 1996; Hooley & Simpson, 1981; Schino et al., 2003). Although differences in maternal restrictiveness were observed in this study, further research in the apes is required in order to determine such effects on NRI alloparental behaviour.

5.4.4 Determining the function of alloparental care in gorillas and chimpanzees

Contrary to the findings of the comparative analyses of Mitani and Watts (1997) and Paul (1999), alloparenting was found to occur in the apes, where infants are slow growing, inter-birth intervals are longer than in most other primates and alloparents are presumed to be lower ranking that the infant's mother in most cases. The following discussion focuses on chimpanzees and gorillas, as quantitative data on bonobo and orang-utan NRI alloparenting are not available to date. Findings compiled from gorillas and chimpanzees in the wild and in captivity support the idea that NRIs alloparent to develop motor and social skills, which are considered advantageous in adulthood. Engaging with infants allows an understanding of the behaviour of infants, whereas, infant carrying allows the development of an appropriate carrying position specific to the infants age, and increased confidence in carrying the infant over long distances. The development of these skills in the pre-reproductive period is proposed in monkeys to assist females with maternal skills, which increase the chance of her first infant surviving (Lancaster, 1971), and to promote a gentle dispensation between ape fathers and their infants (Pusey, 1990). This theory is supported by findings in chimpanzees (Pusey, 1990; Spijkerman *et al.*, 1997), which indicate that alloparenting occurs most frequently in the juvenile period. During this life-stage, other experience-based learning is profuse. To date however, no ape studies are able to determine the success of alloparenting females in raising their first offspring, compared to those who did not alloparent, or to quantify paternal behaviour between males who did and did not have alloparenting experiences. Nor do the current ape studies quantify increasing competency of alloparenting skills in NRIs. Detailed quantitative ape studies providing answers to these questions are necessary to provide further support for the *learning to mother hypothesis,* or perhaps in this study the learning to parent hypothesis.

The *non-adaptive hypothesis* in which alloparenting behaviour is predicted to be a pre-adapted behaviour specific to females are predisposed to care for infants (Manson, 1999) predicts that alloparental care should be a female only behaviour and be apparent consistently throughout the pre-reproductive period and until the birth of her own first offspring. Little evidence from chimpanzee and gorilla studies provides support for the non-adaptive hypothesis of alloparenting. Male and female NRI chimpanzees and gorillas alloparent despite the reduced parental responsibility of adult males and that alloparental behaviour in females often ceased before sexual maturation (Markus & Croft, 1995; Nishida, 1983, this study).

Likewise, testing the *inclusive fitness hypothesis*; both full and half chimpanzee and gorilla siblings were found to engage in affiliative alloparental care with available infants of all ages. This does support the *inclusive fitness hypothesis*, in which closely related NRIs are expected to aid infants to increase their chance of survival, which benefits the NRI through the propagation of common genes into the population (Hamilton, 1964). However, with no longitudinal studies of ape alloparenting available, it is not possible to detect if infant care continues until the infant reaches juvenility and independence, nor indeed how alloparent-infant relationships change over time. Another important consideration is the effect of social system upon alloparenting interactions. In chimpanzees for example, where mothers and associated infants fission away from the social group, full sibling interactions with infants were found to be more profuse (Nishida, 1983). In gorillas however, all NRIs are reasonably closely associated for the majority of their pre-reproductive period, alloparenting with both full and paternal half siblings is documented, supporting the idea that familiarity of the mother to the NRI may be a factor, or simply proximity to the infant. From this therefore, is it difficult to ascertain if relatedness or familiarity influence the time a NRI spends in alloparental behaviour across development, particularly with this data set, which is limited by group size and infant availability. Studies of alloparenting in wild gorillas, where relatedness and time spent in close proximity is less than in the captive environment may shed light on this question.

It is considered likely that interactions with conspecifics across the infant period will increase the competency of those individuals to engage appropriately with older NRIs. Lack of socialisation appears to have the opposite effect; infant chimpanzees raised with only the mother show inappropriate reactions to social interactions from older NRIs when introduced into peer groups (Bloomsmith et al., 2006). In wild bonobos, alloparenting was explained as being a socialisation activity of adult or adolescent males, who engage predominantly in socio-sexual behaviour with infants to encourage the facilitation of species-specific social repertoires

(Enomoto, 1990). Similar may be true for chimpanzees and gorillas in terms of building familiarity and encouraging interaction with conspecifics. The infant benefits through the development of social fitness which can potentially increase future breeding success (Brent et al., 1997; Förster & Cords, 2005).

5.5 Conclusion

Gorillas and chimpanzees show several similarities in alloparental behaviour, which are not apparent in the other apes to date. Current data on alloparenting in chimpanzees and gorillas supports the *learning to 'parent' hypothesis*, where male and female NRIs assume the benefit of social and motor development through carrying and caring for an infant. Although infants are not handled to promote their socialisation, it is likely that infants do benefit from developing relationships with other group conspecifics from a young age. Alloparenting is mediated by the infant's mother, who affects the frequency and duration of interactions; understanding the benefits gained by the mother from allowing alloparenting requires more research effort in all the apes. Infant interactions in the apes to date are comparable to those proposed for monkey species, allowing the application of monkey alloparenting theory to the apes.

Chapter 6

6 EVIDENCE FOR THE NEURAL HYPOTHESIS OF SOCIAL PLAY BEHAVIOUR IN CAPTIVE WESTERN GORILLAS

In this chapter, three hypotheses, which have been proposed to explain the function of social play, are assessed using NRI (non-reproductive individual) play partner preference. Following this, the sequential pattems of social play elements are analysed to assess the potential functional differences in social play of NRIs in the older and younger life-stages.

6.1 Introduction

Animals that have evolved a degree of phenotypic plasticity can modify their behaviour to the changing environment (Stears, 1992). Across evolutionary time this potentially allows them a selective advantage that may increase their chance of survival and increase the number of progeny they produce (Hamilton, 1964). Plasticity is demonstrated to be adaptive in changing environmental conditions and is found to correlate with species-specific life history variables, for example, the influence of infant body mass at birth and at weaning is often dependant upon social group structure (Lee & Kappeler, 2003). However, plasticity is generally less well understood in animals with a long life history and particularly during the pre-reproductive period (Pereira, 2002; Rubenstein, 2002).

In long-lived species, who invest time in growth and delay reproduction for several years, it is expected that a degree of plasticity would be selected for in the pre-reproductive period, to increase the chance of an individual surviving to reproductive age and subsequently to maximise its breeding potential (Rubenstein, 2002). Therefore, mechanisms which potentially increase the development of spontaneous behaviour and which might lead to innovative problem solving or competency in the environment should be selected for within a species.

In primates, the long pre-reproductive period (Janson & van Schaik, 2002) is well documented as a period of cognitive development which leads to progressive social skill and motor enhancement (Pereira, 2002). The pre-reproductive period is thus a period where the role of experience can provide distinct fitness advantages to the individual. Experience can be gained through actual social or environmental interactions and through the simulation of social or environmental interactions through play behaviour.

Play behaviour is found in all primate species and can be defined as postnatal locomotion activity, which appears to have no obvious or immediate benefit to the individual (Burghardt, 2005). Motor patterns can be observed which resemble those found in a functional context but are generally displayed in a modified manner (Bekoff & Byers, 1998). In essence, play resembles species-specific behaviour, but lacks consequence, in that the roles of play partners can be reversed, movements can be exaggerated, repeated and jumbled in sequence and socio-sexual behaviour may be incorporated, although the players are not sexually mature (Bateson, 2005; Burghardt, 2005). Play can be categorised into four different types; *social*, involving other individuals (Lewis, 2005); *object*, incorporating an object into the play bout (Ramsey & McGrew, 2005); *solo*, consisting of sporadic movement such as tumbling and spinning. Finally *fantasy* play, using pretence and imagination to construct adult social situations, is common in children (Smith, 2005) but only minimal support is found for non-human primates and only for the apes (Gomez & Martin-Andrade, 2005).

For the purpose of this chapter, social play will be focussed upon, as social play is the most common form of play in the juvenile and adolescent periods and is presumed to be the most cognitively demanding (Lewis, 2005). This is due to an element of social interaction that is necessary to engage with others, which requires an understanding of the social environment. This understanding of social interactions may emerge in late infancy and progress in complexity across the pre-reproductive period. Social play is also the most relevant type of play to aid our understanding of social development across the pre-reproductive period, as cognitive and social skill are necessary and include paying attention to the partner and the need to react with speed, accuracy and in an appropriate manner for play behaviour to continue (Lewis, 2005; Spinka et al., 2001).

Social play in primates occurs from infancy, peaks in juvenility and then declines until maturation (Burghardt, 2005; Fairbanks, 2002; Lewis, 2005; Smith & Pellegrini, 2005). Social play forms a major component of the daily time budget with the average play allocation for NRI apes (independent of life-stage) being 14% and monkeys 8% (Lewis, 2005). Social play is constructed from multiple different play elements (e.g. chase, gentle play, display, rest, wrestle, spar, solicitation), all of which are distinctly different in form and easily identifiable, which may indicate different evolutionary functions (Bateson, 2005; Fry, 2005). The elements of social play are common and identifiable across the apes (human and non-human, (Pellegrini, 2002)), each is predicted to be functional, in that it would not have evolved unless it contributed towards survival and reproductive success (Fry, 2005). However, the function of each individual element of social play may not be indicative of social play in general (Bateson, 2005). Chase behaviour, for example has been suggested to enable practise of the flight response (Byers, 1998); wrestle and spar behaviour are often depicted as behaviour to develop fighting skill (Fagen, 2002) and resting behaviour as a mechanism to stop play escalating into fighting and to allow an assimilation of the competitive ability of the play partner (Hayaki, 1985). Thus, a disparity in preferred play partners is predicted, where behaviour aids the development of specific competitive skills, i.e. wrestle, spar, would be more likely to occur with older NRIs dyads than with similar-sized NRI dyads where possible. However, behaviour, which does not develop competitive skill, would be more likely to occur with same-sized partners as determined above. To date, the function of these individual play elements has received little attention in the published literature.

Reliable patterns of play-peaks and time investment occur alongside specific periods of brain formation and development in primates. Those primates with a greater capacity to deal with social relations, through the evolution of a relatively larger neo-cortex, engage in greater amounts of social play than those with a relatively smaller neo-cortex (Lewis, 2000). Byers & Walker (1995) also found that a peak in social play occurs both at the time of cerebellum differentiation, which modifies synapse formation and selective retention, controlling motor movement; and towards the end of muscle differentiation, where high levels of play behaviour are expected to influence muscular and motor neurone development for the rest of the individual's lifetime.

The progressive development of motor skills in the pre-reproductive period is supported by Willingham (1999), who determined that with practise (i.e. through play) motor skill learning could increase the spatial and temporal accuracy of movement. The cerebellum however, may also be important in the development of cognitive skills, as not only do cognitive and motor development reflect the same trajectory across development; beginning early in infancy and ending towards maturity but, if cognitive development is perturbed, motor development can be affected (Diamond, 2000). A co-evolved association is proposed to explain this relationship between the cerebellum and social play, which would suggest a role for the cerebellum in both motor and cognitive development (Lewis & Barton, 2004). Growth in other brain areas also reflects play patterns in primates, the size of the amygalda and the hypothalamus, which are involved in emotional development and interpreting signals from the environment, significantly correlate play frequency in primates (Lewis & Barton, 2006). It may be that these brain areas are also involved in social play development, for example interpreting play signals and determining intention to play (Lewis & Barton, 2004). The amygalda is affected by gonadal hormone secretion in adolescence, which may explain the reduction in social play behaviour towards maturity (Lewis & Barton, 2006). In summary, social play behaviour peaks at juvenility, a period of increased independence and maximum plasticity and during a period when the cerebellum, neo-cortex, hypothalamus and amygalda are developing and potentially can incorporate experience into neurological development (Fairbanks, 2000; Lewis & Barton, 2006)

6.1.1 Adaptive function and associated benefits of social play

Since social play is apparent throughout the pre-reproductive period in primates, it is expected to be functionally adapted (Bateson, 2005). The proposed function and assumed benefits of social play fall into two categories: a) where the benefits of social play are immediate to the individual, and b) where benefits are gained in the future. Those who predict that play is for an immediate benefit, propose the pre-reproductive period as a precarious period with specific ecological and social demands which must be met through engaging with the social group and with the environment (Burghardt, 2005; Spinka et al., 2001). Conversely, a delayed benefit seeks to prepare the NRI to reach reproductive potential in adulthood (Burghardt, 2005; Fairbanks, 2000).

Two theories, which predict an ***immediate benefit*** to the individuals, are introduced. The *Theory of Skill Development*, predicts that play in the pre-reproductive period is functional in the acquisition of skills (Fagen, 2002; Fairbanks, 2002; Lewis, 2000). Within this theory the constant practise of skills during the pre-reproductive period conveys the immediate advantages of being able to assess one's own strength compared to others, to receive feedback as to the consequences of actions, to develop communicative ability and to build relationships (Fairbanks, 2002) or to practise species typical behaviour (Fagen, 2002). Support for this theory comes from the fact that all types of play are engaged in across the pre-reproductive period by all NRI primates, regardless of the future roles of males and females. For example, females engage in wrestle behaviour, although in adulthood they do not fight for mates as males do (Fairbanks, 2002).

The second theory, *Training for the Unexpected*, applies to all mammals and predicts that play has evolved as a mechanism to promote training in the environment whereby, losing physical control gives the physiological system experience of improvising in atypical co-ordination of movements (Spinka et al., 2001). This is predicted to be advantageous in predator avoidance, fighting behaviour or in general locomotion. Training for unexpected incidents also gives the individual the cognitive experience of being disorientated and coping with loss of control in potentially dangerous situations, in effect, preparing the sympathetic nervous system for the flight response (Spinka et al., 2001). The assumed benefit of increasing motor co-ordination during unexpected situations is to increase the chance of surviving unexpected events, whereby those without the opportunity to play in the pre-reproductive period are most likely to succumb to accidental death or predation (Spinka et al., 2001). Evidence is provided by the nature of all play behaviour, which may be haphazard and thus more likely to lead to unexpected events, in the form of physical falls, losing control of an object or engaging with others at high speed to reduce the accuracy of engagement (Spinka et al., 2001). However, it has been shown that whilst engaging in social play, NRIs are less vigilant to potential predators, which counteracts the intuitive theory of being preparing for the unexpected (de Oliveira *et al.*, 2003; Fagen, 2002) relying on the protection from the social group, whilst training.

The potential ***delayed benefits*** of social play are explained through the *Neural Hypothesis*, whereby the timing of social play coincides with physiological and developmental systems and maximum plasticity, which together develop to enable the individual to construct the skills necessary to ensure breeding success and survival in adulthood (Fairbanks, 2000). Support for this theory is provided by the fact that the timing of social play is inconsistent with its proposed immediate benefits. For example, play-fighting behaviour, which is proposed to be necessary for males to develop effective fighting skills should not decline in adolescent apes, years before it is needed in adulthood (Byers & Walker, 1995); continued practise of fighting skills would be predicted if play fighting had benefits to the individual in adulthood. In further support of this hypothesis, social play coincides with neurological development (Lewis & Barton, 2004, 2006), which may prime the nervous system to accommodate species-specific behaviour and through the repetition of ordered sequences may lead to the development of understanding social engagement with others (Fairbanks, 2002).

The proposed functions and assumed benefits of social play behaviour across the literature span both motor and cognitive development, but are extremely difficult to find evidence for in a quantitative or experimental manner (Burghardt, 2005). The main confounding factor is that primates engage in motor and social interactions in and out of social play, which cannot be separated, thus the benefits alluded to social play could equally be gained through regular locomotion and social interactions (Brown, 1988). The difficulties in finding evidence to support the functional hypotheses of social play are due to the fact that both immediate and future advantages may be achieved from the same behaviour. For example, an immediate benefit of social play may be survival across the pre-reproductive period, brought about through increased competence in the environment (Fagen, 2002; Lewis, 2000), but the development of these skills - which are still apparent in the behavioural repertoire of adults - may also contribute towards survival in adulthood. Likewise, in relationship formation, an immediate benefit to a NRI may be incurred through development of communicative ability (Fairbanks, 2002), but the relationships formed with individuals may result in allies in the future or allow the development of adult behaviour. Future benefits assumed from social play may further be dependant upon the species' social system, in terms of the likelihood of individual emigration, and the individual's rank in the social group, with regard to the need for allies. Thus, providing unequivocal support for a theory of social play is problematic. Longitudinal studies of individuals across the pre-reproductive period and into adulthood are necessary to understand whether the beneficial aspects of social play, pertained to in the literature are reliably found in populations.

No matter the function, engaging in social play has obvious costs in terms of energy consumption, potential risk of injury and predation (Fagen, 2002; Janson & van Schaik, 2002). Seemingly, there is a critical period for the spontaneous emersion of social play behaviour, as individuals kept in isolation during late infancy/early juvenility may never play when merged into a social group (Lewis, 2005). Further to this, play behaviour in general does not occur under physical or psychological stress (reviewed by, Fagen, 2002). However, primates who do not play in the pre-reproductive period reach adulthood with the same behavioural repertoire as other group members (Bateson, 2005). This indicates that social play is not imperative for normal social development, although non-playing individuals are often found to be less flexible in response to competitive or unexpected situations and may respond to social group members with unnecessary aggression (Bateson, 2005; Bloomsmith et al., 1994). Thus, advantages are assumed by engaging in social play across the pre-reproductive period.

Even within a species, social play behaviour may differ by age and sex of the individuals involved, for example, female vervet monkeys, galagos, gorillas and human children of all cultures engage in less wrestling behaviour than males (Burghardt, 2005; Fairbanks, 2002; Fry, 2005; Gosso *et al.*, 2005). Also, some species may prefer to play with siblings over non-siblings (Markus & Croft, 1995) same sex or opposite sex partners (Burghardt, 2005; Watts & Pusey, 2002). Such differences are likely to be explained by the species' social system and the development of adult roles for each sex and not because of the adaptive function of social play per se, as all individuals will engage in social play behaviour across the pre-reproductive period. Hypotheses relating to such species-specific adaptations which alter the dynamics of social play behaviour without affecting the overall function of social play are referred to as *Social Relationship Hypotheses* (Fairbanks, 2002).

It is likely that play behaviour evolved in a common mammalian ancestor (Burghardt, 2005). The benefits of social play are paramount in human and non-human primates today, thus enabling social play to be stable in form across the primate order. Social play behaviour is found to be similar across the great apes in terms of the elements of social play identified and age and sex differences across species. Some discontinuities in social play between species are found however, concerning the engagement of parents within play, where human and bonobo parents engage in social play with kin, but gorillas and chimpanzee parents rarely do beyond infancy (Enomoto, 1990;

Smith, 2005; Watts & Pusey, 2002) and how social play may function within cultural transmission (Smith & Pellegrini, 2005).

The aim of this chapter is firstly to be able to draw support for and against the functional theories of social play using the trajectory of social play behaviour across the pre-reproductive period in captive western gorillas. Secondly, this chapter will determine if individual elements of social play differ in use, sequence and consequence as an indication of their individual function. The function of social play can be assessed from reliable, measurable similarities across closely related species, which may include the trajectory of social play by age, sex, relatedness or by play partner. Preferred play partners indicate the advantages assumed through social play and for each social play hypothesis, predicted outcomes can be proposed. To provide support for the *Skill Development Theory* it is proposed that younger NRIs gorillas should show a distinct preference to engage in social play behaviour with older NRIs, from which to learn specific skills. For the *Training for the Unexpected Hypothesis* it would be expected that NRIs show no preference in play partners, instead taking any opportunity to engage in play, thus maximising the number of unexpected experiences across the pre-reproductive period. Finally, for the *Neural Hypothesis*, NRIs would be expected to engage in social play with same-sized partners to reduce the risk of injury to the developing systems, whilst regularly practising necessary motor movements during periods of cerebral synaptogenesis and muscle fibre differentiation.

Social play behaviour in NRI gorillas is likely to differ from the other apes, due to the polygynous social system in which they live in contrast to chimpanzees for example who, in a fission fusion society spend less time with like-aged peers compared to gorillas. Social play behaviour should also differ between males and females with regards to who they play with, and the elements of social play, which enable the individuals to develop sex-specific traits as determined by the *Social-Relationship Hypothesis*. For gorillas, it is predicted that males, who must compete against other males for access to breeding females are more likely to play to develop fighting skills with males as opposed to females (Maestripieri & Ross, 2002). Females however, emigrate from the natal group at sexual maturity and unlike many other primate females, may not continue relationships with related females across adulthood (Watts, 2001), to the extent that adult female relationships can be described as agonistic in wild western gorillas (Doran-Sheehy & Lodwick, 2005). It is predicted therefore, that female NRIs should also engage more in social play with males, since in adulthood female relationship with the silverback form the basis of the gorilla social group (Watts, 2001)

6.2 Aims

- To compare the *Neural Hypothesis, Skill Development Hypothesis* and *Training for the Unexpected Hypothesis* to:
    i. Investigate the function of social play behaviour in captive western gorillas.
    ii. Investigate the sequence of social play elements across the pre-reproductive period in captive western gorillas.

- To determine if the social-relationship hypothesis explains the sex and age differences in social play behaviour and play-partner preference in captive western gorillas.

6.3 Methods

6.3.1 Trends in social play behaviour and play partners

Social play is reportedly a combination of specific behaviours in apes and humans (Bateson, 2005; Fry, 2005). The individual elements of social play: chase, gentle, rest, spar, and wrestle, are easily distinguishable in gorillas and are defined in Table 2.4. Analysis of individual elements of social play enables a through investigation of their individual and collective occurrence and function within social play.

The data were standardised to median durations per hour (or frequency per hour for spar behaviour) and analysed using non-parametric statistics or one-way ANOVAs. ANOVAs were used, as they are robust to violations in the distribution of data (Field, 2005). The homogeneity of data variance was checked using the Levene's test and if violated, corrected by reporting the adjusted Welch F. *Post hoc* comparisons were conducted using the Bonferroni test as these were suitable on small data sets and robust to type one errors (Field, 2005). Reported throughout the chapter, exact tests were run; these are appropriate when sample sizes are small and deviations in the distributions of data occur (Field, 2005). In the analysis of partner preference, all available focal individuals who met the criteria of the analysis were included as focal individuals and as partners.

6.3.2 Determining the function of social play

NRIs incorporated into these analyses all lived in social groups where it was possible for them to engage in play behaviour with both a NRI in the younger life-stages (old infant and juvenile) and a NRI in the older life-stages (adolescent male, adult female, or blackback). This enabled an investigation into social play between similar sized partners and social play with partners of disparate size, when a choice of partner was found.

This chapter focuses upon the elements of gentle, chase, rest, spar and wrestle, omitting solicitations and display behaviour. Solicitation is omitted as it does not always lead to social play and social play can occur without solicitation, particularly in older NRIs (Lewis, 2005), thus it does not predictably occur and when it does, it does not lead into social play with certainty. Similarly, display behaviour, which for gorillas were recorded to occur in and out of social play behaviour, and may be used as a signal of intent to continue engagement in social play but may be used outside of the play context (Payne & Pagel, 1997), but is also omitted from analysis and discussion.

To determine the function of social play, the data sets were converted into categorical data, where each potential NRI dyad was recorded to engage in the specific element of social play, or not. Gorillas were categorised as playing together if they had been observed to engage in the play element on more than one occasion during focal data collection. This measure was taken to ensure that play was intended between a dyad, and occurred reliably. Categorising the data was considered the most appropriate way to determine the occurrence of play partners for each element of social play considering that play between some NRIs may be more sporadic compared to others due to NRI age and differences in social group size. For example, NRIs with a large number of play partners in a social group were likely to play with less favourable partners on fewer occasions than if they lived in a smaller social group with fewer potential partners. In such cases, the formulation of a median value would have resulted in a zero value indicating the absence of play between those partners. The categorical data were analysed using log linear analysis and Chi^2 as appropriate, reporting Likelihood ratios as they were considered more robust for explaining phenomenon within small group sizes (Field, 2005). To determine the extent of significant interactions in 2 x 2 contingency tables, the odds ratio was reported, which gives a clear indication of the effect size detected and protects from the effects of inter-subject variability when categorical observations are collected from multiple members of several groups (Bakeman & Gottman, 1997). The calculation for the odds ratio is shown in equation 6.1, using the example of chase play in younger NRI dyads.

$$\textbf{a)}\ \text{Odds ratio} = \frac{\text{Odds}_{(\text{chase with younger NRIs})}}{\text{Odds}_{(\text{chase with older NRIs})}}$$

$$\textbf{b)}\ \text{Odds}_{(\text{chase with younger NRIs})} = \frac{\text{No. of younger NRI dyads who chase}}{\text{No. of younger NRI dyads who do not chase}}$$

$$\textbf{c)}\ \text{Odds}_{(\text{chase with older NRIs})} = \frac{\text{No. of older NRI dyads who chase}}{\text{No. of older NRI dyads who do not chase}}$$

Equation 6.1 - Odds ratio test calculation

The individual elements of social play were examined (chase, gentle, spar, rest, wrestle). It was predicted that wrestle, chase, spar and gentle play occurred for a specific reason within social play, as they are repeatedly reported behaviour across the ape literature (Enomoto, 1990; Fletcher, 1994; Nowell, 2005; Watts & Pusey, 2002) and were recorded within play bouts of all captive western gorillas in this study. However, it is proposed that the function of each play element may change across the pre-reproductive period as social play occurrence declines and that the purpose of social play behaviour in general may alter to meet the demands of a maturing NRI. A further analysis assessed the recurring pattern of social play bouts in younger and older NRIs to predict which social play elements significantly led onto more social play and of those, which social play elements should precede (or follow if any).

6.4 Results

6.4.1 Trends in social play behaviour across the pre-reproductive period

Overall, the time spent engaging in social play (median duration/hour) was found to decline with the age of the NRI (Figure 6.1). For male NRIs however, the time spent in social play significantly declined across the pre-reproductive period (Spearman's $\rho = -0.57$, $N = 13$, $P = 0.04$), whereas the frequency of social play did not ($\rho = -0.39$, $N = 13$, $P = 0.19$), indicating that older males engaged in shorter bouts of play. The reverse was found for female NRIs, where the duration of social play was not found to significantly decline over the pre-reproductive period ($\rho = -0.51$, $N = 9$, $P = 0.16$), but the frequency of social play did ($\rho = -0.82$, $N = 9$, $P = 0.01$). Thus, older females played less often, but when they did, they played for longer periods.

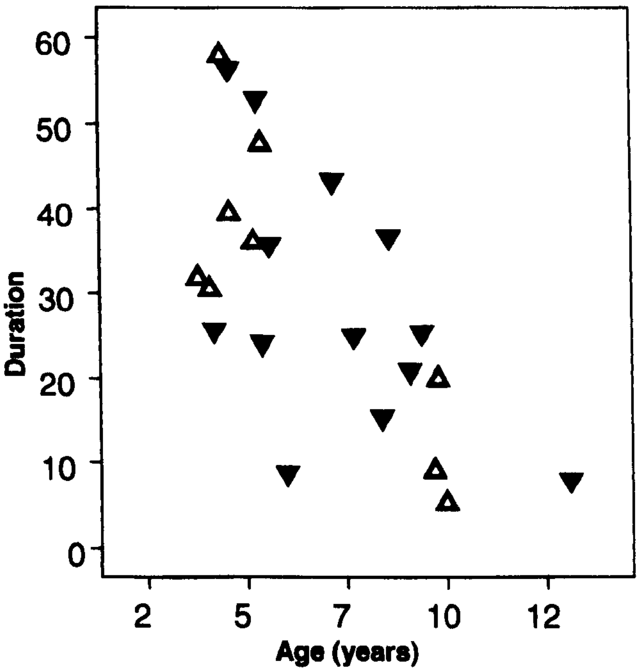


Figure 6.1 – Duration (seconds/hour) of social play with age for male and female NRIs. $\rho = -0.66$, $N = 22$, $P = 0.001$. Open triangles represent females; closed triangles represent males.

The type of social play that NRIs engaged in was investigated both across the pre-reproductive period and between the sexes (Figures 6.2, 6.3). The median duration of chase, gentle and rest play did not significantly differ between old infant, juvenile and adult females of different life-stages (Chase $F_{(2,6)} = 1.12$, $P = 0.39$; Gentle $F_{(2,6)} = 1.66$, $P = 0.27$; Rest $F_{(2,6)} = 0.17$, $P = 0.84$; Spar $F_{(2,6)} = 1.09$, $P = 0.40$). However the median duration of wrestle play did differ ($F_{(2,6)} = 19.15$, $P = 0.002$), with old infants and juvenile females wrestling significantly more than adult females (Bonferroni; Old infant vs. adult female $P = 0.01$; Juvenile female vs. adult female $P = 0.01$). No significant differences were found in the median duration of any aspect of social play by male NRIs between life-stage (Chase, $F_{(3,9)} = 1.88$, $P = 0.21$; Gentle, Welch $F_{(2, 2.30)} = 1.48$, $P = 0.39$; Wrestle, $F_{(3,9)} = 0.47$, $P = 0.64$; Rest, $F_{(2,9)} = 0.17$, $P = 0.85$; Spar, $F_{(3,9)} = 0.72$, $P = 0.56$).

To understand the differences in social play behaviour between the sexes, NRIs of similar life-stages were compared (juvenile males with juvenile females and adolescent males with adult females). No significant differences were found between social play behaviour in juvenile male and female behaviour (Kolmogorov-Smirnov; Chase, $Z = 0.64$, $N = 8$, $P = 0.81$; Gentle, $Z = 0.91$, $N = 8$, $P = 0.38$; Wrestle, $Z = 0.82$, $N = 8$, $P = 0.51$, Rest, $Z = 0.46$, $N = 8$, $P = 0.99$; Spar, $Z = 0.55$, $N = 8$, $P = 0.93$, Figure 6.2, 6.3). Likewise, no significant differences were found between chase, gentle and rest social play behaviour between adolescent male and adult female NRIs (Chase, $Z = 0.64$, $N = 8$, $P = 0.81$; Gentle, $Z = 0.46$, $N = 8$, $P = 0.99$, Rest, $Z = 0.91$, $N = 8$, $P = 0.38$; Spar, $Z = 0.91$, $N = 8$, $P = 0.38$). However adolescent males were found to engage in wrestling behaviour significantly more than adult females ($Z = 1.37$, $N = 8$, $P = 0.05$).

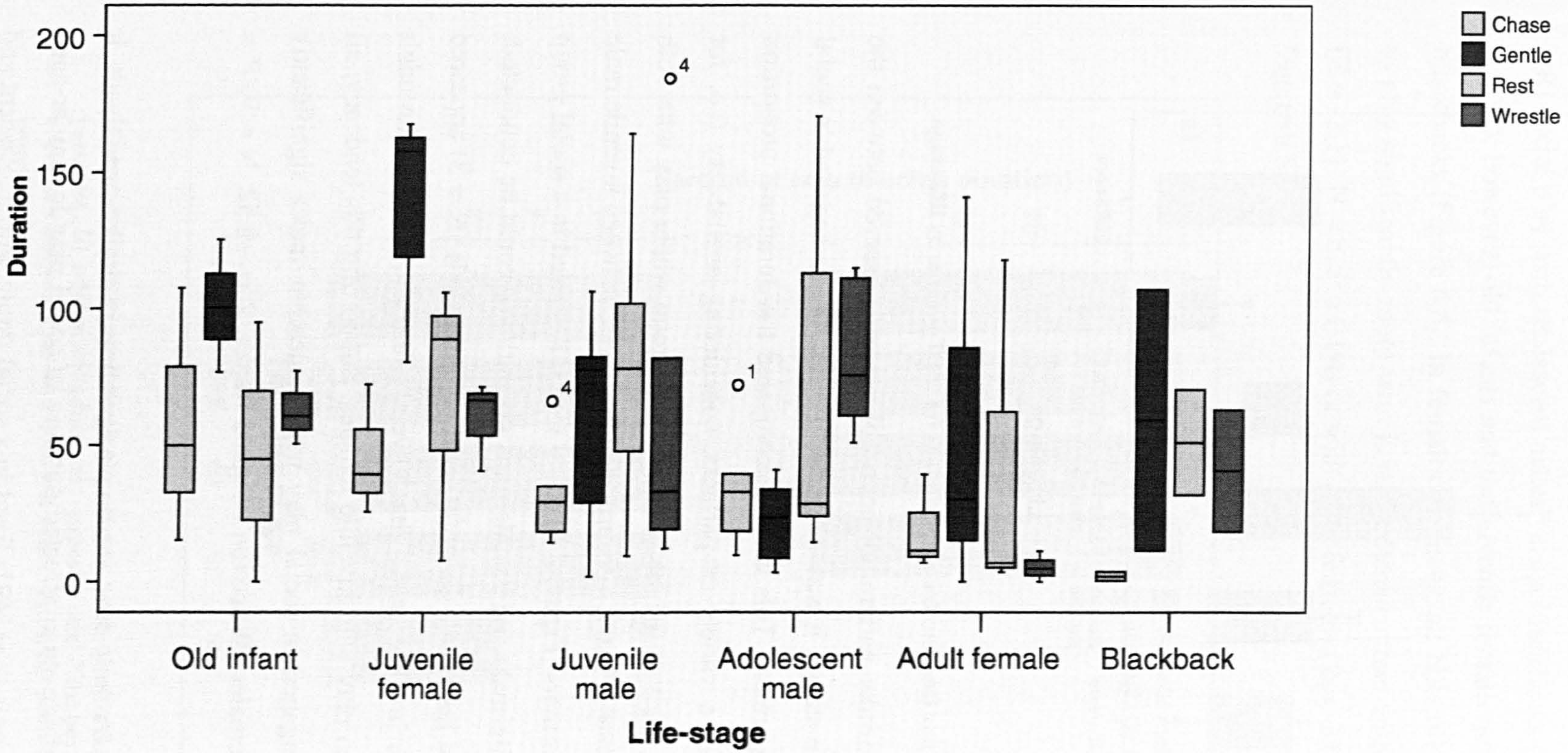


Figure 6.2 - Relationships between the elements of social play (median duration/hour) at each NRI life-stage across the pre-reproductive period.

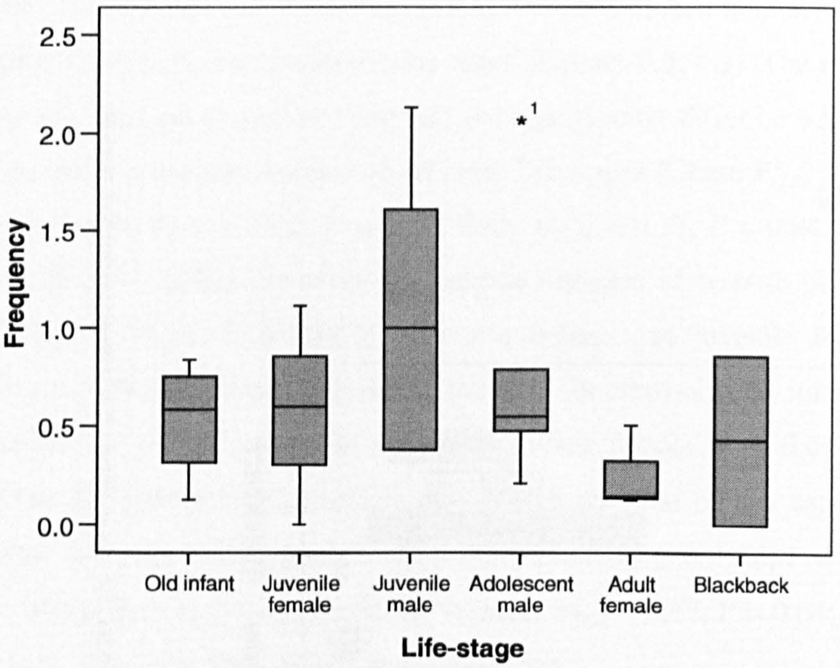


Figure 6.3 - Spar (median frequency/hour) for NRI gorillas by life-stage.

Considering that similar patterns of social play were observed between the sexes at similar life-stages, it was examined if NRI gorillas engaged in social play with similar partners. This analysis compared the durational proportion of social play with a variety of partners, considering availability (i.e. for inclusion into this analysis the NRI must be in a group where play with both partners was possible). Firstly, a comparison was made between juvenile male and female play partners (Figure 6.4). Only four NRIs lived in a social group with both a juvenile male and female, thus no statistics could be conducted; however, on visual inspection old infant and juvenile NRIs (N = 3) appeared to play more with juvenile males than juvenile females, whereas the adult female preferred to play with juvenile females. Supporting this tendency, all NRI life-stages engaged in social play with adolescent males significantly more than adult females (Wilcoxon's Signed Ranks, Z = - 2.52, N = 9, *P* = 0.01, Figure 6.4).

With a preference for male over female play partners in similar-aged dyads, it was investigated if life-stage affected duration of social play in similar-aged dyads. For males, only four NRIs lived in a social group with adolescent and juvenile males, therefore statistics could not be conducted although the time spent in social play with juvenile males appeared greater than for adolescent males (Figure 6.5). No significant difference however, was found between NRI social play with adolescent males versus blackbacks (Z = -0.95, N = 9, *P* = 0.38), however, old infants and the juvenile female rarely played with the blackbacks (Figure 6.5). In females however, all NRI life-stages were found to play significantly more with juvenile females than with old infant females (Z = -2.11, N = 8, *P* = 0.04) or with adult females (Z = -3.0, N = 11, *P* = 0.01, Figure 6.6).

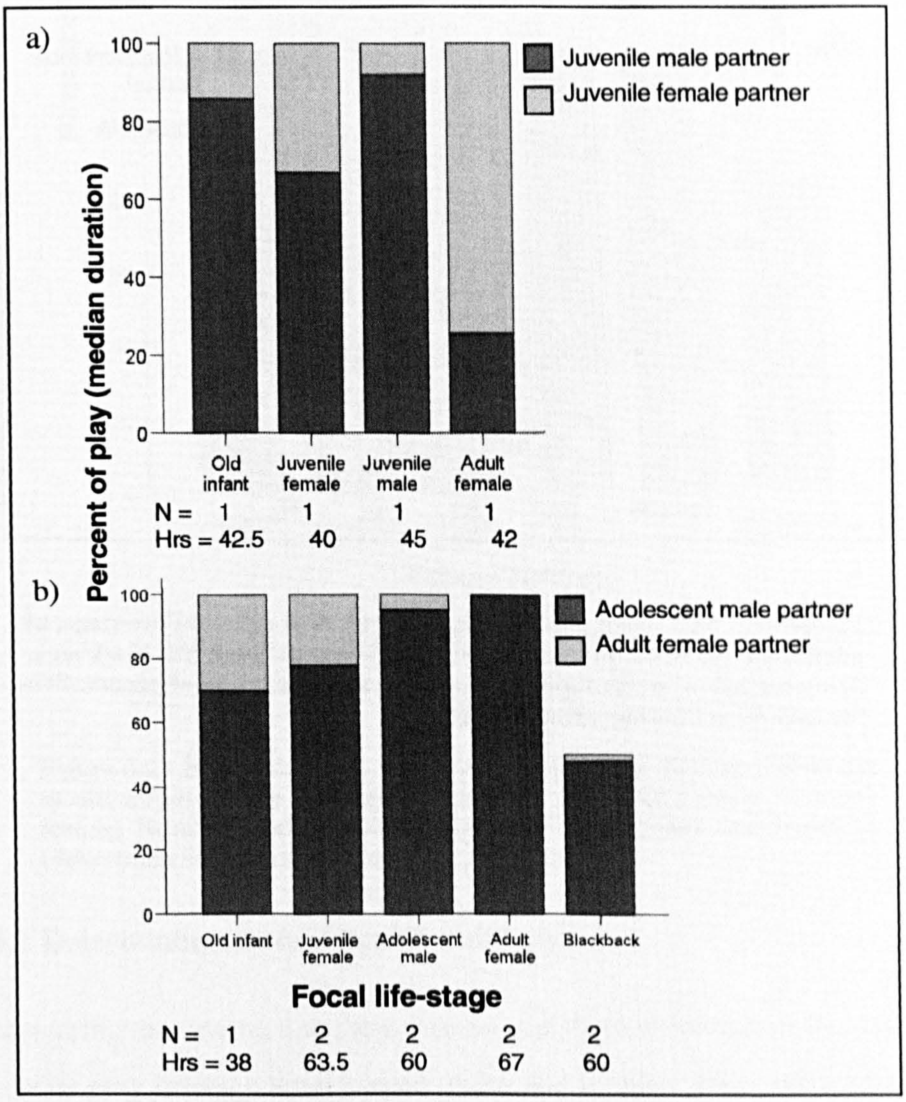


Figure 6.4 - NRI social play partners with similar-aged dyads, a) juveniles, b) adolescent/adult, but opposite sex. Numbers below x-axis represent No. of dyads and hours of observation for each focal life-stage, respectively.

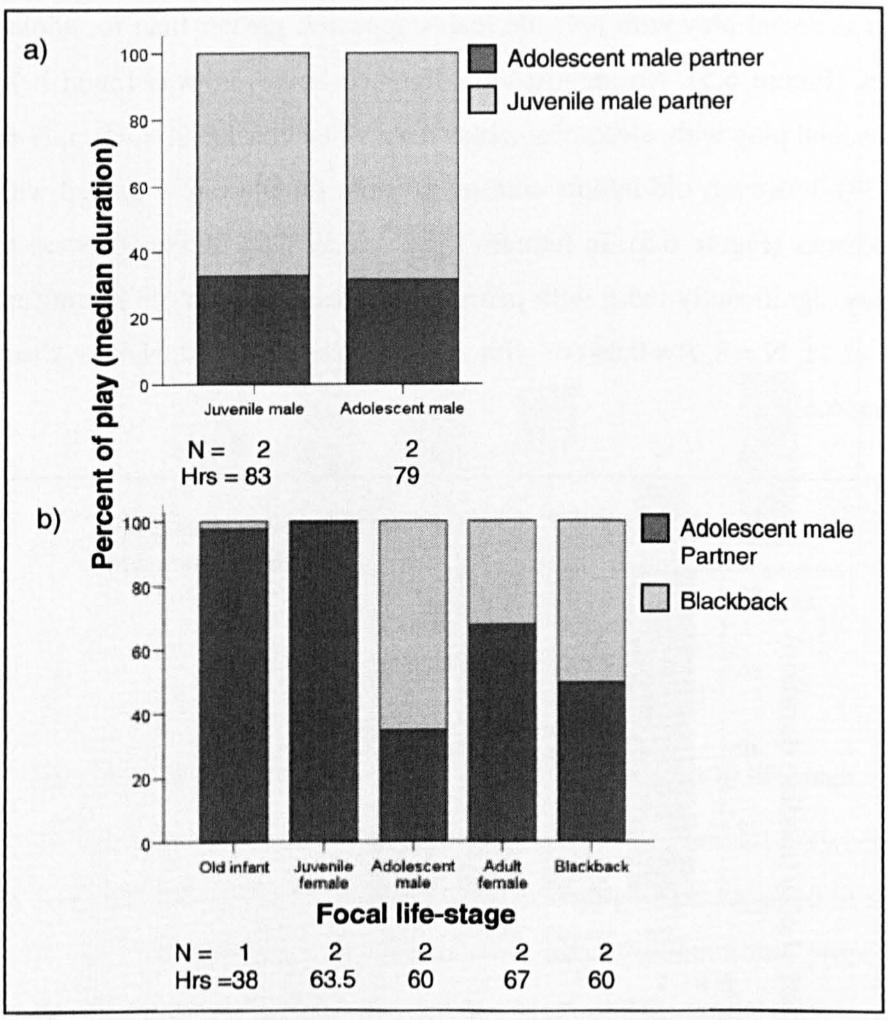


Figure 6.5 - NRI social play with male partners of different life-stage, a) adolescent male vs. juvenile male, b) adolescent male vs. blackback. Numbers below x-axis represent no. of dyads and hours of observation for each focal life-stage, respectively.

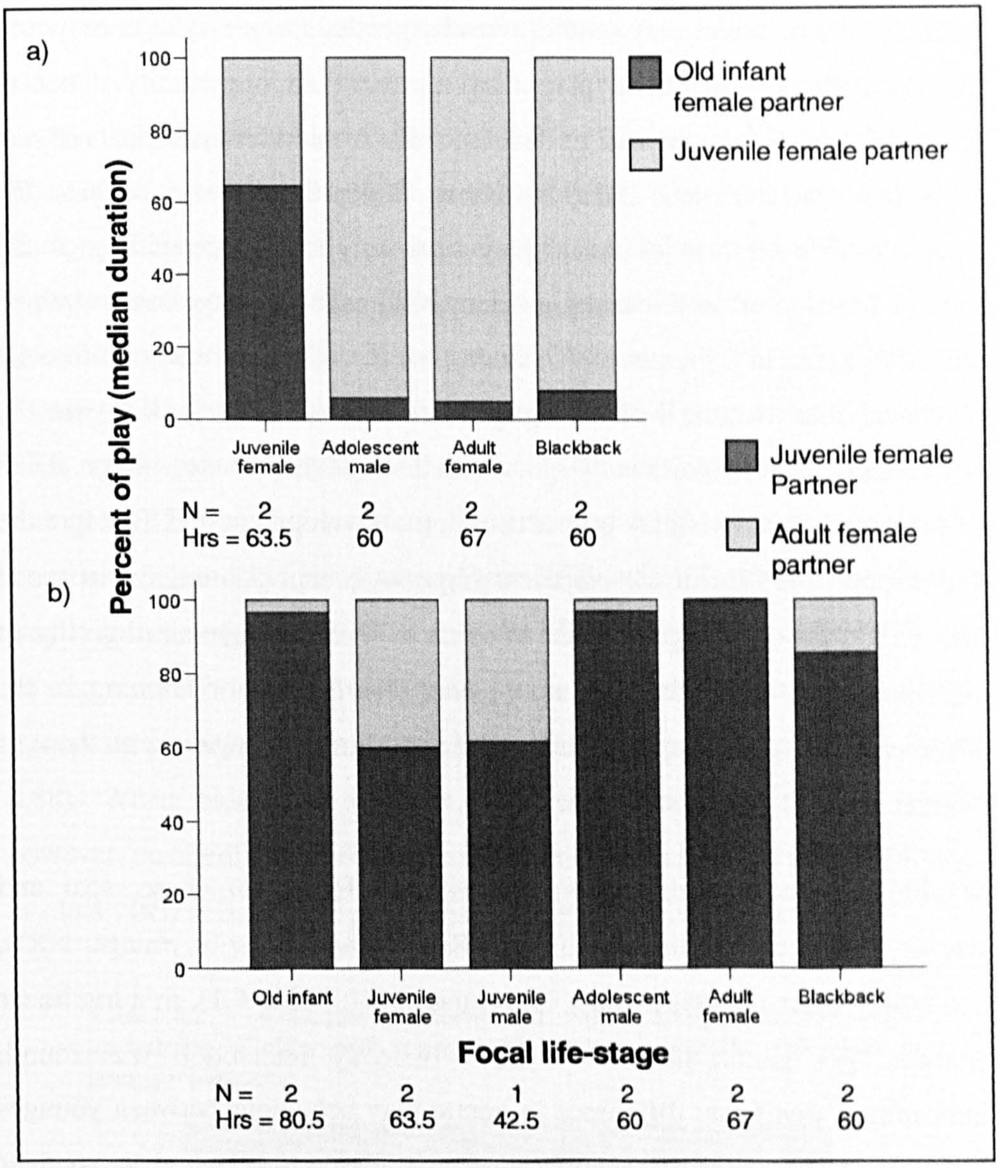


Figure 6.6 - NRI social play, with female partners of different life-stage, a) old infant female vs. juvenile female, b) juvenile female vs. adult female. Numbers below x-axis represent No. of dyads and hours of observation for each focal life-stage, respectively.

6.4.2 Determining the function of social play

Considering the finding that there was no statistical difference in the duration of social play between similar-aged males and females, NRIs were split into two groups. The first contained younger NRIs and incorporated old infants and juveniles of both sexes, and the second contained older NRIs, which incorporated adolescent males, adult females and blackbacks. The function of social play was investigated for both groups through partner preference for each element of social play (chase, wrestle, gentle, spar, rest). It is proposed that each element of social play may represent an opportunity either to practise motor development or to develop skills from older individuals (Byers & Walker, 1995; Fagen, 2002; Fairbanks, 2000; Spinka et al., 2001). By assessing each element of social play separately, an understanding of the relative function of each social play element to each life-stage can be gained which will lead to a greater understanding of the adaptive function of social play behaviour overall. If NRIs engage in each social play element (wrestle, chase, gentle, spar) significantly more with those of the same life-stage, it can be presumed that NRIs play to practise motor development and therefore the data support the *Neural Development Hypothesis.* If NRIs engage in social play with older or younger gorillas as much as with the same-sized gorillas it is proposed that social play may aid the *Skill Development* or *Training for the Unexpected* (where younger NRIs had the opportunity to engage with those of a larger size and greater strength).

Significant three-way interaction effects were found for chase, spar and wrestle behaviour with the variable of NRI life-stage (older or younger NRI), and play partner life-stage (older or younger NRI; Table 6.1), in a log linear analysis. For gentle play however, a two-way interaction was found, indicating a significant difference in gentle play behaviour between younger and older NRIs. A higher frequency of gentle play was found in younger NRIs compared to the older NRIs ($\chi^2_{(1)} = 6.18$, $P = 0.02$). Significant interactions in Table 6.1 indicated that older and younger NRIs had preferences in the age of preferred play partners for each play element.

Table 6.1 - The relationship between NRI, play partner and play element, using Log linear analysis.

Play element	Interaction	χ^2 (d.f.= 1)	P
Chase	NRI life-stage x partner life-stage x chase	8.62	0.003
Gentle	NRI life-stage x gentle play	6.14	0.01
Spar	NRI life-stage x partner life-stage x spar	13.93	<0.001
Wrestle	NRI life-stage x partner life-stage x wrestle	7.14	0.01

To investigate these interactions further, Chi-squared analyses were conducted to determine differences in the occurrence/non-occurrence of each element of play with older or younger NRIs (Table 6.2). Younger NRIs (old infants and juveniles) engaged in all elements of social play with other younger NRIs significantly more than expected and with no difference from expected with older NRIs (Table 6.2). The odds ratio test was used to determine the effect size (Bakeman & Gottman, 1997). For chase play, younger NRI gorillas were 21 times more likely to play with other younger NRIs compared to playing with older NRIs. In gentle and wrestle play younger NRIs were 6 times more likely to play with a younger compared to an older NRI and in spar play younger NRIs were 30 times more likely to play with a younger rather than an older NRI. Conversely, older NRIs were no more likely to play with younger or older NRIs than the expected frequency predicted (odds ratio; chase 0.93, gentle 1.23, spar 0.76, wrestle 0.88). When older and younger NRIs engaged in social play together however, no significant difference was found between which partner (younger or older NRI) solicited the play behaviour ($\chi^2_{(1)} = 0.02$, $P = 0.56$).

Table 6.2 - Chi-squared (likelihood ratio) analysis to determine probability of older and younger NRIs playing equally with older or younger partners.

NRI Life-stage[1]	Play style	χ^2 (d.f. = 1)	P
Younger NRI	Chase	13.24	*0.001*
	Gentle	5.54	*0.04*
	Spar	23.29	*<0.001*
	Wrestle	5.9	*0.03*
Older NRI	Chase	0.015	0.56
	Gentle	0.15	0.79
	Spar	0.15	0.76
	Wrestle	1.53	0.27

[1]Younger life-stage = old infant and juvenile NRIs, older life-stage = adolescent male, blackback, adult female NRIs

The function of older NRIs playing with younger NRIs was investigated by analysing older NRI play duration with full siblings and comparable age-sex paternal half siblings. Five older NRIs (3 x adult females, 1 x adolescent male and 1 x blackback) had younger, female NRI full siblings (2 x old infant, 3 x juvenile female) and lived in social groups with paternal half sibling younger female NRIs (5 x juvenile females). A tendency was found for older NRIs to engage in social play behaviour with full as opposed to paternal half siblings (Kolmogorov-Smirnov; Z = -1.46, N = 5, *P* = 0.06).

Considering the additional effect of sibling relationship on play partner preference in older NRIs, sibling interactions were omitted from analysis and the Chi^2 analysis re-run with the finding that in chase, gentle and wrestle play older NRIs played with other older NRIs, more than expected and with younger NRIs less than expected (Table 6.3).

The *Neural Mechanism Theory* of social play was supported by these analyses in that younger and older NRIs preferred to engage in social play with similar-sized individuals, rather than to play with disparate-sized individuals, except where full siblings are concerned.

Table 6.3 – Chi -squared (likelihood ratio) analysis to determine probability of older NRIs playing equally with older NRIs or younger NRIs (not including full siblings).

NRI Life-stage[1]	Play style	χ^2 (d.f. = 1)	*P*
Older NRIs	Chase	3.80	0.05
	Gentle	4.27	0.05
	Spar[2]	-	-
	Wrestle	5.41	0.02

[1]Younger life-stage = old infant and juvenile NRIs, older life-stage = adolescent male, blackback, adult female NRIs Chi^2 could not be conducted as an expected value was calculated to be less than 5.

6.4.3 The functionality of social play elements

The following analysis sought to understand which elements of social play significantly leads to and which do not lead to the continuation of social play. Differences between the elements may indicate differences in their adaptive function. Significant differences in the subsequent pattern of play were found between younger NRI dyads and older NRI dyads after chase, spar and wrestle behaviour (Table 6.4). In the case of chase for younger NRI dyads it was unpredictable whether more social play would follow, whereas for older NRI dyads, chasing play was significantly more likely to be the end of the play bout.

Table 6.4 - Determining whether social play elements lead significantly onto continuation or cessation of social play in older and younger NRI dyads, using a Kolmogorov-Smirnov test

Element	Younger NRI dyads (N = 10)			Older NRI dyads (N = 15)		
	Z	*P*	Outcome	Z	*P*	Outcome
Chasing	-0.26	0.43	Unpredictable	-2.7	0.002	Play stops
Gentle	-0.42	0.37	Unpredictable	-1.46	0.09	Unpredictable
Spar	-2.14	0.02	Play continues	-1.86	0.04	Play continues
Rest	-0.77	0.24	Unpredictable	-0.42	0.38	Unpredictable
Wrestle	-2.38	0.01	Play continues	-0.56	0.31	Unpredictable

With elements that led significantly more often onto social play (spar, wrestle) it was investigated if the previous and subsequent play element could be predicted in older and younger NRI dyads. Differences in pattern formation or differing patterns between older and younger NRIs may indicate different functions of the play elements and/or a different use of play behaviour across development.

Wrestling behaviour was found to lead onto further social play for younger NRIs, but did not necessarily lead onto social play in older NRIs. In both older and younger NRIs, spar behaviour reliably led onto further social play behaviour. For younger NRI dyads wrestling behaviour led into chase play significantly more than gentle, spar or wrestle ($F_{(3,32)} = 17.54$, $P = <0.001$, Figure 6.7) and spar behaviour led into wrestle behaviour significantly more than gentle, chase or spar behaviour ($F_{(3,32)} = 5.50$, $P = 0.004$). For older NRI dyads however, after wrestle or spar behaviour the subsequent play element (if any) could not be predicted (wrestle, $F_{(3,36)} = 0.36$, $P = 0.78$; spar, $F_{(3,36)} = 2.3$, $P = 0.92$).

In younger NRI dyads, it was possible to determine the behaviour which occurred before wrestle and spar behaviour. Before wrestling, younger NRI dyads chased significantly more than they engaged in wrestle, spar or gentle play ($F_{(3,32)}$ = 10.22, P = <0.001, Figure 6.8), whereas before sparring, younger NRI dyads were significantly more likely to engage in wrestling behaviour ($F_{(3,32)}$ = 4.91, P = 0.01). For older NRI dyads the behaviour which occurred before either wrestling or sparring was not predictable (wrestle, $F_{(3,36)}$ = 0.27, P = 0.84; spar, $F_{(3,36)}$ = 1.11, P = 0.34).

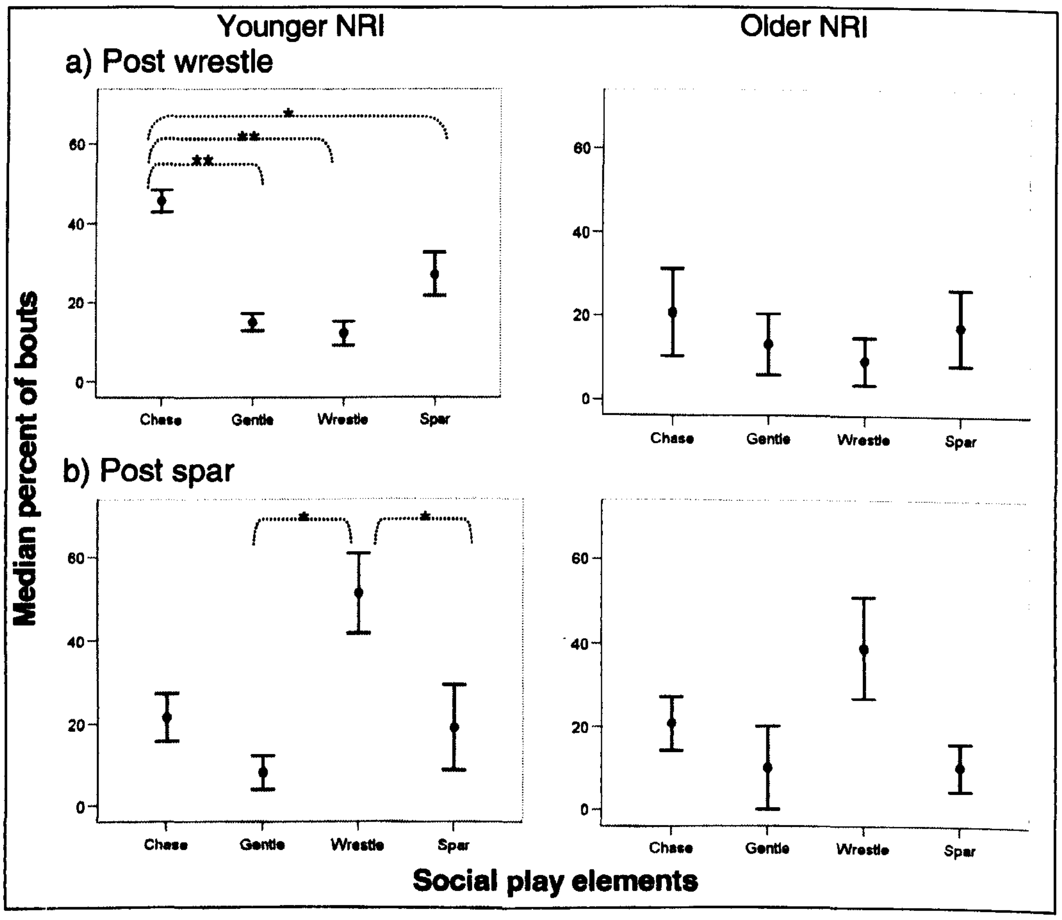


Figure 6.7 - Predicting social play elements after (Lag +1) a) wrestle, b) spar for younger and older NRIs. ** = Bonferroni *Post Hoc P* = < 0.001, * = Bonferroni *Post Hoc*, *P* = < 0.05

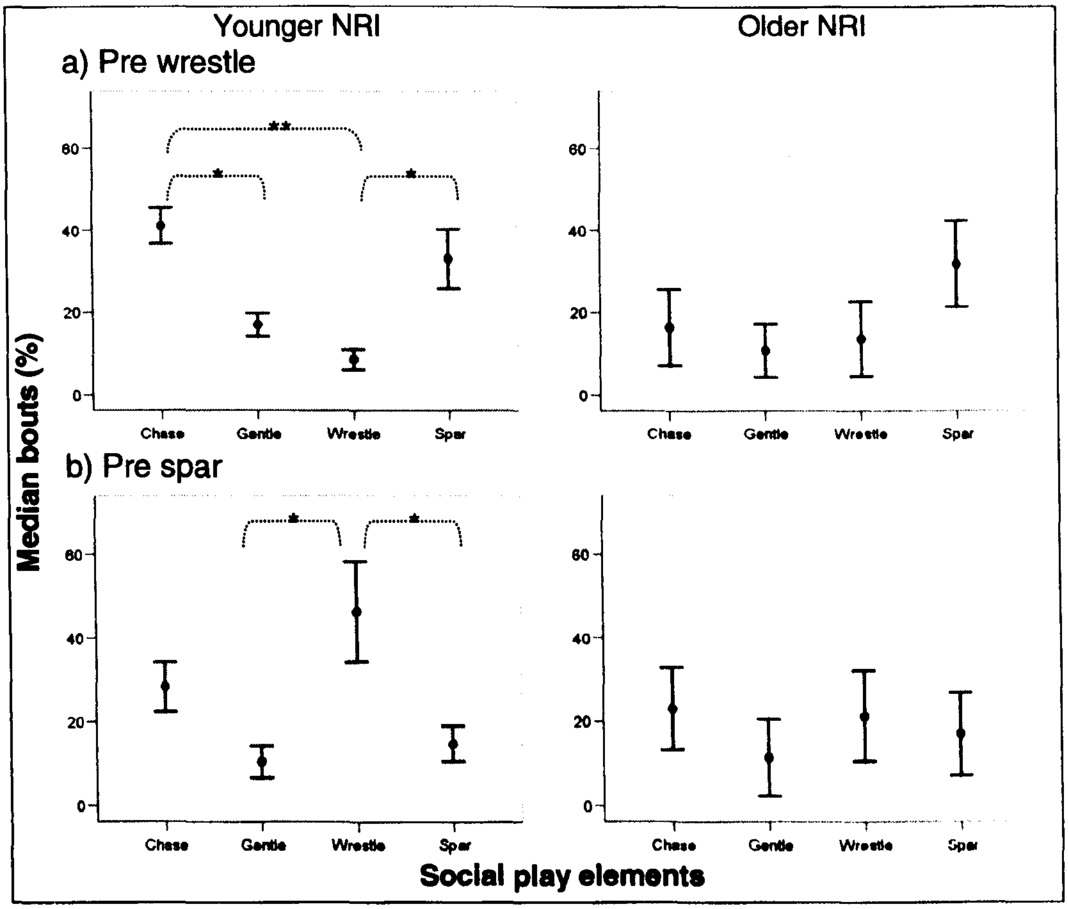


Figure 6.8 - Predicting social play elements before a) wrestle, b) spar for younger and older NRIs. ** = Bonferroni *Post Hoc* P = < 0.001, * = Bonferroni *Post Hoc*, P = < 0.05

In essence, younger NRIs engaged in more predictable play patterns, whereas older NRIs engaged in non-predictable play (Figure 6.9).

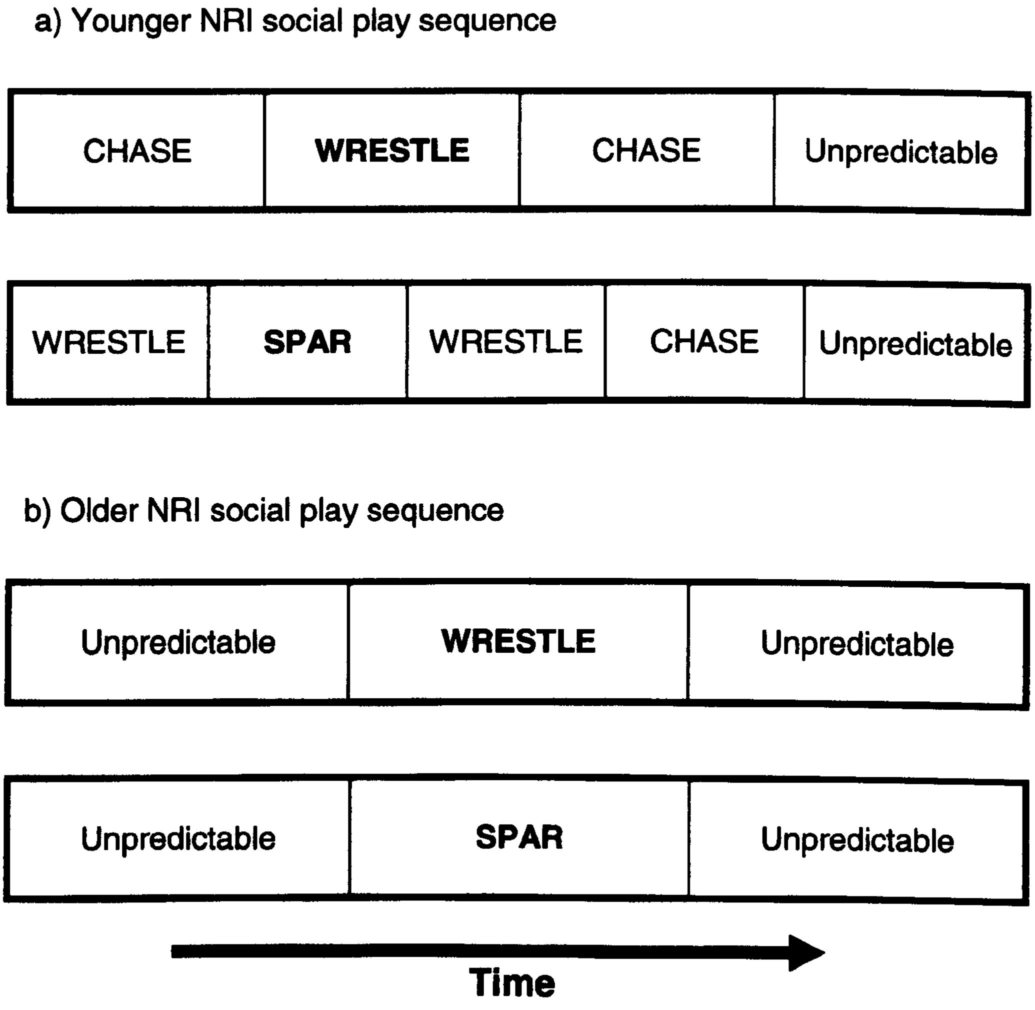


Figure 6.9 - Play sequences, predicted by wrestle and spar behaviour for older and younger NRIs.

6.5 Discussion

6.5.1 Results summary

Social play in captive western gorillas showed a gradual decline across the pre-reproductive period for both male and female NRIs. Although the frequency and duration of social play elements (chase, gentle, rest, wrestle, spar) gradually declined between life-stages, only wrestle play was found to significantly differ in duration between the juvenile female and adult female life-stages. Likewise, wrestle play was found to occur significantly less in adult females compared to adolescent males. In general, male and female

NRIs of all life-stages showed a preference to play with other males over females when both were available, although no preferred male life-stage was apparent. When females were played with however, juveniles were preferred over old infants or adult females.

Younger and older NRIs were found to engage in social play behaviour significantly more with those of a similar-size rather than those of a disparate-size, although there was a tendency for older NRIs to engage in social play more with their younger full siblings, compared to younger paternal half siblings.

Older and younger NRIs were found to use chase, wrestle and spar behaviour in different sequences within social play. The play element chase, in older NRIs was statistically likely to cause the cessation of social play, but in younger gorillas, did not predict whether social play would continue or not. Both wrestle and spar elements led onto continued social play in younger NRIs as did spar play in older NRIs. However, in younger NRIs, chase play was predictable both before and after wrestle play and wrestle play was predictable before and after spar play. For older NRIs the pre and post play elements to spar and wrestle play could not be predicted with any certainty, indicating an unpredictable structure of social play in older NRIs and potentially indicating a difference in social play function, when compared to younger NRI social play.

6.5.2 The proposed function of social play and associated benefits

This chapter aimed to determine the function of social play using partner preferences in social play as an indicator of the advantages assumed by the NRI, then portraying when the benefits of social play occur. The *Neural Hypothesis* predicts that NRIs will engage in social play with individuals of a similar size and strength, enabling them to practise necessary motor development during periods of cerebral synaptogenesis and muscle fibre differentiation (Byers & Walker, 1995; Fairbanks, 2000). In *Skill Development hypothesis* it is predicted that NRIs should engage in social play with older individuals where possible, to develop skills that would be a selective advantage (de Oliveira et al., 2003; Fagen, 2002). No difference in the occurrence of social play with similar versus disparate-aged partners would be expected for the *Training for the Unexpected Hypothesis*, in which it would only be necessary to engage in a precarious manner to practise physical movement skills.

Captive western gorillas were found to engage in social play behaviour with similar sized NRIs more than would be expected and played significantly less than expected with disparate-sized play partners. This finding occurred in both male and female NRIs across the pre-reproductive period suggesting that the advantages assumed by engaging with similar-sized NRIs exist between the sexes in younger and older NRIs. That male and female NRI primates play with like-sized individuals across the pre-reproductive period is supported by play studies in vervet monkeys (Fairbanks, 2000; Govindarajulu et al., 1993) and across the apes (Fletcher, 1994; Watts & Pusey, 2002). Of particular interest is the propensity for wild chimpanzee NRIs to engage with similar-sized play partners in longer lasting and more boisterous play bouts, compared to play with a disparate-sized partner (Pusey, 1990). This is indicative of a specific partner preference as the chimpanzee's fission-fusion society leads to comparatively less time spent in social situations with similar-aged peers, compared to time spent with full siblings.

That similar-sized partner social play is preferred among NRI gorillas indicates that there is a specific advantage assumed by individuals for playing in this formation. Peaks in social play behaviour in old infancy and juvenility correlate with the development of neural structures and cognitive competencies and therefore may be important for maximising the development of these systems (Byers & Walker, 1995), supporting the *Neural hypothesis*. Similar-sized partners allow play that is closely matched by size and ability, which enables individuals to anticipate and judge the relative attributes of others (Fairbanks, 2000). Partners of similar life-stages are also matched by the intensity of their desire to play (Fagen, 2002) and are more likely to be found in the same social group across development. The establishment of play within same-aged partners therefore may enable a situation where repeated exposure to these individuals can promote the development of comparative assessment abilities and increased skill in motor performance. In this way, it would be crucial that social play has immediate as well as future benefits and thus some support for the development of skills and motor training in the *Skill Development* and *Training for the Unexpected* hypotheses were found, supported by the use of repetition of play sequences. In males, for example, training with similar-sized partners are considered necessary, as in conflict situations, competitors would likely be similar in size and strength.

When social play with disparate-sized partners does occur in the apes, it has been found most often between individuals of high relatedness (Lewis, 2005; Markus & Croft, 1995). This may indicate close proximity to one another through mutual maternal relationships (Chapais, 2001), or advantages assumed through inclusive fitness if the older NRI invests in the younger NRI's fitness, or harms the younger partner less. Disparate social play partners in this study were found when older NRIs engaged in social play with younger full siblings. This finding leads some support to the *Skill Development Hypothesis* in that playing with older NRIs may lead to faster development of sex-specific skills in the younger NRI (Fagen, 2002), which would be selectively advantageous if the younger NRI could then use these skills to a competitive advantage (which cannot be determined here). Considering that social play was found mostly between full siblings in the disparate dyads, it could then be the case that such nepotistic social play would lead to an inclusive fitness benefit in the younger NRI (Hamilton, 1964). Likewise, in support of the *Training for the Unexpected Hypothesis*, disparate-sized play partners would allow practise of motor skills against a faster, more proficient partner where the risk of injury is greater for young individuals, or for the older partner to engage in self-handicapping behaviour to enhance the unpredictability of the play situation (Spinka et al., 2001).

In social play between disparate-sized partners it has often been found that the larger animal engages in self-handicapping behaviour (Burghardt, 2005;

Lewis, 2005; Pereira & Preisser, 1998), moderating its play to the relative asymmetry in strength (Lewis, 2005). Any moderation of strength by the older NRI would reduce the relative beneficial properties of social play attained in terms of testing strength and ability and developing the emerging cognitive systems, but would allow play to continue without it escalating into fighting or potential injury to the younger NRI (Hayaki, 1985). If the advantages of social play to one partner are less than to the other, it is predicted that social play with disparate-sized partners should be found less often than social play with similar-sized partners, when social situations allow, which was indeed the case in this study. Disparate-sized social play was generally found between siblings and at a lower rate than similar-sized NRI play partners, which were most profuse, thus supporting the ***delayed benefits*** of social play and the *Neural Hypothesis.*

In summary, some support has been found for all three hypotheses, which is related to the difficulty in separating future and immediate effects of social play, which of course are recorded in the present. Here it is promoted that social play has a ***delayed benefit***, supporting the *Neural Hypothesis*, but that other lesser advantages of social play may be immediate, such as increased competency in the environment. The cumulative nature of behavioural development across immaturity indicates that any behaviour with a future benefit will develop across the pre-reproductive period, where it is likely to be practised.

6.5.3 Form and function of social play elements

Not only was social play most common with similar-sized partners, but all elements of social play were engaged in significantly more with similar-sized NRIs compared to disparate-sized NRIs, regardless of their function, further promoting the *Neural Hypothesis* and providing no support for the *Development of Skills Hypothesis* from older NRIs or *Training for the Unexpected.* If some social play elements were more useful to develop skills or for training, it would be expected that these elements would be more profuse when disparate sized NRIs played, thus providing support for the immediate benefits of social play behaviour. All elements of social play occurred within older, younger, and mixed NRI play dyads, but in the case of chase and wrestle had different effects within the play bouts indicating that the elements may have a different function in different age groups. These differences, due to age are likely brought about by the developmental effects between similar-sized younger and older NRIs. An analysis of play elements showed that after gentle play and rest play in both older NRI dyads and younger NRI dyads, social play was found to continue or stop, without predictability. Highly unpredictable forms of social play are reported in the literature as defining features of social play in general (Fagen, 2002). Unpredictability in continuation or cessation of social play may indicate that the purpose of the particular social play element is only for its occurrence, i.e. to allow practise of that form, or an assessment of previous action, each of which may influence whether or not it is beneficial for the individual to continue to engage (Fagen, 2002).

The chase element of social play was also unpredictable in younger NRIs, but more often preceded play cessation in similar-sized older NRIs. This suggests that chasing is driven by the need to practise this specific behaviour, as opposed to signalling continued desire to continue social play. Considering that the purpose of a flight response would be for one partner to out-run or evade the other (Spinka et al., 2001), this is a predictable outcome for this social play element. Conversely, after spar and wrestle behaviour in similar-sized younger NRIs, social play was more likely to continue than not, which indicates that the function of this behaviour might differ from that of chase, gentle and rest play. This is not the case for wrestling in older NRIs, perhaps due to the escalating competition between males in later adolescence to assert dominance and test skills against that of the partner, which may lead to social play cessation as a mechanism of control, rather than risking the play escalating into a fight (Fry, 2005; Hayaki, 1985).

Developmental differences are documented across the pre-reproductive period in the apes; in this thesis these include increased proximity from the social group in males, decreased investment in social relations with peers

(Chapter 4), reduced interest in alloparental behaviour (Chapter 5) and reduced time spent in social play as age increases (this chapter). Across other ape studies, also reported are changes in hormones, leading to increased aggression and sexual behaviour (Anestis, 2006; Lewis & Barton, 2006; Watts & Pusey, 2002), and increase in growth (Leigh, 1996). Developmentally therefore, a difference in the function of social play behaviour would also be expected to accommodate the somatic, physiological and behavioural development co-occurring during this period, but has not before been investigated.

Although not previously tested in the non-human apes, differences in the social play of juvenile and adolescent boys have been documented in terms of increased dominance, increased intent to injure and lack of restraint with increasing age during adolescence (Fry, 2005) and as such indicate a difference in play function as children increase in age. In this chapter, differences were found in the predictive nature of social play sequences, where preceding and subsequent behaviour for wrestle and spar behaviour could be predicted, indicating a tendency for younger NRI dyads to play in predictable play sequences, which were repeated across play bouts and with similar-sized partners. In older NRI dyads however, play sequences could not be predicted indicating a more sporadic and innovative play sequence. The differences in apparent predictability in social play between younger and older NRIs may indicate a different function in play engagement in younger and older NRIs. This finding can be explained further using the *Neural Hypothesis*. Social play is found to increase just after weaning in primates (Lewis, 2005) at a time of cerebellum differentiation and synapse formation, indicating a period of high plasticity and neurological development to the environment (Fairbanks, 2000). From a motor development perspective, this combination of social play and plasticity leads to the learning of sequences for motor action, which become more accurate with practise (Willingham, 1999). Social play is indeed discussed across the literature as repetitive and proposed as a method of practise, to develop understandings about social interactions and be able to effectively gage the outcome of a fight (Bateson, 2005; Burghardt, 2005; Fagen, 2002). As discussed, such immediate effects may also benefit the younger individual.

The focus on non-human primate adolescent play to date has been much less than for juvenile play, except in the human literature, where a shift in behavioural development is seen in boys from practising skills to developing dominance (Fry, 2005; Pellegrini, 2002). Likewise, in rhesus macaques a difference in social play was documented across the pre-reproductive period, and described as an increase in inhibition during social play and an increase in complexity due to disparate roles and asymmetric play forms (Levy, 1979). Recent research supporting these descriptions shows that the amygalda, which is responsible for social assessment and social response appropriateness, is affected by gonadal hormones during adolescence (Lewis & Barton, 2006), which may reduce the incidence of play behaviour, but may also differentiate between the play exhibited. It is proposed here, that after a period of motor skill practise during juvenility, NRIs must pass through a period of developing spontaneity, which can only occur after adolescent hormone secretions and when the brain is more developed and cognitively aware (Fairbanks, 2000). The development of spontaneity in essence builds on the skills learnt in juvenility, but involves learning how to use the skills in a selective manner, to assert dominance and become competitive with others, whilst remaining in a protected social group and thus reducing the risk of injury. The reduction of social play in adolescence may also be a mechanism to reduce the chance of injury because of fighting when non-predictable play patterns are tested.

Social play with similar-sized partners may be brought about by adolescents being larger and playing in a riskier manner than juveniles do, thus juveniles may increase the chance of injury by playing with them for prolonged periods and therefore avoid doing so (Fagen, 2002). Or potentially, due to the adolescent's greater proximity from the central core of the group, there is reduced opportunity to engage in social play (Pusey, 1990). Social play with similar-sized partners may come about due to the different function of social play at each life-stage, where the advantages of play are reduced for both partners by engaging in prolonged social play with disparate-sized/skilled partners. If such is the case, it is indeed necessary to develop skills and train for the unexpected, in a progressive way, but ultimately these are proposed as necessary stages in combining cognitive and physical development, seen through behaviour change, which allows the necessary benefits to the individual ready for adulthood.

6.5.4 Using the social-relationship hypothesis to explain trends in social play

Due to limited sample size, it was not possible to determine the effects of sex on older NRI social play function. Differences between males and females would be expected however, because NRIs are predicted to develop in a sex-specific manner, (Cords, 1997). Male gorillas are depicted as the group protectors (Stewart, 2001), whilst female gorillas engage more in infant care (Fletcher, 2001), thus it is anticipated that there will be a greater advantage for males to develop effective fighting skills compared to females (Burghardt, 2005).

It has also been predicted that males and females of a species should play more with the sex with which they engage most with in adult life, which Fairbanks (2002) terms the *Social-Relationship Hypothesis.* For male gorillas, therefore it is important to engage with other males and to develop an understanding of fighting ability, to secure breeding females and protect their offspring in the future. Females however, have been documented to have few relationships with other females, potentially due to their emigration upon sexual maturity and thus lack of relatedness with other females in the breeding group (Watts, 2001). It would be predicted therefore, that females too would engage with males more than females during the pre-reproductive period in order to make accurate assessments as to the fitness and suitability of potential mates.

Support for this theory was provided in the current study; all NRIs showed a propensity to engage in social play with males as opposed to females, although social play between females did occur. In particular, adult females played solely with adolescent males and rarely played with other adult females. The same findings were recorded in a study of captive gorilla infants (Maestripieri & Ross, 2002), with some support from juvenile western and mountain gorillas (Brown, 1988; Fletcher, 1994; Nowell, 2005), although adolescent mountain gorilla females were found to engage in social play more with other adolescent females as opposed to adolescent males (Fletcher, 1994).

The function of female and male NRI social play can be assessed by comparing the duration (i.e. amount of time invested in play) of social play elements with similar-aged males. In this study, it was found that wrestling behaviour in juvenile male and females was not significantly different, however, by the older NRI life-stage adult females engaged in wrestling behaviour for significantly less time than adolescent males. Considering in this study that adult females did not play with other adult females, and that older NRIs preferred to engage in social play with other older NRIs as opposed to younger NRIs, it was found that the majority of wrestling play was engaged in with adolescent males. However, the adult female sample size was small in this study (N = 3) and further data would be needed to support this finding. It is proposed that adult females engage in wrestling behaviour as a means of assessment, whereby she can learn to determine attributes of males, which would be beneficial in future mating partners.

6.6 Conclusion

Using partner preference in social play, understanding individual elements of social play and assessing the pattern of social play in similar-sized younger and older play partners together leads to support for the *Neural Hypothesis*, and proposes that social play provides ***delayed benefits*** to the individual. Some evidence also pertains to the immediate benefits of social play supporting the *Skill Development* and *Training for the Unexpected* hypotheses. Social play is proposed to have two age-specific functions. In younger NRIs social play is proposed as a means of practise, using repetitive sequences of behaviour to develop skills, whereas older NRIs, build on the skills formed previously and develop spontaneity within play. During both developmental phases, NRIs played most with similar-sized partners, who are likely engaging in the same style of play and are therefore less likely to harm each other. Male and female gorillas sought to engage in social play with male NRIs of a similar-size, which will prove beneficial to the individuals in competing against other males or selecting a fit male as a breeding partner and supports the *Social-Relationship Hypothesis*.

Chapter 7

7 THE EFFECT OF EARLY SOCIAL DEPRIVATION AND LIVING IN ATYPICAL SOCIAL GROUPS ON BEHAVIOURAL DEVELOPMENT.

The aim of this chapter is to investigate if peer groups are adequate social environments for the development of species typical social development.

7.1 Introduction

7.1.1 The need for social relationships

Primates that live in social groups are held together by strong relationships formed between reproductive individuals (Curley & Keverne, 2005), related females (Hrdy, 1999) and between mothers and their offspring (Broad *et al.*, 2006). In primates, each individual is capable of maintaining several such relationships at any given time. The maintenance of these relationships within a structured social group over long periods of time, along with the ability to solve ecological problems are proposed as the driving force for the evolution of the large relative brain size in anthropoid primates (Dunbar, 1998). Large social groups are considered to be highly beneficial for adult primates, through increased breeding opportunity and protection, whilst for primate non-reproductive individuals (NRIs), opportunities to form social relationships are thought to be essential for the development of skills, knowledge acquisition and species-specific behaviour (Cords, 1997; Russon, 1997).

Primates are predisposed from birth to form intense functional relationships with their mothers (Broad et al., 2006) and later in infancy with other available conspecifics, particularly relatives (Silk, Altmann et al., 2006). In general, mothers form stronger, more permanent social relationships with infants, due to the physiological necessity of investing in a closely bonded relationship with infant offspring (Hrdy, 1999). In many primate species, female remain in the social group as adults and continue their relationship with their mother, past the period of dependency (Hrdy, 1999), forming strong female-female bonded relationships across the social group.

Current neurological research has found that social bonds are maintained through the visual or olfactory recognition of a social partner, which releases oxytocin and vasopressin into the brain (Curley & Keverne, 2005). The release of these neurochemicals is particularly strong upon recognition of an individual's own infant. This release acts as a reward mechanism, positively reinforcing the social relationship and strengthening the relationship between the two individuals. Mother-offspring relationships, which in anthropoid primates typically last for several years and are highly robust, proposed to be the building blocks for the formation of other strong relationships which occur with increasing maturity of the individual within a cohesive social group (Curley & Keverne, 2005). It is the development of these relationships and the prolonged maintenance of multiple strong bonds within social relationships that are deemed to set apart anthropoid primates from other social species (Shultz & Dunbar, 2007).

7.1.2 The effect of early social deprivation on normal social development

Infants are born predisposed to develop into functioning social group members, but their ultimate success is limited by their fitness and the available social experiences between birth and adulthood (Sanchez *et al.*, 2001). The rearing environment, including mothering style, mother's dominance status, group composition and habitat of a primate have been shown to affect survival and the success of social development (MacKinnon, 2007). Individual differences add to the social complexity of primate groups.

In captivity, primates can be reared under social conditions in which they would not survive in the wild. Experiments that, for example, have isolated individuals from birth or in infancy, have enabled an understanding of the necessary social environments in which normal development will occur, as well as documenting the effect of an inadequate social environment on behaviour (Sackett *et al.*, 2006). Social deprivation in infancy has been found to affect normal behavioural and physiological development patterns and lead often to the development of abnormal behaviour (defined as that which differs in pattern, frequency or context to behaviour displayed by wild counterparts) in animals (Broom & Johnson, 1993; Sanchez et al., 2001) and in humans (Dettling *et al.*, 2007). Two types of captive environments have extensively shown the effects of inadequate social rearing conditions on normative primate social development: firstly, in the laboratory, where infants have been removed from their mother at birth to study the effect of reduced social stimulus on social development (reviewed by Novak & Sackett, 2006) or the effect of infant deprivation on subsequent behaviour and physiological development (Sanchez et al., 2001). Secondly, inadequate social rearing is found in zoos, where mothers have rejected their infants, or infants have been removed from their mothers to increase the rate of ape infant survival in captive conditions (reviewed by Porton & Niebruegge, 2006).

7.1.2.1 Effects of social deprivation during infancy

Very severe social deprivation was found when infant macaques were raised in total isolation, which led to highly abnormal cognitive, social and physiological development (Harlow *et al.*, 1966). Infants raised in this way were found to have deficiencies in communication and in the ability to establish relationships, impaired motor development and immune response, increased expression of fear and aggression and were characterised through stereotypical rocking, clutching and huddling behaviour (reviewed by Novak & Sackett, 2006). Similarly, chimpanzee infants that were human-raised without conspecifics exhibited high levels of abnormal behaviour and reduced social and cognitive abilities compared to those raised by the mother (Bloomsmith et al., 2006). Across the pre-reproductive period, human-raised gorillas can show increased self-injurious behaviour, solitary play and inappropriate aggression (Gold, 1992; Meder, 1989a), whereas in adulthood such chimpanzees and gorillas often exhibit signs of social and sexual incompetence, which lead to a low social status and a decreased ability to cope with stress (Meder, 1989b; Porton & Niebruegge, 2006). Recent studies which assess the effect of early social deprivation on the physiological system of marmosets report heightened basal systolic blood pressure and low cortisol receptor levels in juvenile and adolescent primates, which are comparable to depressed human patients (Pryce *et al.*, 2004; Pryce *et al.*, 2005)

Reducing abnormal behaviour which has developed across the pre-reproductive period is extremely difficult, particularly in NRI rhesus monkeys who have been isolated from birth (Novak & Sackett, 2006). Placing the isolated monkeys in a social situation with peers or surrogates was not found to reduce the incidence of abnormal behaviour in juvenility, unless the conspecific was in a younger life-stage than the isolated monkey and thus at a more immature stage of development (Novak & Sackett, 2006). For chimpanzees raised in isolation from a young age, full socialisation and acceptance into a social group may not be possible (Bloomsmith et al., 2006) and can lead to social exclusion and increased aggression from conspecifics. Clearly, relationships with conspecifics from a young age are essential for normative social development in primates.

Subsequent experiments with monkeys and baboons (reviewed by Brent & Bode, 2006; Novak & Sackett, 2006) assessed the relative role of peers and mothers in the progression of normal social development. Infants raised with only their mother and those raised in peer-only groups were both found to develop a full range of species-specific behaviour, with few behavioural differences and little abnormal behaviour observed. However, mother-raised infants were found to exhibit more aggression towards peers upon immersion into a social group, demonstrating the role of peers in moderating behaviour through play (Novak & Sackett, 2006). In stressful events, peer-raised baboons began to exhibit maladaptive abnormal behaviour and a reduction in the ability to cope with new situations. These were presumed to be due to the lack of an attachment figure, or altered stress physiology related to early maternal deprivation (Brent & Bode, 2006; Sanchez et al., 2001).

In peer-reared chimpanzees and gorillas, abnormal and/or stereotypic behaviour (defined as repetitive, invariant behaviour without a goal or function, (Mason, 1991)) are commonly found (Bloomsmith et al., 2006; Hill, 2004; Meder, 1989a), ranging from finger sucking to regurgitation. Male gorillas raised in peer groups were found to be more aggressive than parent-reared gorillas (Gold, 1992), particularly when raised in pairs rather than in larger groups (Meder, 1989a) and in chimpanzees raised in peer groups sex differences in behaviour emerged later in juvenility compared to parent-reared chimpanzees (Spijkerman et al., 1997). When introduced to conspecifics or a stressful situation, peer-raised gorillas of both sexes react with increased aggression and a greater incidence of stereotypic behaviour than parent-reared apes (Meder, 1989a), again showing the reduced ability of peer-reared apes to cope in new circumstances. In adulthood, reproductive incompetence is common in peer-raised chimpanzees (Bahr, 2002): female chimpanzees who had spent less than a year with the mother having an increased chance of rejecting their offspring, compared to those raised by the mother (Bloomsmith et al., 2003) and males often using incorrect copulatory positions (Ryan *et al.*, 2002).

Further experiments have sought to determine the behavioural effect of a forced separation between mother and infant or between juvenile peers. Upon prolonged separation from the mother, gorilla, chimpanzee and orang-utan infants showed heightened agitation, with increased vocalisation and locomotors behaviour, before declining into a period of behavioural depression and general inactivity, which was more extreme if the individual was caged alone (Hoff et al., 1994). The same result was found in more recent research separating rhesus macaque infants from mothers (Sanchez *et al.*, 2005). Likewise, the separation of a NRI monkey from a peer during juvenility has been seen to lead to the development of abnormal and even pathological, self-mutilating behaviour (Novak, 2003). Upon reunion with the mother, infants from all ape species did not immediately repair their attachment with the mother, but remained in close contact with conspecifics for some days before gradually increasing proximity from the mother.

In summary, a lack of social contact with peers and/or the mother decreases the likelihood of normative social development in infant primates. Living in functional social groups however, allows the NRI to learn adult behaviour through social learning from adults (Hook *et al.*, 2002), whilst peers engage in play behaviour aiding the development of motor skills and moderating social behaviour (Bateson, 2005). Disruption of the maternal bond has a significant negative effect on infant behaviour, which is not immediately rectified upon reunion with the mother. However, some primates raised in normative social groups in captivity also exhibit abnormal behaviour and much current research in zoos and laboratories seeks to understand why.

7.1.3 Effects of stress in the captive environment

The captive environment differs from the wild in complexity, perceived and actual control, available space, enrichment and food availability; animals predisposed for life in a specific habitat must attempt to adapt into managed routines and static environments, with no control over emigration (Carlstead, 1996). The ability of an individual, or indeed a species, to adapt differs. Continued high or low stimulation or frustration beyond the individual's capacity to cope leads to a stressful state, which can be exhibited as species-atypical or abnormal behaviour (Broom & Johnson, 1993). Such behavioural responses to stress are shown as a robust measure of primate well being (Wolfensohn & Honess, 2005), whereby the more species-typical the behaviour of an individual in a stressful situation, the better the welfare of the animal is likely to be.

Atypical or abnormal behaviour only mainly in captive individuals (Wolfensohn & Honess, 2005) and is not of any advantage to the individual. In primates, abnormal behaviour is highly variable between species, for example, posterior presenting in captive gibbons (Cheyne, 2006), high frequencies of coprophagy in captive gorillas and chimpanzees (Hill, 2004;

Hook et al., 2002) or digit sucking in primates raised without the mother (Hook et al., 2002; Meder, 1989a). Abnormal behavioural profiles differ greatly between individuals as such behaviour occurs spontaneously when the individual is under or over-stimulated in the environment (Hook et al., 2002).

Stress may lead to the development of stereotypical behaviour: easily observable aberrant behaviour patterns. Examples in primates include pacing (Bellanca & Crockett, 2002), or hair plucking (Hill, 2004). Stereotyped behaviour indicates a change in cognitive functioning (Novak *et al.*, 2006) which, in the case of self-injurious behaviour such as self-biting, can cause bodily harm to the individual. Such stereotypic behaviour are learnt reinforced behaviour patterns, which can become permanent and difficult to extinguish (Mason, 1991). A recent meta-analysis of the effect of enrichment in zoos found that stereotyped behaviour was often reduced with enrichment provisions, but never abolished completely (Swaisgood & Shepherdson, 2006). Thus, stereotypies, which may simply be used as a short-term coping mechanism under certain circumstances (e.g. relocation, Hill, 2004; Mason, 1991), can become permanently ingrained into the behavioural repertoire of the animal.

Abnormal behaviour and stereotypies are obvious, observable behavioural patterns indicating stress in an individual, however other, harder to distinguish changes in a species-specific behavioural repertoire can also be useful to indicate the welfare of an individual. Social and solitary play, for example, occur when an individual has time to pursue extra activities (Bateson, 2005). In the wild in times of stress due to food shortage, or death of a caregiver, play behaviour decreases in NRI primates (reviewed by Fagen, 2002). Likewise, increased stress in the environment, caused by overcrowding or increased competition for food may also lead to increased aggression and reduced tolerance of other group members (Broom & Johnson, 1993). Conversely, captive primates may become apathetic in conditions under which they have no control, or under forced separation from other group members. This is typified by reduced activity and a lack of interest in the environment and can be an indicator of depression (Broom & Johnson, 1993).

Understanding the welfare issues surrounding captive primates is essential for the appropriate social development of NRIs. Reducing the stress of a captive primate can have many positive effects, such as increasing effective breeding, lifespan and cohesion within a social group. Less stressed captive primates are considered to be better subjects in laboratory experiments, more naturalistic exhibits in zoos and better candidates for conservation programmes (Wolfensohn & Honess, 2005).

7.1.4 Ape peer groups in sanctuaries

Peer groups were previously introduced as sufficient social environments in which species-typical normal development can develop (Bloomsmith et al., 2006). Peers provide an appropriate social context for correct social development and indicate that the presence of adults may not be necessary to learn species-specific skills, although currently there is a lack of data to show this effect.

In chapter 4, it was shown that western gorillas form a spatially robust proximate orientation in breeding groups. Peer groups provide the opportunity to investigate whether a comparable social structure emerges in the absence of adults. However, most peer groups in captivity are composed of two or three individuals, who are often not kept together for the whole day and upon sexual maturity, are housed in different social formations (Porton & Niebruegge, 2006). The opportunity for such a studies however is now emerging, using the large ape peer groups rescued from the bushmeat trade and held in African sanctuaries.

Increased access to forest habitat through road development and the extension of logging concessions across Central Africa have led to increased hunting of native fauna (Tutin et al., 2005). In addition, hunting with firearms for ape meat has increased to supply the demand for bushmeat in African cities and overseas (Wilkie & Carpenter, 2001). NRI apes, captured upon the death of their parents, but considered too small to kill for meat, are generally taken to villages or sold in markets as pets (Farmer, 2002). Under the CITES regulations for the trade in endangered species, it is illegal to either keep an ape as a pet or remove it from its native country (CITES, 1979). Thus, apes found alive in markets or villages are confiscated by government officials and placed in the care of an in-country sanctuary. Over the past ten years, as regulations for the protection of apes have become more frequently enforced, NRIs have been confiscated and the number of captive apes, along with the number of sanctuaries in Central Africa, has increased (Farmer, 2002). In 2000, to co-ordinate the sanctuaries' efforts and represent primate sanctuaries across Africa, the Pan African Sanctuary Alliance (PASA) was created. In 2006, it had 18 sanctuary members (PASA, 2006) and in 2005 held 711 chimpanzees, 69 gorillas and 44 bonobos.

NRI apes arriving at a sanctuary generally suffer from anxiety and depression due to the forced separation from the mother and social group coupled with insufficient treatment prior to arrival (Farmer, 2002). From earlier studies, it would be predicted that such social deprivation in infancy may cause behavioural and physiological changes in development, which may lead to a predisposition for the development of stress-related disorders, notably depression (Sanchez et al., 2005). In addition, many have physical injuries from gun shot wounds, parasitic infections and dehydration/diarrhoea from inadequate food consumption (Farmer, 2002). Usually, individuals have suffered unmeasured stress from being taken from the forest, kept in a village, transported and kept in isolation for days or sometimes years. Upon arrival at a sanctuary, individuals need first to be medically attended to in quarantine before being rehabilitated through the introduction into similar-aged peer groups, where they are raised to adulthood. The age of newly confiscated apes is determined by veterinarians, based on tooth emergence and for very young apes, size of the individual. However, these methods can be inaccurate, particularly with apes that have been malnourished for a long period, affecting growth and tooth emergence patterns. Stressful situations, loss of an attachment figure, peer group living and being in captivity have all been demonstrated in laboratories and zoos to bring about abnormal behaviour and at times, ineffectual relationship formation (Bloomsmith et al., 1994; Meder, 1992). Similarly, in the sanctuaries NRI apes may develop abnormal behaviour, which is predicted to affect their rehabilitation, socialisation into a peer group and social development.

The aims of PASA are to provide a safe and secure environment, where primate welfare is prominent. The eventual aim is for each PASA sanctuary to be able to release some individuals back into protected native habitat (PASA 2006). However, little research to date seeks to understand the effects of social separation and being raised in a peer group on normative social development in the sanctuary context (but see Farmer *et al.*, 2006), nor indeed, the level of social adjustment in adult sanctuary apes compared to their wild counterparts. Research into abnormal behaviour, social development and the social functioning of peer social groups under sanctuary conditions, is essential to implement effective strategies to raise the sanctuary population and to apply effective management procedures to decrease the incidence of aberrant behaviour. For an enriched captive life in a peer group, or to be considered for release into the wild, sanctuary apes need to develop correct social functioning, be able to cope with stressful situations and eventually to breed and raise young successfully.

The following chapter uses data from peer-raised gorillas in sanctuaries and compares them by life-stage to parent-raised gorillas to determine differences in development brought about by early stress and peer-group living. Specific details pertaining to the sanctuary NRI can be found in Appendix 6 & 6 deemed necessary since unlike the parent-raised NRIs each has had a different early life experience.

7.2 Aims

- To compare how the spatial orientation and social structure of NRIs in peer groups differ from NRIs in breeding groups.

- To assess behavioural disparity in parent-reared verses peer-reared NRI gorillas, using behaviour that has been established to represent stress and abnormal characteristics.

- To investigate if peer groups are adequate social environments for the development of normal social development following periods of social deprivation.

7.3 Methods

Limbe Wildlife Centre (LWC) and Cameroon Wildlife Aid Fund (CWAF), both in Cameroon, have been established for over ten years and are now financially supported by external institutions, Pandrillus Foundation, USA and Bristol Zoo, U.K respectively. Both sanctuaries, from their founding have been reliant upon charity funds, which have led to periods of financial hardship and regular changes in management staff and long-term volunteers. As a result, few records exist of management practice or details of the previous circumstances of confiscated animals, which limits the demographic information available to understand the impact of the bushmeat trade on peer-raised gorillas. Data collection methods followed the same protocol as for parent-raised gorillas and are detailed in Chapter 2.

7.3.1 Statistical analysis

7.3.1.1 Spatial proximity and group structure in peer-raised gorillas

Following the analyses described in Chapter 4, the proximity relationships of the gorillas at each of the sanctuaries were mapped using proximity (0-5m) scan data from NRI gorillas (Appendix 3) and using the PROXSCAL programme.

7.3.1.2 Comparing developmental disparity between parent-raised and peer-raised gorillas using a behavioural model

The justification for the use of the specific statistical analysis to determine life-stage using behavioural variables is described in detail in the methods section of Chapter 3. Four behavioural variables were used in the analysis, these were mean values for each NRI for feeding (frequency/hour), lying (duration/hour), locomotion (duration/hour) and social play (frequency/hour).

A life-stage category (based on Chapter 3) was estimated for each sanctuary gorilla (Table 7.1), based on the NRI gorillas' estimated age from the sanctuary records. Behavioural disparity between parent and peer reared gorillas were detected using non-parametric statistics as the data were non-normally distributed and negatively skewed.

7.3.1.3 Comparing the behavioural disparity of parent-raised and peer-raised gorillas.

Using a range of behaviours stated across the primate literature that change in frequency or duration in times of stress, the peer-raised gorillas were compared to the parent-raised gorillas by life-stage to determine the effect of peer group living at each developmental stage. A value for abnormal behaviour and human orientated behaviour were derived by adding all occurrence of abnormal behaviour or human orientated (Table 2.4) together to give two values per NRI. The frequency of agonism, display behaviour and solo play and the duration of self-grooming and social play (Table 2.4) were used as median tendencies. All information on sexual competency was taken from ad hoc notes and scan samples taken during data collection (Table 2.4).

Table 7.1 - Estimated age and associated life-stage of NRI peer-raised gorillas in Cameroonian sanctuaries.

Sanctuary Group	Name of gorilla	Estimated age (years)	Estimated life-stage[1]
LWC	Ak	5	Juvenile ♀
	Ar	6	Adolescent ♂
	Bt	6	Adolescent ♂
	Be	9	Blackback
	Ch	11	Blackback
	Pi	8	Adult ♀
	Tw	8	Adult ♀
CWAF group 1	Av	8	Adult ♀
	Bb	7	Adolescent ♂
	Ja	8	Adult ♀
	Ku	7	Adolescent ♂
	Nm	7	Adolescent ♂
CWAF group 2	Mv	3	Old infant
	Nk	5	Juvenile ♂
	Nu	3	Old infant
	Ss	4	Juvenile ♂

[1] based on estimated age and using the classification tested in Chapter 3

Each peer-raised gorilla was compared to all parent-raised gorillas in the current study (Chapter 3) of the same estimated life-stage to determine if, based on behavioural variables, the peer-raised gorillas' estimated life-stage was justified or if re-classification into a different life-stage was more appropriate. In preparation for this, the mean of the four standardised behavioural variables (Feeding- freq/hr, Lying- dur/hr, Locomotion- dur/hr, Social Play- freq/hr) used in Chapter 3 to determine life-stage in parent-raised gorillas were compiled and transformed where necessary (see Chapter 3) for each of the peer-raised gorillas. The mean calculated value for each sanctuary gorilla was added into a discriminative analysis along with the equivalent data for parent-raised gorillas of the same life-stage, which were used as a comparative base. Peer-raised gorillas that were signalled in the discriminative analysis as belonging to the incorrect life-stage were considered for re-classification. Reclassification was determined by the appropriateness of the life-stage category that the discriminative analysis proposed. In addition, analyses were conducted to determine if peer-raised gorillas differed behaviourally from parent raised captive gorillas of the same life-stage. To do this, a t-test was conducted on the two discriminative analysis functions that were produced to represent the four co-varying behaviours, where Function 1 represents a scale of maturity and Function 2 represents a measure of activity.

7.3.2 Comparing the behaviour of peer-raised and parent-raised gorillas

To study developmental differences, as a result of being raised with peers as opposed to in a family group, a behavioural comparison of peer-raised and parent-raised gorillas of each life-stage was conducted (individuals indicated in Table 7.2). Behaviour to be analysed was chosen as it had been shown in published studies ((Bloomsmith et al., 2006; Bloomsmith et al., 2003; Brent & Bode, 2006; Gold, 1992; Meder, 1989a, 1994; Porter, 2001) to illustrate atypical social development in other primates in captivity or those raised in peer groups. Abnormal and stereotypic behaviour was recorded and defined as stated in Chapter 2. Human-orientated behaviour was described as that in which the focal gorilla watches, follows or tries to interact with the Keeper (who typically was involved in the hand-rearing process and daily feeds), and in doing so ceases all attention to the social group. Agonism, display, self-groom and play behaviour were all compared between peer-raised and parent-raised gorillas of the same life-stage. Primates in peer groups have been previously shown to have altered frequencies of occurrence of such behaviour, compared to parent-raised primates (Brent & Bode, 2006; Gold, 1992; Meder, 1989a; Nakamichi & Kato, 2001; Novak & Sackett, 2006; Spijkerman et al., 1997). Sexual competence was determined by watching copulations and assessing the success of intromission and assessing pregnancy success since data collection was completed.

Table 7.2 - NRI subjects of comparable life-stage in parent and peer-raised groups

Life-stage category	Peer-raised gorillas	Parent-raised gorillas
Old infant **(N = 2, 3)**	Mv ♀, CWAF Nu ♀, CWAF	Gy ♀, Apenheul Kw ♀, La Vallée Si ♀, Burgers'
Juvenile female **(N = 1, 3)**	Ak, LWC	Ne, Apenheul Ny, Burgers' Zo, Apenheul
Juvenile male **(N = 2, 5)**	Nk ♂, CWAF Ss ♂, CWAF	Bd, La Vallée Bg, Zurich Bs, Zurich Kb, La Vallée Li, Burgers'
Adolescent male **(N = 4, 5)**	Ar, LWC Bb, CWAF Bt, LWC Ku, CWAF Nm, CWAF	Az, Zurich Kd, Apenheul Mk, Apenheul Vi, Basel Vz, Basel
Blackback **(N = 2, 2)**	Be, LWC Ch, LWC	Mb, Apenheul Uz, Apenheul
Adult female **(N = 4, 3)**	Av, CWAF Ja, CWAF Pi, LWC Tw, LWC	Bi, Apenheul Ki, Apenheul Sh, Burgers'

N = peer-raised, parent-raised gorillas.

7.4 Results

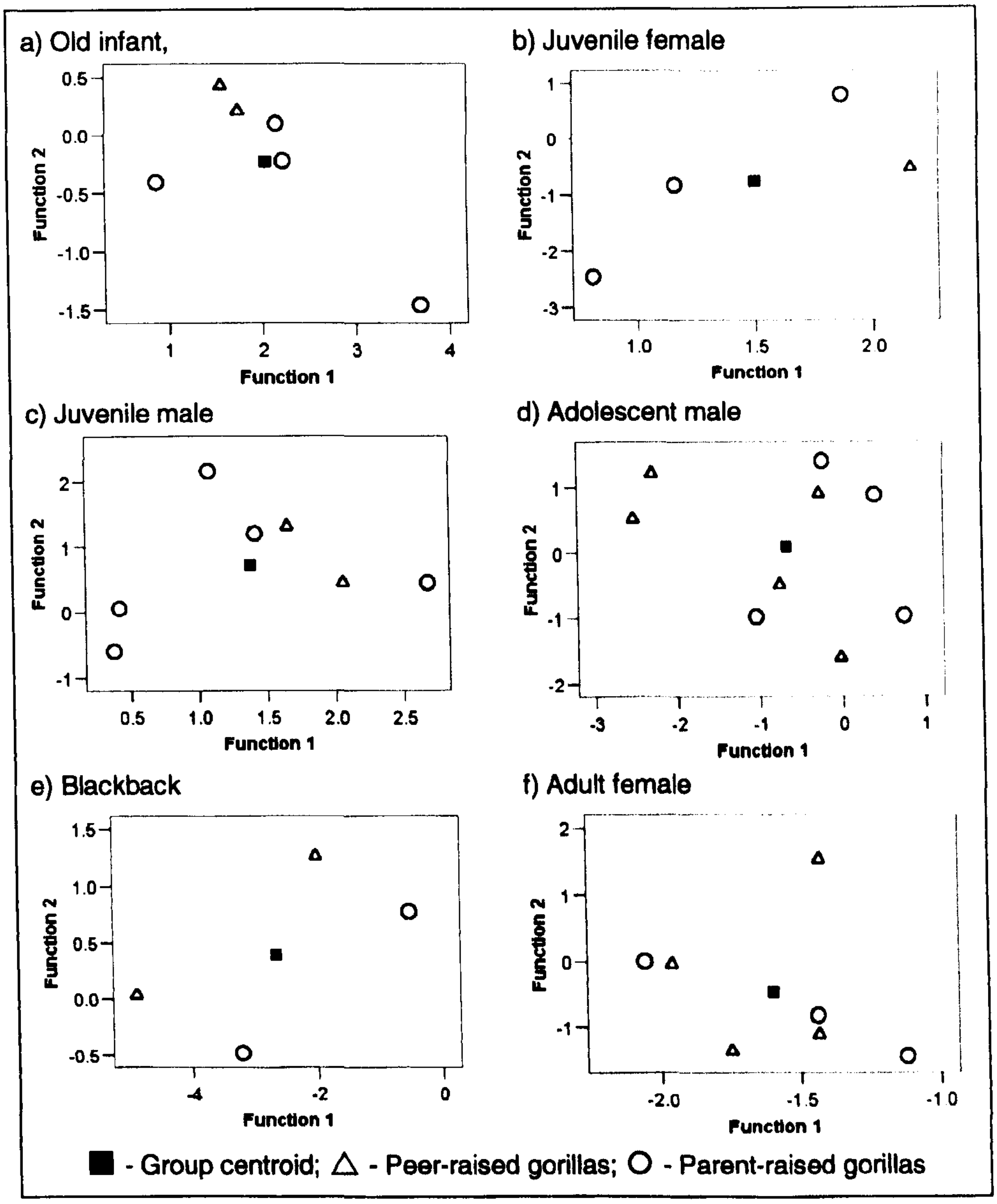
7.4.1 Determining behavioural disparity between parent-raised and peer-raised gorillas

A discriminative analysis was conducted on four behavioural variables following the methods of Chapter 3. The following section of results uses separate group plots to illustrate the disparity in behaviour between peer-raised and parent-raised gorillas, by life-stage.

Overall, no significant behavioural differences were found on either Function 1 (depicted as maturity) or Function 2 (depicted as activity) between parent raised and peer-raised gorillas in any life-stage (Table 7.3). However, disparity between maturity and activity levels were found between individuals within these life-stages. Old infant peer-raised females had a tendency to score higher on Function 2 than parent-raised gorillas (Figure 7.1a). Similarly, the peer-raised juvenile female scored higher on Function 1 than other parent-raised juvenile female gorillas (Figure 7.1b). Two peer-raised adolescent male gorillas scored lower on Function 1 and higher on Function 2 than other parent-raised or peer-raised gorillas (Figure 7.1d), whereas one peer-raised adult female gorilla scored higher on Function 1 than the other adult female (Figure 7.1f). Although disparity occurred, NRI gorillas in the sanctuaries were not found to be behaviourally different from gorillas in captive family groups.

Table 7.3 - Comparing the function values of peer-raised and parent-raised gorillas, by life-stage using a Kolmogorov-Smirnov test.

Life-stage	N (Parent-raised, peer-raised)	Function 1		Function 2	
		Z	***P***	***Z***	***P***
Old infant	2, 4	0.86	0.44	1.16	0.14
Juvenile female	3, 1	-	-	-	-
Juvenile male	5, 2	1.20	0.12	0.72	0.68
Adolescent male	4, 5	1.12	0.16	1.12	0.16
Blackback	2, 2	0.5	0.96	0.5	0.96
Adult female	3, 4	0.98	0.29	0.70	0.79



a) Old infant,

b) Juvenile female

c) Juvenile male

d) Adolescent male

e) Blackback

f) Adult female

Figure 7.1 - Spatial representations of peer-raised and parent-raised gorillas, based on four significant co-varying behavioural composites, arranged by life-stage

7.4.2 Spatial distribution and relationship formation within peer-raised gorillas.

PROXSCAL MDS was successfully applied to the durational proximity data (contact – 5 metres) for all focal gorillas in the three peer-raised gorilla groups. The resulting co-ordinates was presented in Tables 7.4, 7.5, 7.6, arranged alphabetically. A two-dimensional configuration per gorilla group, which gives the nature of epistemic space were proposed in Figures 7.2 - 7.4. A criterion using a stress value of 0.004 and a DAF of 0.98 or above was adopted to ensure a high degree of accuracy, following Kruskal (1964).

7.4.2.1 CWAF Group 1

The CWAF Group 1 associated spatially around the adolescent male (AM1) (Figure 7.2). The three adult females and the other two adolescent males (AM 1 and 2) were spatially separated from each other, in a circle around AM1. Spatial orientation was not linked by age or sex of the adolescent. The gorillas did not have any specific close associations, but were cohesive as a group, with no individuals outlying from the social group.

Table 7.4 - MDS scores of gorilla proximity for the CWAF group 1 gorillas.

Gorilla	Life-stage categorisation	Co-ordination	
		Dimension 1	**Dimension 2**
Av	AF1	.625	-.279
Bb	AM1	.003	.078
Ge	AF2	-.488	.599
Ja	AF3	-.635	-.201
Ku	AM2	.604	.444
Nm	AM3	-.110	-.641

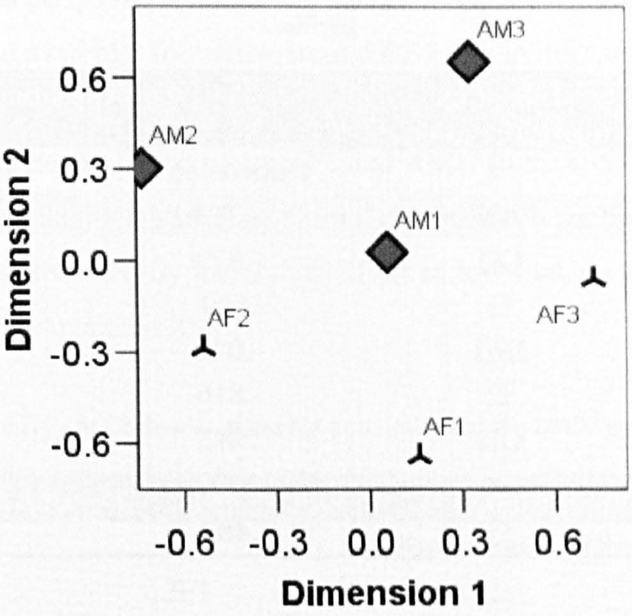


Figure 7.2 - A two-dimensional MDS configuration for proximity values among the gorillas in the CWAF group 1. S-stress = 0.002. DAF = 0.999

7.4.2.2 CWAF Group 2

In this group, the Keeper was added into the MDS configuration as his constant presence inside the enclosure likely influenced the spatial orientation of the other gorillas. CWAF group 2 associated spatially around the juvenile male (JM1, Figure 7.3). The remaining juvenile male and the two female old infants were equally spaced around JM1, whereas the infants (I1, I2, and I3) were spatially arranged towards the Keeper. Two infant gorillas (I2, I3) remained in close proximity to each other; likewise the two female old infants (OI1, OI3) were found to be in close association, which can be explained as they were confiscated together from a village and it was presumed that they had been together for a few days. The juvenile male (JM2) was spatially the furthest away from both the Keeper and the infant gorillas.

Table 7.5 - MDS scores of gorilla proximity for the CWAF group 2 gorillas.

Gorilla	Life-stage categorisation	Co-ordinations	
		Dimension 1	Dimension 2
Keeper	KE	-.213	-.430
Mv ♀	OI1	-.829	.046
Nc ♀	I1	.549	-.489
Nk ♂	JM1	-.025	.136
Nn ♀	I2	-.816	-.033
Nu ♀	OI3	.582	.312
Ss ♂	JM2	.263	.945
Ye ♂	I3	.489	-.488

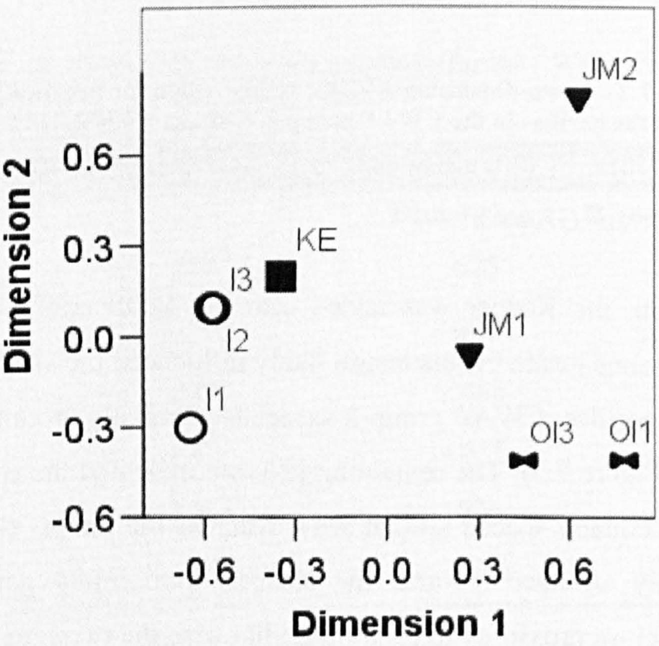


Figure 7.3 - A two-dimensional MDS configuration for proximity values among the gorillas in the CWAF group 2. S-stress = 0.004, DAF = 0.999

7.4.2.3 LWC

Gorillas associated around a blackback gorilla (BB1). Interestingly, this was not the largest, or estimated oldest blackback gorilla in the group (Figure 7.4). The other blackback gorilla (BB2) often behaved agonistically towards individuals in the group (Appendix 1) and in the spatial plot, was found situated on the periphery of the social group (Figure 7.4). The adult female gorillas formed a circular formation around BB1, but in the case of AF2, AF3, at a large distance from BB2. Close associations were found between two of the youngest members of the group, JF1 and AM2. Both AF5 and AM1 were found close together, slightly away from the central core of the group. These gorillas were considered by the author (JEH) as low ranking and were often chased by BB2 (Appendix 2).

Table 7.6 - MDS scores of gorilla proximity for the LWC gorillas.

Gorilla	Life-stage categorisation	Co-ordinations	
		Dimension 1	**Dimension 2**
Ak	JF1	-.222	-.498
Ar	AM1	.816	-.270
Bt	AM2	-.065	-.241
Be	BB1	-.125	.230
Br	AF1	-.475	.471
Ch	BB2	.739	.715
Ju	AF2	-.764	.158
Ny	AF3	-.818	-.217
Pi	AF4	.349	.188
Tw	AF5	.565	-.536

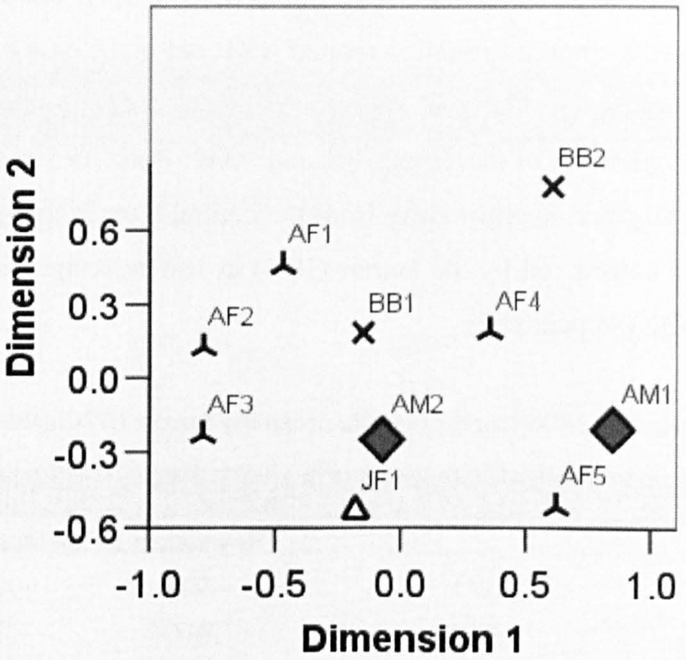


Figure 7.4 - A two-dimensional MDS configuration for proximity values among the gorillas in the LWC group. S-stress = 0.04, DAF = 0.98

7.4.3 Comparing the behaviour of peer-raised and parent-raised NRI gorillas.

For the purpose of this analysis, play, display behaviour, self-grooming, abnormal and human-orientated behaviour were compared between peer-raised and parent-raised NRI gorillas to determine the specific difference in social development of NRI gorillas of each sex and life-stage. The behaviour tested is reported in the literature to indicate stress disruption in social development due to separation from the mother; atypical social group and living environment (see Methods). When sample size allowed, additional statistical comparisons were made between parent-raised and peer-raised gorillas of the same life-stage, these are shown in Figures 7.5 and 7.7 by an asterisk (*) .

Abnormal behaviour was recorded in 14/16 peer-raised gorillas, who were categorised to range from old infancy to blackbacks. No data were collected from female gorillas who were predicted to be over 8 year of age, or males predicted to be over 11 years of age. Of those who did not produce abnormal behaviour one was a juvenile male at LWC and the other an adult female at CWAF. For a breakdown of the specific abnormal behaviour displayed by each individual, see Table 7.7. Gorillas generally exhibited more than one abnormal behaviour style (9/14). There was a tendency for some abnormal behaviour to occur specific to social group, such as coprophagy, digit sucking and masturbation at CWAF and plucking at LWC (Table 7.7). In adolescent males, abnormal behaviour were found to be higher for males who were peripheralised from the central cluster, (see Figures 7.2 and 7.4, median frequency/hour = 4.33), compared to those in the centre of the social group (median frequency/hour = 0.53). Conversely, in the CWAF Group 2, the central male displayed more abnormal behaviour (median frequency/hour 1.56) than the peripheralised male (median frequency/hour = 0.89, Table 7.3, Figure 7.8). Human-orientated behaviour was recorded in all NRIs raised in peer groups.

Table 7.7 - Abnormal and stereotypic behaviour recorded for each peer-raised gorilla

Sanctuary	Code	Gorilla	Abnormal behaviour									Total abnormal behaviour median (freq/hr)
			Coprophagia	Clasping	Digit Sucking	Masturbation	Nipple suckling	Plucking	Posterior presenting	Regurgitation & reingestion	Repetitive behaviour	
CWAF adolescent	AF1	Av										0
	AM1	Bb	✓			✓			✓			0.56
	AF3	Ja	✓								✓	0.07
	AM2	Ku	✓		✓						✓	1.64
	AM3	Nm			✓	✓						2.06
CWAF infant	OI1	Mv♀	✓							✓		0.6
	JM1	Nk♂	✓	✓	✓	✓				✓	✓	1.56
	OI2	Ny♀	✓									0.13
	JM2	Sh♂								✓		0.89
LWC	JF1	Ak					✓	✓				0.13
	JM1	Ar										0
	JM2	Ba						✓		✓		0.8
	BB1	Be						✓				0.5
	BB2	Ch						✓			✓	4.54
	AF4	Pi						✓		✓		6.7
	AF5	Tw								✓		0.13

Abnormal behaviour and human-orientated behaviour were found to be highly correlated, across all parent-raised and peer-raised gorillas (Spearman's Rho, $\rho = 0.79$, N = 38, $P = <0.001$, Figure 7.5), though levels of both were low in parent-raised groups. In the peer groups, the frequency of abnormal behaviour and human-orientated behaviour did not significantly change with estimated age of the NRI (abnormal behaviour, $\rho = -0.8$, N = 16, $P = 0.77$; human-orientated, $\rho = 0.364$, N = 16, $P = 0.17$, Figure 7.5), or between the sexes (abnormal behaviour, Kolmogorov-Smirnov Z = 0.69, N = 16, $P = 0.72$; human-orientated, Z = 0.57, N = 16, $P = 0.91$). However, at CWAF, males were found to have a significantly higher frequency of abnormal behaviour than females (Z = -2.2, N = 9, $P = 0.03$), although no significant difference in human orientated behaviour was found between the sexes at CWAF (Z = -1.23, N = 9, $P = 0.29$). No significant difference in abnormal behaviour was found between groups (Kruskal Wallis $\chi^2 = 0.22$, N = 16, $P = 0.90$), however in human-orientated behaviour the CWAF group 1 reacted to and attracted the attention of Keepers more than the other two groups (Figure 7.6, $\chi^2 = 6.32$, N = 16, $P = 0.04$,).

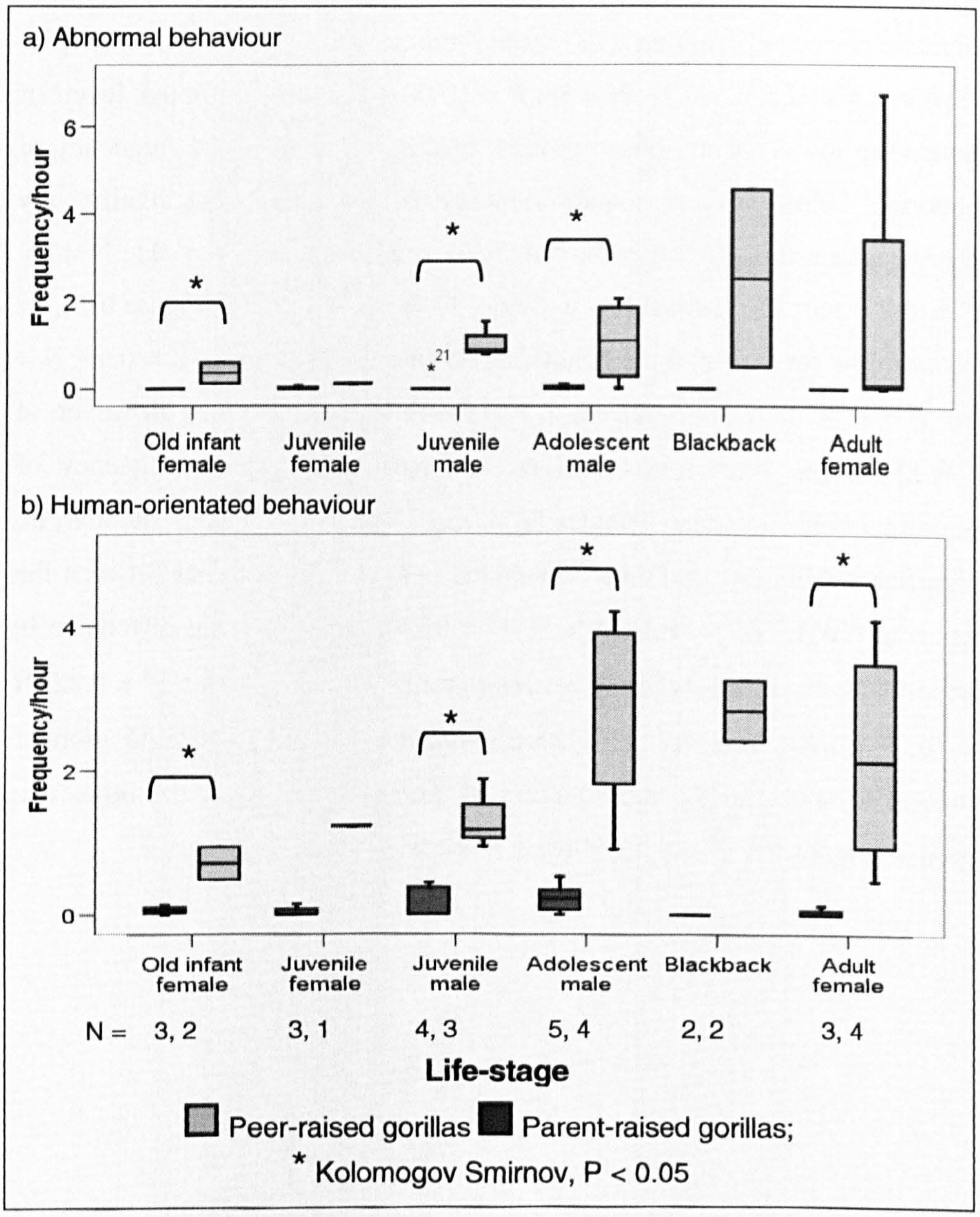


Figure 7.5 - Comparison of abnormal and human-orientated behaviour between parent-raised and peer-raised gorillas in each life-stage.

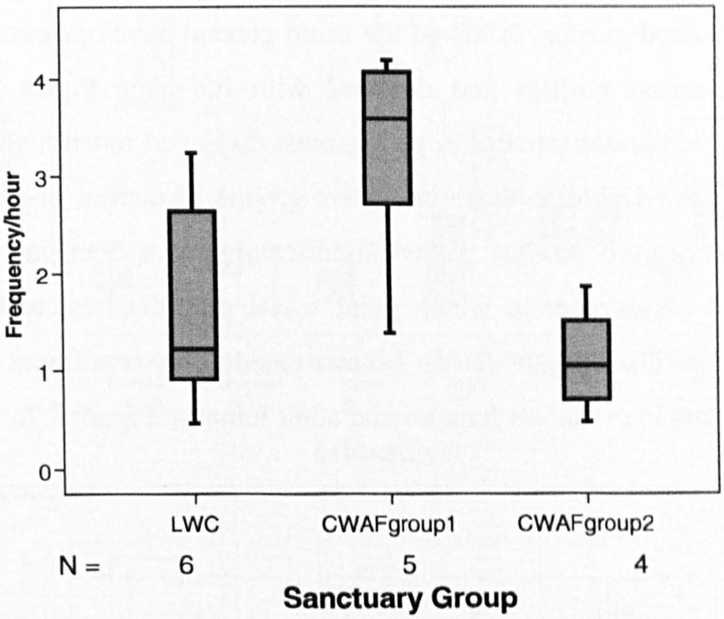


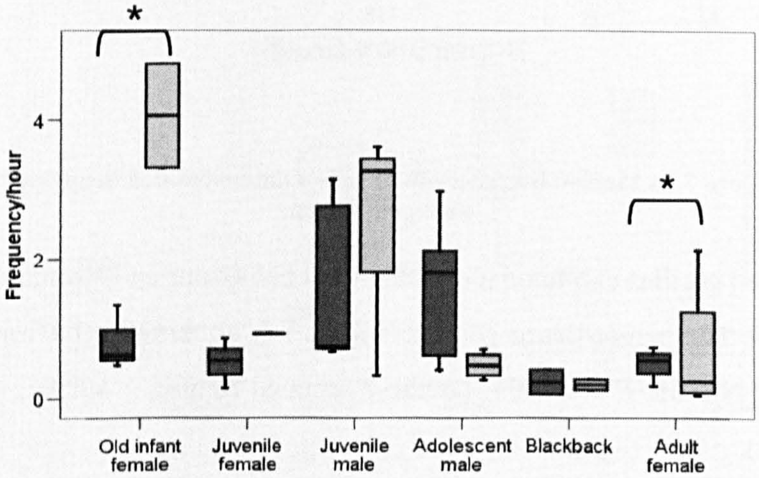
Figure 7.6 - Median frequency/hour of human-orientated behaviour in each peer group.

Peer-raised gorillas exhibited more abnormal behaviour and human-orientated behaviour than parent-raised gorillas (Figure 7.5, abnormal behaviour freq/hr, Z = 2.25, N = 38, *P* = <0.001; human-orientated freq/hr, Z = 2.91, N = 38, *P* = <0.001).

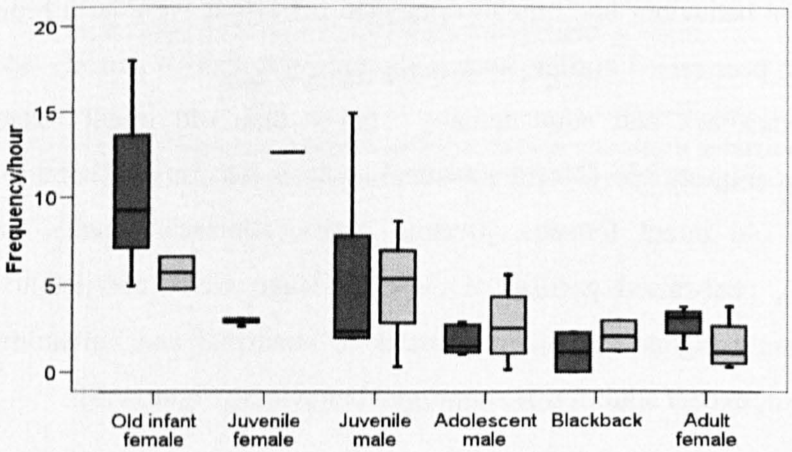
Abnormal behaviour and human-orientated behaviour were both found to be higher in peer-raised gorillas later in the pre-reproductive period - adolescent male, blackback and adult female - rather than old infant females and juveniles (Figure 7.5). Where statistical analysis was possible due to sample size (in old infant females, juvenile males, adolescent males and adult females), peer-raised gorillas of each life-stage were recorded to exhibit significantly higher median frequencies of abnormal and human-orientated behaviour, except adult female abnormal behaviour (Figure 7.5).

When comparing rates of species-specific behavioural repertoires (Figure 7.7), self-grooming behaviour was found to be significantly higher in peer-raised gorillas compared to parent-raised gorillas of the same life-stage, Figure 7.7c. In peer-raised gorillas, self-grooming was higher in the early pre-reproductive period, but was reduced to less than parent-raised gorillas in the later pre-reproductive period. Agonism, display behaviour, social and solo play in peer-raised gorillas followed the same general developmental pattern as in parent-raised gorillas and declined with life-stage Figure 7.7b,d,e. Interestingly, old infant females in peer-groups displayed much higher levels of agonistic behaviour than those in captive groups. However, in social play behaviour peer-raised gorillas played significantly more than parent-raised gorillas, until adolescence at which point social play declined to less than parent-raised gorillas, (Figure 7.7d). Likewise, solo play was found to occur significantly less in old infant females and adult females, Figure 7.7e.

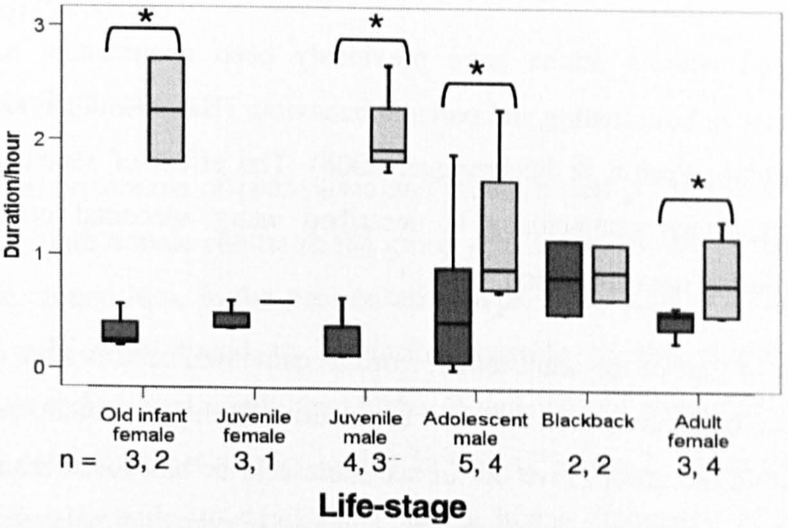
a) Agonism



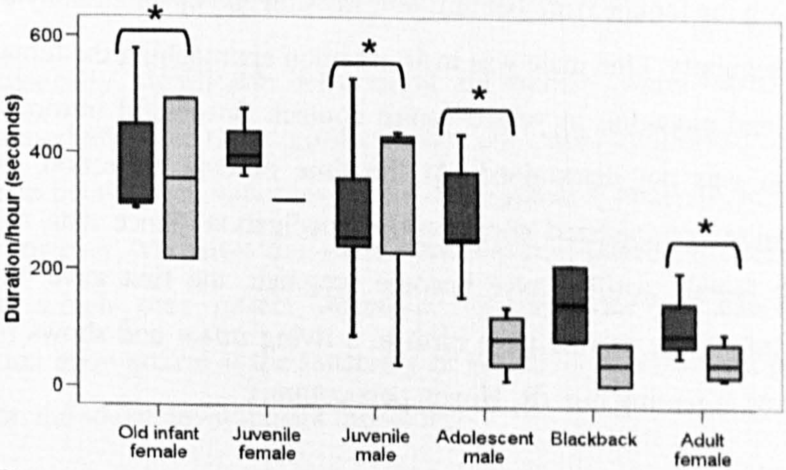
b) Display behaviour



c) Self grooming



d) Social Play



e)Solo Play

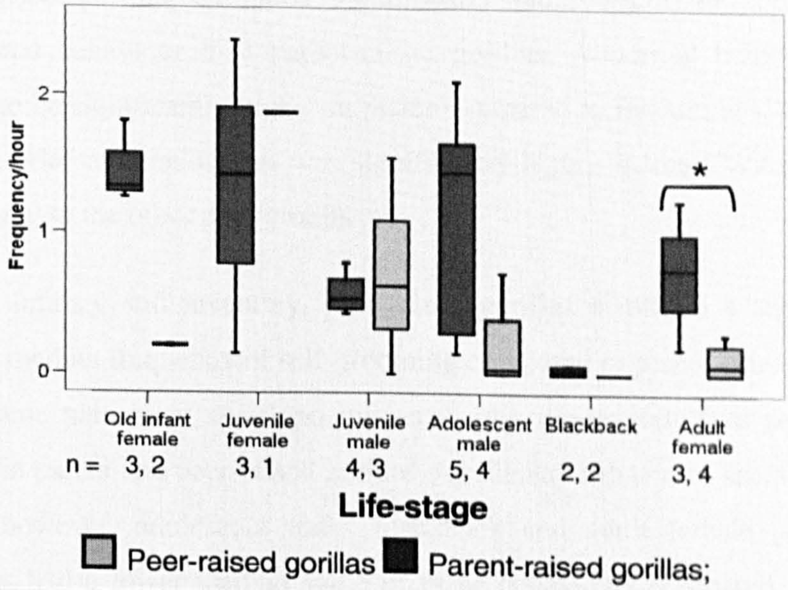


Figure 7.7 - A comparison of. a) agonism, b) display behaviour, c) self-grooming, d) social play and e) solo play; between parent-raised and peer-raised gorillas of each life-stage. * Wilcoxon's Rank Sum, P < 0.05

7.4.4 Sexual competency

Apes raised without adults have previously been documented to show inadequacies in both mating and parental behaviour (Bloomsmith et al., 2006; Meder, 1989b; Porton & Niebruegge, 2006). The effect of sanctuary peer groups on sexual competency is described using anecdotal copulations recorded during data collection.

Three out of four of the adult female gorillas came into oestrus once or more during data collection, each solicited copulations from individually preferred males within the group. Five out of six adolescent or blackback males were witnessed to engage in copulations, 4/5 engaged in correct copulatory stance, approaching the female from behind; intromission and ejaculation by the male occurred regularly. One male was insistent upon approaching the female from the front and engaging in ventro-ventro contact. Successful intromission or ejaculation was not determined. At the time of data collection, no adult females were administered contraceptive medication. Since data collection two adult female gorillas have become pregnant, the first gave birth to a stillborn infant; the second gave birth to a living infant and shows maternal competence in rearing him (R. Hogan pers comm.).

7.5 Discussion

7.5.1 Results summary

The spatial orientation of peer-raised and parent-raised gorillas was found to be similar with a male central to the group and the remainder of the gorillas clustered around him. In the peer-raised groups, males similar in age to the central male were found to be further outside of the cluster and in adolescence, these males exhibited higher frequencies of abnormal behaviour than the central male. Contrary to this, in CWAF group 2, where the central male was a juvenile, this individual had a higher frequency of abnormal behaviour than the peripheral male, of the same life-stage.

No statistically significant behavioural differences were found between parent-raised and peer-raised gorillas, when compared by life-stage, using the composite behavioural variables on the discriminative analysis. In some life-stages however, variation did exist between peer-raised and parent-raised gorillas, which may reflect mistaken life-stage due to inaccurate age estimation upon arrival at the sanctuary or the effect of stress and peer group living on the social development trajectory.

Peer-raised gorillas exhibited significantly more abnormal and human-orientated behaviour than parent-raised gorillas. Abnormal behaviour was found to be significantly higher in males compared to females at CWAF, and human-orientated behaviour was significantly higher in the CWAF group 1 compared to the other peer groups.

In old infancy and juvenility, peer-raised gorillas displayed a significantly higher median frequency of self-grooming compared to parent-raised gorillas. The same pattern of development across the pre-reproductive period was found in parent and peer-raised gorillas, for display behaviour, social and solo play; however, adolescent male, blackback and adult female peer-raised gorillas had a lower median value of these behaviours compared to parent-raised gorillas.

Four out of five males engaged in a correct copulation position, engaging in intromission and ejaculation. Only one male gorilla showed a different style in his approach to copulation. The female who successfully gave birth since this study is successfully raising her infant, the father of the infant remains unknown.

7.5.2 Social development of NRIs in peer groups

The results from this chapter support the reviewed findings of Brent & Bode (2006) and Novak & Sackett (2006) and the study of peer-raised chimpanzees (Spijkerman et al., 1997), that peer groups are sufficient social settings for the occurrence of species-specific social development in primate species. Further to this, sanctuaries in native habitat country, raising gorillas in peer groups after immeasurable stress from capture and confiscation, are adequate environments to allow the full range of gorilla behaviour to occur. However, infants which have undergone extreme stress over a prolonged period are reported to be more likely to become predisposed to high basal blood pressure, be prone to stress-related disorders and to react in an extreme manner to novel situations (Pryce et al., 2004; Sanchez et al., 2001), which can not be tested here.

NRI primates grow through predictable species-specific behavioural, physical and physiological patterns (Pereira & Altmann, 1985). Each distinct stage of development can be defined into a life-stage, which in sexually dimorphic primates differs between males and females in the duration and pattern of the pre-reproductive period (Leigh, 1995; Taylor, 1997). Comparing individuals raised in different social environments by life-stage allows an understanding of disparity in social development due to social environment. In this study, the overall behavioural trajectory of parent-raised and peer-raised gorillas was not found to differ significantly. To understand overall behavioural discrepancies in social development between life-stage groups, comparing similar life-stages is highly effective, but it did not allow a detailed understanding of individual behavioural differences between different life-stages or rearing strategies, or response to stress in infancy. The following discussion compares behaviour, which has been documented in previous studies of peer groups to differ from parent-raised groups, due to stress or social environment, such as play, agonism, self-groom, sexual behaviour and social relationship formation. This comparison then allows an assessment of how peer-raised gorillas in sanctuaries compare to the other peer-raised individuals in laboratories and zoos and parent-raised gorillas in breeding groups. Understanding behavioural differences brought about due to stress and deprivation is beneficial in managing the gorillas in peer-groups over the course of their lifetime and particularly if release back into the wild is to be considered.

7.5.2.1 Behavioural disparity between parent and peer raised NRIs

Play behaviour is considered to be an essential component of NRI social and skill development across the pre-reproductive period (Bateson, 2005; Fagen, 2002). Its absence in wild NRI primates is documented in cases where the individual is under conditions of extreme stress (Dettling et al., 2007; Fagen, 2002; Sanchez et al., 2001). Greatly reduced play behaviour in peer-raised gorillas compared to parent-raised gorillas at each life-stage would likely indicate high levels of stress. In previously studied peer groups rates of social play are comparable to parent-raised apes (Porton & Niebruegge, 2006), but inappropriate use of display behaviour is common in peer-raised gorillas (Gold, 1992). In this study, the same pattern of play development was found between parent and peer-raised gorillas in social play and in frequency of display behaviour across the pre-reproductive period. This suggests that the development between the two rearing conditions is indeed similar and indicates the absence of extreme stress in the peer-raised groups.

Although the general pattern of social play in peer-raised and parent-raised gorillas was found to be similar, in peer-raised gorillas the duration of social play was significantly higher than in parent-raised gorillas until adolescence at which point peer-raised gorilla play dropped to below that of parent-raised gorillas. An explanation may be that this is due to the apparent accelerated maturation of individuals in these life-stages, who were at this stage either sexually mature or competing for access to cycling females. In the parent-raised groups by comparison, males had less access to females due to the presence of the silverback and often, adult females were administered contraceptive medication to stop oestrus. In relation to social structure, the sanctuary peer-groups had a reduced age range of individuals thus there was no opportunity for these individuals to be solicited into play by younger gorillas. Play between NRIs of different life-stages with juvenile NRIs was common in parent-raised groups (see Chapter 6) and may explain why parent-raised gorillas in later NRI life-stages played until later in the pre-reproductive period.

An increase in agonistic interaction is a predictable reaction to stress in animals (Broom & Johnson, 1993). This coupled with a lack of mediation in the appropriate use of aggression by adult group members in the sanctuary environment, means that agonistic interactions would be expected to be higher in peer-raised NRIs. In addition, stress, coupled with the lack of parental support, can lead to a reduced tolerance of other group members which may in turn lead to the perpetrated use of agonism (Broom & Johnson, 1993). Other peer-raised studies have shown increases in agonistic interactions in infant gorillas (Gold, 1992) and in monkeys (Novak & Sackett, 2006). In this study, old infant females were found to engage in agonism significantly more than parent-raised old infant females. However, in other life-stage groups, agonistic interactions in peer-raised gorillas were not found to be significantly different from parent-raised gorillas. This may be due to the process of maturation mediating the use and purpose of agonism, or having spent longer in the same social group and having accepted a social position within the group hierarchy, which would reduce the need for conflict.

Increased self-grooming is also recognised as a behavioural response to stress (Broom & Johnson, 1993). Self-grooming in peer-raised gorillas, in this study and in the literature, was found to be significantly higher compared to parent-raised gorillas between infancy and juvenility (Gold, 1992; Meder, 1989a). However, the frequency of occurrence was not found to be significantly higher in peer-raised compared to parent-raised adolescent and blackback males or adult females in this study. This result was also found in a study of adolescent peer-raised baboons, where no significant species-specific behavioural differences were found between parent and peer-raised individuals from adolescence onwards (Brent & Bode, 2006). It would seem that younger peer-raised gorillas, who also exhibited higher agonistic interactions, either were under greater stress than older peer-raised gorillas, or compensated for a lack of maternal grooming through self-grooming behaviour.

Due to a limited sample size, it was not possible here to provide quantitative analysis of agonism and self-grooming behaviour between the sexes in old infancy and juvenility. Previous studies have shown that peer-raised gorilla males are more agonistic than females (Gold, 1992). Tentatively in this study, juvenile males were found to be more agonistic than the one juvenile female of this study but, in contrast, old infant females were found to be more agonistic than juvenile males. The rate of self-grooming however did not differ between old infant females and juvenile males. The difference may be due to these sanctuary gorillas living in larger social groups than the parent-raised gorillas, which has been shown to reduce agonistic behaviour, compared to peers raised in pairs (Brent & Bode, 2006).

Although anecdotal in nature, the records of copulation competency in older NRI peer-raised gorillas suggests that in these sanctuaries, the majority of individuals were developing normal sexual behaviour. The incidence of sexual incompetence recorded (1/5 males) across the two peer-groups holding adolescent males or blackbacks was lower than reported in other primate peer groups where, for example 46% of hand-reared chimpanzees, (Porton & Niebruegge, 2006) and 33% of hand-reared gibbons were found to be sexually incompetent (Mootnick & Nadler, 1997). Likewise, 36% of hand-reared gorilla males were not witnessed to copulate with females, compared to 88% of parent-reared gorillas which were recorded to instigate copulations (Meder, 1989b). To reduce sexual incompetence in chimpanzees Porter (2006) found that hand-reared chimpanzees should be introduced to conspecifics by 19 months of age. The lower incidence of sexual incompetence in the sanctuary peer-raised gorillas, compared to the zoo peer-raised gorillas supports these findings. Sanctuary gorillas were all raised in species-typical social groups and were mostly introduced into a peer group or to conspecifics before 19 months of age.

The main factor influencing maternal competency in captive zoo apes is whether the individual was raised by the mother or has witnessed other females caring for infants (Abello & Colell, 2006). A similar finding has been reported in female chimpanzees, where a third of those raised by their mothers for at least a year rejected infants, compared to two-thirds of females who were separated from their mothers before six months of age (Bloomsmith et al., 2003). Although only one infant born to a peer-raised female has survived in the sanctuary groups to date, it would be expected that females, who like the sanctuary males, were raised by their mothers for a period and then immersed into peer groups at the youngest possible age would likely show fewer maternal deficiencies.

7.5.2.2 Spatial proximity in peer groups

Recent physiological and behavioural studies have found mammals to be predisposed to form social relationships from infancy (Broad et al., 2006; Curley & Keverne, 2005). Gorillas are found to form specific patterns of proximate association in breeding groups (Nakamichi & Kato, 2001, this study), which is based on dyadic social relationships which are dependant upon adult females having offspring, or maturation (Kappeler, 1999). Peer-raised gorillas are predicted to form social relationships with available individuals in the absence of kin, but as they are raised in the absence of adults, is it is unknown if proximate group structure is comparable to breeding gorilla groups. Peer groups in this study were found to form the same spatial orientation as captive breeding groups (see Chapter 4), with a male in the centre of the social group, surrounded by females and younger gorillas. This similarity in spatial formation of peer-raised gorillas despite the lack of adult leaders, suggests that a natural grouping pattern exists within individuals. Considering that the same social grouping pattern was found in a peer group in which the oldest individuals were juvenile males, this pattern of social organisation was apparent from at least the juvenile period. In this study, in the absence of adult gorillas, cohesive relationships were formed with like-aged conspecifics and collectively towards one of the oldest males in the social group. Whether group spatial proximity, i.e. surrounding one specific male, over other like-aged males, is driven by the central male's behaviour or collective conspecific choice cannot be determined in this study. However, this is interesting considering the immature age of the peer-groups and specifically in the juvenile peer group that species-specific grouping patterns emerge even with a lack of breeding possibility. Comparable studies are not apparent in the literature.

7.5.3 Causes of abnormal behaviour in peer-raised groups

Social deprivation in infancy has been found to affect normal development patterns and lead often to the development of abnormal behaviour (Broom & Johnson, 1993). However, abnormal and stereotypical behaviour are reported to occur for a variety of reasons. Pertinent to this study they include: a reduced ability to cope with the captive environment, periods of social deprivation in infancy (Porton & Niebruegge, 2006; Sackett et al., 2006; Sanchez et al., 2001), or as a residual behaviour adopted into the behavioural repertoire during a previous period of stress (Mason, 1991). Recent physiological studies suggest that this brain formation is due to developmental plasticity not being buffered into a specific range by the mother, with the effect being that development occurs out of the species-typical range, with resultant abnormal phenotypes expressed (Pryce et al., 2004).

Each of these reasons for atypical behaviour is incredibly difficult to test due to the individualistic nature of the aberrant behaviour demonstrated by each individual in captivity (Hook et al., 2002) and because little is known about the period from capture until confiscation in these focal subjects. Abnormal and stereotypic behaviour are however, an aberrant reaction to stress from the captive environment, which are not documented in wild populations (Broom

& Johnson, 1993; Mason, 1991). Variation in the frequency of abnormal behaviour between individuals can be attributed to the amount of stress that an animal can cope with (Broom & Johnson, 1993), which in turn is related to level of deprivation and age at which it occurred in infancy.

In this study of peer-raised gorillas, the occurrence of abnormal behaviour was not found to differ between specific peer groups. Therefore, there was not found to be one environment more stressful than the others. If abnormal and stereotypic behaviour cannot be attributed to the specific environment in which the gorillas lived at the time of data collection, the occurrence of such behaviour may be considered an individual reaction to the other stressors named above.

The ability to cope with stress is linked to the prolonged occurrence of a mother-infant bond (Maki *et al.*, 1993; Sanchez et al., 2001). Chimpanzees separated from their mothers in infancy have less ability to cope with stress compared to those raised by their parents (Maki et al., 1993). This is supported in this study where abnormal behaviour occur at a higher frequency in peer-raised individuals compared to parent-raised gorillas.

7.5.3.1 Sex differences in atypical behaviour in peer-raised groups

Sex differences may also explain some variation in the occurrence of abnormal behaviour. In chimpanzees, rhesus monkeys and gorillas, females were found to show more abnormal behaviour than males (Gold, 1992; Hook et al., 2002), whereas males showed higher abnormal behaviour in pig-tailed macaques (Bellanca & Crockett, 2002). However, as peer-raised primates in the laboratory and zoos are usually socialised in groups of between two and four individuals (Bloomsmith et al., 2003; Gold, 1992; Meder, 1989a; Porton & Niebruegge, 2006), and often only in the infant and juvenile life-stages, this may not be comparable to individuals who live in large social groups such as gorillas in peer groups. Atypical behaviour in large peer-groups is investigated for the first time here. Abnormal behaviour was found to be greater in males than females at CWAF. In adolescent males, this may be explained in terms of social position within the social group. For mountain gorilla males, the position within the social group is an important factor, and determines access to cycling females (Robbins, 1999). The dominant male thus controls access to receptive females; other males contest this position and if successful may take over the group to assume the breeding advantage (Robbins, 2007). In peer groups however, adolescent males who were not spatially central to the social group and perhaps could not dominate the central male had a higher median frequency of abnormal behaviour than those in the central position. In peer-raised males of this study, it may be that, the stress of reduced access to sexually receptive females is exhibited through aberrant behaviour.

7.5.3.2 Atypical behaviour brought about by hand-rearing

The process of hand-rearing infant gorillas in the sanctuary setting is essential. Firstly, infant gorillas could not survive without regular nutrition and secondly gorillas suffer extreme depression upon separation from their mothers (Hoff et al., 1994). Gorillas separated from their mothers and other peers become withdrawn and refuse to eat or drink and can die within a few days (R. Hogan pers comm.). Chimpanzees also become depressed upon separation from their mothers (Hoff et al., 1994), but are less likely to die from withdrawal-associated symptoms (R. Hogan pers comm.). This sensitivity of gorillas compared to chimpanzees, is considered by the author to explain the lower number of gorillas compared to chimpanzees confiscated from villages and fewer gorillas surviving in the two Cameroonian sanctuaries, considering that chimpanzees and gorillas are sympatric in much of Cameroon's forests (Tutin et al., 2005). Clearly, upon admittance to the sanctuary it is essential for infant gorillas to form strong relationships with a human caregiver, the process of which reduces their depression, increases their appetite and therefore increases their chance of survival (R. Hogan, pers. comm.).

A strong attachment relationship in infant chimpanzees is essential to reduce the incidence of stress-induced abnormal behaviour (Maki et al., 1993). Those who have a strong attachment bond in infancy are shown to develop the capability to cope with stress in adulthood, compared to those who do not (Maki et al., 1993). However, bonding with humans may have the negative effect of increasing abnormal behaviour as was found in peer-raised baboons (Brent & Bode, 2006), or in decreasing species-specific social and cognitive functioning as was found in peer-raised chimpanzees and gorillas (Bloomsmith et al., 2006; Meder, 1989a). The attachment with mothers and human caregivers with NRI gorillas in this study was found to differ substantially. Attachment to the mother declines with immature age in gorillas (Fletcher, 1994, 2001; Nowell, 2005, this study) and in adulthood it is common for gorillas to have no contact with their mother due to emigration from the natal group. In the sanctuaries however, relationships with the human caregivers continues across the pre-reproductive period through the provisioning of food and daily keeper contact. Attraction towards caregivers was not found to decline in the peer-raised gorillas as maternal relationships decline in wild gorillas (Fletcher, 1994; Nowell, 2005, this study) and in fact was found to be greatest in adolescent and blackback males and adult females, specifically the CWAF adolescent peer-group, where the same keepers who raised them were still working.

Compared to parent-raised gorillas, peer-raised gorillas of all ages and both sexes were more orientated towards humans in this study. Human orientation in peer-raised gorillas is not advantageous for the development of species-specific behavioural patterns; human relationships after infancy were found to reduce the social cohesion within the gorilla group (LWC, see Appendix 2) and lead to an increase in stereotypic or abnormal behaviour upon absence of or anticipation of caregiver contact (pers. obs). This relationship between human caregiver and peer-raised gorillas needs further study in order to: a) investigate the correlation between length of time with the caregiver in infancy and human orientation in later life-stages, b) to determine if such a dependency illustrates the individual has decreased ability to cope in a gorilla peer group, or without the presence of a keeper.

7.5.4 Management considerations

PASA aims to provide apes with environments where their welfare is a priority, with the eventual aim of releasing some individuals back into the wild (PASA, 2006). The two sanctuaries in Cameroon have been able to raise gorillas to adulthood with, in the majority of cases, species-specific behavioural repertoires. However, further research into causes of abnormal behaviour specifically in 'bushmeat trade orphans' will allow implementation of enrichment from an early age to decrease its incidence. Such is an important consideration for the welfare of the gorillas in light that aberrant behaviour patterns become hard to extinguish the longer they have been established (Swaisgood & Shepherdson, 2006), or when individuals are socially deprived from a young age (Bloomsmith et al., 2006). Not addressed in this study, but of importance in light of PASA's aims to release apes back into the wild, are the coping mechanisms of the peer-raised gorillas in new situations. Peer-raised baboons for example show maladaptive response patterns to new situations, which they find stressful and are not seen in parent-raised baboons (Brent & Bode, 2006). In this study, increasing human-orientation with older NRIs may be indicative of a maladaptive coping mechanism to stress, group cohesion and attachment figures, which should be addressed before considering release programmes.

7.5.5 Conclusion

Sanctuary peer-raised gorillas develop species typical behaviour, comparable to parent-raised captive gorillas, although the patterns of behaviour occurrence may differ between the two captive regimes between specific life-stages. Behavioural differences were generally found in the old infant and juvenile life-stages, compared to adolescent male, blackback and adult females. Species-specific grouping mechanisms occurred in peer-raised gorillas from juvenility onwards, were highly comparable to captive breeding group social orientation, and were apparently a pre-disposed behaviour within individuals. Peer-raised gorillas, specifically males, exhibit abnormal behaviour, which probably occurred as a coping mechanism in peer group situations without the support of a secure attachment to parents and adult conspecifics. Unlike the mother-infant relationship, the gorilla-human-caregiver relationship did not decline with gorilla age and was found to be most prevalent in adolescent males and blackbacks. This dependant relationship decreases social cohesion and may promote aberrant behaviour patterns. In general, sanctuaries are suitable environments to allow species typical behaviour to develop in gorillas, but more research into stress, causes of abnormal behaviour and methods to reduce them are needed to promote long-term welfare of these gorillas. This chapter promotes the sanctuary methods of raising individuals in large peer-groups and illustrates some areas of potential management change if gorillas are to be engaged in release programmes in the future.

Chapter 8

8 GENERAL DISCUSSION

The success of adults in a species is proposed to be largely dependant upon social and environmental experiences within the pre-reproductive period, concerning either surviving to adulthood (Janson & van Schaik, 2002; Rubenstein, 2002) or developing the necessary skills and knowledge to be successful in adulthood (Cords, 1997; Fairbanks, 2000; Russon, 1997, 2003). It seems odd then that the study of NRI (non-reproductive individual) primate behaviour and development is severely lacking compared to studies of adult primates. Studies that focus on aspects of NRI primate development that lead to the erudition of survival and enhancement of future breeding success are essential to understand a species' life history and to allow comparative analyses between phylogenetically similar species. A research focus is needed to promote an understanding of the specific factors that lead to divergent development trajectories within and between a species (Pereira & Leigh, 2003), to understand the function of behaviour in the pre-reproductive period with regards to specific life-stages and to understand how events in the pre-reproductive period affect success and fitness in adulthood. Such a focus would increase the understanding of primate evolutionary theory, considering the variation and complexity of immaturity, based on robust, detailed studies of life history.

This thesis contributes to the understanding of western gorilla social development across two types of captive environment, with consideration for changes in behaviour due to divergent sex-based trajectories. This has led to the development of new methods to broaden our understanding of gorilla social development beyond traditional behavioural data analysis and pose research questions, using a novel approach. The aim is to contribute towards the area of NRI primate behavioural development and to provide evidence to explain the functional aspects of specific behaviour occurrence and trajectories across the pre-reproductive period.

8.1 Methodological advancements towards the study of NRIs

The most common behavioural sampling methods used to collect behavioural data are discussed in Altman (1974) and Martin & Bateson (2002); these are used extensively across the literature, and are considered effective in the collection of adequate behavioural data from multiple individuals (Martin & Bateson, 2002). Methods to analyse behavioural data however, are more varied and driven by the research question posed.

In areas of scientific research that have not been extensively studied, for example social development in *Gorilla* species, general questions as to the pattern, frequency and duration of the behaviour are asked. In the case of gorilla social development, Fletcher (1994) and Nowell (2005) provide an broad understanding of social development from infancy to adulthood and have generated hypotheses to explain functional adaptations. Using these studies as a basis, this thesis was able to focus on specific aspects of social development and provide further understanding of these areas. This was achieved by formulating procedures, which are less limited than typical methods currently accepted in the general study of social development, and by testing hypotheses to explain the function of specific behaviour. To enable such hypothesis testing it was therefore pertinent to develop new analytical methods or to introduce methodology that is used in other scientific areas and adapt these in a novel manner. Potential advances in the field of primatology and within the discipline of social development, through the contribution of these analytical methodological considerations, are discussed below.

8.1.1 Using behaviour to classify life-stages

Classifying primates into a life-stage provides a framework from which to compare similar individuals, within or between species (Bolter & Zihlman, 2007). However, across primatology, life-stage classifications are non-quantified and often static, which ignores the effect of individual rates of development and phenotypic plasticity, leading to large variability of data within life-stage groups. A new method presented in Chapter 3, compared individuals and determines the acceptance of individuals into a life-stage using behaviour as a flexible indicator of development.

Composite behavioural variables can accurately determine life-stage, sex differences in captive western gorillas, and most importantly, allow a degree of flexibility with regard to individual development and thus, strongly support the use of a quantitative system to determine primate life-stages. Further to this, support was found for the variability in life history trajectory between similar species, in this case mountain and western gorillas, most likely brought about by the divergent habitats to which they are adapted (Doran et al., 2002; Ganas et al., 2004). A future study aims to develop this finding by assessing the success of the four mountain gorilla classifications using mountain gorilla behavioural data collected by Fletcher (1994) and by testing the classification proposed for captive western gorillas on behavioural data from wild western gorillas collected from Mbeli Bai, collected by Nowell (2005). This planned analysis will provide essential wild comparisons and determine the effects of the captive environment, which may occur due to the gorillas' restricted range and managed daily routine. Further to this, error caused by using static life-stages and thus causing unnecessary variability across data sets will be assessed to estimate how this might affect results within quantitative research.

A behavioural classification is highly applicable for the field of primatology, challenging the appropriateness of employing static age-based classification systems, particularly alongside non-quantified developmental variables. It is proposed that future studies, where the selection of study subjects is necessary, should at least use a strong justification for incorporating or eliminating an individual from analysis of a particular life-stage. This must consider environmental or social factors that could lead to individual divergence in developmental timings. The promotion of a quantitative classification system, such as the one presented in this thesis, is important to reduce variability in data sets brought about by accepting individuals into an age-based life-stage, from which they differ developmentally. It is argued that by encouraging rigor in experimental and field based research allows stronger comparative analysis, thus highlighting, in this case, behavioural and developmental differences and similarities between species.

It should also be considered, based on these findings that classification systems formed for a species in one habitat, may not be applicable to the same species living in a divergent habitat, as adaptation to an environment is proposed to affect life history events (Kappeler & Pereira, 2003). This has been recognised at some field sites, where different age-based life-stage classifications are used for different spider monkey populations, one in Southern Mexico and another in Costa Rica, regardless of the lack of quantified analysis to determine where developmental differences arise between populations (Claire Santorelli, pers comm.). However, one limitation of this method, if used over multiple primate species is that a different range of behaviours may be used to determine the life-stages, which may reduce the comparability of life-stages between species. Since this method has so far only be used on one species researchers using this method in the future should assess the effect of this potential error.

8.1.2 Understanding NRI social relationships within social groups

The length of the extended juvenile period in primates is linked to social group complexity (Joffe, 1997). Therefore, it is assumed that the development of relationships is highly important as the basis of learning skills and knowledge from other group members (Russon, 1997). Traditionally, primate social relationships are measured by the proximate relationship between two individuals. Although the likelihood is that those who are regularly in close contact have stronger social relationships than those at greater proximity, the social dynamics of the remainder of the social group need to be considered since group social relationships based on interactions between individuals, with each interaction affecting subsequent ones, with a network of interwoven relationships resulting (Hinde & Hinde, 1988). For example, in previous studies of gorilla social development, it was found that there was increased proximity from the mother with increasing age of the NRI (Fletcher, 1994;

Nowell, 2005). However, distance from the mother was not a significant correlate of NRI behavioural development in Chapter 3, indicating that proximity alone does not determine relationship strength but that other social behaviour (e.g. grooming or affiliation) are likely to be used to reinforce the social relationship and may provide a more robust indicator of relationship strength. Chapter 4 expands the understanding of relationship development in NRIs by incorporating a spatial representation of the social group, using proximity and developing a sociality index (SI) using behaviour that is prominent in the NRI behavioural repertoire. Together, these methods build an understanding of where NRIs are spatially orientated within the social group and document the strength of social relationships between individuals in different life-stages. Understanding the social complexity that NRIs must endure in a species is essential to understand the roles of specific partners in influencing development and the predicted trajectory of relationships from birth to adulthood. These are likely to be influenced by the species social system, the group composition and the environment. This study does not assess these factors, which leads to little understanding of how the sample size and composition of NRI gorillas in this study has affected the analysis and subsequent understanding of relationships development. Within this study there were no NRIs categorised as adolescent females and only one male old infant, future studies should seek to study a larger sample of NRI gorillas, which incorporate multiple gorillas of each life-stage.

Application of the MDS packages in future studies must be administered with care. In this study, there is some missing proximity data as scans of proximity measures were only taken from the NRI focal gorilla towards all other gorillas in the group, hence no scan data exist therefore between adult females or between adult females and the silverback. MDS (PROXSCAL), unlike logistical regression, is robust to such perpetrations as long as appropriate proximity measures are used, here scan samples are standardised by each dyad following (Nakamichi & Kato, 2001). Using data sets with proximity data between all possible dyads would ensure even higher accuracy of spatial maps.

Future studies could build on the current study by assessing social group relationships more consistently, using focal data collected from all group members. This would enable an understanding of adult and NRI social relationships in a population, along with understanding specifically how adult social dynamics affect NRI relationship development. In gorillas, for example, the general close proximity of many adult females towards the silverback will affect the proximity of younger NRIs. In this way, a future study, using data from Mbeli Bai, intends to assess how specific social situations (e.g. presence of another gorilla group in the bai, females in oestrus) influence the spatial orientation of individuals in the gorilla group. This will further investigate how group orientation changes in specific social circumstances and provide an important understanding of the function of a social group to a silverback, adult female and NRI.

The application of spatial proximity and social interactions, to other species and on longitudinal data will can provide a complex understanding of social relationships, both in the wild and in captivity. The effect of social system demography on, for example, male and female NRI relationship formation will likely prove an interesting comparative area of research, indicating how species-specific behaviour is learnt and developed and how such adult-NRI relationships affect future individual fitness.

8.2 Significant relationships across NRI pre-reproductive period and future directions

A common premise within this thesis has been to execute analyses, which provide a greater understanding of relationships between specific members of the social group and the trajectory of these across the pre-reproductive period. This has commonly led to a discussion of the functionality of the behaviour in question within the studied populations, but when applied to primatology in general, this can lead to a discussion of the assumed benefits of specific dyadic relationships for both partners. Individual dyadic relationships are important to understand the prolonged occurrence of relationships between specific group members where the benefits assumed may differ between partners or over time. The following sections focus on relationships between specific dyads, and the activities in which they commonly engage.

8.2.1 Mother-NRI dyads

The role of the mother is considered to be necessary for species-specific social development and increased success in adulthood (Bloomsmith et al., 2003; Fletcher, 2001). Cognitively, the mother is proposed to act as a buffer between the infant and the environment, protecting the developing brain from social or environmental stress (Pryce et al., 2005) and allowing postnatal development to occur gradually and cumulatively (Pereira & Altmann, 1985). The plasticity within cognitive development potentially allows beneficial adaptation to the specific environment to which the individual is born (Deaner et al., 2003), but is considered detrimental without the mother, where stress can negatively affect the homeostatic environment (Pryce et al., 2004). Thus increasing independence across the pre-reproductive period, leads to reduced input from the mother. The decline in the relationship between mother-NRIs beyond infancy has been previously reported in gorillas (Fletcher, 1994; Nowell, 2005) and is supported here in terms of increased spatial proximity, but also in terms of frequency of social engagement. Ape mothers may engage in social play with infants (Watts & Pusey, 2002), but this is uncommon with juvenile and adolescents in this study, perhaps driven by the benefit to NRIs of interacting with similar-sized peers.

The absence of the mother (coupled with an inappropriate environment) during the pre-reproductive period can alter the normal trajectory of behavioural development and have a negative impact on adult social competency and breeding success in the apes (Porton & Niebruegge, 2006). However, in the current study, NRI behavioural development in peer groups occurred at comparable rates to that in NRIs raised with their mother. From a developmental point of view, this research suggests that species-typical behaviour will emerge from individuals kept with peers, in the absence of the mother. This is interesting since observing adult behaviour is often promoted as a means for species typical skills to develop e.g. food processing in mountain gorillas (Byrne, 1999), or infant handling (this study), as well as the mother being the primary agent to facilitate infant survival and social development (Fletcher, 2001). Understanding which behaviour is innate and which needs to be learned in a species is still an area of much controversy, but this study supports that an environment with other members of the same species is sufficient to develop some typical behaviour even when conspecifics are also immature. The development of behaviours necessary for adult breeding success, i.e.-parenting skills and competing for mates however, could not be quantitatively assessed in this study due to short-term cross-sectional data collection methods, which limit inferences on individual trajectories. Future studies could address this limitation by monitoring individuals in peer groups though the pre-reproductive and into adulthood to determine if peer-groups are sufficient to allow the development of essential parenting/competitive skills.

The impact of maternal deprivation and stress in the pre-reproductive period is predicted to affect the individual's physiological stress response and ability to cope (Sanchez et al., 2001), which was perhaps demonstrated through the occurrence of additional atypical behaviour in peer-raised gorillas which was not addressed in this study, again due to the short data collection periods. To understand the occurrence and prevalence of abnormal behaviour further in peer-raised apes would require more information on physical experience and physiological response, the age of separation from the mother, extent of physical injuries incurred, the length of time kept in the villages as well as physiological measures such as blood cortisol levels. These could then be related to the specific stage of development and the amount of species atypical behaviour displayed. Such future studies could further understand the effect of maternal deprivation on cognitive development and associated behavioural traits, in non-experimental situations, which would further the understanding of the role of the mother on NRI development.

8.2.2 Peer-NRI dyads

Relationships common to a species or across the primate order are considered to have evolved for a specific purpose and to have a specific fitness advantage to NRIs born in the present (Pagel & Harvey, 2002). Engaging with peers from the same social group is likely to be beneficial by allowing skill development and knowledge of social relationships, as well as building future alliances in some species. In wild mountain and western gorillas juveniles show a propensity to associate with like-aged gorillas (Fletcher, 1994; Nowell, 2005), who exhibit similar levels of socialisation. In this study, similar-aged peers intentionally spent time in close proximity in juvenility, but not so in adolescence. However, social play between similar-sized peers was most common in all NRIs, which it is proposed, provides practise and opportunity to develop behaviour in a non-confrontational relationship (Fagen, 2002). Relatedness however, affects NRI relationships in primates (Berman, 2004), within this study, full siblings engaging in affiliative behaviour more and continued to engage in alloparental behaviour until later in maturity than disparate-aged paternal half siblings. What it has not been possible to detect in this study is any strong support for the inclusive fitness explanation of kin relationships (Hamilton, 1964), or if indeed these relationships are driven by proximity and close relationship to the mother (Chapais, 2001). Future studies could focus on full and paternal half sibling relationship across a range of similar species to determine the likely benefit of this documented relationship and to provide support for the alternative functional hypotheses.

Understanding how an individual develops relationships across the pre-reproductive period and how relationships affect the occurrence of specific behaviour such as alloparenting and social play and together how these behaviours affect future reproductive success is necessary to understand the disparate life history patterns. Relationship formation however, is affected by variation in family group size and composition i.e. demography. Within this study, no analysis has been conducted to accommodate the effects of conspecific availability, nor size of the social group. Gorillas in the European Zoos are all part of a breeding programme, to maintain maximum genetic diversity in the captive populations restrictions are placed on the number of offspring an adult female is allowed to have. The effect is often that some zoos have multiple NRIs, whilst others (e.g. Jersey and Twycross Zoo (Schmidt, 2005)) have one or two. Future studies could assess the effect of an absence in conspecifics or divergent group size on NRI development. Such is likely relevant to wild western gorillas as group size varies considerably, affecting conspecific availability (Nowell, 2005). From this study, it is predicted that NRI conspecific relationships are highly beneficial for development as shown through prominent relationship development.

Future research must also consider the nature of the captive environment and how this compares to the wild. Play behaviour for example is found to occur at higher rates in the captive environment as captive animal groups spend less time travelling and securing food (Thompson, 1996). The same may be true for alloparenting behaviour, it may occur less frequently in the wild due to the time constraints of other activities, or maternal restrictiveness may increase in natural habitat where the risk to the infant may be perceived as higher than in captive enclosures. Currently only one field site in Africa has a habituated western gorilla group of ten individuals that can be followed daily throughout their habitat (Doran-Sheehy & Lodwick, 2005), making it impossible at present to replicate this study using wild western gorilla data. It may be advantageous in the future, however, to determine how the energetic factors of travel and securing food in a forested, seasonally changing environment affect typical NRI behaviour such as play and alloparenting, particularly when NRIs are free to emigrate from the natal group.

The study of NRIs in general and NRI – conspecific relationships specifically remains a neglected area of study (but see, Barrett et al., 2006; Setchell & Wickings, 2004; Setchell *et al.*, 2006), which has the potential to highlight the function of the immature period in primates. Additionally, longitudinal studies of NRIs are particularly rare but are increasingly necessary to understand the pre-reproductive period both from an individual NRI and from a species perspective (Fairbanks & Pereira, 2002).

The welfare of primates kept in the captive environment has been an area of increasing investigation over the past few decades leading in general, to better standards of care and provisions specific to the species needs, naturalistic social groupings and changes in enclosure design to reduce the effects of visitors and limitation of space (Wolfensohn & Honess, 2005). Still however, captive primates, often show abnormal or stereotypical behaviour, often concluded to be due to the social and environmental stress of the restricted environment (e.g. Hill, 2004). Gorillas in particular have been shown to be vulnerable to the captive environment in terms of social groupings, enclosure design and husbandry regime (Hill, 2004; Lukas, Hoff et al., 2003; Lukas, Stoinski et al., 2003; Lukas, 1999; Meder, 1989a, 1992, 1994). However, throughout this thesis no consideration has been taken for the divergence in captive environments in which the five European breeding groups are kept and managed and thus the effect that this could have on the behaviour exhibited by the NRIs. In a future analysis of this data, the following factors will be considered.

Firstly, the enclosures in which the gorillas are kept varied in size, from Basel and Zurich zoos, each of which held large family groups in small indoor enclosures (under 140m^2) to Apenheul Primate Park where data were collected from a 4000m^2 island,. This fundamentally limited the opportunity of NRIs of Basel and Zurich to move greater distances away from other group members. Likewise, feeding routine and diet differed between zoos, with the groups at Apenheul Primate Park and La Vallee des Singes being fed large amounts of willow branches in the morning and encouraged to move to public feeding platforms for multiple feeds throughout the day. This compared to Burgers' Zoo where willow was fed ad hoc, only two fruit feeds were administered during the afternoon, subsequently the gorillas at each zoo had a different daily routine and potentially a different daily activity pattern.

Finally, data were collected in Europe over the spring and summer periods, when visitor numbers are much greater than across the winter. A study of gorillas during periods of high visitor density found increased aggression and stereotypies, indicating higher stress levels in the group compared to low visitor levels (Wells, 2005), again the effects of visitors need to be taken into consideration when analysing the behaviour of NRI gorillas.

8.3 Final comments

This thesis begins by formulating a quantitative method to determine gorilla life-stages and uses this method throughout. It investigates relationship development strategies, skill and knowledge development in the form of alloparenting and social play behaviour and finally compares NRI gorillas living in disparate social grouping patterns. Gorillas with their prolonged development period, large sexual dimorphism and polygamous social structure are excellent subjects from which to exemplify behaviour change with age, divergence in the development of the sexes and disparate behaviour due to relatedness. It is hoped that research generated here will allow a comparative base for similar studies on other primate species to develop the field of life history, incorporating in-depth understanding of the pre-reproductive period.

Appendices

APPENDIX 1 Demography of observed gorilla groups (subjects as highlighted text)

a. Apenheul Primate Park

Name	Gorilla Code	Age(yrs)	Sex[2]	Sire	Dam
Bongo	Bo	*Wild caught*	M		
Dalila	Da	*Wild caught*	F		
Lobo	Lo	*Wild caught*	F		
Mintha	Mi	*Wild caught*	F		
Mandji	Ma	*Wild caught*	F		
Uzuri	Uz	11	M	Bongo	Mandji
Bibi	Bi	8	F	Bongo	Lobo
Kisiwa	Ki	8	F	Bongo	Dalila
M'Bewe	Mb	8	M	Bongo	Mintha
Kidogo	Kd	7	M	Bongo	Mandji
M'Kono	Mk	6	M	Bongo	*Transferred 2004*
Zoezi	Zo	5	F	Bongo	Lobo
Nemsi	Ne	4	F	Bongo	Mandji
Gyasi	Gy	3	F	Bongo	Dalila
Loango	La	1	M	Bongo	Lobo

b. Basel Zoo

Name	Gorilla Code	Age(yrs)	Sex[2]	Sire	Dam
Kisoro	Ks	17	M		
Goma	Go	47	F		
Kati	Ka	*Wild caught*	F		
Quarta	Qu	38	F		
Faddama	Fa	23	F		
Joas	Jo	17	F		
Wima	Wi	7	F		
Vizuri	Vz	9	M	Kisoro	Quarta
Viatu	Vi	8	M	Kisoro	Faddama
Zungu	Zu	3	M	Kisoro	Joas
Chelewa	Cw	6mns	F	Unknown	Wima

c. Burgers' Zoo

Name	Gorilla Code	Age(yrs)	Sex[2]	Sire	Dam
Bauwi	Ba	16	M		
N'Gayla	Ng	12	F		
Shatilla	Sh	8	F	*Deceased*	*Deceased 2004 (full sibling of Si)*
N'Yaounda	Ny	4	F	Bauwi	N'Gayla
Shinda	Si	3	F	Bauwi	*Deceased 2004 (Full sibling of Sh)*
Likale	Li	3	M	Bauwi	*Deceased 2004*
N'Aika	Na	6mns	F	Bauwi	N'Gayla

d. La Vallée des Singes

Name	Gorilla Code	Age(yrs)	Sex[2]	Sire	Dam
Yaounde	Ya	22	M		
Gaja	Ga	*Wild caught*	F		
Virunga	Vi	*Wild caught*	F		
Moseka	Mo	21	F		
Badongo	Bd	6	M	Yaounde	Virunga
Kibali	Kb	4	M	Yaounde	Moseka
Kwanza	Kw	3	F	Yaounde	Gaja
Sango	Sa	1	M	Yaounde	Moseka
Lomako	Lm	1	M	Yaounde	Virunga

e. Zurich Zoo

Name	Gorilla Code	Age(yrs)	Sex[2]	Sire	Dam
N'Gola	Nl	29	M		
Mamitu	Mm	29	F		
Nache	Nh	26	F		
N'Yokumi	Ni	5	F		*Transferred in 2005*
Azizi	Az	6	M	N'Gola	*Deceased 2002*
Bonsenga	Bs	4	M	N'Gola	Nache
Binga	Bg	4	M	N'Gola	Mamitu
Eyenga	Ey	2	M	N'Gola	Nache
Enea	En	1	F	N'Gola	Mamitu

f. CWAF (Group 1)

Name	Gorilla Code	Age (yrs)	Sex[2]
Geri	Ge	10	F
Jasmine	Ja	8	F
Avishag	Av	8	F
Bobo	Bb	7	M
Nkamum	Nk	7	M
Kibu	Ku	7	M

g. CWAF (Group 2)

Name	Gorilla Code	Age (yrs)	Sex[2]
Nkan	Nk	5	M
Shai	Ss	4	M
Mvie	Mv	3	F
Nyum	Nu	3	F
Ncarla	Nc	2	F
Yeba	Ye	1	M
Nona	No	1	F

h. LWC

Name	Gorilla Code	Age (yrs)	Sex[2]
Nyango	Nn	16	F
Brighter	Br	11	F
Chella	Ch	11	M
Jumbo	Ju	9	F
Emma	Em	9	F
Benito	Be	8	M
Pitchou	Pi	8	F
Twigs	Tw	8	F
Arno	Ar	6	M
Batek	Bt	6	M
Akiba	Ak	5	F

APPENDIX 2 Configuration for focal sampling

Code	Behavioural definition	State(s)/ Event(e)	Modifier 1	Modifier 2
	Feeding and Grooming			
su	Suckling	s	position	termination
fx	Feeding on vegetation	s		
fb	Feeding on bark	s		
fg	Feeding on grass	s		
fw	Drinking water	e		
fv	Feeding on vegetables	s		
ft	Food taken from within 1metre of another	e	initiator	
fs	Food snatched from another's hand	e	gorilla code	initiator
fm	Food manipulation	s		
gs	Self grooming	s	body part	
gr	Receiving grooming	s	gorilla code	body part
gg	Grooming another	s	gorilla code	body part
ge	Touch another gorilla's genitals	e	gorilla code	
rg	Another touches subjects genitals	e	gorilla code	
	Modifier – gorilla code[1]			
	Modifier – position			
pd	Clinging in a dorsal position			
pv	Clinging ventrally and unsupported			
ps	Clinging ventrally and supported			
pi	Clinging onto the side			
pr	Clinging onto the rump			
pa	Clinging onto the arm			
	Modifier – initiator			
fo	Focal initiates contact with another			
an	Another gorilla initiates contact with focal			
	Modifier – body part			
bh	Head			
ba	Arm			
bl	Legs and feet			

bf	Ventral			
br	Rump			
	Modifier - termination			
sm	Mother terminates suckling			
sf	Focal terminates suckling			
	Movement			
rl	Lying down	s	gorilla code	distance
rt	Sitting	s	gorilla code	
tr	Locomotion	s		
tc	Climbing	s		
rc	Rump cling	s	gorilla code	initiator
td	Focal is carried dorsally	s	gorilla code	initiator
tb	Focal carries another ventrally	s	gorilla code	initiator
tv	Focal carries another dorsally	s	gorilla code	initiator
	Modifier – distance			
dc	In contact			
dt	Within 2 metres			
df	Between 2 and 5 metres			
de	Between 5 and 10 metres			
do	Over 10 metres			
	Interactions			
fp	Focal approaches another gorilla	e	gorilla code	
ap	Another gorilla approaches focal	e	gorilla code	
fl	Focal leaves another gorilla	e	gorilla code	
al	Another gorilla leaves focal	e	gorilla code	
ao	Another gorilla follows focal	e	gorilla code	
ff	Focal follows another gorilla	e	gorilla code	
fd	Focal displaces another gorilla	e	gorilla code	
ad	Another gorilla displaces focal	e	gorilla code	
ts	Focal restrained from leaving	e	gorilla code	
tt	Focal retrieved by another	e	gorilla code	
lo	Focal looking at another gorilla	e	gorilla code	
if	Focal interacts with another gorilla	e	gorilla code	focal interaction
an	Another gorilla interacts with focal	e	gorilla code	another interaction

	Modifier – focal/another interactions			
it	Touch			
ih	Hug			
ip	Peer			
ic	Charge			
is	Swipe			
il	Lunge			
ia	Slap			
ib	Bite			
	Self or human directed behaviour			
ss	Repetitive movements	s		
sp	Hair plucking using hand	s	gorilla code	body part
sl	Hair plucking using teeth	s	gorilla code	body part
sc	Clasping	s		
sr	Regurgitation	s		
si	Re-ingestion	s		
sg	Coprophagia	s		
hd	Interacting with the public	s		
hw	Watching the public	s	human watching	
sm	Masturbation	s		
sf	Finger sucking	s		
	Modifier – human watching			
pu	Public			
ke	Keepers			
ob	Observer			
	Play			
pc	Chase	s	gorilla code	initiator
pg	Gentle play	s	gorilla code	initiator
pw	Wrestle	s	gorilla code	initiator
pa	Spar	e	gorilla code	initiator
pp	Parallel play	s	gorilla code	initiator
ch	Chest beat	e		
pi	Solicit play	e	gorilla code	solicitation
pf	Foliage in mouth display	e		
re	Rest play	s		
px	Socio-sexual play	s	gorilla code	distance
pl	Play face	e		
po	Object play	s		

ps	Self play	s	self play	
co	Object used in display	e		
cs	Strut stance	e	gorilla code	
cc	Handclap display	e	gorilla code	
cb	Body beat display	e	gorilla code	
	Modifier – solicitation			
il	Solicit by looking			
ia	Solicit through an action			
it	Solicit through touch			
	Modifier – sex position			
sv	Ventro-ventro			
sd	Dorso-dorso			
so	Dorso-ventro			
	Modifier – self play			
pt	Tumble			
pp	Spin			
pe	Explore			
	Play solicitation			
so	Focal solicits play bout	e	gorilla code	solicitation
as	Another solicits play bout	e	gorilla code	solicitation

[1] See Appendix 1

APPENDIX 3 Configuration for scan sampling

Code	Code definition	Modifier 1	Modifier 2
	Group activity		
xr	Majority (over half of the group) are resting (stationary, seated or lying)		
xt	Majority of the group are travelling (active movement)		
xf	Majority of the group are feeding (consuming food items)		
xe	Some (over a third of the group) rest, some feed		
	Focal distance to other gorillas		
yy	Distance in metres to another gorilla	gorilla code	distance
	Modifier – gorilla code[1]		
	Modifier – distance		
dc	In contact		
dt	Within 2 metres		
df	Between 2 and 5 metres		
de	Between 5 and 10 metres		
do	Over 10 metres		

[1] See Appendix 1

APPENDIX 4 Configuration for all occurrence sampling

Behaviour	
Alloparenting	*(Collected on a Dictaphone)*
Beginning time	
Ending time	
Name of alloparent	
Name of infant	
Initiator of carrying	
Terminator of carrying	
Activities during alloparenting	
Contact with other gorillas	
Position carried	

APPENDIX 5 Results of Spearman's Rank correlation of all behavioural variables with NRI age

Behavioural group	Behaviours within the group	Measure	Spearman's Rho	N
Proximity to mother (in contact)		f	-0.56*	17
Proximity to mother (in contact)		d	-0.63*	17
Proximity to the mother (within 2 metres)		f	-0.51*	17
Proximity to the mother (within 2 metres)		d	-0.68**	17
Proximity to the mother (within 5 metres)		f	-0.53*	17
Proximity to the mother (within 5 metres)		d	-0.63**	17
Proximity to the silverback (in contact)		f	-0.18	21
Proximity to the silverback (in contact)		d	-0.23	21
Proximity to the silverback (within 2 metres)		f	-0.09	21
Proximity to the silverback (within 2 metres)		d	-0.09	21
Proximity to the silverback (within 5 metres)		f	-0.18	21
Proximity to the silverback (within 5 metres)		d	-0.14	21
Proximity to a similar aged peer (within 2 years of age difference, within 2 metres)		f	-0.32	19
Proximity to a similar aged peer (within 2 years of age difference, within 2 metres)		d	-0.29	19
Proximity to a similar aged peer (within 2 years of age difference, within 5 metres)		f	-0.29	19
Proximity to a similar aged peer (within 2 years		d	-0.31	19

of age difference, within 5 metres)				
Autogrooming		f	0.06	22
Autogrooming		d	0.29	22
Grooming (gives to another)		f	-0.33	22
Grooming (gives to another)		d	-0.9	22
Grooming (receives from another)		f	-0.24	22
Grooming (receives from another)		d	-0.27	22
Social grooming	All giving and receiving of grooming	f	-0.44*	22
Social grooming	All giving and receiving of grooming	d	-0.32	22
Approach mother		f	-0.68**	17
Approach silverback		f	-0.24	21
Lying		f	0.33	22
Lying		d	0.82**	22
Sitting		f	-0.26	22
Sitting		d	-0.09	22
Resting	Sitting + lying	f	-0.09	22
Resting	Sitting + lying	d	-0.15	22
Travelling		f	-0.25	22
Travelling		d	-0.65**	22
Climbing		f	-0.63**	22
Climbing		d	-0.80**	22
Locomotion	Travelling + climbing	f	-0.68	22
Locomotion	Travelling + climbing	d	-0.62**	22
Displacement (focal displaces another)		f	-0.34	22
Displacement (another displaces focal)		f	-0.30	22
All displacement	Focal displaces another + another displaces focal	f	-0.21	22
Feeding		f	-0.45*	22
Feeding		d	0.05	22
Focal snatches food from another		f	-0.16	22
Focal peers at another		f	-0.44*	22
Chase play		f	-0.59*	22
Chase play		d	-0.52*	22
Gentle play		f	-0.80**	22
Gentle play		d	-0.48*	22
Spar play		f	-0.30	22

Wrestle play		f	-0.43*	22
Wrestle play		d	-0.29	22
All social play	Chase, gentle, spar, wrestle	f	-0.58**	22
All social play	Chase, gentle, wrestle	d	-0.66**	22
Spin		f	-0.36	22
Tumble		f	-0.34	22
All solo play	Spin + tumble	f	-0.49*	22
Object play		f	-0.08	22
Object play		d	-0.13	22
Chestbeat		f	-0.53	22
Sex play		f	-0.06	22
Sex play		d	0.03	22
Solicit play		f	-0.51	22

f = frequency, d = duration
* = P <0.05, ** P = < 0.01

APPENDIX 6

University of Chester

Gorilla Social Development & Management Report

For Limbe Wildlife Centre

January 2006

Johanna Hutchinson MSc.

University of Chester, UK

Executive Summary

Several differences occur between the LWC gorillas and the family gorilla groups held in European zoos, mainly, their lack of a defined leader and reduced social cohesion, resulting from their young age and strong attachment to humans. Although alliances are seen between individuals in the group, the gorillas are highly independent for the majority of each day. Play behaviour occurs much less at LWC than in European family gorilla groups, potentially due to a stressor in their environment, or in some cases accelerated social development. However, when play does take place each gorilla has a preferred play partner, with higher ranking gorillas being involved in play more than lower ranking individuals.

Each gorilla is developing at his or her own rate; individual behaviour is determined by age and thus stage of social development. Chella, has begun to show dominance of the group and seeks for ways to assert his strength over other group members, often chasing lower ranking individuals. Benito shows alliance building with the group by chasing Chella away from others and intervening in female disputes. Pitchou has developed strong mothering tendencies towards the younger gorillas, as well as becoming a popular female through her plucking behaviour. Twigs and Amo are both low ranking in the group, however Amo has a concerning status in that he is not holding this position and at times is ignored or attacked by other group members. Batek shows good social development and a good play relationship with Chella as well as being mothered by Brighter. Akiba although only 5 years old, has developed at a fast rate and shows dominance over all except Chella, Brighter and Pitchou

Several self directed behaviour have been observed across the group, including plucking (Pitchou, Chella), regurgitation/re-ingestion (Nyango, Jumbo), repetitive movements (Jumbo), anxiousness (Amo, Twigs) tooth grinding (Chella) some occur as a result of daily frustrations, other as a result of rearing experience and previous early stress. These are discussed in relation to the individual.

The management of these gorillas in one group will be problematic; suggestions are made to ease the current group stressors to enable the group to live together for a few more years. These include empowering Chella as silverback, by allowing him access to the group at all times, increasing social cohesion by reducing the incidence of separating individuals, increasing naturally consumed food items, to increase feeding and resting time and scattering food over the entire outdoor enclosure to reduce feeding competition in the group.

Introduction

The LWC study forms part of a larger piece of research which seeks to understand and compare social development and behaviour of immature gorillas in captivity. The social organisation of primates is highly diverse and is dependent upon the interaction of many variables. The development of relationships, which ultimately create the social structure of a group, is understudied in gorillas, as continuous observation of western lowland gorillas is not yet possible.

Captive gorillas provide a valuable resource to further our knowledge of the development of behaviour and relationships in groups of differing size and structure. Established populations of gorillas held in European zoos enable a comprehensive study of juvenile and adolescent behaviour in environments familiar to them and without the environmental stressors of the forest habitat.

In addition the bushmeat trade has led to an increase in immature gorillas taken into captivity after enduring periods of stress and mis-management. Hand-rearing, rehabilitation and reintroduction of individuals into social groups are necessary for the survival of these gorillas. However, the long-term success of these projects is dependant on managing the gorillas in captivity for their lifetime. Research into gorilla social development and behaviour links this need specifically with the sanctuary gorillas' behaviour. This pioneer research will enable an understanding into the prevailing differences in gorilla behaviour across establishments.

Throughout the months of November and December 2005 the researcher (JH) spent a total of 203 hours conducting focal observations on the immature gorillas at Limbe Wildlife Centre. Immaturity was defined as a female gorilla under 8 years old or a male gorilla under 11 years old, in accordance with the literature on wild mountain and lowland gorillas. Using LWC records to determine approximate age gorillas included in the study were Akiba, Batek, Amo, Benito, Twigs, Pitchou and Chella. On each day of data collection one gorilla subject was chosen and followed for their duration in the outdoor enclosure. Data were collected on feeding, resting and play behaviour as well as proximity and interactions with other gorillas.

This report:

- Highlights the findings of LWC data collection
- Provides a summary of the behaviour of all 11 gorillas
- Compares the immature gorilla social development with that of contemporaries in European zoos
- Makes suggestion for the future management of the group taking into consideration the animals as they behave now.

Summary of group behaviour

In essence, the gorillas at LWC should be considered a success story, after the unknown ordeal of each gorilla to survive and live as part of a group at all shows a resilience and strength of character that not all gorillas possess. However, certain traits not seen in family groupings in European zoos have been documented, purely as a result of their experiences and subsequent necessary living arrangements. The most obvious difference is the lack of a defined leader and thus the lowered cohesion of the group. Although a hierarchy exists in the group this is not split into male and female roles probably due to the youth of the males in the group. Dominance is achieved by stronger individuals such as Brighter and Chella, but also more assertive individuals such as Akiba. This is a situation likely to change as the males grow in size and confidence and challenge the smaller group members more. Currently each gorilla acts as an individual within the group, their proximity to others and behaviour are independent of each other. The greatest influence is seen by Chella towards the lower ranking gorillas (Twigs, Nyango & Amo), who actively move away as he approaches. Alliances between gorillas in the group are seen, but these do not determine proximity during feeding or resting periods with any reliability as is seen in family gorilla groups where for example a mother-infant or two adolescent males would regularly be seen resting in close proximity.

Each gorilla shows a strong attachment to humans, particularly their keepers and much daily behaviour is determined by the keeper activity. Although this is partly food expectation, they will follow the keeper around the enclosure and move to watch the keeper cleaning the enclosure, or eating lunch. Although this is common in hand raised gorillas within this group it does emphasis their lack of interest in each other and their focus on activities outside the enclosure. Often during periods of 'keeper watching' self orientated behaviour such as teeth grinding (Chella), repetitive movements (Jumbo), self plucking (Pitchou) and regurgitation and re-ingestion (Nyango) become more prevalent than at other times indicating frustration or stress.

Play behaviour forms an important component of social development in all primates as it promotes the physical development of the body and builds social bonds among peers. In comparison to their European counterparts the younger gorillas at LWC play less frequently and in shorter duration than those in family groups, sometimes with days passing without any play behaviour being documented. Play bouts in family units typically occur during rest periods and can often last up to 45 minutes. At LWC play rarely lasted longer than 20 minutes and typically occurred in the mid morning or briefly before entering the indoor enclosure. However during play bouts preferred play partners are recorded for each individual and a range of play positions and dominations are seen typical of gorillas of their ages. Two theories are proposed for the reduced play behaviour in the group, firstly play does not occur in wild primate populations during times of stress. Certain stressors in captivity could include Chella's attacks or incorrect diet, which would reduce or stop play behaviour. Secondly, hand raised gorillas can show advanced behaviour for their age, indicating accelerated social development, in such a case play behaviour would not be as essential for the individual and therefore would be seen to occur less frequently.

All the LWC gorillas show a good use and interest in their environment, using climbing apparatus, making use of the all the space in the outdoor enclosure and using novel objects in play and displays opportunistically. In addition the gorillas are seen to feed on vegetation growing in the enclosure and will spend time trying to acquire vegetation out of bounds to them.

Summary of individual behaviour

Chella

Chella exhibits normal social development for an eleven year old gorilla, choosing to remain away from the group for most of the day. He has a close relationship with Pitchou and both will seek each other to allow Pitchou to groom and pluck hair on his back. Low levels of play are documented with the younger gorillas (Batek and Akiba), which is usually initiated by Chella. It is common for dominant males to play with the youngest males of the group, but this is the first instance documented during this research of an older adolescent male playing with a juvenile female. It would be expected that most of Chella's play bouts be focused towards Benito who is closest in age and strength to him; however, no play behaviour was seen between them, perhaps as Benito seems to take a protector role for the rest of the group chasing Chella away when he attacks group members. Chella exhibits high levels of object play, often banging stones together and most recently digging a hole in the enclosure, however self play (tumbling, spinning etc.) was not seen, correct for his age.

As the eldest male and with no guidance from a silverback he does show an over aggressive behaviour to other members of the group, which is disruptive to normal group functioning. On 40% observation days Chella would enter the outdoor enclosure and begin to follow the group around the enclosure strutting, tooth grinding and displaying to them. Regularly during these occasions he would choose a 'victim' and pursue this gorilla for 30 minutes, chasing, slapping, biting and lunging onto them. Victims were most usually the lowest ranking in the group, Nyango, Amo, Twigs & Emma, with Brighter and Pitchou not receiving any aggressive attention. After direct contact with the victim Chella was chased away by several of the group, led by Benito and the victim on most occasions. The chase would end with Chella demonstrating a strut stance until the group moved away, at which point he would begin to follow his victim again. For the rest of the day after such attacks the group would avidly move away if Chella approached and Chella was not seen to participate in any play behaviour.

Chella shows sexual interests in cycling females, following them, sniffing their genitals and mounting them however, with the exception of Pitchou the females seem uninterested in mating with him. Chella's mating attempts are currently unlikely to result in the pregnancy of the females as he initiates an incorrect copulatory style, thrusting in a ventro-ventro position, instead of a dorso-ventro position. This is a result of his limited experience learning from an adult male and is common of some hand raised males in European zoos.

Through display behaviour Chella defends his outdoor territory from noisy members of the public, birds and the guenons in their neighbouring cage. This is very typical behaviour for a blackback gorilla, testing his strength against his environment. He also will strut and display in front of known people as a show of strength, and also for a reaction, which he searches for through sideways glances at the person.

Currently Chella exhibits self directed tooth grinding when he is frustrated, common sources of this frustration seem to be being kept in the indoor enclosure after the group have entered the outdoor enclosure and waiting to be fed by the keepers. Recently he has also begun to pluck his arms during rest periods, perhaps an indication of boredom.

Pitchou

As an adolescent female Pitchou holds an excellent position in the group, she has strong relationships with most group members through approaching them to groom and pluck and because of a close relationship with Chella will become more dominant in the group as time passes. Mothering behaviour is seen towards Batek and in particular Akiba. With Batek, Pitchou approaches him to groom often restraining his movement. Akiba initiates contact with Pitchou up to four times a day by approaching and whimpering with pursed lips, Pitchou then allows her to access to her nipple, where Akiba will attempt to suckle whilst Pitchou plucks her head and arms, typically it is Akiba who ends this association and moves away from Pitchou. No play behaviour has been seen by Pitchou, typical for a female her age.

The reason for the emergence of plucking behaviour over the past few months, is unclear, however, most gorillas accept her plucking them. Only Nyango refuses her attentions, although Pitchou still approaches and attempts resulting in Nyango typically moving away. The most destructive plucking is seen on Chella's lower back, where Pitchou has created a large bald patch. Considering few other gorillas approach

Chella this demonstrates the closeness of their relationship in the outdoor enclosure. Only Brighter is not approached to be plucked probably due to her more dominant position. Pitchou also plucks herself along her arms, legs and around her face. Such self directed behaviour may be due to boredom as it occurs mostly during resting periods. Pitchou plucks in two ways, either she will pull out hairs using her fingers, at other times using her teeth, hairs that have been pulled out she generally holds in her fingers and pulls through her front teeth.

Twigs

Although the lowest ranking female in the group Twigs holds this position and is not subjected to any excessive negative behaviour from other gorillas. Her paralysed arm often makes her slower to move or feed than others in the group, but she is well adapted and climbs, chest beats, displays and plays with ease. However being low ranking has several disadvantages that Twigs suffers from; she often feeds after the group and will not secure as much good quality food as higher ranking gorillas. She can also be chased by Chella and is the first gorilla (with Amo) to move as he approaches, this makes her fairly nervous and she is often much more vigilant of Chella's behaviour than others in the group. After being attacked by Chella she will chase him away, however, when he chases other gorillas she rarely joins the group in chasing him away. Brighter daily approaches Twigs to groom her able arm. This Brighter does by holding Twigs paralysed arm to restrict her from moving away.

Twigs is exceptionally playful for her age and probably uses play to reaffirm bonds in the group. However, being low ranking she is not a preferred play partner and thus although she initiates play more than any other gorilla through chest beats and throwing objects she is less likely to be played with. Benito and Akiba are her most common play partners, both play well with her, Benito being more careful probably due to her paralysed arm. Akiba already shows dominance over Twigs and will play more aggressively, often taking objects or food items away from her. Chase play between Akiba and Twigs is commonly seen before they enter the indoor enclosure at the end of the day.

Benito

Benito is a calm adolescent male, who is exceptionally popular with the younger gorillas and females alike. His social development is at a normal level for his age and position in the group, showing little aggression to the females and being the preferred play partner of Akiba, Amo, Twigs and Batek. Due to having an elder male in the group as a role model and his calm temperament he is likely to develop into a good leader and a manageable silverback. With regards to play Benito frequently makes use of objects, especially old elephant grass, hiding under it, nest making and using it in his play displays. During wrestling play with the younger or weaker gorillas he is exceptionally considerate and will play at the level of his partner instead of showing his strength. Chasing play is most common with Brighter and Jumbo at the end of the day, which often becomes very energetic.

Chella and Benito have not been seen to play during the study period and due to their separation at night it can be assumed that they are playing very irregularly. This is interesting as at this age it would be expected for Benito to be constantly testing his strength against Chella through spar bouts. However, when Chella attacks the group Benito is the main challenger chasing, barking and baring his teeth. In addition in the indoor enclosure during aggression between the females Benito often plays the role of the intermediary, usually a dominant male job. If these two behaviour continue to be seen without any play behaviour it could lead to increased tension between Chella and Benito which could end in serious aggression, thus it would be more beneficial if Benito could remain in a subordinate position until after maturity and not challenge the authority of Chella within the group.

Amo

Amo is the most vulnerable gorilla in the group, holding the lowest rank and struggling to be accepted by the group. This situation may stem from the constant negative interactions from Chella who does not accept his presence, leading Amo to be constantly vigilant and nervous in the outdoor enclosure. After receiving aggression from Chella, Amo remains unsettled for the rest of the day, constantly moving around and not resting for more than a few minutes. Obviously this is a very stressful situation for him, causing him much anxiety.

Like Twigs, Amo moves away from Chella on sight and feeds after the majority of the group, consuming much less than other group members. Amo plays much less than would be expected for a young male gorilla; however he does initiate play with Akiba, Batek, Benito and Twigs everyday. Unfortunately the other gorillas will only accept 50 % of his play offers, either ignoring him or moving away from him. Even when play does occur his play partners have a tendency to change partners for a more dominant gorilla. Amo has a good relationship with Brighter, who will often pull him onto her back to move around the enclosure. When Brighter was in oestrus she took to pulling Amo onto her back multiple times over a day and Amo exhibited thrusting behaviour onto her back. It is possible that through this behaviour Amo is learning the correct copulatory position and could impregnate her in the future.

Batek

Through much of the research Batek suffered from a cough which affected his behaviour and led to him being less active than normal. Batek shows good adjustment to the group and although his play behaviour is much less than young males in European zoos his development is normal. Typical of juvenile males Batek was involved in much play with older males, playing most frequently with Benito. Chella also prefers to play with Batek and initiated play with him on several occasions by pulling Batek towards him and tickling him. Batek would often try to evade Chella by moving away from him, but would then play when Chella did grab him. Batek is accepted into the group although he does not have any one attachment figure. Instead he is groomed regularly by Brighter, Pitchou and Jumbo and rests at random within the group. During his illness Brighter would approach, pull him onto her back and move to new areas of the enclosure with him, when Batek tried to get off her back she would often pull him back on and hold his arms to restrain him.

Akiba

Akiba shows accelerated social development and behaves more like a 7 year old female than a 5 year old. She is very dominant already in the group, overpowering all except Pitchou, Brighter and Chella. Her assertiveness and confidence have led her to develop a number of displays using objects found in the enclosure and she is the most capable in the group of problem solving. On one occasion Pitchou was trying to pull some vegetation from a palm tree fenced off in the outdoor enclosure, but she could not reach. Akiba approached, failed to reach, then climbed onto Pitchous back and pulled the whole branch down.

Akiba is very playful, still playing by herself, spinning and tumbling a lot, typical of juvenile gorillas. Being in a dominant position she can choose her play partner and will often initiate play with gorillas much older than herself and interrupt the play of other gorillas to be involved. Unlike other less dominant gorillas she is rarely refused play and can be insistent if refused. This is seen mostly with Chella, she approaches him cautiously and invites him to play by touching him or with a play face, and eventually he will grab her and pull her closer. Akiba uses displays frequently outside of play behaviour, asserting her dominance through stone throwing and chest beating around the group, although she shows no aggression to any group member.

A good relationship has developed between Pitchou and Akiba, whereby Akiba is comforted and allowed to suckle from Pitchou. Again she is insistent to be allowed access to the nipple and will scream at Pitchou if her initial pleas are ignored. It some cases 5 year old gorillas would still be allowed to suckle in captive groups, usually when the mother has another infant and thus has milk available. It is likely that Pitchou is seen as a mother figure to Akiba, although when not suckling Akiba does not approach Pitchou to feed or rest close by.

Adult females

It is difficult to provide an in-depth comparison of adult female gorillas to the same in European zoos as typically European zoo females would be pregnant or with offspring and thus display much different behaviour from those at LWC. In brief are some aspects of their relationships within the group and any self directed behaviour documented.

Brighter

As the dominant gorilla of the group Brighter holds an interesting position in that she is the only gorilla in which Chella does not show aggression. On one occasion he displayed near to her and she chased him away baring her teeth and barking at him, he did not re-approach her. However as Chella grows in strength it will be harder for her to retain this position and it will be interesting how her position in the group alters due to this. She uses her dominance mostly during feeding times when she can take preferred food items from other gorillas'

Brighter exhibits mothering behaviour towards the younger gorillas, pulling Amo and Batek onto her back and insistently approaches Twigs and Akiba to groom them. For her age she is incredible playful and late in the day will initiate play with Akiba or Benito, often play chasing for up to 10 minutes. Brighter is the only gorilla that Pitchou does not approach to pluck, possible due to her similar dominance status in the group. She shows no self directed behaviour, with the exception of regurgitation and re-ingestion of peanuts - a preferred food item.

Jumbo

Jumbo shows no strong association to other gorillas in the outdoor enclosure, she is openly accepted into the group and rests and feeds within the group at random. She is exceptionally attached to humans, Bouma in particular and will spend much of the day watching activities outside the enclosure and approaching humans to initiate contact. Occasional play is seen with Akiba when Akiba initiates play with her but most commonly is seen to exhibit self play, spinning, head shaking, chest beating and jumping into the air at random. With regards to objects Jumbo has a fascination with all articles from outside her enclosure, particularly if taking them elicts a response from a human. Pitchou approaches Jumbo daily to pluck her and Jumbo turns away from Pitchou to have her back plucked. Jumbo exhibits self directed behaviour at a greater frequency than others in the group including repetitive nose picking and hand movements, regurgitation and re-ingestion, these mostly occur whilst watching humans.

Nyango

The lethargy, lack of interest in her surroundings and other gorillas and consistent slow movements indicate that Nyango is depressed. She makes no initiation of contact with any other gorilla in the group or any human, does not play and refuses grooming attention from Pitchou. Nyango spends most of the day sat close to the fence watching out, often with Benito or Pitchou in close proximity. Food is a main priority to Nyango during the day, although she often will forfeit food in the indoor enclosure to stay in the outdoor enclosure at night. Chella will often chase Nyango but Nyango shows little tolerance of him; during the day she will move to the opposite side of the enclosure to avoid his movements and can refuse to go outside if Chella is released first. However if Chella attacks her she chases him aggressively, screaming and baring her teeth. Whether her daily slow movements are due to depression or a physical problem impairing her movement remains to be seen.

Her appearance and behaviour is typical of a gorilla hand raised away from other gorillas where introductions to gorillas occurred late in the juvenile period. Unfortunately most gorillas raised in this way never fully integrate into their social groups, always remaining aloof and antisocial and refusing any breeding attempts by their silverbacks.

Emma

Throughout the study Emma has been very quiet, she is active, accepted as part of the group and rests frequently with other adult females. No play behaviour, contact with immature gorillas or self directed behaviour were documented. When chased by Chella her tactic is to curl up in a ball, he grabs her legs and runs away, pulling her behind him. However, Emma was seriously ill during the study and it is therefore difficult to know how her behaviour has been affected by this.

Management Recommendations

Encourage Chella as group leader. To keep all 11 gorilla living together peacefully over the next few years it is important to support the largest male in the group as group leader. This will reduce challenging by younger males, reduce aggression between the females and enable the group to be managed as one. For this to be achieved it is important for Chella to be with the group day and night and will require careful integration of him into the group in the indoor enclosure. To encourage support of Chella he should also be the first into the indoor enclosure in the morning to enable him to protect him territory and during keeper feedings he should be fed first

Increase group cohesion. The greater the activity and interest between the gorillas in the group the less self directed and human directed behaviour will be seen and a strengthening of bonds between immatures and adults. The separation of weaker or lower ranking individuals is counter productive to this as the individual has to then re-establish his/her position into the group, which may or may not be accepted by other group members. Keeping the gorillas together at all times (with the exception of veterinary attention) helps to build cohesion and enables lower ranking individuals to hold their position without challenge.

Feeding of brouse material. In the wild gorillas spend much time feeding on brouse, which is often mimicked in European zoos by feeding willow branches. Brouse feeding has several advantages, it is time consuming, if available in large quantities can provide a group activity without competition and induces group rest periods for digestion. Again for the LWC gorillas this would reduce self directed behaviour and keeper watching and if used regularly would provide a more rigid routine to the group's day.

Scatterfeeds. The morning is the most important feed of the day and it is necessary to provide sufficient food for the group in a non-competitive way. Scattering a number of different foods in small pieces across the outdoor environment is beneficial as it allows all to feed equally and also allows foraging of the remaining food for the rest of the day.

Conducting research at LWC has been an enlightening experience, to work closely with a successfully working sanctuary and the gorillas directly affected by the bushmeat trade. This could not have been achieved as quickly or efficiently without the dedicated and committed management and staff at LWC who permitted access to the gorillas on a daily basis, provided no end of information and support and whose hard work results in 11 well cared for gorillas. Thank you!

APPENDIX 7

University of Chester

Gorilla Social Development & Management Report

For Cameroon Wildlife Aid Fund

March 2006

Johanna Hutchinson MSc.

University of Chester, UK.

Executive Summary

Several similarities occur between the CWAF gorillas and those mother raised in captivity, mainly, their strong social cohesion and the dominance of age orientated play behaviour between peers. However, being hand raised away from a family group has led to the gorillas having a strong human attachment, exhibiting minor abnormal behaviour and the development of age orientated hierarchies within each group. The adolescent group are now entering a phase of change, which will involve growth of the males, changes in dominance and potential aggression between males for food and female access. Currently the group still incorporate long morning play bouts into their routine, forage across the enclosure, but always rest together in the same area. However, changes to the group assemblage and enclosure will be necessary to hold the gorillas long-term in stress free conditions, suggestions to deal with these situations are discussed. The juvenile and infant group are a diverse and active bunch. Play occurs most frequently between Nkan and Shai, whilst Mvie shows most interest in allomothering Nona. The infants show good adjustment to the group and when a keeper is present are accepted into group play, rest, feeding and grooming periods. Play between the males and the infants are very common, although Yeba often becomes aggressive with the older males. Regurgitation and re-ingestion is witnessed multiple times each day by both Shai and Nkan indicating some stress within the group, however the group show little long term interest to events outside the enclosure and have a good habituation to humans. Management strategies are discussed with regards to sustaining group relations, keeper involvement and the long term keeping of adult gorillas.

Introduction

The CWAF study forms part of a larger piece of research which seeks to understand and compare social development and behaviour of immature gorillas in captivity. The social organisation of primates is highly diverse and is dependent upon the interaction of many variables. The development of relationships, which ultimately create the social structure of a group, is understudied in gorillas, as continuous observation of western lowland gorillas is not yet possible.

Captive gorillas provide a valuable resource to further our knowledge of the development of behaviour and relationships in groups of differing size and structure. Established populations of gorillas held in European zoos enable a comprehensive study of juvenile and adolescent behaviour in environments familiar to them and without the environmental stressors of the forest habitat.

In addition the bushmeat trade has led to an increase in immature gorillas taken into captivity after enduring periods of stress and mis-management. Hand-rearing, rehabilitation and reintroduction of individuals into social groups are necessary for the survival of these gorillas. However, the long-term success of these projects is dependant on managing the gorillas in captivity for their lifetime. Research into gorilla social development and behaviour links this need specifically with the sanctuary gorillas' behaviour. This pioneer research will enable an understanding into the prevailing differences in gorilla behaviour across establishments.

Throughout the months of January and February 2006 the researcher (JH) spent a total of 260 hours conducting focal observations on the immature gorillas in Mefou National Park. Immaturity was defined as a female gorilla under 8 years old or a male gorilla under 11 years old, in accordance with the literature on wild mountain and lowland gorillas. Using CWAF records to determine approximate age gorillas included in the study were Bobo, Nkamum, Kibu, Jasmine, Avishag, Nkan, Shai, Mvie & Nyum. On each day of data collection one gorilla subject was chosen and followed for their duration in the outdoor enclosure. Data were collected on feeding, resting and play behaviour as well as proximity and interactions with other gorillas.

This report:

- Highlights the findings of CWAF data collection
- Provides a summary of the behaviour of all 13 gorillas in relation to same age and sex peers in the European captive population.
- Makes suggestion for the future management of the gorillas

General

In essence, the gorillas at CWAF should be considered a success story, after the unknown ordeal of each gorilla to survive and live as part of a group at all shows a resilience and strength of character that not all gorillas possess. However, certain traits not seen in family groupings in European zoos have been documented, purely as a result of their experiences and subsequent necessary living arrangements. Most obvious is the strength of attachment to their keepers and within the adolescent group an intense curiosity of unknown people. Although this is partly food expectation from known keepers can affect the behaviour of the gorillas with interest being drawn outside of the enclosure and often an interaction demanded. Neither group readily accept unknown people close to their enclosure and both groups took several days of observations to habituate to the researcher, however this was more difficult to achieve with the adolescent group due to their distance from the village and thus relatively in-acquaintance with unknown people. Subsequently Kibu, Gerri and Avishag interacted with the researcher on a daily basis and although no attention was given these behaviour did not extinguish.

Both groups show a high level of social cohesion, acting as a group throughout the day and moving together to forage or rest. Within the juvenile group cohesion is based around the keeper for much of the day, but when the keeper and infants are absent the juveniles move around the enclosure in close proximity. All gorillas are accepted into their social group with little daily aggression seen between individuals; small disputes are settled by the weaker gorilla moving away from the more dominant, or through play bouts. Documented aggression was directed towards food possession or with regards to the adolescent group access to females in oestrus (Bobo & Nkamum). All individuals show high levels of play behaviour, many playing at a higher rate than found for their age and sex compatriots in European zoos. Play is regularly an energetic and intense period in the morning and consists of fewer slower bouts in the afternoon, all gorillas show appropriate play behaviour and play with multiple group members. Play behaviour is a positive sign of group health as it strengthens bonds between group members, builds cohesion and rank order without use of aggression, promotes good physical development and reduces boredom. Both groups have a defined and accepted male leader, although in the adolescent group Gerri still holds dominance overall. Nkan and Bobo's leadership may be accepted currently but this may not hold true for the future with Nkamum and Shai constantly testing their strength against the leader, challenges for dominance are likely to begin in the adolescent group where cycling female provide a resource to compete for. Both groups make good use of the enclosure space, with individuals often moving independently throughout the day to forage in the available vegetation, although the juveniles spatial arrangement is largely determined by the position of the keeper the juveniles do move further away which encourages the infants to forage in the same way.

The Adolescent Group

Gerri

As the oldest female in the group Gerri shows more independence from the others, often moving away to feed, find sticks or rest. This is correct behaviour for her age and demonstrates her maturity and slight detachment from the group. A wild gorilla of her age would have migrated and probably would be caring for her first offspring. In line with this Gerri shows unusual possession of sticks, often carrying and resting with them for long periods under her arm and initiates much copulation with Bobo when in oestrus. Kibu is also allowed to copulate with Gerri on occasion but Nkamum is not accepted as a sexual partner. Bobo does not need to mate guard Gerri as she follows and approaches him for sexual contact. When play behaviour occurs within the group Gerri is often a central role chasing with Jasmine and Kibu for possession of favoured food items (vines, branches). Play often lasts for an hour and Gerri often plays for the duration, asserting her unchallenged dominance over the group, without using aggression. Gerri is especially dominant with regards to food, and is seen to take items from other group members and chase those who take food from her. Gerri shows excellent tool use with sticks through the electric fence and has been photographed using two sticks to secure a food item, one to hold up the fence, one to pull the food item closer. Attachment to humans remains strong, particularly when in oestrus when she insisted on copulating in front of the observer. She will often separate from the group to watch the keepers in their duties or investigate unknown noise.

Avishag

Avishag has a strong, autonomous character, often acting alone and moving independent of the group. She uses aggression to assert herself, often with the result of being dominated by Bobo. On a couple of occasions, after Avishag has displayed or attacked a group member Bobo has physically restrained her until she submits to him. During play she is highly aggressive, using physical contact to instigate chase behaviour with the males, although she plays regularly, she is as likely to sit close to the play bout and not participate. Avishag actively protects the territory, displaying through object displays and charges to visitors and unknown keepers alike. This behaviour has been shown to be highly robust with Avishag still displaying to the researcher after several weeks of observation. Territory protection is often taken upon with Nkamum, frequently with both charging and object throwing in unison. Her persistence in this behaviour and lack of tolerance to new situations leads to Avishag having less adaptability than other group members. When is oestrus Avishag is mate guarded by Bobo, but only copulates with him due to his dominance. She has a strong alliance with Nkamum and tries to approach him for copulations; however this has led to confrontations between the two males. During resting periods Avishag has one particular resting area within the bushes, out of sight. Although the rest of the group lie close by only Kibu and Bobo will follow her into the bush. At night Avishag is most likely to refuse entry to the indoor enclosure, remaining outside without food or other gorillas, which may be linked to the males dominance over food and limited space in the satellite enclosure. Avishag shows no self directed behaviour.

Jasmine

Jasmine is a calm, mature female, more aloof from humans than the rest of the group, but a central gorilla with regards to play, copulations and escapes. She is the main instigator of much play and escape behaviour by finding preferred food items or appropriate sticks in the enclosure. This creates a lot of excitement from the rest of the group, who will challenge her and intercept her find. This often leads to long play bouts with Gerri, Bobo, Kibu and Nkamum where possession of the favoured object is the aim. Play with Jasmine is highly energetic, but not aggressive and can involve more than one partner at a time. Jasmine is interested in copulations in and out of oestrus and invites all the males to mount her by presenting her rump to their faces. If mounting does not occur she will force herself on top of the male in a ventro-ventro position, thrusting onto the male. She prefers to copulate out of sight of the observer and to enable this will carry Bobo on her back to a suitable area. With regards to the enclosure Jasmine uses all the space provided and forages more than other group members, she is often out of sight in bushes, or high in the trees, moving independent of other gorillas. She shows appropriate social development for her age and no signs of self directed behaviour

Nkamum

As a subdominant male Nkamum has a lot to prove to the group and a difficult position to maintain. Although bigger in size than Bobo he is clearly subordinate and after aggressive play, or a fight he is the first to move away. However the pressure of securing females and dominating the group is likely to change this situation and more aggressive behaviour is likely towards Bobo in the future. Currently Nkamum is the main male protector of the group, defending the territory through charges and using objects in his displays, regularly he struts in front of the group, particularly if a female is in oestrus. This is correct behaviour for his age, representing his advancement into sub-adulthood, not seen yet in Bobo. Although Nkamum will approach other group members to play he is not a preferred play partner when Bobo is around and can be pushed out of group play activities, or not allowed to rest close to the others. However, when play occurs between Nkamum and Bobo good demonstrations of male-male play are seen, long chases are seen interceded with spar displays and short wrestling sessions. These important play sessions aid each male to know the strength of each and thus reduce aggressive tension between the two. Being subordinate leaves Nkamum with limited access to females in oestrus, even when certain females (Avishag) prefer to mate with him. All aggressive encounters between Nkamum and Bobo were recorded when a female was in oestrus and Bobo was guarding them. Nkamum does secure opportunities to mate with all females and demonstrates the correct copulation positions as well as ventro-ventro mounting, although ejaculations were not witnessed. Nkamum shows consistent finger sucking behaviour during rest periods and before receiving food, this habit developed during infancy is unlikely to extinguish at this age, but may be reduced through regular scatter feeding in the enclosure to reduce food anticipation.

Bobo

Bobo is a good group leader, dominating all except Gerri without use of excessive aggression. Gerri still shows her dominance to Bobo, especially where food acquisition is involved, Bobo is not permitted to take food from her and indeed rarely begs, during play Gerri also dominates Bobo and even when in oestrus Gerri pushes herself onto Bobo and determines the time of copulations. Play is Bobo's major vice for dominating the group, initiating long play bouts with all group members and maintaining highly energetic displays in-between play. Being the dominant male he is the most sexually active of the group, guarding all females when in oestrus and mating consistently throughout the day. Bobo does show a correct copulation stance, but in an unusual position perhaps due to being too short to enter the females in this position, although grunting noises are made and Bobo often licks fluid off his penis after intercourse. In addition Bobo daily masturbates during resting periods, rubbing his penis for long periods and licking/sniffing his hand afterwards, again no ejaculation was seen. Bobo demonstrates a number of behaviour probably learnt from the keepers including blowing raspberries, lip smacking and a bizarre rump beat display, behaviour not usually seen in gorillas and mostly not copied by other gorillas in the group.

Kibu

Although the lowest rank in the group Kibu is accepted as a group member and maintains this position well. He behaves much younger than his age or his male peers and shows several self direct behaviour, although in nature seems very content and not stressed by his environment. Kibu initiates play regularly with other group members but is the least likely to be accepted, he also tries to initiate play during group resting periods, and is ignored, showing a mis-understanding of that time period. During group play he is very active with all group members, but is played with in a less aggressive fashion, such as with a younger gorilla. Kibu still plays alone regularly, spinning round, tumbling and jumping from tree to tree. Worryingly, he also incorporates repetitive movements into self play sessions and can spend minutes nodding his head between his legs. He shows an interest in the fence and a lack of fear of electric shocks and objects that could be used to escape, spending much time with banging sticks against the fence. During female oestrus' he is accepted by Bobo and the females to attempt mating and although he shows the correct position and movements has little enthusiasm. Often during attempted copulations Kibu does not have an erection, thus penetration is unlikely. Kibu shows a strong attachment to humans, always seeking contact and trying to initiate play with keepers and the observer, even after several weeks of ignoring him he would still follow the observer around the enclosure, trying to gain eye contact and approval. In addition he regurgitates and re-ingests his food multiple times a day and sucks his finger during resting periods and before receiving food.

The Juvenile/Infant Group

Nkan

With regards to social behaviour Nkan is an active and inquisitive male, whom instigates play more than others, forms the preferred play partner for the majority of the group and is accepted in his dominance. Being the oldest male it is common for younger males to want to test their strength and younger females to gain his attention, thus he is in a good position to gain ample gorilla stimulation and develop into a good leader for the group. Currently he is dominant male of the group, although Shai, Mvie and Yeba will challenge him if he is too persistent with play attempts, when the keepers are close by. His play style differs with his play partner and this shows good understanding of his peers. With Shai and Mvie he will play wrestle for long periods, which often result in chases when one or the other gorilla become aggressive. With Nyum, Ncarla and Nona Nkan plays in a calmer, restrained manner, using gentle play and long bouts of slow chase. Here he uses the 'eyes closed' manner which many of the group have copied, moving after each other with their eyes tight closed, until they make contact. Nyum, Ncarla and Nona have much less control of play with Nkan compared to play between themselves. Nkan dictates play with them, beginning and ending play when he chooses, despite the younger gorilla's attempts to leave. Nkan also determines type of play with the infants often forcing them into submissive positions for sex play, but gently playing with them afterwards. With the exception of Yeba, Nkan shows a good relationship with the younger gorillas, allowing them to climb over him and he often initiates small grooming bouts with them. Although he does not initiate alloparental behaviour he will allow the infants to climb onto his back, but generally will then sit down until they have chosen to leave. With regards to Yeba, Nkan antagonises him into a temper and then continues to interact with him until Yeba attacks and a keeper intervenes. These attempts and the lack of play behaviour resemble Nkan asserting his dominance, but Yeba refuses to be submissive to him.

Although the oldest in the juvenile group Nkan shows a stronger human attachment and a more insecure disposition than other gorillas. Nkan spends more of his time than other juveniles in the close vicinity of the keepers and is dominant over their time and whom they choose to interact with. He often uses domination of the other gorillas to stop them playing with the keepers and displaces them to seek keeper attention. With the keepers he is insistent on getting his own way and reacts badly to discipline, throwing himself on the ground and screaming. In addition Nkan is constantly testing keeper strength, using rougher displays than necessary to get their attention and at times it is important for both keepers to enforce their domination. Nkan also shows high levels of regurgitation and re-ingestion behaviour, particularly after feeding, but often at intervals throughout the day, although he shows little other stereotypical behaviour on a regular basis.

Shai

Shai is a confident young gorilla, already showing specific male behaviour such as territory protection and wariness of visitors. His position in the group as second male allows him to demonstrate displays of struts and lunges towards Nkan more than others, many of which are ignored. The constant testing of strength against Nkan and the keepers through play bouts and displays is a typical male behaviour and will increase in intensity over the next few years. It is likely that Shai will always contend with Nkan's dominance, in a similar way that Nkamum challenges Bobo. Play between Nkan and Shai becomes very active, often incorporating spars, long chases and energetic wrestling bouts. Shai has more equal play relationship with the younger gorillas than Nkan, attending to their initiation of play more and playing specifically at their level. The occurrence of gentle play with Yeba has specifically increased over the past few weeks, with Yeba approaching Shai to play regularly. Play with Yeba is becoming more equal, with aggressive interactions diminishing. Yeba also tries to climb onto Shai's back, but leaves again before Shai can carry him. Nona and Ncarla also play with Shai daily, often in long wrestling bouts. Shai does not groom or initiate

sex play with the infants, but will carry Nona away from the group and 'allomother' her, often restraining her from leaving. Play bouts between Mvie and Shai are always secondary to play with Nkan, although they play both prefer to play with Nkan and thus the incidence of play between the two is lower.
In a similar fashion to Nkan and Mvie, Shai regurgitates and re-ingests his food during the day at high levels, but unlike Nkan there seems to be little variation in the rate of regurgitation across days, perhaps indicating a base level stress experienced in the enclosure.

Mvie

Mvie shows a good level of social development for her age, with some signs of accelerated development in allomothering and foraging behaviour. Mvie behaves as a typical female, seeking the males as play partners and playing predominantly with them, foraging more than the males and being less dependant on the keepers for support and reassurance. During the day she makes good use of the enclosure, moving away from others to climb and rest or forage. Typically she finds more preferred food items than the males, who can follow her and subsequently snatch the food item away. Grooming behaviour is exhibited most by Mvie in the group, or by others directed towards Mvie to instigate contact with her. She is recorded to groom all group members, including the keepers, but shows special interest in grooming infants and Nyum for longer periods. Nona receives most grooming from Mvie as she is often carried away from the group and 'mothered' for periods up to twenty minutes. Although Nona often protests and tries to move away from Mvie, Mvie will restrain her to continue grooming or place her on her back (often with an incorrect holding style - facing backwards) and move further away from the keepers. She is often followed by Shai, Nkan and Nyum when in procession of Nona who try to instigate play with Mvie, allowing Nona to escape, it is rarely seen that Nona is taken by another group member from Mvie. Although Mvie will play and groom Ncarla and Yeba she does not allomother them and will only carry them when they initiate contact. Her determination and persistence in allomothering, even when Nona is trying to escape is typical of female gorillas older than her, showing her acceleration in this behaviour. During play bouts Mvie uses many displays, such as chest beating to initiate play with the males, which is usually fast, fluid and on a par with male-male play seen between Shai and

Nkan. Displays are absent when play begins with Nyum and the infants, although this play is often much slower, less intense and lasts for shorter periods of time. Mvie shows little interest in events outside of the enclosure, she is the first to move away from visitors investigates noises from the village much less than the males Mvie is set to grow into an independent and confident female gorilla, who will probably dominate other females within the group and become a mediator in group politics as the males compete for dominance.

Nyum

As a result of the meningitis that Nyum suffered from last year there are several physiological aspects of her behaviour that differ from the other gorillas. At times she seems uncoordinated in her ground movement, particularly when trying to move fast, which often results in her falling over. However when climbing or involved in contact play behaviour she shows much better coordination, perhaps as a result of the greater concentration needed with these activities. With regards to social development again this differs between whom she interacts with, often playing and acting more like a juvenile when participating with peers as opposed to infants. Thus for Nyum in the next few years it is important for her to be in an environment which facilitates better movement and appropriate behaviour for her age. Although she may never achieve a full repertoire of adult gorilla behaviour, she will develop more in a peer group rather than being housed with gorillas at an earlier stage of development. Currently her group and enclosure support these needs. She is fully accepted within the group, despite her disabilities and her frequency of play is only slightly less than Mvie. She forages alone and with Mvie and is successful at finding appropriate food in the environment. However she does show a lack of understanding of certain 'rules' within the group, particularly with regards to initiating play with another gorilla, often lunging on other playing gorilla dyads, with the effect of being ignored instead of incorporated into the play. The group's infants often try to initiate her to carry them dorsally by climbing onto her; she seems not to understand their reasoning and will either stop walking or initiate play with them, resulting with the infant leaving her. Nyum has good relationships with Nkan and Mvie, both of whom interact with her regularly. Through resting close to Mvie she is copying grooming behaviour, often grooming an infant that Mvie is grooming or grooming Mvie after receiving grooming from her. Nyum shows a strong attachment relationship with the keepers, staying in closer proximity to them than other juveniles and insisting on interacting with them. During rough play she will often return to the keepers for protection much as the infants do.

Ncarla

Ncarla is growing into an independent young female gorilla, spending more time away from the keepers than the younger infants and only initiating contact for defence or reassurance. She has good relationships with other group members, especially Nkan, whom will play with her for long periods of time, chasing, gently wrestling and sex play. Again as a female she prefers to play with male gorillas and is the most frequent play partner of Yeba, which presents an equal play relationship. Although she does try to initiate contact with Mvie to play, Mvie ignores her but does spend time grooming her during rest periods. Ncarla often plays with Nyum but only for short bouts before Ncarla moves away from her. Ncarla is beginning to show good use of the environment as her confidence grows moving away from the keepers to forage and climb for periods of time. She will spend more time away from the keepers when foraging in the same area as Mvie. Ncarla uses objects in her own play repertoires frequently and is seen demonstrating displays, including strut stances to visitors. Finger sucking is seen in anticipation of food, but generally not until the keepers have begun to prepare the milk, Ncarla does not nap in the outdoor enclosure, thus it is unknown if finger sucking also occurs when tired.

Yeba

The strong determined character of Yeba, along with the reluctance to be submissive to other males and the high incidence of strut displays lead to the conclusion that Yeba understands that he is male! In turn his development is accurate for his age, with limited independence away from the keepers and higher levels of self play than peer play. Male infant gorillas have been found to wean slightly later than females and show more reliance on their mothers til a later age. In line with this Yeba shows reluctance to move independently from the keepers and rarely feeds or plays far from them and screams if left behind. Yeba plays most with Ncarla and is developing 'fairer' wrestling play with Shai, Mvie regularly grooms him and he is often insistent on being carried by other gorillas by climbing onto their backs, however, they rarely carry him far. Play with Nkan is rare and ends in aggressive actions by Yeba due to Nkans antagonistic displays. Generally such aggression is initiated by Yeba fuelled by Yeba refusing to be submissive to the older male, leading to the keepers separating them. When hungry or tired Yeba sucks his fingers, this occurs more readily at lunch time than in the evening.

Nona

As the youngest of the group Nona is currently treated as the group baby and is protected, played with and allomothered much more than either Yeba or Ncarla. Through this Nona is exceptionally confident in the enclosure and will spend long periods away from the keepers close to older gorillas. Nona shows an advanced social development with respects to securing her own food by climbing in small trees, playing with objects found in the environment and not being dependant upon the keepers during agonistic interactions. However, being the youngest she is encouraged to spend more time close to the keepers and is equally content interaction and playing with the keepers, often napping with them before milk time. Due to the older gorillas affinity to her Nona plays mostly with the juvenile gorillas as opposed to the infants, in particular Nkan and Shai. She clearly understands the play rules of chasing and wrestling, but has not yet understood when a play bout is finished, leading to the older gorillas moving away from her to signal the end. Nona instigates play with the males often through direct contact, but does not yet use action displays to show her interest in play. Although Mvie often tries to play with Nona does not readily accept to play unless she is being restrained and will often move away from Mvie when the opportunity arises. Mvie's interest in Nona is not reciprocated, with Nona often resenting being allomothered and resisting through moving away from Mvie, or showing aggression towards her. Nona regularly does not rest close to Mvie and actively moves away if Mvie approaches, or tries to groom her. Nona too demonstrates finger sucking behaviour in anticipation for milk feeding, but not at other times during the day.

Future management considerations

Use of keepers

Both groups show excellent social cohesion and acceptance of their keepers within the group is due only to the long term relationship between the keepers and the gorillas. The nature of these relationships may change in the future but it is and will continue to be evident that this primary secure relationship has enabled good social development in all gorillas, alongside the early establishment of peer groups allowing species-specific behaviour to develop. Although the role of the individual keepers may become less evident in day to day management of the groups it should be ensured that their relationships will always be a positive influence on the group's management over the long term. Keepers relationship with both groups will move from individual primary caregiver to group manager; a role of equal importance and an understanding of the needs of adult gorillas must be sought. The development of this new relationship is now beginning within the adolescent group whereby the gorillas accept the keepers as dominant, but can refuse to obey daily tasks such as entering the satellite cage and willingness to accept keepers during feeding and copulation periods may follow. A situation should be avoided whereby a gorilla feels the need to assert dominance over a keeper. The use of a keeper as a central adult figure in the juvenile group is highly effective in monitoring the group development but also individual behaviour, particularly in light of introducing infants into the group. The keeper is used as a base for protection, comfort and shelter throughout the day as well as providing food and initiating resting or feeding sessions. Although the keepers encourage independence in all gorillas, the keepers have different expectation of each gorilla depending on their age and development stage, which allows each to develop and initiate into the group at their own rate, without undue stress.

Diet

Wild gorillas spend large periods of each day in food acquisition feeding mainly on vegetation and supplementing with fruits as available. In this way resting becomes necessary periodically to digest cellulose structures and facilitates times of play in younger gorillas. Due to the expanse and composition of the enclosures all gorillas have the opportunity to forage on vegetation, the amount and quality of vegetation available may differ across the seasons with less available in the dry seasons and due to daily degradation it is likely that preferred vegetation is found in greater quantities in the surrounding forest. The daily feeding of high sugar, low protein fruits however are not considered beneficial to the gorillas as it provides little cellulose fibre to aid digestion and is consumed quickly. A substitution of vegetation (either bought or cut from the surrounding forest) in the morning feed would benefit the gorillas taking longer to eat, providing a more natural diet and stimulating a more active routine. Examples include; banana plants, papaya leaves, maize still on the stalk or small branches with edible bark. Both groups show long periods of inactivity in-between fruit feeding, with the adolescent group resting for up to four hours such periods can be expressed as boredom, with high frequency of self directed behaviour, providing more activity during the day by extending the feeding periods will help to decrease these behaviour.

Effect of oestrus in the adolescent females

During the study all the females exhibited signs of oestrus, pinker genital region and showed increased sexual interest. Female oestrus lasted 3 or 4 days, during which time multiple copulations were documented. All females were mate guarded by Bobo, who followed and rested with them, refusing copulation access to Nkamum. Kibu was allowed restricted access to the females, but upon observation was often not seen to have an erection or insert his penis. Aggression was only documented between Nkamum and Bobo when a female was in oestrus. Generally aggressive encounters occurred later in the day, were short in nature, initiated by Bobo and ended by Nkamum moving away, or Gerri separating the males. Females showed distinct mating preferences, Jasmine & Gerri mated mostly with Bobo and occasionally with Kibu, Avishag accepted all 3 males, but sought Nkamum and showed preference to be close to him. Female oestrus has been documented as a period of heightened aggressive interactions between Bobo and Nkamum. Increases in aggression over time will be determined by the amount which Nkamum challenges Bobo's possession of the females Although this may not happen for a couple of years to come, it is likely that such challenges will lead to injuries in the males and potentially a chance in dominance. It may be necessary in the future to separate one or two males from the group during a female's oestrus to reduce tension and potential injury, thus the building of an adequate holding facility adjoining to the enclosure is necessary.

Managing adult gorillas in captivity

As the male gorillas at CWAF reach adulthood they are more likely to compete for dominance and thus access to food and females. Several management strategies can reduce the competition between males, which in the short term may decrease tension in the groups. Firstly the use of contraception in the females will stop the females cycling and thus stop competition for sexual access. However, some oral contraception's can make the female 'smell' like she is in oestrus and thus increase copulations with the males, thus care should be taken as to which contraception in chosen. An alternative is to keep the female or males in the indoor enclosure until the oestrus is over. Secondly competition for food can be reduced by providing excess food and scattering it throughout the enclosure. If males can feed out of sight of each other, tension can be reduced. Thirdly, the indoor enclosure is often an area of increased tension between males due to the confined space and relative length of time inside compared to outside. Segregating males into isolation for indoor feeding and/or sleeping can be a short term option to reduce male injury and aggression.

In the long term in a sanctuary setting it will advantageous to have a system of keeping all gorillas in relative stress free groupings. The options are to hold the gorillas in mixed sex non breeding groups, mixed sex breeding groups, or a mixture of one male breeding/non breeding groups and bachelor groups.

Keeping multiple males with females in captivity is a difficult task and rarely achieved within the European population. Of the 59 gorilla exhibits in Europe, a total of 388 gorillas, only 7 zoos hold multiple adult males in breeding groups (*La Palmyre, France; St. Martin la Plaine, France, Munich Zoo, Germany, Madrid Zoo, Spain; Howletts & Port Lymme, UK; Belfast Zoo, UK and Twycross Zoo*). It would certainly be advantageous to contact these institutions to find how they achieve this before the males at CWAF become adults. The above management aids may help to achieve a multi male/female group, alternatively there is evidence to suggest that castrated males will live alongside breeding males without any problems. (An example of this is a male, castrated at 1 year old in Apenheul Primate Park, now lives alongside a breeding male in Belfast Zoo and provides an additional play partner for the youngsters). However castration will affect the development of the individual and may not be in the best interest for the gorilla in question.

The formation and maintenance of bachelor groups is still in its infancy in the captive population, but bachelor groups are being held in several establishments in America and Europe with little associated problems. The stability of such groups over the long term are as of yet unknown, but introducing males at a young age, housing them away from any cycling females and providing an enclosure large enough for males to disperse away from tension are all advantageous. However rates of aggression in bachelor groups in captivity and in wild mountain gorillas are higher than in breeding groups, thus the potential injury rate is higher. Aggression is generally found to be greater from older males towards younger males and can increase as the number of males in a group increases.

To be able to walk into an establishment and begin to collect data, day to day without interruptions or hassles is a rarity. For this to be possible in CWAF shows a strong management and a dedicated team of keepers, for which I am extremely grateful. I wish you every success with the future management of the gorillas and look forward to hearing of your successes in the future. A special thanks to Rachel, Bruno, Alfred, Appolinaire and Thierry for making research at CWAF such a pleasurable experience and sharing with me those special gorillas in your care!

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