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BEHAVIOURAL DEVELOPMENT IN WILD WESTERN LOWLAND GORILLAS (*GORILLA GORILLA GORILLA*)

Thesis submitted in accordance with the requirements of the University of Liverpool for the degree of Doctor in Philosophy by

ANGELA ANDERSON NOWELL

February 2005

DECLARATION

I declare that the work undertaken and reported throughout this thesis is my own, and has not been submitted in consideration of any other degree or award.

Angela A. Nowell

ABSTRACT

Behavioural development has received little attention in primates, despite having important influences on infant mortality, interbirth intervals, and therefore, growth of populations. Gorillas have long developmental periods, exhibit strong maternal bonds and integrate into intricate social systems, making them an ideal species in which to investigate non-human primate development. Gorillas exist across a range of habitats, and differences in behaviour, both within and between species reflect socioecological differences, for example, in the availability and distribution of food. Consequently, by using gorillas as a model, opportunities also exist to investigate environmental constraints on the development of independence. This study provides the first detailed analysis, with reference to ecological factors, of the development of behavioural skills and relationships in wild western lowland gorillas (*Gorilla gorilla gorilla*). Behavioural development of western lowland gorillas is then compared with published accounts of development in mountain gorillas (*Gorilla beringei beringei*) to determine the extent to which differing ecology influences behaviour.

The study was conducted at Mbeli Bai in the Republic of Congo, a large, marshy clearing, visited by gorillas predominantly for feeding purposes. Data were collected using scan, focal, all-occurrence and ad libitum sampling methods from 58 gorillas below 8 years of age. Spatial relationships, suckling, and the nature of interactions involving immature individuals were analysed. The distribution of time between different behaviours by immatures, and the development of independent feeding and travelling behaviour was also investigated, and all were tested for differences as a result of immature age, sex and social group, or the mother's parity.

Towards the end of infancy, individuals showed competent feeding behaviour in the bai. However, western lowland gorillas were not weaned until the juvenile period, and until this time, close association was common between mothers and offspring. With increasing independence from the mother there was limited investment in *relationships* with other individuals, and instead, a greater emphasis was placed on developing *skills* through play, alloparenting and agonistic interactions. When results were compared with those of mountain gorillas, there was evidence of increased investment in relationships, particularly with the silverback, by immature mountain gorillas, which was assumed to reflect lower rates of natal dispersal by mountain gorillas, and the greater likelihood that relationships with individuals in the natal group could prove useful in the future. Suckling and close proximity to the mother continued until later ages in western lowland gorillas, resulting in clear differences between them mountain gorillas in the duration of investment by mothers. More frugivorous western lowland gorillas required increased levels of investment by the mother before independence could be achieved, demonstrating the effect that resource availability can have on behavioural development in species where resources are widely and unpredictably dispersed.

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CHAPTER ONE

INTRODUCTION

1.1. INTRODUCTION

Non-human primates exist in a vast array of social systems (Wrangham, 1987; Kappeler & van Schaik, 2002) within a wide range of habitats. The behaviours that enable individuals to survive within these social systems and habitats must be sufficiently developed before complete independence from the mother can be achieved. Primate populations are subject to variation in environmental factors, such as predation pressure, and the abundance and availability of food in the environment. By studying behavioural responses to these, it may be possible to discover the effects of environmental factors, not only on primate social organisation and behaviour (see also Doran-Sheehy & Boesch, 2004), but also on the development of behaviour. For example, the size and composition of social groups, the amount of time spent searching for food, and the degree of range overlap between different groups (potentially influencing future transfer decisions (Harcourt & Stewart, 1981; Cheney, 1987b)) are all affected by ecological factors, and primates' responses to them determine the immediate physical and social environment in which individuals mature.

Gorillas exhibit strong maternal bonds (Stewart, 1981; Fletcher, 2001; Nowell, 2001) and long periods of immaturity (Pereira & Altmann, 1985). They integrate into dynamic and intricate social systems (Tutin, 1996; Doran & McNeilage, 1998), and exist within a complex environment in which resources must be located and predators avoided (e.g., Watts, 1991c; Byrne & Byrne, 1993; Fay et al., 1995). Because of these attributes, gorillas are ideal species in which to document the process of non-human primate development, an area that has received little attention (Pereira & Fairbanks, 1993; Kappeler & van Schaik, 2002) despite providing contributions to our understanding of human behavioural development (Fletcher, 1994; Harcourt, 1998). Additionally, within the genus *Gorilla*, variation exists in habitat type, diet, ranging behaviour, and group structure (e.g., Watts, 1984; Williamson et al., 1990; Watts, 1991c; Watts, 1996b; Doran & McNeilage, 1998; Doran et al., 2002; Parnell, 2002a), and by comparing populations of western lowland (*Gorilla gorilla gorilla*) and mountain gorillas (*Gorilla beringei beringei*) in which these factors differ, an analysis can be made of their effects on behavioural development within the framework in which maturation occurs.

1.2. DEVELOPMENTAL STUDIES

In primates, the transition from complete dependence upon the mother to independence begins at an early age, but intensifies as the mother begins investment in subsequent offspring (Walters, 1987). Social skills, feeding skills, and independent locomotion must be sufficiently developed to enable survival by this time. Although the development of behaviour has previously been studied in mountain gorillas (Fletcher, 1994; Fletcher, 2001; Stewart, 2001), captive western lowland gorillas (Hoff et al., 1981a; Hoff et al., 1983; Maestripieri et al., 2002), and a number of other primate species (e.g., in chimpanzees: Pusey, 1978; Pusey, 1983, baboons: Altmann, 1980, and macaques: Eaton et al., 1985; Worlein & Sackett, 1997), no detailed analyses have been made of behavioural development in wild western lowland gorillas. This study, therefore, provides an important account of previously undocumented behaviour in this species, and allows insight into how the differing ecology of mountain and western lowland gorillas may influence their behavioural development.

1.2.1. Definitions of Developmental Periods

Infancy is the period during which offspring cannot survive without the mother (Walters, 1987). In some species, it culminates in a clear display of parent-offspring conflict with the process of weaning, where a mother ceases investment in her current offspring to begin investment in the next (Trivers, 1974). Suckling infants prevent the mothers from returning to oestrus and conceiving (Stewart, 1988; Sievert et al., 1991), resulting in mothers being selected to provide less than infants are selected to demand (Trivers, 1974).

Juveniles are capable of surviving in the absence of their mother, but have not yet reached puberty (Walters, 1987; Pereira & Fairbanks, 1993). Juvenile mortality rates tend to be high, since juveniles must behave as adults do to integrate into the social unit, but without the same levels of support that they received from the mother during infancy (Janson & van Schaik, 1993). During this period, juveniles take full responsibility for their own locomotion (e.g., Doran, 1997b; Wells & Turnquist, 2001), and refine processes of food selection and preparation (e.g., Watts, 1985a; Byrne & Byrne, 1993).

The period between puberty and being capable of successfully reproducing comprises adolescence, or *sub-adulthood* (Walters, 1987; Pereira & Fairbanks, 1993). In sexually dimorphic species, where males and females take differing amounts of time to reach reproductive status, physical characteristics begin to diverge during adolescence (e.g., Cords, 1987; Janson & van Schaik, 1993; Watts, 1991b). Gorillas usually remain in the natal group during sub-adulthood, and it is during this period that immature individuals refine their social repertoire. Sub-adults are often the most active group members in initiating inter-group interactions (e.g., Parnell, 2002b), increasing their awareness of individuals in the population beyond their social unit, which promotes the successful transition to adulthood.

1.2.2. Social Development

An immature gorilla usually develops in a social group with between two (a female and silverback) and up to 47 other group members (Watts, 1996b; Doran & McNeilage, 1998; Kalpers et al., 2003), with a median weaned group size of 8.5 individuals (Parnell, 2002a). Immature gorillas must learn how to behave appropriately within the group to avoid being the target of aggression from other gorillas. Initially, the mother monitors the behaviour of her infant, for example, by retrieving it if it strays too far (Fletcher, 1994; pers. obs.) or by intervening in interactions involving her infant (Nowell, 2001; Stokes, 2004). As the relationship between mother and infant wanes in intensity, young individuals begin to regulate their own interactions with other group members and learn the social etiquette appropriate to group living.

1.2.3. Development of Feeding Skills

Young primates are nutritionally dependent on their mother (Nicolson, 1987), who provides or supplements the diet of her infant with milk for as long as is necessary. Western lowland gorillas feed on a huge number of food items (up to 230 items and 180 species (Rogers et al., 2004)), and many of these foodstuffs require some degree of processing before they can be ingested (Parnell, 2001; see also Byrne & Byrne, 1993). Young gorillas must learn which foods are palatable from the vast selection available in their habitat, and how to ingest them. The development of these skills is a prerequisite for survival without the mother.

1.2.4. Development of Locomotor Skills

In addition to being nutritionally dependent on the mother, gorillas are also dependent on her for transport during, at least, the first few months of life (Nicolson, 1987; Fletcher, 1994). In many primate species which are carried by the mother rather than being "parked" (see Ross, 2001), locomotion progresses from being supported ventrally by the mother, to clinging ventrally. Infants then begin to travel dorsally, before finally travelling independently (e.g., Hoff et al., 1983; Fletcher, 1994). Competence in independent travel is a further prerequisite for survival without the mother.

Once young gorillas become competent in their feeding and travelling behaviour, and in their interactions with others, the necessary skills are likely to be sufficiently developed to allow the survival of offspring in the absence of the mother.

1.3. STATUS OF THE GENUS *GORILLA*

1.3.1. Taxonomy

Gorillas are currently recognised as two distinct species, *Gorilla beringei* and *Gorilla gorilla*, each comprising two subspecies (Clifford et al., 2002). Mountain gorillas (*G. b. beringei*), found only in the tri-national area of Rwanda, Uganda and the Democratic Republic of Congo (Harcourt, 1996); and eastern lowland gorillas (*G. b. graueri*), found only in the eastern Democratic Republic of Congo, comprise the eastern subspecies. Two populations of mountain gorillas exist; in the Virunga Volcanoes, and in Bwindi Impenetrable Forest (Stewart et al., 2001). Recent population estimates place the Virunga's population at 360 gorillas (Kalpers et al., 2003), and Bwindi's at 300 gorillas (McNeilage et al., 2001). The IUCN status of *G. b. beringei* is "critically endangered" (Hilton-Taylor, 2000).

The majority of eastern lowland gorillas (75%) are found in their largest continuous habitat in Kahuzi-Biega National Park (Hall et al., 1998; Yamagiwa & Kahekwa, 2001). A survey carried out in 1995 placed the population estimate for eastern lowland gorillas at 11,020 weaned individuals (Hall et al., 1998). However, large-scale poaching occurred within Kahuzi-Biega National Park in 1999, and decimated the gorilla population. More than half of the gorillas (including groups habituated for tourism) in the park are thought to have been killed (Yamagiwa & Kahekwa, 2001), further confirming their “endangered” status (Hilton-Taylor, 2000).

The western species comprises western lowland gorillas (*G. g. gorilla*), and the newly recognised Cross River gorillas (*G. g. diehli*) (Sarmiento & Oates, 2000). Western lowland gorillas are found across central Africa, in Gabon, Republic of Congo, Cameroon, Central African Republic, Nigeria, and Equatorial Guinea (Harcourt, 1996). Recent genetic analyses have identified three distinct sub-groups: the gorillas of northern Congo and Central African Republic, those of Equatorial Guinea, and those of Gabon and south central Congo (Clifford et al., 2002). The total population estimate in 1996 was 100,000 (Harcourt, 1996), making this sub-species the most numerous with its consequent IUCN listing of “vulnerable” (Hilton-Taylor, 2000).

Cross River gorillas were acknowledged as a distinct subspecies in 2000, and occur only along the border of Nigeria and Cameroon in approximately nine isolated populations (Oates et al., 2003). Population estimates describe a dire situation with around 250 individuals remaining (Oates et al., 2003), hence, their status of “critically endangered” (Hilton-Taylor, 2000).

1.3.2. Current Threats to Gorillas

The remaining populations of *Gorilla* face numerous threats (Tutin, 2001), and the immediacy of these threats increases the need for detailed information on behavioural development in undisturbed populations, since the successful progression through immaturity and into adulthood necessarily affects rates of population growth. Threats faced by gorillas include the loss or fragmentation of habitat (due to logging, and loss of forest for cultivation or exploitation for minerals (Tutin, 2001; White & Tutin, 2001)); increased exposure of gorillas to disease due to the closer proximity of humans to ape populations (Lilley et al., 2002); capture of infants for the pet trade, and perhaps most importantly, the bushmeat trade (Peterson & Ammann, 2003). Many of these factors are exacerbated by political situations in host countries (Tutin, 2001). The effects of logging are greater than the immediate loss of habitat. Logging fundamentally changes forest structure by fragmenting and destroying habitats (Wilkie et al., 2000; White & Tutin, 2001). The resulting disappearance (whether long or short-term) of animals such as gorillas, chimpanzees and elephants, major players in seed dispersal, for example (Rogers et al., 1998), means that the impact is not limited to reduced numbers of such species. Rather, the botanical structure and composition of the forest is altered (Tutin & Vedder, 2001), thus affecting the viability of the habitat for future populations of these, and many other species.

In addition to its effects on the habitat, the logging industry, directly or indirectly, facilitates the commercial bushmeat trade through the road infrastructure created (Wilkie et al., 2000; Tutin, 2001), rendering previously unreachable tracts of forest accessible (Tutin & Vedder, 2001; Peterson & Ammann, 2003; Walsh et al., 2003). Gorillas have been hunted subsistently for thousands of years by local people, but with the commercialisation of the bushmeat trade, the growing demand in cities, and the increasing ease with which meat can be transported to meet demand, the level at which hunting is carried out is no longer sustainable (Tutin, 2001; Peterson & Ammann, 2003).

Recent data have prompted a movement for the immediate upgrading of western lowland gorillas' IUCN status to that of critically endangered, partly due to the effect of outbreaks of Ebola haemorrhagic fever on their density (Walsh et al., 2003). If Ebola, together with deforestation and hunting continue at the present rate, ape populations are predicted to decline by 80% within 33 years (Walsh et al., 2003). Following a recent catastrophic outbreak of Ebola at Lossi Forest, Congo, seven of 143 individually identified gorillas have been found alive after intensive searches (Walsh et al., 2003). These figures demonstrate the immediacy of the problem, and it is clear that action must be taken now to ensure the survival of *Gorilla*.

1.4. GORILLA STUDIES: PAST AND PRESENT

Savage and Wyman first described gorillas scientifically in 1847, and the extent to which scientists have studied the different *Gorilla* species differs considerably. Behavioural data, in particular, from western lowland gorillas are lacking (although see Parnell & Buchanan-Smith, 2001; Parnell, 2001; Stokes, 2004). The current study will fill this gap in the knowledge of western lowland gorillas, and in addition, *compares* behaviour between species, something that has only recently become possible, and to date, has only considered the differing socioecology of gorillas

(Doran & McNeilage, 2001; Yamagiwa et al., 2003), rather than actual behavioural differences.

1.4.1. Mountain Gorillas

The mountain gorillas of the Parc National des Volcans are by far the best known and well studied of all gorillas. George Schaller initiated a study of these gorillas in 1959 (Schaller, 1963), which was continued by Dian Fossey in 1967. This become one of the longest running studies on any one animal population, and is still ongoing. (Fossey, 1983; Stewart et al., 2001). Researchers based at the Karisoke Research Centre collected data, mostly from three habituated groups on a wealth of topics which give a huge amount of detail on the lives of the Karisoke mountain gorillas (see Stewart et al., 2001 for a review). However, mountain gorillas inhabit one extreme of *Gorilla* range, and therefore, cannot be considered truly representative of the genus (McNeilage, 2001; Robbins et al., 2004). Among those conducted at Karisoke, detailed studies of behavioural development were carried out (Stewart, 1981; Fletcher, 1994). One aim of this study is to evaluate the effects of environment on the development of behaviour in different subspecies.

1.4.2. Eastern Lowland Gorillas

Studies of eastern lowland gorillas have been more limited than those on mountain gorillas, primarily due to the political instability of the Democratic Republic of Congo. Studies have been frequently disrupted, but researchers in Kahuzi-Biega have nonetheless, managed to maintain a remarkable degree of continuity. Groups have been successfully habituated for both tourism and research, and data collected have focussed on topics such as feeding behaviour, ranging and nesting behaviour, rates of dispersal and transfer for males and females, and the effects of sympatry with chimpanzees (e.g., Yamagiwa et al., 1987; Yamagiwa et al., 1993; Yamagiwa & Mwanza, 1994; Yamagiwa et al., 1994; Yamagiwa et al., 1996; Yamagiwa & Kahekwa, 2001; Yamagiwa, 2001). However, the tragic slaughter of four of the five habituated groups in the highland sector of Kahuzi-Biega in 1999 means that the apparently unique social organisation of gorillas in Kahuzi is in danger of being lost (Yamagiwa & Kahekwa, 2001).

1.4.3. Western Lowland Gorillas

The vast majority of gorillas in captive institutions are western lowland gorillas (Schmidt & Hilsberg, 2001), but until recently, little was known about their ecology and behaviour in the wild. The establishment of various long-term field sites (Tutin & Vedder, 2001) followed censuses carried out in the 1980s that increased the estimated population of western lowland gorillas by ten-fold (Tutin & Fernandez, 1984; Fay et al., 1989; Fay & Agnagna, 1992; Blake et al., 1995).

Western lowland gorillas, for the most part, have proven themselves to be resistant to habituation, unlike mountain and eastern lowland gorillas (Tutin & Fernandez, 1991). Early studies gleaned information from feeding trails and nest sites (e.g., Tutin & Fernandez, 1985; Rogers et al., 1990; Williamson et al., 1990; Tutin et al., 1995; Tutin, 1996; Remis, 1997a; Remis, 1997b; Goldsmith, 1999). Some habituation studies are now enjoying good levels of contact with their groups, and much needed data on the behaviour of gorillas in the forest is emerging (e.g., Bermejo, 1997; Doran et al., 2002; Cipolletta, 2004; Doran et al., 2004).

In the mid-1990s, the discovery in central Africa of large, open clearings (called *bais*) that attract large numbers of forest-dwelling species, including gorillas, mainly for feeding purposes, provided new potential for answering questions about demography and the social behaviour of western lowland gorillas (Olejniczak, 1994; Fay, 1997). The major benefit of bai studies is that over time, the structure of the entire population using the bai can be determined. Data being collected from bai studies include accurate measures of group size and structure, which are difficult to achieve with counts from nest sites (Tutin et al., 1995), rates of emigration and immigration, interbirth intervals, age at first parturition, details of social relationships, interactions between social units, and other behaviours that are impossible to observe in the forest (e.g., Magliocca et al., 1999; Parnell & Buchanan-Smith, 2001; Latour, 2002; Parnell, 2002b; Gatti et al., 2004a; Gatti et al., 2004b; Stokes, 2004). To supplement these data, genetic studies are now being carried out on various populations of western lowland gorillas (Bradley et al., 2000; Clifford et al., 2002; Jeffery et al., 2004).

Such details are available for mountain gorillas, and to some extent, eastern lowland gorillas, but have been lacking in western lowland gorillas, primarily due to poor levels of habituation (Doran-Sheehy & Boesch, 2004). Although gorillas spend very little of their total time in bais (Parnell, 2002b), bai studies currently provide the best opportunity to analyse the social behaviour of gorillas in the wild.

Data from captive gorillas complement the work on wild populations, although they often concentrate on necessary captive management issues (e.g., Hoff et al., 1982; Hoff et al., 1996; Stoinski et al., 2001). Others have focussed on social relationships within groups (e.g., Tilford & Nadler, 1978; Enciso et al., 1999; Scott & Lockard, 1999), infant behaviour (e.g., Hoff et al., 1981a; Hoff et al., 1981b; Meder, 1990), and physiology and morphology (e.g., Sievert et al., 1991; Remis, 2000; Stoinski et al., 2002). The captive environment may influence behaviour and alter certain demographic factors; however, these studies provide useful data for comparison with those conducted in the wild.

1.5. GORILLA ECOLOGY AND BEHAVIOUR

The environment in which an individual lives plays a major role in behavioural development. Ecological factors necessarily affect behaviour, resulting in differences in the behaviour of populations that are subject to different ecological conditions (e.g., Yamagiwa et al., 2003; Barrett et al., in press). To help determine how such factors might influence the development of behaviour in gorillas, a summary of gorilla socioecology is given below, focussing on differences between mountain and western lowland gorillas.

1.5.1. Group Structure and Composition

The main social units in gorillas are stable groups, which are led by at least one silverback male, consist of a number of females plus their offspring, and can include other non-sexually active adolescents (Stewart & Harcourt, 1987; Doran & McNeilage, 1998; Parnell, 2002a). In all populations, solitary males are also present (Tutin, 1996; Watts, 1996b; Doran & McNeilage, 1998). Western lowland gorilla groups tend to be smaller than those of mountain gorillas (but not significantly so (Parnell, 2002a)), and are more likely to contain only one silverback male (Parnell, 2002a; Robbins et al., 2004). Up to six adult males have been documented in mountain gorilla groups (Kalpers et al., 2003), all of whom may copulate with females, but the dominant silverback tends to father most offspring (Watts, 1991b;

Robbins, 1995). Genetic analyses are underway in most study sites collecting long-term data to confirm the paternity of individuals. Bachelor groups (consisting solely of mature and immature males) have been observed at a low frequency in mountain gorillas (Robbins, 2001). Until recently they had not been described in western or eastern lowland gorillas (Magliocca et al., 1999; Yamagiwa & Kahekwa, 2001; Parnell, 2002b), but a study at Lokoué Bai, Republic of Congo has now reported their presence in western lowland gorillas (Gatti et al., 2004b).

The group sizes recorded during the last census of mountain gorillas in the Virungas probably represent the largest gorilla groups recorded (Parnell, 2002a) (a maximum group size of 47 was recorded (Kalpers et al., 2003)). Despite variation in western lowland gorilla group size, very large groups (of 20 and 32 individuals) have been observed at only one site in Congo, which is extremely rich in terrestrial herbaceous vegetation (THV) (Bermejo, 1997). Maximum group size appears to be limited by both social (access to females and sufficient protection against infanticide (Watts, 1989; Watts, 1990a)) and ecological (access to sufficient food resources (Watts, 1985b)) constraints.

1.5.2. Transfer of Individuals Between Groups

Both males and females may emigrate from the natal group upon reaching sexual maturity (at a mean age of 13.5 years for male mountain gorillas (Robbins, 1995), and between six and ten years for females (Watts, 1991b)). Females seldom travel alone, and usually transfer directly from one social unit to another (Stewart & Harcourt, 1987; Watts, 1996b; Stokes et al., 2003). Eastern lowland gorillas seem to be the exception, but experience levels of infanticide that are unusually low (Yamagiwa & Kahekwa, 2001), which may be a factor that allows movement of females in the absence of males. Data for western lowland gorillas are currently limited, but to date, the rate of natal emigration appears higher than in mountain gorillas, with the majority of young adults dispersing from their natal groups (Stokes et al., 2003; Robbins et al., 2004). Emigration from the natal group by nulliparous females has been associated with the absence of mating partners other than the putative father (Watts, 1990b; Sicotte, 2001). Therefore, with a higher occurrence of multi-male groups in mountain gorillas, female reproduction in the natal group may be more common (Parnell, 2002a; Yamagiwa et al., 2003). Secondary transfer is also common in female gorillas and is thought to represent attempts to reduce feeding competition and improve protection by males (Watts, 1996b; Stokes et al., 2003).

Males may disperse from the natal group (either abruptly, or over a period of months or years (Tutin, 1996; Parnell, 2002b)) to travel alone, or in some cases, to join a bachelor group before attempting to recruit females to form a breeding group (Harcourt, 1978b; Robbins, 1996; Watts, 1996b; Parnell, 2002b). Alternatively, maturing males may remain in the natal group and reproduce there. Robbins (1995) documented that 36% of mountain gorilla males underwent natal emigration while the remaining 64% would breed in their natal groups, given the appropriate circumstances, such as access to unrelated females.

1.5.3. Relationships Within and Between Groups

Strong relationships exist between adult female and male gorillas (Harcourt, 1979b; Stokes, 2004), and females spend more time in proximity to adult males than to each other (Stewart & Harcourt, 1987; Stokes, 2004). The transfer of females from their natal group upon reaching maturity (Watts, 1996b; Doran & McNeilage, 1998; Stokes et al., 2003), means they are usually unrelated to other females in the group, and tend to merely tolerate each other's presence, showing little evidence of an established hierarchy (Watts, 1994a; Stokes, 2004). Rates of agonism between males and females are higher than between females, and possibly represent a tactic adopted by males to retain mates (Stokes, 2004).

The predominant relationship of infant gorillas is that with the mother (Stewart, 1981; Fletcher, 2001; Nowell, 2001). Mountain gorillas (Fletcher, 1994; Stewart, 2001) and captive western lowland gorillas (Tilford & Nadler, 1978; Enciso et al., 1999) also exhibit strong relationships with the group silverback, but the extent of this relationship in wild western lowland gorillas has not previously been studied in detail. Interactions between immature gorillas include those of play behaviour with others in the same (e.g., Stewart, 1981; Fletcher, 1994; Nowell, 2001), and different social groups (e.g., Parnell, 2002b).

Given their increased dependence on fruit and the uneven distribution of this resource, western lowland gorillas are predicted to experience higher levels of feeding competition than mountain gorillas, both within and between groups (Stokes, 2004). Therefore, it has been suggested that western lowland females (who are more sensitive than males to ecological changes since their reproductive success is dependent on access to resources (Stokes, 2004)) may exhibit a more pronounced hierarchy than mountain gorilla females (Stokes, 2004), although such a hierarchy is not evident in a bai environment. Coalitions between females over defence of a food source are rarely seen (Tutin, 1996; Stokes, 2004).

Overt feeding competition between gorilla groups appears low in all subspecies. Home ranges often overlap, but groups are unlikely to concurrently use the same area and no groups have exclusive access to an area, (Tutin, 1996; Watts, 1996b; Doran & McNeilage, 1998). Mountain gorilla groups seemed more likely to engage in agonistic interactions than western lowland gorillas when in proximity to each other (Sicotte, 1993; Bermejo, 2004; Parnell & Nowell, in prep.), but may be more related to the acquisition of females rather than feeding competition. The peaceful mingling of western lowland gorilla groups is often observed in bais when groups converge to feed on plentiful herbaceous vegetation (Olejniczak, 1994; Parnell, 2002b), and feeding competition is likely to be at its lowest levels for western lowland gorillas during these periods. Recent genetic evidence has shown that at one western lowland gorilla site, silverbacks of neighbouring groups are highly related to each other, which may be account for the apparently lower frequency of aggressive interactions than in mountain gorillas (Bradley et al., 2004).

Male mating competition is likely to be the cause of many of the wounds seen on silverback males, although contact aggression has rarely been witnessed in western lowland gorillas (Tutin, 1996; Parnell, 2002b). Observed interactions in mountain gorillas between groups, or between groups and solitary males, during which female transfer takes place have been severe and have resulted in infanticide and home range shifts (Watts, 1989; Watts, 1994b).

1.5.4. Feeding Ecology and Ranging Behaviour

Variation in resource abundance and distribution exists between the habitats in which gorillas live, and is reflected in their feeding ecology and ranging behaviour. Mountain gorillas inhabit areas where abundant THV is constantly available (Watts, 1996b) and their folivorous diet varies little throughout the year (with the exception of bamboo used by some groups (Watts, 1998b)). Their diet is the narrowest of all gorillas, consisting of 106 different food types from 62 families; only six of which are fruits (Watts, 1996b). With abundant and evenly distributed food, day journey length (about 500m) is short, and correspondingly, home range size (approximately 8.2km^2) is small (Watts, 1991c; Watts, 1996b).

Eastern lowland gorillas feed in a manner intermediate to that of mountain and western lowland gorillas (Watts, 1996b; Yamagiwa et al., 1996). The distinct highland and lowland populations also differ from each other: the diet and ranging behaviour of highland populations resembles that of mountain gorillas feeding on THV and seasonally on bamboo, whereas more fruit (20 species) is seasonally incorporated into the diet of the lowland populations (Watts, 1996b). Correspondingly, day journey length (600-1100m) and home range size (30-40 km^2) fall between that of mountain and western lowland gorillas (Casimir, 1975; Yamagiwa et al., 1996).

Contrary to previous assumptions, western lowland gorillas are not restricted to secondary forests, and are also found in large numbers in primary and seasonally flooded swamp forests (Fay et al., 1989; Fay & Agnagna, 1992; Tutin & Vedder, 2001). They have been described as “opportunistic frugivores” (Tutin et al., 1991; Kuroda et al., 1996), and will feed on fruit whenever it is available (Tutin, 1996; Doran et al., 2002; Rogers et al., 2004). Around 98% of faecal samples contain fruit remains, and fruit parts account for 55% of plant food items (Tutin & Fernandez, 1993; Doran et al., 2002). During periods of fruit scarcity, increased quantities of pith and leaves are incorporated into their diet (Rogers et al., 2004). Ranging behaviour reflects the distribution of food resources, and western lowland gorillas travel further when fruit is plentiful to reach widely dispersed resources (Tutin, 1996; Doran et al., 2004; Rogers et al., 2004). Likewise, gorillas exploiting resources within swamps travel further to reach them than they would otherwise (Doran et al., 2004). Core home range (areas that account for 75% of use) of a group of western lowland gorillas was 5.32km^2, compared to 2.4 km^2 in mountain gorillas (Watts, 2000b), suggesting that western lowland gorillas experience increased foraging costs in order to meet their nutritional requirements (Doran et al., 2004).

1.6. AIMS OF THE THESIS

Details of the ecology and social behaviour of gorillas has been outlined, and the need for greater detail of behaviour for western lowland gorillas is clear. Using the information presented here, predictions will be formulated regarding the influence of ecology and future social relationships on the development of behaviour in immature western lowland gorillas. Specific hypotheses are presented in each of the data chapters, however, the main aim of this thesis is to provide the first detailed account of how socioecological constraints influence the development of behaviour in wild western lowland gorillas. To achieve this, previously unrecorded behaviour in wild western lowland gorillas will be investigated to determine:

- The development of feeding and processing skills in combination with differential investment in other behaviours, which together allow the development of nutritional independence from the mother.
- The development of mother-offspring relationships, focussing on spatial proximity, modes of travel, suckling and weaning, and interactions between mother and offspring. Changes in these behaviours with increasing immature age will be analysed to demonstrate the development of physical and emotional independence from the mother.
- The development of relationships with other group members (and individuals within the population), as young gorillas leave the proximity of the mother. Spatial relationships and interactions between immature gorillas and individuals other than the mother will be investigated to determine which aspects of adult social relationships are sufficiently important to shape the nature of immatures' relationships with others.
- Differences in the behavioural development of western lowland and mountain gorillas (and captive western lowland gorillas where possible) to determine the extent of ecological and environmental constraints.

Behaviours will be investigated to take account of factors that have previously been shown to affect the behaviour of primates. These include the age and sex of study subjects (Stewart, 1981; Brown, 1988; Nikolei & Borries, 1997), parity of the mother (Hooley & Simpson, 1981), size and composition of the social group (which ultimately result from socioecological factors) (Berman et al., 1997; Brent et al., 1997).

CHAPTER TWO

STUDY AREA, POPULATION AND METHODS

2.1. STUDY AREA

This study was carried out in Congo-Brazzaville, located on the Atlantic coast of Central Africa and straddling the Equator at 3° 41'N-5° 2'S, 11° 9'E-18° 39'E (Blake, 2002). Congo shares borders with Cameroon, Central African Republic, Gabon, Angola and the Democratic Republic of Congo. The population of Congo is low, at around 2.75 million people, the majority of whom are distributed within Brazzaville, Point Noire, and along the railroad joining them. Much of the 341,500km^2 of Congo (approximately 222,300km^2) is uninhabited forest (Parnell, 2002b).

2.1.1. The Nouabalé-Ndoki National Park

The Government of Congo and the Wildlife Conservation Society (WCS) initiated the Nouabalé-Ndoki Project in 1991, which led to the formation of the Nouabalé-Ndoki National Park in September 1993 (Nishihara, 1995). The park is located in the north of Congo between 1.5° to 3°N and 16° to 17°E (Blake, 2002), covering 392,169 hectares between the north-eastern Sangha Province and north-western Likouala Province of Congo (**Figure 2.1**). It forms part of an important contiguous tract of protected forest, which also includes Dzanga-Ndoki National Park in Central African Republic, and Lac Lobéké National Park in Cameroon. Congolese and expatriate researchers, WCS administrative staff, and Congolese Government representatives have maintained a continuous presence in Nouabalé-Ndoki National Park since its formation in 1993.

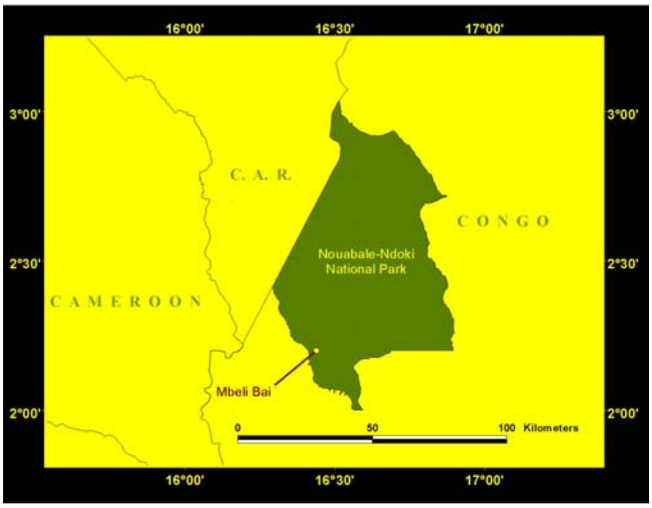


Figure 2.1. Location of Nouabalé-Ndoki National Park and the study site in northern Congo. Map courtesy of Emma Stokes.

2.1.2. Vegetation

Vegetation in the Ndoki Forest (which has the Nouabalé-Ndoki National Park at its core) has been categorised into twenty-four distinct types (Blake, 2002) The majority of the national park consists of large patches of mono-dominant *Gilbertiodendron dewevrei* forest along watercourses and upland plateaux (Blake & Fay, 1997), mixed forest and swamp forest types. Clearings in the forest, known as "bais", are found throughout the landscape and provide large quantities of aquatic herbaceous vegetation.

2.1.3. Logging History

In the north of Congo, the amount of forest lost to logging remained low until recent years, due primarily to its remoteness and the lack of infrastructure in these areas. Consequently, current logging concentrates on high-grade timber, and is largely restricted to two species of African mahogany (Blake, 2002). Although 62% of Congo's forests still stand, only 29% remains undisturbed, with selective logging having already been carried out throughout much of the south of the country (Blake, 2002).

The Nouabalé-Ndoki National Park forms part of the undisturbed area of forest: logging has never occurred within its boundaries resulting in minimal disturbance to the habitat and mammal populations.

2.2. STUDY SITE

2.2.1. Mbeli Bai

Mbeli Bai is a 12.9-hectare clearing in the south-west of the Nouabalé-Ndoki National Park, situated at 2°15'30.6 N 16°24.'39.8 E, and at an altitude of approximately 300m (see **Figure 2.1**). The intricacies of bai formation are not known, but elephant activity is thought to be important in the formation and maintenance of such areas (Parnell, 2002b).

Almost all of Mbeli Bai is permanently flooded with water reaching depths of up to 2m, and the surrounding forest is swampy. Two tributaries of the Mbeli River run through the bai (**Plate 2.1**) and two large pools are found in the north-east and south-east corners, both of which are used by forest elephants (*Loxondonta africana* *cyclotis*). A third, deeper pool, is found towards the middle of the bai and is used almost exclusively by bull elephants, who appear to dig for minerals in the waterbed. The areas used by gorillas tend to be concentrated along watercourses where growth of their preferred foods is plentiful.

The bai is dominated by species of aquatic and semi-aquatic vegetation, which form a floating mat, the level of which varies according to season. Hydrocharitaceae, Cyperaceae and Gramineae families are the most prevalent (Parnell, 2002b).

2.2.2. Climate

Temperature and rainfall have been measured daily at Mbeli Bai since 1998 (**Figure 2.2**). There tends to be a long dry season between December and March and a rainy season between June and November, although considerable variation is present between years. The highest temperatures are generally recorded during the drier months, and maximum daily temperature decreases during the rainy months. There is less annual variation in daily minimum temperatures, but lowest temperatures tend to occur during the long dry season.

2.2.3. Mammal Species Using the Bai

The abundance of vegetation in and surrounding bais makes them extremely valuable resources to many forest mammals. At Mbeli, the most frequent bai visitors include forest elephants (*Loxodonta africana cyclotis*), sitatunga (*Tragelaphus spekei*), forest buffalo (*Syncerus caffer nanus*), red river hogs (*Potamochoerus porcus*), black and white colobus (*Colobus guereza*), Congo clawless (*Aonyx congicus*) and spot-necked otters (*Lutra maculicollis*) (Mbeli Bai Study, long term records). Many other species of mammal can be observed on and close to the bai edge, including eight primate species, six duiker species, and leopards (see Parnell, 2002b; or www.wcs-congo.org for a complete mammal list).

Plate 2.1. Aerial photo of Mbeli Bai taken in 2001. Photo courtesy of Jeffry Oonk and Marleen Azink / Foto Natura.

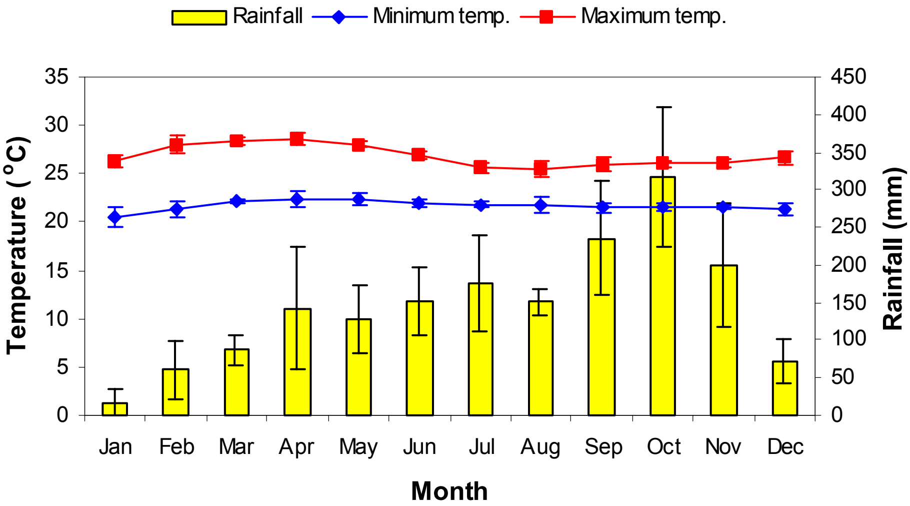


Figure 2.2. Mean monthly minimum and maximum temperatures, and mean monthly rainfall (with standard deviation bars shown). Data taken from Mbeli Bai Study, long-term records.

2.3. GENERAL METHODOLOGIES

After initial pilot studies by Blake in 1993 (Fay, 1997) and Olejniczak in 1994 (Olejniczak, 1994), the Mbeli Bai Study was established in 1995 and continues to the present day. Gorillas are the main focus of the study, but visits made by other regular bai users are also recorded in detail. Observers can individually identify all gorillas that have used the bai since the start of the study, and when personnel change, every effort is made to ensure that researchers overlap, thus maintaining continuity in the identification of individuals. When previously unidentified gorillas visit the bai (all drawings of "missing" gorillas made by previous researchers are reviewed to ensure that they are unidentified gorillas), they are assumed to be new and drawings are made so they can be re-identified on their next visit.

During the present study, observations were made from a 9m high platform (**Plate 2.2**) located halfway along the south edge of the bai. Throughout the study, a Bausch and Lomb 15-45 x 6 zoom telescope, and Opticron 10 x 50 binoculars were used for identification of animals. To record the location of gorillas (and other animals) in the bai, the area was divided into nine distinct zones using natural boundaries on the forest edge (**Plate 2.3**). Zones one to seven were divided further into nine areas based on compass bearings, for example, two north centre, three south west; zones eight and nine were divided into north, centre and south sectors.

Plate 2.2. Mbeli Bai observation platform, the second floor of which was used for research activities.

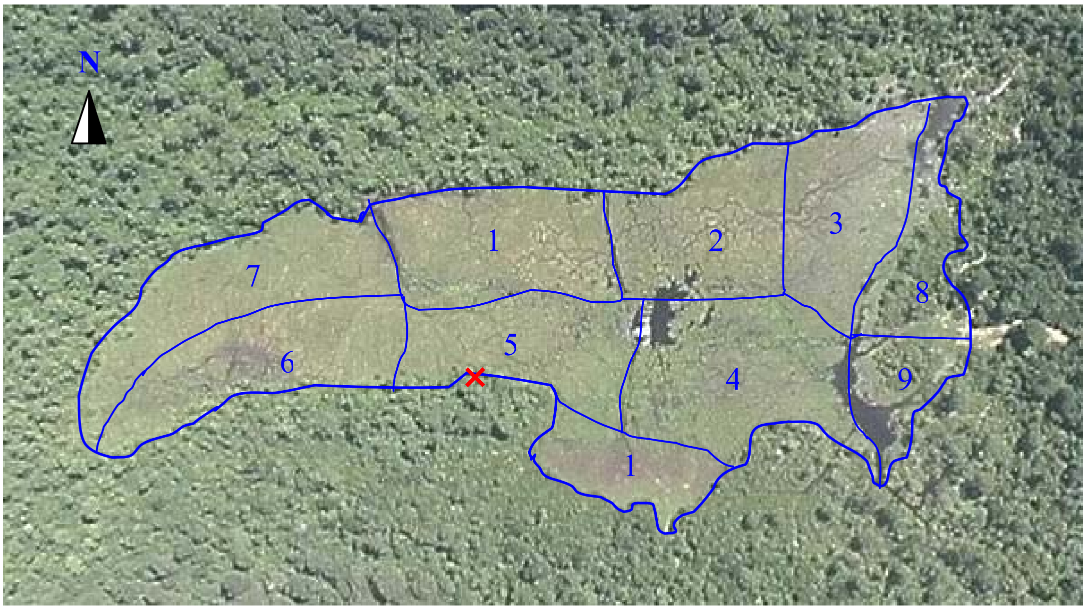


Plate 2.3. Mbeli Bai, showing divisions into zones. x marks the location of the mirador. Photo courtesy of Bryan Curran.

2.3.1. Gorilla Identification

Gorillas were identified using a number of methods employed by gorilla researchers (Magliocca et al., 1999; Parnell, 2002b), in particular, the marks and indentations above the nostrils – the noseprint, which is thought to be unique for each gorilla. Other distinguishing features used in this study include the form of the brow ridge, shape of the nostrils, colouration of pelage, distinguishing ear notches or other scars, sagittal crest development, and the size of the individual also plays an important role. **Plate 2.4** shows solitary silverback, Vince. His distinguishing features include a deformed right ear, eyes with red rims, vertically aligned nostrils, a small vertical mark above his right nostril, a short curved brow ridge, and a fully developed chestnut crest.

Plate 2.4. Solitary silverback, Vince.

2.3.2. Age Classification

The Mbeli Bai Study has good birth estimates for all individuals born into the population since 1995. The ages of older gorillas and those immigrating into the population must be estimated, based on size and behavioural comparisons with gorillas of known age. For those thought to be over eight years of age, females are classed as adult females, and males are classed as blackbacks until signs of silvering on the saddle appear. Gorillas aged between 8 and 10 years of age can often be difficult to assign to a sex, either by physical or behavioural characteristics. In these

situations, classification into an age-sex category is postponed until a definitive identification of sex can be made (giving birth, or silvering of hair). Copulations in the bai were rarely observed so were not useful for identifying sex.

Various different systems of age classification have been used for gorillas and consequently, it is important to classify individuals into age categories that are comparable with other populations. The system used in this study is that of Watts & Pusey (1993) (**Table 2.1**), which has previously been used to describe the population at this site (Parnell, 2002b), and in a study of development in mountain gorillas (Fletcher, 2001). In this study, all gorillas under the age of eight years were selected as study subjects, and collectively referred to as "immatures".

Table 2.1. Age classification of gorillas used in the study (Watts & Pusey, 1993).

Age Class	*Males*	*Females*
Infant	0 – 3 years	0 – 3 years
Juvenile	3 – 6 years	3 – 6 years
Sub-adult	6 – 8 years	6 – 8 years
Adult female		8 years plus
Black back	8 – 12 years	
Young silverback	12 – 15 years	
Adult silverback	15 years plus	

2.4. MBELI GORILLA POPULATION

2.4.1. Study Subjects

Throughout the study data were collected from 58 study subjects. Individuals less than 8 years of age at the start of the study were classed as study subjects. Data collection continued on those who reached 8 years during the study to permit comparison of immature behaviour with that of young adults.

2.4.2. Population Structure

Throughout the study period thirteen groups containing study subjects and eight solitary silverbacks visited the bai. **Table 2.2** provides details of the composition of all visiting units on the final date on which they were observed (hereafter, the abbreviation of the unit's full will be used). **Table 2.3** shows the distribution of visits by study groups throughout the study period.

Table 2.2 Composition of all units (and unit abbreviations) visiting Mbeli Bai on the final date on which they were observed. Study subjects emigrated from the population and transferred between groups, so the number of study subjects presented here does not equal the number of study subjects in the population. ASB = adult silverback, YSB = young silverback, AF = adult female, BB = blackback, AF/BB = individual aged 8-12 years of unknown sex, SAD = sub-adult, JUV = juvenile, INF = infant, SS = study subjects.

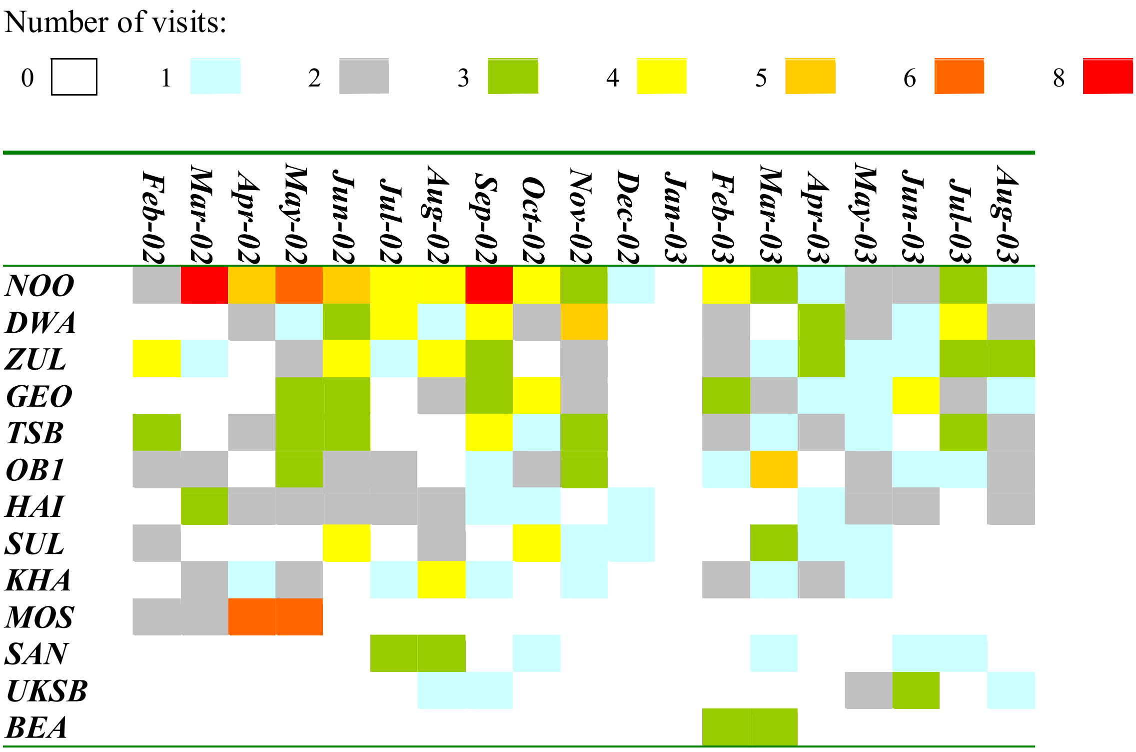
	ASB	*YSB*	*AF*	*BB*	*AF/BB***	*SAD*	*JUV*	*INF*	*SS***	*TOTAL*
Khan (Kha)	1	-	8	-	-	-	6	2	8	**17**
Dwayne (Dwa)	1	-	5	-	-	2	3	2	7	**13**
Zulu (Zul)	1	-	-	6	-	-	1	5	6	**13**
Noodles (Noo)	1	-	3	4	1	1	-	2	6	**12**
George (Geo)	1	-	6	-	-	-	1	4	5	**12**
OB1	1	-	2	1	1	2	2	1	6	**10**
Hairy (Hai)	1	-	4	-	-	1	-	2	3	**9**
Unknown silverback (UKSB	-	-	5	-	-	-	-	4	4	**9**
Mosombo (Mos)	1	-	1	1	-	2	1	1	4	**7**
Sangha (San)	1	-	3	-	-	1	1	1	3	**7**
TSB	1	-	1	1	1	-	1	-	2	**5**
Bear* (Bea)	1	-	1	1	-	1	1	-	2	**5**
Sulatalu (Sul)	1	-	-	2	-	-	-	1	1	**4**

Solitary Silverbacks										
Bayleaf (Bay)	-	1	-	-	-	-	-	-	-	**1**
Gretsky (Gre)	1	-	-	-	-	-	-	-	-	**1**
Stockwell (Sto)	1	-	-	-	-	-	-	-	-	**1**
Vidal (Vid)	1	-	-	-	-	-	-	-	-	**1**
Taragon (Tar)	1	-	-	-	-	-	-	-	-	**1**
Isaak (Isa)	-	1	-	-	-	-	-	-	-	**1**
Vince (Vin)	1	-	-	-	-	-	-	-	-	**1**
Lemmy (Lem)	1	-	-	-	-	-	-	-	-	**1**

* Bear was a solitary silverback throughout the first study period, but formed a group during the second study period.

** Individuals older than 8 years were still considered study subjects if they had contributed to data collection before the age of 8.

Table 2.3. Distribution of visits by groups containing study subjects during the study period. Groups are presented in order of decreasing visit frequency. Note that observations were not carried out between 11th December 2002 and 6th February 2003 (see **Figure 2.4**).



Number of visits:

0 ☐ 1 2 3 4 5 6 8

	Feb-02	*Mar-02*	*Apr-02*	*May-02*	*Jun-02*	*Jul-02*	*Aug-02*	*Sep-02*	*Oct-02*	*Nov-02*	*Dec-02*	*Jan-03*	*Feb-03*	*Mar-03*	*Apr-03*	*May-03*	*Jun-03*	*Jul-03*	*Aug-03*
NOO	2	8	5	6	5	4	4	8	4	3	1		4	3	1	2	2	3	1
DWA			2	1	3	4	1	4	2	5			2		3	2	1	4	2
ZUL	4	1		2	4	1	4	3		2			2	1	3	1	1	3	3
GEO				3	3		2	3	4	2			3	2	1	1	4	2	1
TSB	3		2	3	3			4	1	3			2	1	2	1		3	2
OB1	2	2		3	2	2		1	2	3			1	5		2	1	1	2
HAI		3	2	2	2	2	2	1	1		1				1	2	2		2
SUL	2				4		2		4	1	1			3	1	1			
KHA		2	1	2		1	4	1		1			2	1	2	1			
MOS	2	2	6	6															
SAN						3	3		1					1			1	1	
UKSB							1	1								2	3		1
BEA													3	3					

2.4.3. Demographic Changes

Details of changes in group structure that affected study subjects and occurred during the study are given in **Table 2.4.**

Table 2.4. Summary of demographic events affecting study subjects. * indicates the same individual.

Event	*Individual (group)*	*Details*	*Mother*
Births:			
	Columbus (Sul)	Born in June 2002	Ramona
	Kojak (Hai)	Born in July 2002	Amber
	Likouala (San)	Born in September 2002	Lefini
	Jola (Zul)	Born in October 2002	Ndebele
*	DO(Tabaqui) (Kha)	Born in October 2002 (twin)	Tabaqui
	Toomai (Kha)	Born in October 2002 (twin)	Tabaqui
	Hitchcock (UKSB)	Born in October 2002	Jewel
	Howsa (Zul)	Born in February 2003	Hadza
	Lando (OB1)	Born in February 2003	Simone
	Piment (Dwa)	Born in March 2003	Primrose
	DO (Agatha) (UKSB)	Born in May 2003	Agatha
	DO (Niari) (San)	Born in June 2003	Niari
Deaths:			
	Mosombo (Mos)	Old group silverback, disappears from population and is assumed dead	
*	DO(Tabaqui) (Kha)	Twin offspring of Tabaqui. Assumed to have died at approx. 1 month of age	
	Yoda (OB1)	Mother Cindy transferred to SUL group; Yoda assumed to have died, aged 32 months. Infancticide?	

Transfers:	
Winona/Whisky (Mos)	Immigrate into NOO group after death of Mosombo, group silverback
Iook (Mos)	“ “ “ “
Lyle (Mos)	“ “ “ “
Peter (Mos)	Emigrates from population after death of Mosombo, group silverback
Livingston (Bea)	Immigrates into BEA from outside population
Stanley (Bea)	“ “ “
Picard (OB1)	Immigrates into OB1 from outside population
Kirk (OB1)	“ “ “
Cindy/Yoda (OB1)	Transfers from OB1 to SUL group, infant Yoda disappears
Moses (TSB)	Emigrates from population

2.5. SPECIFIC DATA COLLECTION METHODS

2.5.1. Scan Sampling

After all group members present in the bai were identified, study animals located and the group had settled down to feed, scan sampling (Altmann, 1974) commenced. Scan samples were conducted every 20 minutes and recorded using a dictaphone. For each study individual present, scan samples recorded their current behaviour and the approximate distance to all other group members present. The presence or absence of the group silverback and the presence and approximate distance to any other groups present in the bai were also recorded. Usually, scans were limited to periods during which all group members were present (to gain a picture of overall group spatial patterns). However, in some groups, one or more members often entered later, left earlier, or did not enter the bai, and scans were carried out without all group members being present. This typically occurred with the UKSB group, whose silverback was never seen in the bai, although one was heard chest beating and hooting from the bai edge in proximity to the rest of the group. In some cases, data where not all group members were present were removed from the analyses due to an effort to keep the data as comparable as possible. Distances were recorded as:

contact, 0-2m, 2-5m, 5-10m and 10m plus. Distances to other groups were estimated to the nearest 10m. Data were entered daily into Excel check sheets on a laptop.

2.5.2. Focal Sampling

Between scan samples, a study subject was selected and a 15 minute focal sample (Altmann, 1974) was carried out. All behaviours performed during this period were recorded continuously. Focal individuals were selected by choosing the individual of whom the best view was available (i.e., not obscured behind vegetation or another individual) at the start of the focal sample, but an effort was made to collect equal amounts of data on all individuals. If no study individual was clearly visible at the start of a sample, one was chosen randomly. A previous study demonstrated how the majority of behaviours had bout lengths shorter than fifteen minutes, so this period was selected to allow complete behavioural bouts to be recorded (Nowell, 2001). A period of 15 minutes also allowed each study subject in a group to be sampled at least once, unless the visit was unusually short. If a group stayed in the bai long enough for a focal sample to be recorded for each study individual, further focal samples were collected during the same visit. Subjects were selected using the same protocol as for the first focal sample. Repeated focal samples carried out during the same visit were not independent and not analysed as such. Median values for behaviours recorded during focal samples on the same individual on the same day were calculated.

Focal samples were conducted using The Observer software and a hand-held Psion Workabout. A “configuration file” was designed using The Observer programme, which allowed all behaviours in the ethogram to be recorded. The configuration file was downloaded onto the Psion for use during data collection. During the 15 minute focal samples, each behaviour performed by the focal animal was recorded by entering a three-letter code, defined in the configuration file. After data were collected on the Psion they were downloaded onto a laptop for analysis.

2.5.3. All-Occurrence Behaviours

Additional behaviours (**Table 2.5**) that were of interest to the study were recorded each time they were observed in any study subject (Altmann, 1974).

Table 2.5. Details of behaviours recorded using all-occurrence sampling.

Behaviour	***Details recorded***
Method of entry/exit	The method of travel used by each study subject entering the bai in contact with its mother.
Breaking contact	The length of time taken by an individual entering the bai in contact with the mother to break contact with her. Termed "latency to independence".
Suckling	The start and stop time (to the nearest second) of suckling bouts, the position in which the offspring suckled, terminators of bouts.
Interactions	*Active* behaviour directed from one individual to another.

If any of these behaviours occurred during scan samples or focal samples on other subjects, another member of the research team alerted me. With respect to suckling, a study subject would occasionally be out of sight at the start or end of the bout making it unclear when the bout actually commenced or was terminated. A bout could consist of suckling from both nipples consecutively and was ended by separation from the nipple for over 15 seconds. It is impossible to ascertain whether milk was obtained during these periods, and suckling may be more correctly defined as "nipple contact", but for ease and for comparative purposes, such behaviour will be referred to here as suckling.

2.5.4. Ad Libitum Recording

Details of any unusual behaviour (for example, obvious wounds or injuries, close proximity to other mammals using the bai, descriptions of the general behaviour of the group, and impressions gained throughout the visit, such as whether a female may be pregnant, or the peripheralisation of group members) were noted and later transcribed into field notes. The field notes record gave a summary of these behaviours and interactions that occurred during a visit and were not recorded during scan or focal sampling.

2.6. GORILLA ETHOGRAM

The behaviours recorded during focal and scan sampling in this study were determined during a previous study (Nowell, 2001) (**Table 2.6**). Modifiers (e.g., initiator etc.) are used by The Observer software: the type of behaviour performed is entered, and then when appropriate, one or two modifiers (listed towards the end of the ethogram) are used to further define the behaviour. For example, suckling behaviour can be modified by giving details of the positional behaviour of the offspring when suckling, as well as the terminator of the bout. Likewise, approaches and departures made to and by the focal animal were modified by adding the name of the individual to whom the approach/departure was made/received, and the distance to which the approach/departure was made/received.

Table 2.6. Ethogram showing all recorded behaviours throughout the study, including modifiers, which further define behaviours.

Behavioural Code	**Definition**	**Modifier 1**	**Modifier 2**
FEEDING BEHAVIOURS:			
Fhz	Feeding on *Hydrocharis chevalieri* rhizomes		
Fhr	Feeding on *H. chevalieri* roots		
Fls	Feeding on *H. chevalieri* leaves and stems		
Fhl	Feeding on *H. chevalieri* leaves		
Fhs	Feeding on *H. chevalieri* stems		
Fh?	Feeding on an undetermined part of *H. chevalieri*		
Fhy	Feeding on multiple parts of *H. chevalieri*		
Fhn	Feeding on *H. chevalieri* root nodes		
Dre	Dredging up parts of *H. chevalieri*		
Sor	Teasing apart and selecting parts of *H. chevalieri*		
Was	Manipulating *H. chevalieri* in water prior to consumption		
Ffs	Feeding on *Fimbristylis sp.*		
Frs	Feeding on *Rhynchospora corymbosa*		
Fcs	Feeding on *Cyperus sp.* stems		
Fcr	Feeding on *Cyperus sp.* roots		
Fky	Feeding on Kyllinga		
Fu7	Feeing on unknown species 7		
Fuk	Feeding on an unknown species		
Suc	Suckling	Position	Miscellaneous
Fdt	Food transfer between two individuals	Miscellaneous	Miscellaneous
Plf	Play feed – manipulation of food item with negligible or no ingestion		
PLAY BEHAVIOURS:			
Cha	One individual chasing or being chased by another		
R+t	Rough and tumble play behaviour – wrestling and rolling around with another individual		
Gra	Grapple play behaviour – “wind milling” of arms towards another individual, often making contact		

Par	Parallel play behaviour – individuals engaging in play behaviour with another without direct contact		
Dis	Play displays – chestbeating, clapping, mock charges outside an agonistic context		
Sep	Solitary play, including twirling, rolling, flopping about, manipulation of objects other than food items		
Cli	Solitary play, but on mother's back		
MOVEMENTS IN RELATION TO OTHERS:			
Apr	Approach received from another individual	Name	Distance
Apa	Approach made to another individual	Name	Distance
Ler	Another individual leaves the focal animal's proximity	Name	Distance
Lea	Another individual approaches the focal animal's proximity	Name	Distance
For	Another individual follows the focal animal's departure	Name	Distance
Foa	The focal animals follows another individual's departure	Name	Distance
Dir	The focal animal is displaced by the approach of another	Name	Distance
Dia	The focal animal approaches and displaces another	Name	Distance
Col	Collected and moved by mother	Position	
Modifier: Distance			
Con	In contact with another individual		
0-2	Between 0 and 2m of another individual		
2-5	Between 2 and 5m of another individual		
5m+	Greater than 5m from another individual		
INTERACTIONS WITH OTHERS:			
Afa	Affiliative behaviour performed towards another individual	Name	Affiliative
Afr	Affiliative behaviour performed by another individual towards the focal animal	Name	Affiliative
Aga	Agonistic behaviour performed towards another individual	Name	Agonistic
Agr	Agonistic behaviour performed by another individual towards the focal animal	Name	Agonistic
Pac	Peer towards another individual	Name	Distance
Pre	Peer received by another individual	Name	Distance
Modifier: Affiliation			
Tou	Reaching towards and touching another individual (and vice versa)		
Hug	Wrapping arms around another individual (and vice versa)		

Pro	Moving towards and remaining in the immediate proximity of another individual (and vice versa)	
Gro	Manipulating the hair or skin or another individual with hands, lips or teeth (and vice versa)	
Modifier: Agonism		
Cha	Charge towards or by another individual	
Chb	Chest beat directed towards or by another individual	
Swi	Swipe at or by another individual with no contact being made	
Lun	Lunge towards or by another individual	
Cog	Cough grunts directed towards or by another individual	
Sla	Slap, making contact with or by another individual	
Modifier: Initiator		
Foc	Focal animal initiates the interaction	
Oth	The other individual initiates the interaction	
OTHER:		
Vig	Vigilance characterised by staring towards another gorilla, animal or location in the bai	Miscellaneous
Res	Default - period where no other activity is performed and the subject is inactive	
Tra	Movement within the bai	Position
Out	Temporarily out of sight due to presence of another animal or vegetation between the subject and the observer	
Exi	Exit from the bai	
Fac	Change in facial expression	Miscellaneous
Modifier: Position		
Ind	Independent	
Dor	Dorsal on (usually) the mother	
Clv	Clinging ventrally on (usually) the mother	
Suv	Supported ventrally by one or two arms of usually the mother	
Arc	Clinging to the arm of (usually) the mother	
Ruc	Clinging to the rump of (usually) the mother while she is moving	
Qua	Standing with all four limbs in contact with the ground	
Bip	Standing on hind legs	

Lie	Lying down on the ground
Sit	Sitting down
Con	Sitting with one part of the body in contact with one part of the body of another individual
Modifier: Miscellaneous	
Ele	Elephant
Sit	Sitatunga
Owg	Own group
Otg	Other group present in the bai
Mir	Mirador
Foe	Forest edge
Mot	Mother
Off	Offspring
Nor	Normal facial expression
Pla	Play face expression – drawing back lips and exposing teeth
Til	Tight-lipped face – pursing lips, usually accompanied by stare avoidance of the individual to which the expression is directed
M2o	Food transferred from the mother to the offspring
O2m	Food transferred from the offspring to the mother
Modifier: Name	
3 letter codes denoting all known members of the population, as well as codes allowing for the presence of unknown animals e.g. af1, af2, do1 (where af – adult female, do = dependent offspring)	

2.7. DATA COLLECTED

Observations were generally made between the hours of 0730 and 1700, and I was present at the bai for a total of 3943 hours from February 2002 through December 2002, and February 2003 through August 2003.

Gorillas were present on an average of 75% of observation days throughout the study period (**Figure 2.3**) and were visible in the bai for over 990 hours. Mean visit length was 115 minutes (range: 1-510 minutes). Each study subject was present for a median of 34.2 hours in total (0.7 to 118.4 hours).

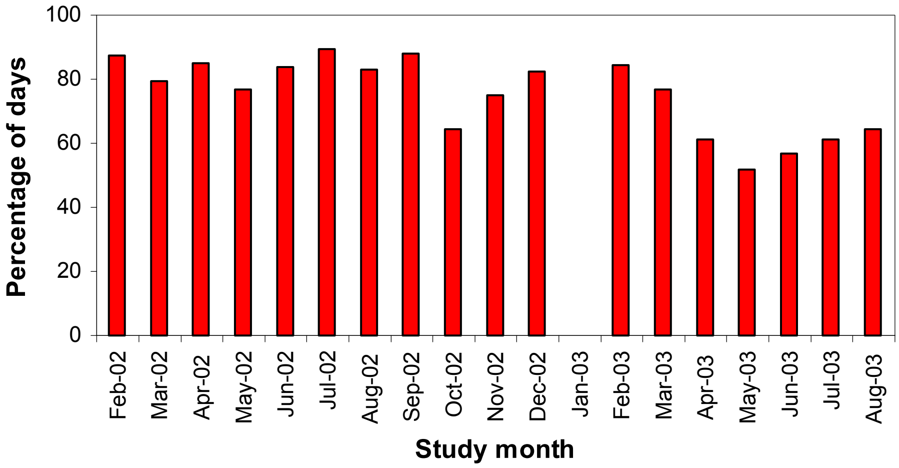


Figure 2.3. Percentage of days on which gorillas were present in the bai.

The total time for which study subjects in each 6-month age category were present in the bai over the course of the study period is shown in **Figure 2.4**. **Appendix 1** shows the number of hours that each individual was present in the bai during the study period. It should be noted that each age category was not independent. Subjects could be represented in up to four age categories as they increased in age throughout the 16 months of the study. It was impossible to collect an equal amount of data for each study subject, since data collection was dictated by the visiting frequency of groups. Not only did groups visit with different frequencies, resulting in differing amounts of data being collected for individuals in different groups, but also within groups, individuals were not always visible for equal amounts of time. This must be borne in mind when interpreting results of analyses: it is possible that the results may be biased due to a disproportionate amount of data being contributed from one individual.

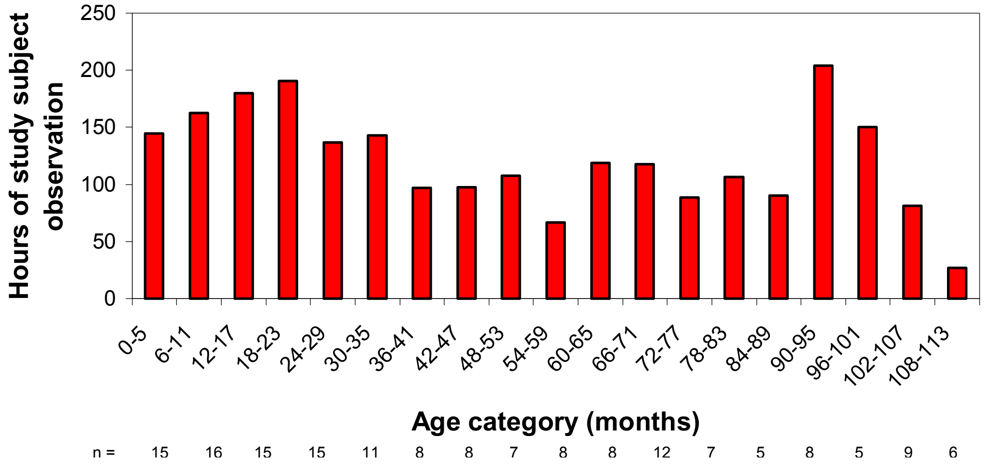


Figure 2.4. Total hours of observation of study subjects in each age category. Numbers below the graph indicates the number of subjects contributing to each age category. Total number of contributing subjects: $N_{TOTAL} = 58$.

A total of 4538 scan samples were collected during the study period **(Figure 2.5)**. The median number of scan samples per study subject was 54, with a range of 1 to 239.

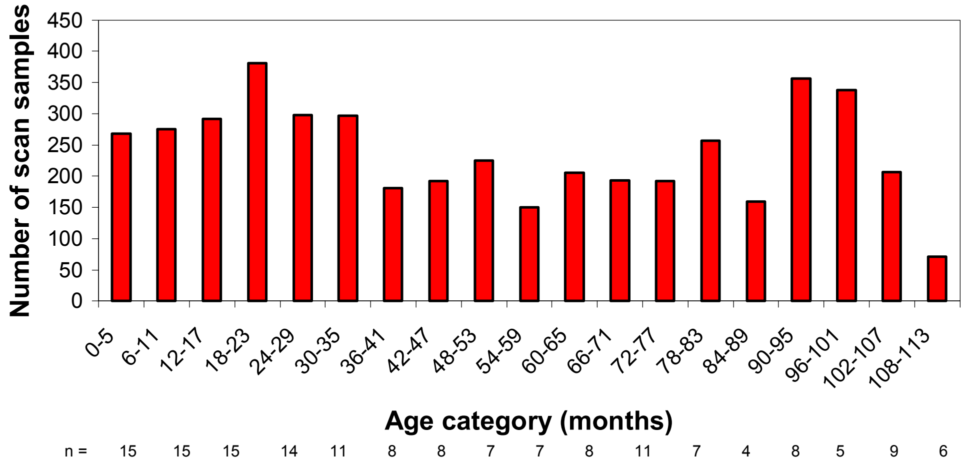


Figure 2.5. Total number of scan samples collected for each age category throughout the study period. $N_{TOTAL} = 58$.

A total of 11,040 minutes of focal sampling were amassed **(Figure 2.6)**. Study subjects were each sampled for a median of 8 hours, with a range of 0 to 11 hours.

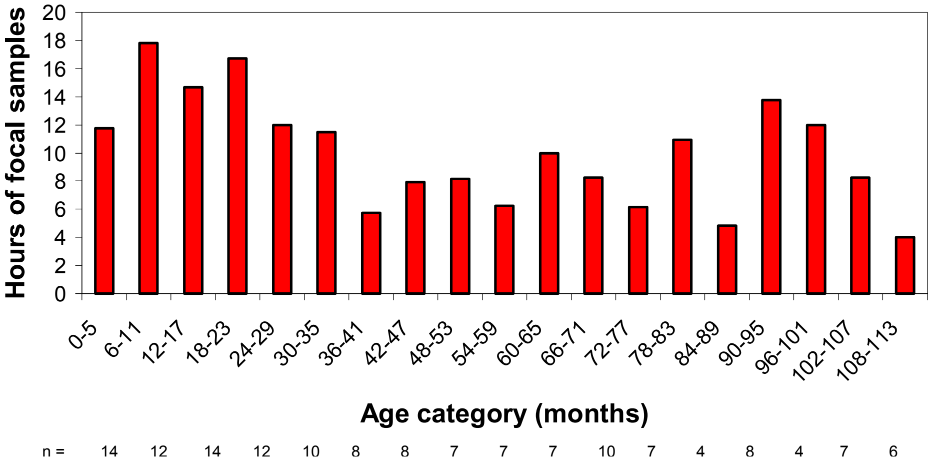


Figure 2.6. Total focal time for which each age category was sampled. $N_{TOTAL} = 56$.

2.8. DATA ANALYSIS

For all analyses (except where otherwise indicated), data for study individuals were summarised in 6 month categories according to the age of the individual when the data were collected. An interval of 6 months was chosen as sufficient time for behavioural change to take place, so the behaviour of those in the 0-5 month category was expected to differ from that in the 6-11 month category, and so on. A median (or, in some cases, a modal value, but the methods used were the same) value for all analysed behaviours was calculated from each individual during the 6 month age categories. Individual median values within an age category were used to calculate age category medians (see Fletcher, 2001). Some individuals made a transition between age classes during the study. Consequently, when comparisons were made between age classes rather than age categories, a median value was calculated for each individual in the age class to which they contributed most data, and individual medians were used to calculate age class medians. Median and modal values used in the analyses, for age classes and age categories, were always calculated in this way, unless otherwise stated.

All statistical tests were non-parametric as a result of large amounts of variation between individuals and relatively few individuals contributing data. To investigate the development of behaviour with age, Spearman rank correlations were conducted. To establish differences between two variables (e.g., sex, presence or absence of siblings), Wilcoxon matched-pairs tests were used for matched data, and

Mann-Whitney U tests were used when data were not matched. For differences between more than two variables (e.g., age class, parity of mother, group), results were tested using Kruskal-Wallis tests for non-matched data, and Friedman ANOVA tests for matched data. In cases where more than five tests were carried out, Bonferroni corrections were carried out to reduce the possibility of making a type one error (Uitenbroek, 1997). All Kruskal-Wallis tests looking at differences between groups compare within group variances to between group variance. This may not be the most effective analysis to conduct in order to determine the effect of group size and composition on behaviour, but was conducted in order to gain an idea of trends within groups, for example, whether groups with a higher proportion of younger members have a different general behavioural profile when in the bai.

When Kruskal-Wallis tests produced significant results, attempts were made to quantify these differences by using post hoc multiple comparison tests (Siegel & Castellan, 1988). The following formula was used:

$$| R_u - R_v | \geq z_{\alpha / k(k\text{-}1)} * \sqrt{} N(N+1)/12 * (1/n_u + 1/n_v)$$

See Siegel & Castellan (1988) for details of the test.

Details of all other analyses are explained in the relevant chapters. For all statistical tests, the level of significance above which the null hypothesis was rejected was 0.05. All tests were two-tailed.

2.8.1. Data Presentation

Throughout the thesis, data are presented, as far as possible, in a similar form. Numbers below the x-axis labels indicate the number of individuals contributing to each age category, and the total number of individuals who have contributed data is given in the legend (and referred to as $N_{\text{TOTAL,}}$ or $N_{\text{males, females}}$, etc). Error bars on graphs represent the interquartile ranges. Vertical hashed lines on graphs separate different age classes.

It is considered that this thesis provides as full and comprehensive an analysis of behavioural development in western lowland gorillas as the data allow.

CHAPTER THREE

ACTIVITY BUDGETS AND THE DEVELOPMENT OF FEEDING BEHAVIOUR

3.1. INTRODUCTION

As young primates increase in age, they must learn to perform behaviours that promote their survival and increase their reproductive success (Watts & Pusey, 1993). Not only must they learn the behavioural elements that are involved, they must also learn to combine the elements in ways that allow them to meet their energetic costs (Watts, 1988; Milton, 1993). In addition to the development of social behaviour (which is considered in later chapters), the development of independent locomotion, and feeding skills is crucial to the survival of young primates.

Throughout this introduction, predictions, indicated by bullet points, are presented with respect to the development of activity budgets, arboreal skills and feeding behaviour. These predictions form the basis for the analyses in the chapter, and will be fully addressed and expanded in the discussion section.

3.2. DISTRIBUTION OF TIME IN PRIMATES

The partitioning of time and energy into different activities, such as feeding, travelling, resting and social behaviours has important ramifications for survival, and eventually, reproduction (Watts, 1988; Matsumoto-Oda & Oda, 2001). The way in which time is budgeted is constrained by factors such as body size, digestive physiology and spatio-temporal variation in a habitat (Watts, 1988). Individuals must gain energy through feeding, and conserve energy through resting in order to perform other behaviours such as travelling, reproduction and social interaction. Ultimately, the nutritional requirements of an individual dictate how much time must be spent feeding in order to obtain sufficient resources. Differences exist between age-sex classes in their nutritional requirements, with infants and juveniles requiring less overall energy, however, energy requirements per unit body weight decrease with increasing body weight (Hanya, 2003).

Adult mountain gorillas spend the majority of an average day feeding, usually interspersed with bouts of travel, and resting is the second most common activity (Harcourt, 1978a; Watts, 1988). These patterns are predicted to differ for young gorillas, since the mother initially provides all necessary nutrition, and infants are dependent on their mother for travel until they are strong enough to travel independently (Hoff et al., 1983; Fletcher, 1994; Doran, 1997b).

Juvenile primates face a diversity of challenges not faced by infants (Pelaez et al., 2000). They must survive in a society dictated by adults despite being smaller, less experienced, and without the same levels of support from the mother that they received during infancy (Janson & van Schaik, 1993). While younger infants continue to suckle, and are allowed to pick discarded food items and debris from the mother's body, juveniles must locate, obtain, and process foods by themselves (Watts, 1985a; Tomasello, 2000). Once weaned, juveniles are responsible for obtaining all their nutritional requirements and combining them in nutritionally adequate proportions (Watts, 1985a).

Likewise, sub-adult, and young adult primates must divide their time adequately between activities in order to obtain sufficient nutrition, in addition to refining social skills that will later facilitate transfer into another group for females, or the eventual acquisition of mates in males. So, as gorillas mature, the manner in which they proportion their time is predicted to change:

- An increase is expected in the percentage of time spent feeding as infants become more responsible for locating their own food. The increase in time spent feeding is predicted to be accompanied by a decrease in other behaviours, and to continue until individuals are weaned.

In many primate species, males and females exhibit behavioural differences, for example, in levels of grooming and play behaviour, and association patterns, and these differences are often apparent before sexual dimorphism or lactation imposes metabolic costs (e.g., Brown, 1988; Nakamichi, 1989; van Noordwijk et al., 1993; Nikolei & Borries, 1997; Brown & Dixson, 2000; Maestripieri & Ross, 2004). Data will be tested to see if this is the case in western lowland gorillas.

Ecological and social factors, such as the seasonality and distribution of food items (Doran et al., 2004), vulnerability to predation (Pelaez et al., 2000), and levels of feeding competition both within and between groups (Watts, 1984; Tutin & Fernandez, 1993; Malenky et al., 1994) are all predicted to determine how time is apportioned to different activities (see Watts, 1988). For example, in gelada baboons, the frequency of immature play behaviour is a good indicator of environment quality, with higher levels of play occurring at times of the year when better quality resources are available (Barrett et al., 1992). In white-headed langurs, more time is spent playing when the habitat quality is high (Li & Rogers, 2004). Chimpanzees in the Taï

National Park, Ivory Coast, spent more time solitary and feeding during the dry season when fruit was less readily available than they did during the wet season (Doran, 1997a). Although in Mbeli gorillas, levels of predation and disturbance are low, the seasonality and distribution of potential food items is predicted to lead to a higher level of feeding competition within and between groups than is observed in mountain gorillas (Doran & McNeilage, 1998; Stokes, 2004). Consequently, larger groups should experience increased feeding competition (see Watts, 1985b).

- Any differences detected between groups in their activity budgets are predicted to reflect levels of intra-group feeding competition.

An analysis of the partitioning of time between behaviours and the development of locomotor and feeding behaviour in immature gorillas will ultimately provide information on how the distribution of resources within the environment drives the attainment of behavioural skills.

3.3. THE DEVELOPMENT OF ARBOREAL SKILLS

In species that feed, travel and sleep arboreally, competent locomotion through the canopy is an essential skill. It is hypothesised that in apes, the demands of arboreal locomotion are related to cognitive abilities, since some degree of self-concept is necessary for large-bodied apes to negotiate safely among thin branches (Hunt, 2004). Arboreal locomotion is essential in western lowland gorillas, as much of their feeding is carried out in trees at heights of up to 30m (Williamson, 1988; Doran et al., 2002). Since the vast majority (96.2%) of mountain gorilla feeding is terrestrial (Watts, 1984), development of arboreal locomotor skills would not appear to be as critical as for western lowland gorillas. Doran (1997b) found that the highest levels of arboreal locomotion in mountain gorillas were recorded between 17 and 21 months of age, and occurred often during play, before becoming less frequent with increasing age.

Trees are also used for nesting in western lowland gorillas (Tutin et al., 1995; Mehlman & Doran, 2002), whereas mountain gorillas nest predominantly on the ground (Schaller, 1963). Unweaned individuals share their mother’s nest, and all weaned gorillas build a new nest each night (Tutin et al., 1995; Mehlman & Doran, 2002). Few details are available of when wild western lowland gorilla infants first show nesting behavioural patterns, but in mountain gorillas, infants were observed manipulating vegetation at 8 months of age and to build nests by 18 months, although these were not slept in (Fossey, 1979; Fossey, 1983).

The use of trees recorded on the bai edge in this study is likely to be qualitatively different from that in the forest. However, an investigation into the arboreal behaviours that were observed gives some information on the developing abilities of immatures in an arboreal environment, and in this study:

- Western lowland gorillas are predicted to increase levels of arboreal locomotion with increasing age, as they become responsible for finding their own food, much of which is located in tree canopies.

3.4. THE DEVELOPMENT OF FEEDING BEHAVIOUR

The diet of gorillas consists mainly of two different food types: plant foods that are easily obtainable throughout the year, but tend to be low in energy and sparsely distributed; and ephemeral items, which provide abundant and readily available energy (Rogers et al., 1990; Byrne, 2001). Western lowland gorillas have been described as seasonal frugivores (Tutin et al., 1991; Remis, 1997b), feeding on up to 100 different species of fruit (Williamson et al., 1990), compared to the six species fed on by mountain gorillas in the Virunga Volcanoes (Watts, 1996b). During periods of fruit scarcity, the proportion of lower quality plant foods and herbaceous vegetation in the diet of western lowland gorillas increases (Remis, 1997b; Doran et al., 2002; Rogers et al., 2004), and it is thought to be their large size that allows them to process sufficient quantities of these items to meet their needs (Remis, 1997b).

With the exception of learning about diet in utero (spontaneous selectivity shown by newborn fawns may be due to this (Tixier et al., 1998)), infants generally receive their first information on diet choice through close contact with the mother (Watts, 1985a; Byrne & Byrne, 1993; Wiens & Zitzmann, 2003), and this is further reinforced by observation of conspecifics (Wiens & Zitzmann, 2003). However, in some species, for example, roe deer (Tixier et al., 1998) and spider monkeys (Milton, 1993), young animals can develop species-typical diets in the absence of adults, suggesting that observational learning is not the only way in which knowledge of food items is gained. In the case that observational learning does play an important role:

- Close proximity between mothers and infants is predicted to continue during early stages of independent feeding, allowing infants to gain information on diet breadth and food choice through observational learning.

Play-feeding behaviour, defined in this study as the manipulation of food items without their ingestion, provides immatures with further information about the qualities of food and non-food items within their environment. During play-feed sessions, individuals appear to attempt some aspect of adult feeding behaviour, but without the fine motor skills, and often the attention span, to execute the behaviour in its adult form (Byrne & Byrne, 1993; Corp & Byrne, 2002). Therefore,

- The incidence of play-feeding behaviour is predicted to increase during the early part of infancy, as individuals begin to incorporate solid items into their diet. Its frequency is then predicted to decrease, as competence in processing and ingesting food is gained.

The transfer of food items between infants and most often the mother, is common in some species such as tamarins (Ruiz-Miranda et al., 1998; Roush & Snowdon, 2001), chimpanzees (de Waal, 1989; Nishida & Turner, 1996) and titi monkeys (Starin, 1978), and is defined as the movement, or attempted movement of solid food between individuals (Ruiz-Miranda et al., 1998). It is likely that this serves to provide information on appropriate food items, which parts are fed on by adults, and how they are fed on, representing parental investment in offspring (see Ueno & Matsuzawa, 2004). The transfer of food may contribute towards earlier weaning as it can provide access to items that immatures could not otherwise obtain, and to rare, but nutritionally rich foods (Ruiz-Miranda et al., 1998). Rates of food transfer decrease with age of the offspring, since juveniles can access previously unattainable items, and also have a broader experience of palatable food items (Ruiz-Miranda et al., 1998).

No previous documentation on food transfer in gorillas was found in the literature, but it was observed during this study, and therefore, was investigated:

- The movement of food between individuals was predicted to be from an older (most likely the mother) to a younger individual, to allow the younger individual to gain information on food items that comprise the adult diet, or to provide access to otherwise unattainable and desirable food items.

3.4.1. Feeding Selectivity

Different plant species vary greatly in the quantity of minerals and energy they contain, and feeding selectivity by primates, e.g., in chimpanzees (Takemoto, 2003), red colobus (Chapman & Chapman, 2002), and baboons (Hill & Dunbar, 2002) often reflects this, with species or parts with high levels of minerals and/or energy being selected. Western lowland gorillas have been shown to consistently feed on items with high mineral levels (Remis, 1999; Magliocca & Gautier-Hion, 2002; Remis, 2002). Growing infants require increased nutrition to build new tissue, maintain existing tissue and support higher actvity levels (Altmann, 1980), and the relatively greater energy requirement of smaller compared to larger individuals (Altmann, 1980; Hanya, 2003) means that juveniles in particular, are expected to rely on high-quality (Hill & Dunbar, 2002; Hanya, 2003), easily processed (Altmann, 1980) foods. “Weaning foods”, i.e., those that are easily obtainable and readily digested are important as young animals’ attempts to obtain milk from the mother are denied with increasing frequency (Altmann, 1980; Barrett & Henzi, 2000). Based on this:

- Initially, food species and parts selected by immatures are expected to be those that are easily digestible and require little processing, but as they mature, their selections are expected to correspond with species and parts chosen by adults that are highly nutritive and/or high in energy.

Learning to select and process food items will not be restricted to infancy. Some trees do not produce fruit on an annual basis, for example, *Gilbertiodendron dewevrei* is thought to fruit on a 5-year cycle (Blake & Fay, 1997), and certain fruit trees fed on by gorillas (e.g., *Diospyros s*p. (Williamson et al., 1990), *Dialium lopense* (Rogers and Parnell, 1991, cited in (Parnell, 2002b)), and *Nauclea vanderguchtii*) appear unable to fruit in certain years following extensive damage to trees caused by intensive gorilla feeding during the previous year (Parnell, 2002b). Consequently, gorillas may encounter important fruit species for the first time as juveniles, and must then learn to recognise and process them. Differences exist between populations of western lowland gorillas in which species are fed on, suggesting that in gorillas, food selection may develop by observational learning and perhaps tradition (Fragaszy, 2003; Huffman & Hirata, 2004). For example, *Greenwayodendron suaveolens* is found in both Lopé National Park, where gorillas do not feed on it (Williamson et al., 1990), and in Nouabalé-Ndoki National Park, where they do (Nishihara, 1995; pers. obs.).

For many folivores, learning *what* to eat is neither complex or risky: for example, herbs constituting mountain gorilla diets are low in indigestible fibres and tannin-based inhibitors (Byrne & Byrne, 1993; Byrne et al., 2001). However, they are defended by hooks, stings and fibrous outer casings, so learning *how* to eat can be more problematic (Byrne & Byrne, 1993). Likewise, the herbaceous components of western lowland gorillas' diets often require some degree of processing before they can be ingested (Parnell, 2001; pers. obs.), and individuals must learn the appropriate balance of processing and consumption to gain the optimum benefit from their food. A study on yellow baboons has shown that processing efficiency is at a premium during weaning (Altmann, 1980), further illustrating the importance of being able to locate, process and digest appropriate items at the time when a mother's investment in her current offspring begins to be directed elsewhere. Adults are expected to combine the processing and ingestion elements of feeding behaviour optimally, so:

- Immatures are predicted to develop a similar balance of feeding and processing behaviour by the age at which they are weaned, and to remain constant thereafter.

3.4.2. The Costs of Being Immature, and Implications for Feeding Behaviour

Although juveniles and sub-adults are capable of processing their food and identifying edible species, they face problems in feeding that infants, with less developed skills do not. They must compete, with less aid from their mother (Janson & van Schaik, 1993) with larger, dominant adults, and each other, for access to food. However, their size may confer some advantages: they can travel along smaller branches to harvest fruits and new leaves not available to larger individuals (pers. obs.) as also seen in immature Japanese macaques (Hanya, 2003). Perhaps this, together with a lower daily-required intake than adults allows juvenile and sub-adult gorillas to obtain adequate nourishment without the protection and guidance of their mother.

3.4.3. Influence of Immature Social Group and Sex

The size and composition of social groups influences feeding behaviour, primarily in the form of feeding competition (Sterck et al., 1997; Chapman & Chapman, 2000). This can result in a reduced group food net intake than in smaller groups, increased time spent foraging, and often lower female reproductive rates and increased mortality (Sterck et al., 1997; Chapman & Chapman, 2000), particularly during periods of food scarcity. Feeding competition within mountain gorilla groups is low (Watts, 1988; Watts, 1991c), presumably as a result of the abundant and ubiquitous distribution of their diet, whereas more frugivorous western lowland gorillas are expected to experience higher levels of feeding competition (Robbins et al., 2004; Stokes, 2004). Increases in within-group contest competition predict a trend towards female philopatry, with females remaining in the natal group and forming coalitions with relatives to defend resources (van Schaik, 1989). However, voluntary female dispersal (Stokes et al., 2003) and relatively infrequent aggression between females (Stokes, 2004) suggests that within-group contest competition in the Mbeli population is low. Therefore,

- Differences between groups in feeding behaviours are predicted to be minimal. However, feeding behaviour in the bai may reflect the levels of competition experienced by groups in the their normal forest environment, with larger groups facing greater levels of competition, and therefore, being "hungrier" as a result when in the bai.

Males and female primates often behave differently from one another, either in terms of the actual behaviours performed, or the frequency with which behaviours are performed (e.g., Harcourt, 1979b; Seyfarth & Cheney, 1984). These differences may be more prevalent in species where one sex is philopatric, and can gain future benefits by investing in relationships with members of the natal group (Fairbanks, 1993). Although sex-specific costs in some species are manifested during immaturity (e.g., Brown, 1988; Nakamichi, 1989; van Noordwijk et al., 1993; Brown & Dixson, 2000):

- Any differences between the sexes in activity budgets or feeding behaviour are expected to be minimal, given that both are subject to increased energy requirements to compensate for higher activity levels, and the generation and maintenance of tissue, in addition to the high rate of natal dispersal for both male and female western lowland gorillas.

Based on these predictions, influences on activity budgets, and the development of arboreal skills and feeding behaviour will now be considered.

RESULTS

3.5. ACTIVITY BUDGETS

Developing individuals must partition their time appropriately in order to obtain the necessary nutritional requirements imposed on them by their increasing size and higher levels of activity. Smaller, younger individuals, whose mothers assist in meeting costs are expected to spend less time feeding, leaving more time available for resting, social interactions and exploration of the environment (Barrett et al., 1992; Hanya, 2003). To investigate changes in the activity budgets of immature gorillas, the behaviour of study subjects was classified into five categories (**Table 3.1**).

Table 3.1. Behaviour categories and their definitions. See also **Table 2.6** for the full gorilla ethogram.

Behaviour	***Definition***
Feeding-related	All feeding behaviours, including the ingestion and manipulation of food items (play-feed and processing) and suckling
Terrestrial locomotion	Locomotion in the bai independent of the mother
Resting	The subject is inactive and no other behaviour is performed (includes dependent travel as the offspring is not responsible for the direction or duration of travel)
Social	All active behaviours involving another individual: affiliative and agonistic interactions, display, and social play behaviour.
Solitary	Self directed behaviours, such as self-groom, and self or object play, and vigilance

3.5.1. Effects of Age on Activity Budgets

For study subjects in each 6 month age category, the percentage of scan samples spent engaging in the five behaviour types was calculated from scan samples. These individual values were then used to give a median value for each age category.

Overall, feeding-related behaviours (57.6%) and resting (29.1%) accounted for 87.7% of all scan samples. There was a significant negative correlation between the median percentage of scans spent feeding and the median percentage of scans spent resting ($r_s = -0.845$, n = 19, $P < 0.0001$), and with increasing age, feeding behaviour replaced resting as the predominant behaviour performed by immatures in the bai.

Over the entire immature period, there was a significant increase in the frequency with which feeding-related behaviours ($r_s = 0.936$, n = 19, $P < 0.0001$) and terrestrial locomotion ($r_s = 0.717$, n = 19, $P < 0.0001$) were observed, showing a significant increase during infancy (feeding-related: $r_s = 1.000$, n = 6, $P < 0.0001$; terrestrial locomotion: $r_s = 0.845$, n = 6, $P = 0.034$). Time spent resting significantly decreased over the immature period ($r_s = -0.889$, n = 19, $P < 0.0001$), and the decrease was also significant during infancy (r_s = -1.000, n = 6, $P < 0.0001$) and the juvenile period (r_s = -0.698, n = 6, $P = 0.005$). Levels of feeding-related behaviours, resting and terrestrial locomotion remained constant during sub-adulthood and adulthood. No correlations were observed between age category and solitary behaviours (r_s = -0.161, n = 19, $P = 0.509$), and median values for social behaviours equalled 0 for all age categories.

Tests were carried out to investigate differences between age classes, as they represented particular life stages where particular patterns might be expected. Significant differences between age classes were found (**Figure 3.1**) in the median percentage of scan samples that immatures engaged in feeding-related behaviours (χ^2 = 36.292, d.f. = 3, $P < 0.0001$), terrestrial locomotion (χ^2 = 22.675, d.f. = 3, $P < 0.0001$), resting (χ^2 = 39.715, d.f. = 3, $P < 0.0001$), and social behaviour (χ^2 = 11.179, d.f. = 3, $P = 0.011$). Solitary behaviours were performed at low frequencies in all age classes (χ^2 = 0.707, d.f. = 3, $P = 0.872$). Multiple comparison tests (Siegel & Castellan, 1988) showed that infants differed from all other age categories for feeding-related behaviours and resting, and they differed only from juveniles and sub-adults in levels of terrestrial locomotion. Levels of social behaviour differed between infants and sub-adults. These results were significant at the 0.05 level.

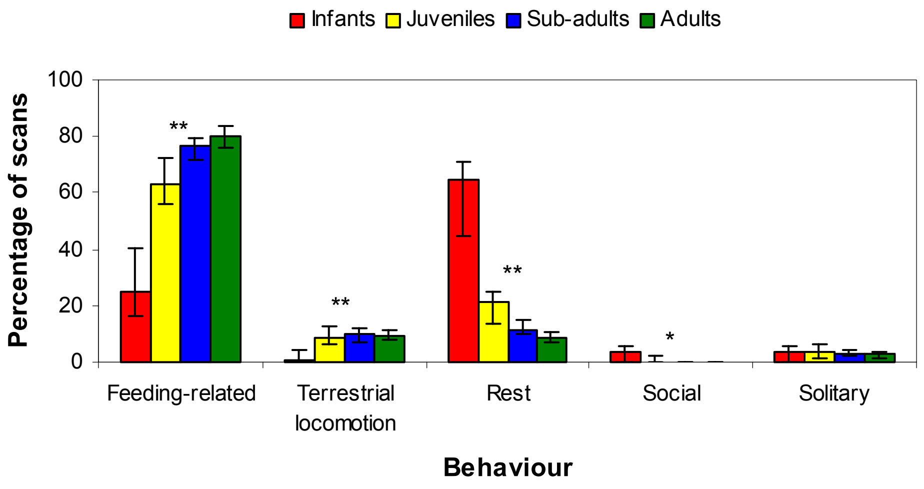
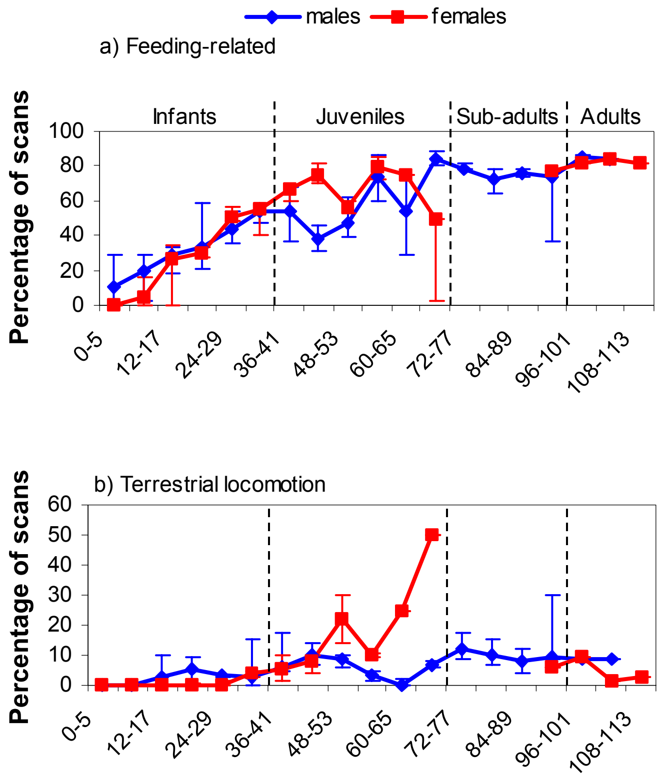


Figure 3.1. Differences between age classes in the median percentage of time spent engaging in each behaviour. $N_{infants} = 26$, $N_{juveniles} = 15$, $N_{sub\text{-}adults} = 10$, $N_{adults} = 4$. * indicates a difference significant at the 0.05 level, ** indicates a difference significant at the 0.01 level.

3.5.2. The Effect of Immature Sex

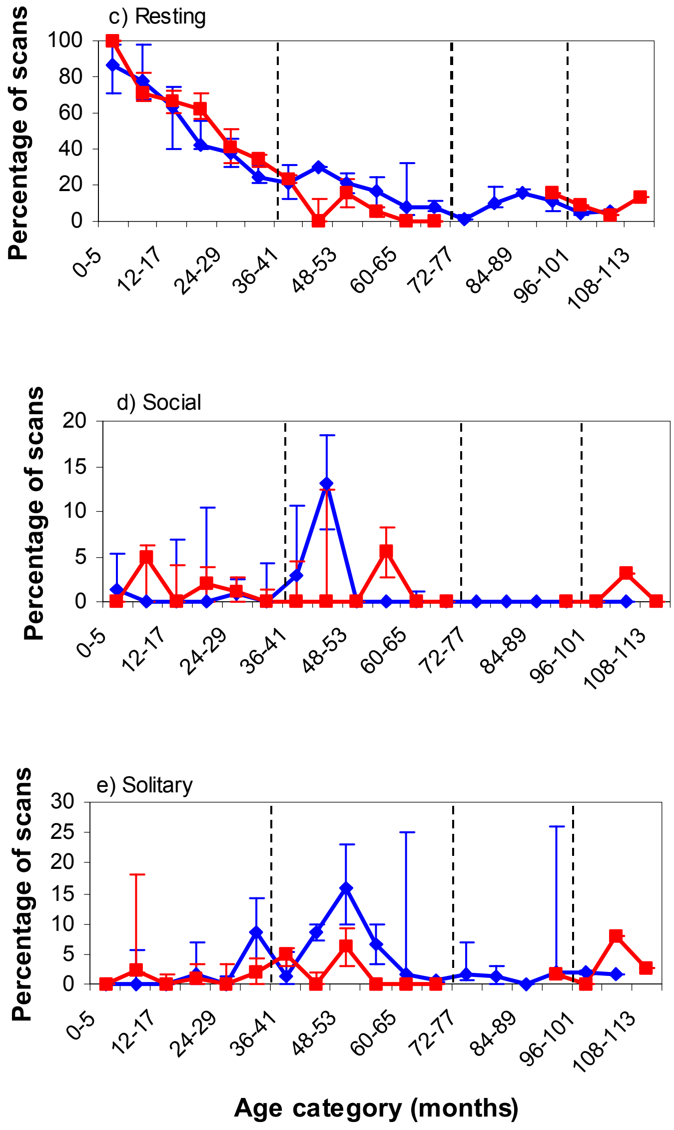
Immature sex was investigated to determine if sex-specific costs had begun to exert their influences on the behaviour of study subjects. During infancy and the juvenile period, the frequency with which behaviours were performed remained unaffected by the sex of the individual, but a lack of sub-adult females, and adult study subjects prevented comparisons in these age classes (**Figure 3.2**).

For the most part, the percentage of scans in which behaviours were recorded was similar between males and females. However, during the juvenile period male and female behaviour appeared to diverge. Females appeared to spend more time engaging in feeding-related behaviours and terrestrial locomotion than males, who were more involved in resting, social and solitary behaviours. However, a small number of females in the sample mean that results may have been influenced by variation between individuals rather than sex differences: results should, therefore, be interpreted cautiously.



a) Feeding-related

b) Terrestrial locomotion



males	10	9	9	9	6	5	4	2	4	2	4	2	3	4	2	3	2	1	0
females	3	5	5	4	4	4	4	3	2	2	1	1	0	0	0	1	1	1	1

Figure 3.2. Comparisons of the median percentage of scan samples that male and female study subjects engaged in a) feeding-related behaviours, b) terrestrial locomotion, c) resting, d) social, and e) solitary behaviours. $N_{\text{males}} = 30$, $N_{\text{females}} = 11$.

3.5.3. Effect of the Social Group on Activity Budgets

Results were tested to investigate the effect of group size and composition on the way in which time was partitioned, for example, if larger groups experienced greater feeding competition (either in the forest or in the bai), which influenced their behaviour in the bai. No differences between groups were found in the frequency with which behaviours were performed in tests carried out within age classes.

However, activity budgets *were* related to the group composition: a significant positive correlation was found between the median age of study subjects within groups (ages taken at the end of the study) and the median percentage of scan samples spent feeding (**Figure 3.3**: $r_s = 0.933$, n = 13, $P < 0.0001$), and negative correlations were found between median group age and the frequency of terrestrial locomotion ($r_s = -0.711$, n = 13, $P = 0.006$), resting ($r_s = -0.966$, n = 13, $P < 0.0001$) and social behaviours ($r_s = -0.831$, n = 13, $P < 0.0001$). So, "older" groups spent more time feeding, and "younger" groups spent more time resting, and engaging in terrestrial locomotion and social behaviour. The frequency of solitary behaviours was not correlated with median group age ($r_s = -0.166$, n = 13, $P = 0.588$). The availability of partners may increase the likelihood of social behaviour between individuals (e.g., Brent et al., 1997), however, groups with more members did not engage in more social behaviour (number of study subjects: $r_s = 0.171$, n = 13, $P = 0.577$; median group size: $r_s = 0.231$, n = 13, $P = 0.447$) or fewer solitary behaviours (number of study subjects: $r_s = -0.288$, n = 13, $P = 0.340$; median group size: $r_s = -0.308$, n = 13, $P = 0.305$).

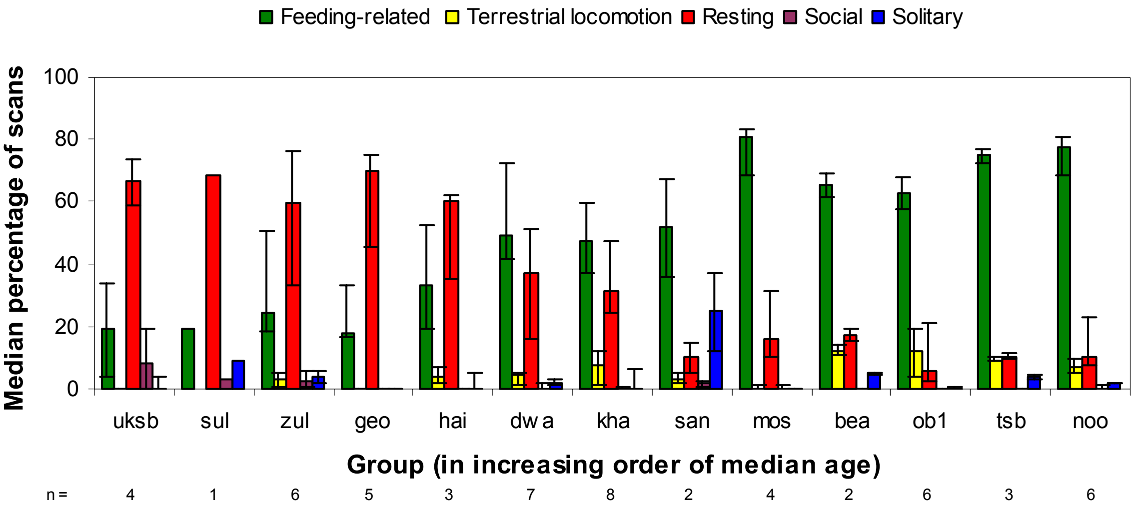


Figure 3.3. The median percentage of scans spent by individuals in different groups engaging in each behaviour type. $N_{TOTAL} = 55$.

3.6. THE DEVELOPMENT OF ARBOREAL SKILLS

The ability to travel independently and successfully through trees is essential for feeding and nesting purposes in western lowland gorillas (Williamson, 1988; Tutin et al., 1995; Mehlman & Doran, 2002). Although the majority of this study focuses on behaviours observed during visits to the bai, the bai/forest interface provided an intermediate habitat between the open, relatively infrequently visited bai, and the closed, more familiar forest environment. *Ad libitum* observations of tree use on the bai edge gives an indication of immatures' ability and confidence in trees, although it is recognised that only very limited conclusions can be reached since tree use in the forest probably had different functions to that observed on the bai edge.

Juveniles were the age class most likely to be seen in trees (**Figure 3.4**), and all juvenile individuals were observed in a tree at some point during the study. The purpose for which study subjects used trees was judged to belong to one of six categories (**Table 3.2**), the frequencies of which can be seen in **Figure 3.5**. Median ages for each type of tree use (calculated from individual median ages) differed significantly from each other: $\chi^2 = 24.055$, d.f. = 5, $P < 0.0001$. Post hoc multiple comparison tests showed that individuals using trees for entry/exit, feeding and resting were older than individuals using trees for playing; those using trees for resting were also older than those using them for quadrupedal locomotion.

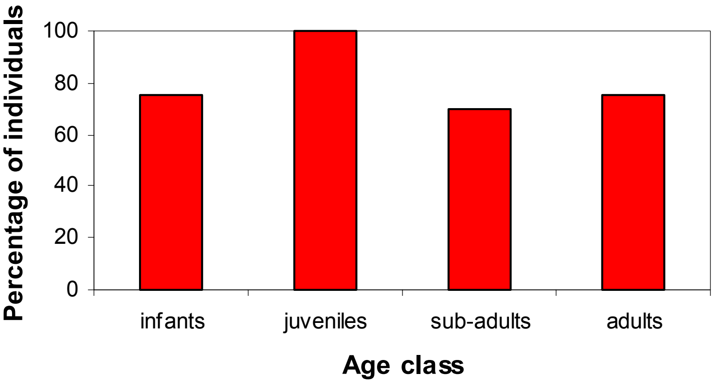


Figure 3.4. Percentage of each age class observed in trees during the study. N_{TOTAL} = 48.

Table 3.2. Definitions of different types of tree use by study subjects.

Tree Use	***Definition***
Entry/exit	Subjects entered or exited the bai via a tree
Feed	Subjects fed on the leaves, fruit or flowers of a tree, while in a tree
Nest	Subjects showed elements of nest building behaviour: folding and patting of vegetation and sitting on folded over branches
Play	Subjects exhibited play behaviours in the branches: swinging from one or both hands, and swinging from lianes. Social and solitary play was observed
Rest	Subjects sat or lay in trees, engaging in no other activity
Quadrupedal locomotion	Quadrupedal locomotion in the branches of a tree

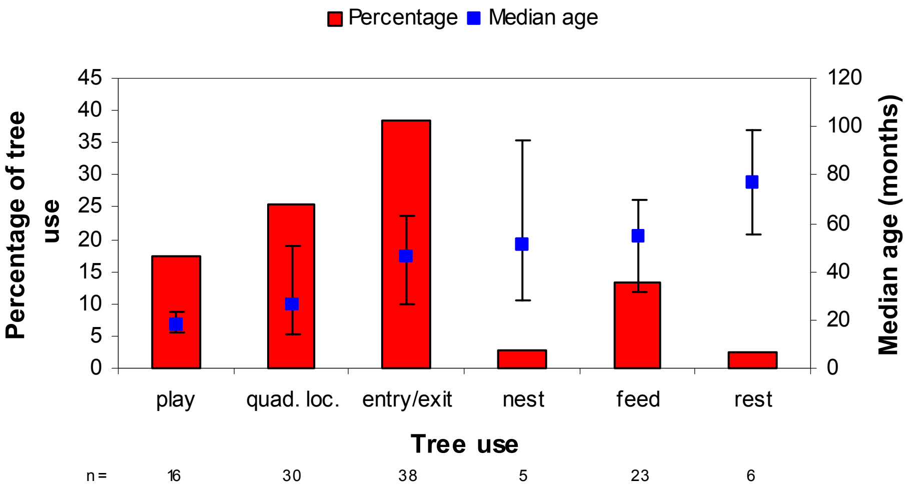


Figure 3.5. The frequency with which each type of tree use was observed, and the median age for individuals performing the type of tree use. $N_{TOTAL} = 48$.

There were no sex differences (within infant and juvenile age classes) in the proportion of visits on which immature gorillas used trees, although sample sizes, particularly for juveniles, were small (infants: $U = 63.5$, $N_{\text{males, females}} = 20, 7$, $P = 0.717$; juveniles: $U = 5.5$, $N_{\text{males, females}} = 4, 5$, $P = 0.268$). Adults of both sexes in the Mbeli population were often seen in trees, mainly for the purposes of entry/exit or feeding, so differences between the sexes during immaturity were not necessarily expected.

Some groups seemed to show a greater tendency than others to use the trees on the bai edge more than others during bai visits, and the median percentage of visits on which tree use occurred in a group was calculated from medians from all individuals within each group and then tested for differences. Significant differences were found (**Figure 3.6**: $\chi^2 = 23.745$, d.f. = 11, $P = 0.014$), with individuals in Hai, Geo and Bea groups being particularly likely to engage in arboreal behaviour. Since juveniles were most likely to participate in arboreal behaviour (see **Figure 3.4**), this difference may have arisen due to group composition. However, the percentage of visits on which individuals were observed in trees per group was not correlated with the number of juveniles in a group ($r_s = -0.368$, n = 12, $P = 0.239$), suggesting that differences were real rather than simply reflecting group composition. In addition, and although sample sizes were small, tests for differences in tree use within age classes all provided non-significant results (infants: $\chi^2 = 15.096$, d.f. = 9, $P = 0.088$; juveniles: $\chi^2 = 5.431$, d.f. = 6, $P = 0.490$; sub-adults: $\chi^2 = 6.261$, d.f. = 6, $P = 0.395$; adults: $\chi^2 = 2.700$, d.f. = 2, $P = 0.259$).

Furthermore, there were no significant correlations between the percentage of visits on which immatures used trees and groups' median visit lengths ($r_s = -0.119$, n = 12, $P = 0.712$), suggesting that tree use did not occur solely as a result of satiation and "boredom" in immatures, waiting on adults to finish feeding.

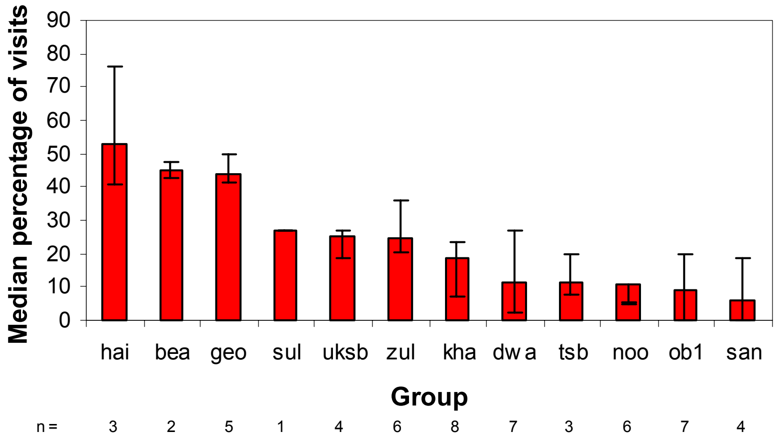


Figure 3.6. Differences between groups in the percentage of visits on which immature group members used trees. $N_{TOTAL} = 48$.

When individual levels of tree use were investigated, certain individuals showed particularly high levels of arboreal behaviour (considered as using trees in more than one third of visits), and to some extent this reflected the differences between the groups. Half of these individuals were infants, 36% juveniles, and 14% were sub-adults. Both immatures in Bea group, 80% of those in Geo group and 66.7% of those in Hai group were included among those with the highest levels of tree use, and reflected the general behaviour of these groups during visits to the bai. When Bea group visited the bai they tended to spend a lot of time on the forest edge. Likewise, Geo group, although much more regular visitors to the bai, spent a high proportion of their visits on the forest edge, possibly as a result of their silverback showing a great tendency to move in and out of the forest during visits. Hai group tended to have long visits, during which Axel (infant) and particularly Ike (juvenile/sub-adult), would retreat back to the forest edge and rest or feed while adult group members continued to feed in the bai.

3.7. FEEDING-RELATED BEHAVIOURS

In this section, all elements of feeding-related behaviour observed in immature study subjects are investigated, including selectivity, play-feed behaviour, the ontogeny of processing and feeding behaviour, and the combination of these elements.

3.7.1. Species and Parts Eaten

Gorillas at Mbeli Bai fed predominantly on species from two families: Hydrocharitaceae and Cyperaceae (**Table 3.3)**. The aquatic herb, *Hydrocharis chevalieri* was the species most commonly fed upon (Parnell, 2002b), and consists of rhizomes (**Plate 3.1**) connected to one to four main roots and one to four stems, each of which bears a single leaf (**Plate 3.2**). All parts were eaten by gorillas (Parnell, 2001). From the Cyperaceae family, *Rhynchospora corymbosa* was also a preferred food item for adult gorillas (Parnell, 2002b). This resembles a narrow garden leek, and requires considerable effort to remove from the ground (Parnell, 2001) (**Plate 3.3**). Other Cyperaceae eaten by gorillas include *Fimbristylis* sp. and *Cyperus sp.,* both grasses that require very little processing (Parnell, 2001). In this study, *H. chevalieri* was the most commonly fed upon item in all immature age classes, and its preferred parts seemed different during infancy than in other age classes, with considerably more time being spent feeding on leaves and stems (**Figure 3.7**). Species other than *H. chevalieri* were fed on by immatures infrequently.

Table 3.3. Details of species and parts eaten by study subjects. $N_{TOTAL} = 59$.

Species	***Part***	***Age range (months)***	***Number of individuals***	***Number of observations***
Hydrocharis	Leaves	6 – 109	14	19
chevalieri	Roots	6 – 110	23	52
	Rhizomes	12 – 110	38	269
	Stems	18 - 101	44	417
	Leaves/stems	33 – 109	12	19
Unknown species		6 – 101	17	28
Fimbristylis sp.	All of it	9 – 105	10	13
Cyperus sp.	Stem base	30 – 100	6	18
R. corymbosa	Stem base	65 – 107	4	6

Plate 3.1. Silverback, Dylan feeding on *H. chevalieri* roots and rhizomes (photo by Emma Stokes).

Plate 3.2. Sub-adult Lyle, feeding on *H. chevalieri* leaves and stems.

Plate 3.3. Blackback, Dill feeding on the base stems of *R. corymbosa*.

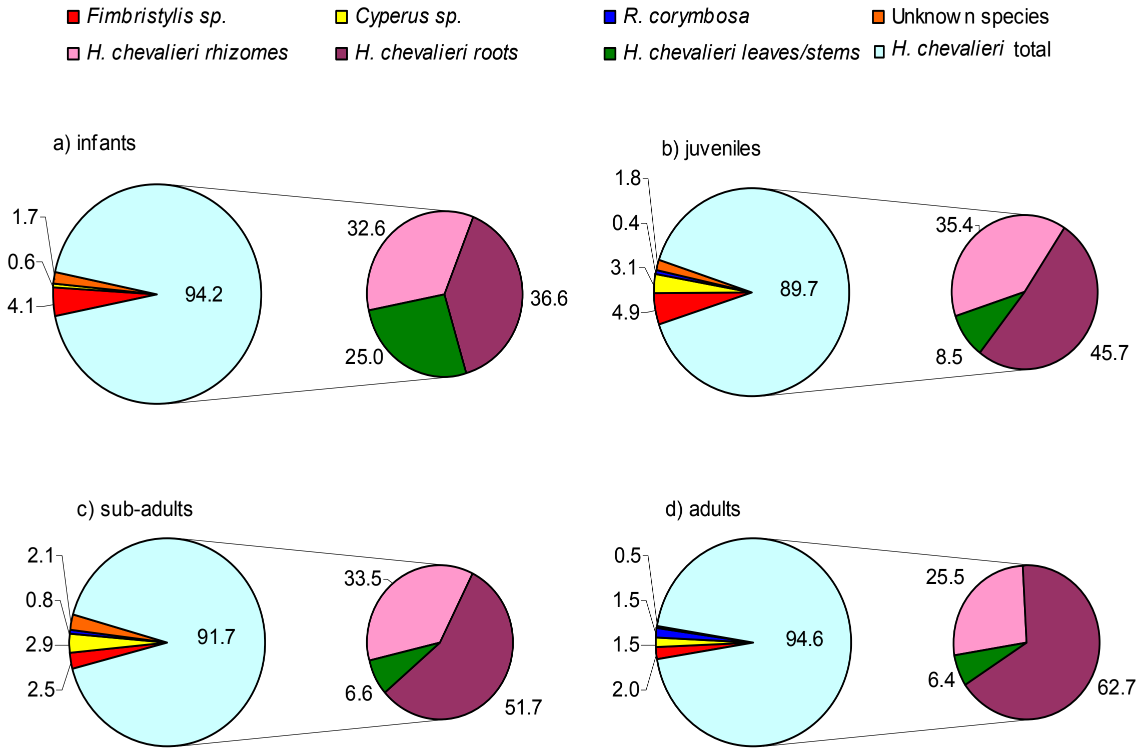


Figure 3.7. Percentage of feeding scans in which each species/part was fed on in a) infant, b) juvenile, c) sub-adult and d) adult study subjects. Values indicate percentages. The exploded pie charts illustrate how *H. chevalieri* feeding was divided between rhizomes, roots and leaves and stems. $N_{infants} = 23$, $N_{juveniles} = 19$, $N_{sub\text{-}adults} = 15$, $N_{adults} = 6$.

3.7.2. Mother-Offspring Distance During Feeding Behaviour

If observational learning is important to immature gorillas in order to receive information on diet choice and feeding behaviours, younger individuals are predicted to feed in close proximity to the mother (e.g., Watts, 1985a). To determine whether this was the case, an index was calculated for individuals using distances to the mother while feeding, and while engaging in non-feeding activities within each 6 month age category (by assigning increasing values to increasing distance categories (contact = 1, 0-2m = 2, etc., and then subtracting the non-feeding distance value from the feeding distance value). Age category median indices were calculated from individual indices. Using this index, a negative value indicated that offspring were closer to the mother when feeding, with positive values indicating that they were closer to the mother when not feeding. A value of zero denoted no difference in the distance from the mother as a result of activity.

During infancy, offspring activity had no influence on distance to the mother, but infants were generally found within 5m of the mother (see Chapter Four), so there was little room for variation in their distance as a result of behaviour. During the juvenile period, however, there was a greater tendency for juveniles to be closer to the mother while feeding than when engaging in other activities (**Figure 3.8**). There was a significant difference between infants and juveniles in index values (U = 12.5, $N_{\text{infants, juveniles}}$ = 12, 11, P = 0.001): the median index for juveniles was –0.75, and +1 for infants. Infants were not found at closer distances to the mother when feeding than when engaging in other behaviours, but juveniles were. Both infants (Z = -2.201, n = 6, P = 0.028) and juveniles (Z = -1.997, n = 6, P = 0.046) were found at significantly closer distances to the mother than to other group members. The mother is likely to be the individual in a group who is most tolerant of her infants' close proximity. If infant gorillas do learn about diet by observational learning, then it will probably be from the mother, as she is individual that they are usually closest to, and therefore, the most easily observed.

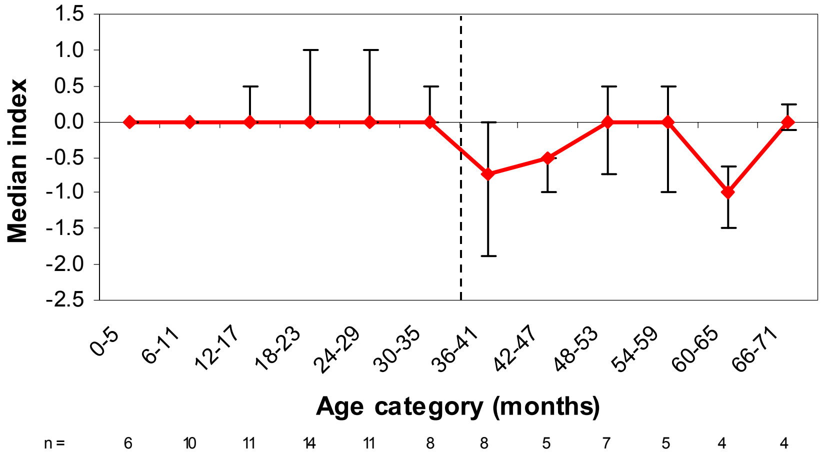


Figure 3.8. Median indices of study subjects investigating distances to the mother when study subjects are engaged in feeding and non-feeding behaviour. Positive indices indicate a closer mother-offspring distance when not feeding; negative indices indicate a closer distance when feeding. N_{TOTAL} = 23.

3.7.3. Play-Feed Behaviour

Play-feed behaviour was defined as the *manipulation of food items but without their ingestion* (**Plate 3.4**), and was thought to occur as a precursor to feeding, and a means by which food processing behaviours were learned. Thus, investment in play-feeding was expected to increase initially as infants began to manipulate food items, and then decrease as it was replaced by the ingestion of solid food items.

Plate 3.4. Infants Bofi (left) and Axel (right) engaging in play-feeding behaviours.

Seventeen (49%) study subjects aged between 5 and 45 months (with a modal age of 17 months) engaged in play-feed behaviour (**Figure 3.9**), which was observed on 47 occasions. Its median duration was calculated for each age category using individual median values with data were taken from the 15 minute focal samples. Results were as expected, with an initial increase in the duration of play-feed behaviour, followed by a significant decrease during the rest of the immature period ($r_s = -0.842$, n = 14, $P < 0.0001$), most notably during infancy and remaining at low levels thereafter (**Figure 3.10**). The total duration of play-feed behaviour, calculated from all contributing subjects within each age category also showed that the most investment in this behaviour occurred during infancy, with only small amounts occurring after this period.

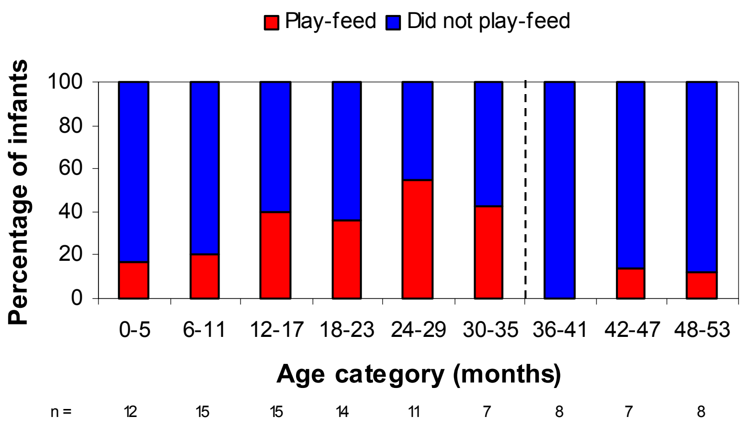


Figure 3.9. The percentage of study subjects engaging in play-feed behaviour. $N_{TOTAL} = 35$.

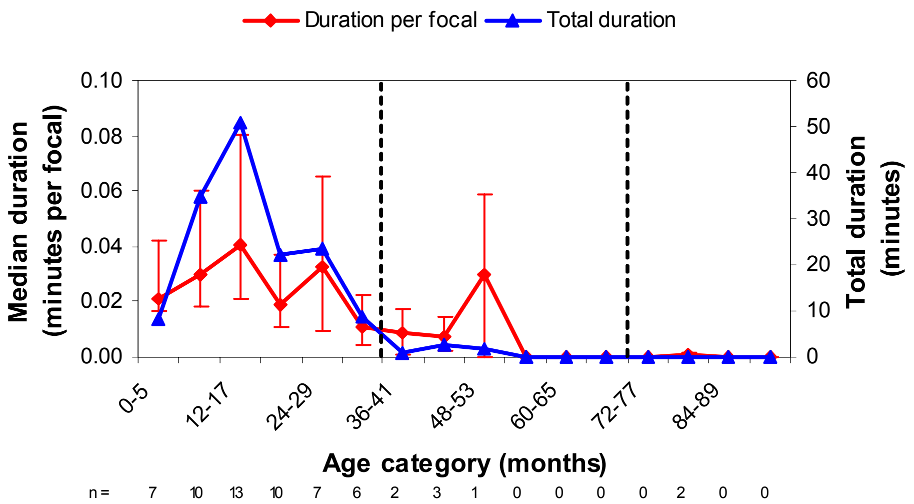


Figure 3.10. Median and total duration of play-feed behaviour and its relationship with offspring age category. $N_{TOTAL} = 35$.

3.7.4. Food Transfers

Food transfer was defined as the *movement*, or *attempts at movement* of solid food between individuals (nursing was not considered a form of food transfer). During failed attempts at food transfer, an individual grabbed at an item in the possession of another who did not relinquish it. In some species, the transfer of food plays a role in the attainment of adult feeding behaviour (e.g., Roush & Snowdon, 2001; Ueno &

Matsuzawa, 2004), and the extent to which this was the case with bai foods in the Mbeli population of gorillas was investigated in this section.

In all observed cases of food transfer, the item involved was a part of *H. chevalieri*. Twenty-one individuals between the age of 4 and 70 months (modal age: 17 months) engaged in this behaviour: 46.7% of males (n = 14), 41.7% of females (n = 5), and 14.3% (n = 2) of individuals of unknown sex. There were 55 actual instances of food transfer between individuals (**Table 3.4**), six of which involved two study subjects.

Table 3.4. The frequency with which each dyad type was observed engaging in food transfer interactions, which member of the dyad took, or attempted to take from the other, and the number of immatures involved.

Dyad Type	*Frequency*	*Frequency with which each was the "taker"*	*Number of immatures*
Infant-mother	42	Infant: 37, mother: 5	15
Juvenile-mother	5	Juvenile: 1, mother: 4	3
Juvenile-infant	3	Juvenile: 1, infant: 0	4
Juvenile-juvenile	2	In both instances, Brie (oldest) took from Peapod	2
Sub adult-adult female	1	Sub-adults: 0, adult female: 1	1
Sub adult-infant	1	Sub-adults: 0, infant: 1	2
Infant-infant	1	Fang (youngest) took from Kung	2

Of the 38 documented cases of offspring taking food from their mother, food was not obtained, or not fed on after it was obtained in 19 of cases (50%). Of the nine cases where a mother took food from her offspring, it was fed on in eight occasions (88.9%), and discarded only once (11.1%). In seven other cases where an immature took from an individual other than the mother, the item was fed on in three cases (42.9%) (**Figure 3.11**). The motivation for initiating food transfers did not appear to be hunger and therefore, any food gained was unlikely to represent a necessary contribution to diet. It is suggested then, that the purpose of food transfers may be to allow young "takers" to learn which foods, or parts of food can be fed on.

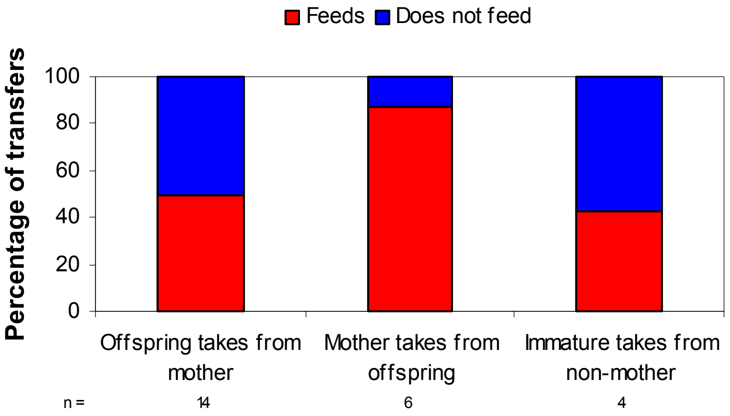


Figure 3.11. Percentage of food transfers in which the obtained item was fed on. N represents the number of immatures. $N_{TOTAL} = 21$.

When an infant interacted with its mother, infants were more likely to obtain, or try to obtain food (the initiator), rather than to have food taken, or an attempt made to take food (the target). Juveniles and sub-adults were more likely to be the target than initiators of interactions. Generally, infants initiated food transfers with all individuals, whereas outside of infancy, older individuals were more likely to be the target of younger individuals.

3.7.5. The Effects of Age on Feeding-Related Behaviours

The total food intake of an individual will reflect its size (Altmann, 1980), and as study subjects mature they will be met with increased costs as a result of growth and higher activity levels. Therefore, total food intake, and also the time invested into learning how to feed or processing food was expected to increase with age. Learning to feed was expected to gradually be replaced by the actual processing and ingestion of food items as the appropriate techniques were refined. In this and subsequent sections, when percentages are involved they were calculated as percentages of the total time spent engaging in feeding-related behaviours.

With increasing age, there was little change outside infancy in the percentage of feeding-related scans that were spent feeding on *H. chevalieri* ($r_s = 0.551$, n = 6, $P = 0.257$), processing ($r_s = 0.365$, n = 19, $P = 0.124$) feeding on other species ($r_s =$

0.405, n = 19, *P* = 0.086) or play-feeding (r_s = -0.562, n = 19, *P* = 0.012) (**Figure 3.12**). Infancy was the period during which the majority of changes in feeding behaviour occurred, and particularly during the first 18 months for the percentages of time spent feeding on *H. chevalieri* and play-feeding. During and after the juvenile period, the percentage of time spent feeding on *H. chevalieri* and other species, and the level of processing involved remained fairly constant, while play-feeding decreased to zero.

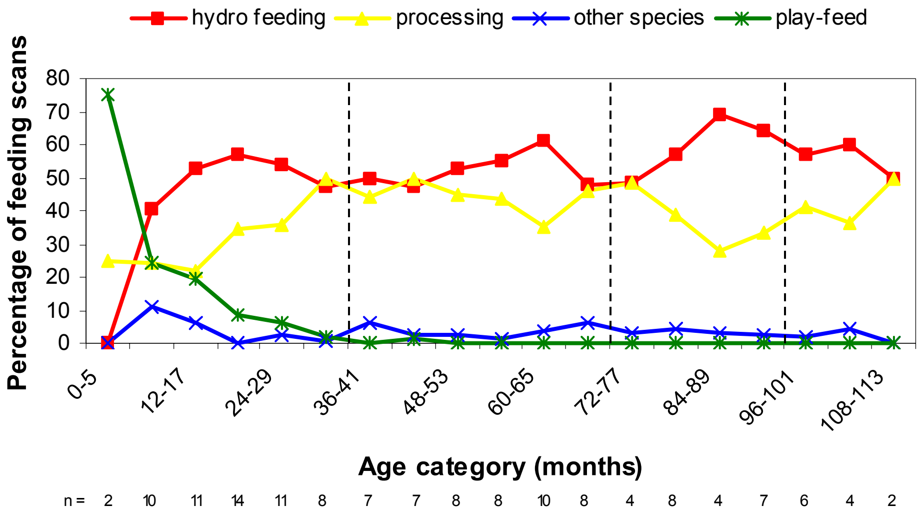


Figure 3.12. The percentage of feeding-related scans that study subjects of different ages engaged in different elements of feeding behaviour. N_{TOTAL} = 50.

3.7.6. The Ontogeny of Feeding Behaviour: **Hydrocharis chevalieri**

As individuals become nutritionally independent, their diet is expected to show less variation between individuals, and begin to resemble the species-typical diet (Watts, 1985a; Milton, 1993). Therefore, *H. chevalieri* was expected to be the species selected most frequently, with all parts being eaten.

The median percentage of the feeding-related time that was spent feeding on parts of *H. chevalieri* was calculated for each age category, and individual values were then used to give age category medians (**Figure 3.13**). Over the whole immature period, the percentages of time spent feeding on *H. chevalieri* roots (r_s = 0.913, n = 19, *P* < 0.0001) and *H. chevalieri* rhizomes (r_s = 0.657, n = 19, *P* = 0.002) were positively correlated with age category. In addition, feeding on *H. chevalieri* roots showed a significant increase during infancy ($r_s = 0.880$, n = 6, $P = 0.021$). Apparent increases during the juvenile period in the percentage of time spent feeding on roots and rhizomes were not significant. The frequency with which *H. chevalieri* leaves and stems were fed on was not significantly correlated with age category ($r_s = 0.443$, n = 19, $P = 0.064$), but showed two slight peaks: one towards the end of infancy, and then again in sub-adult and early adulthood.

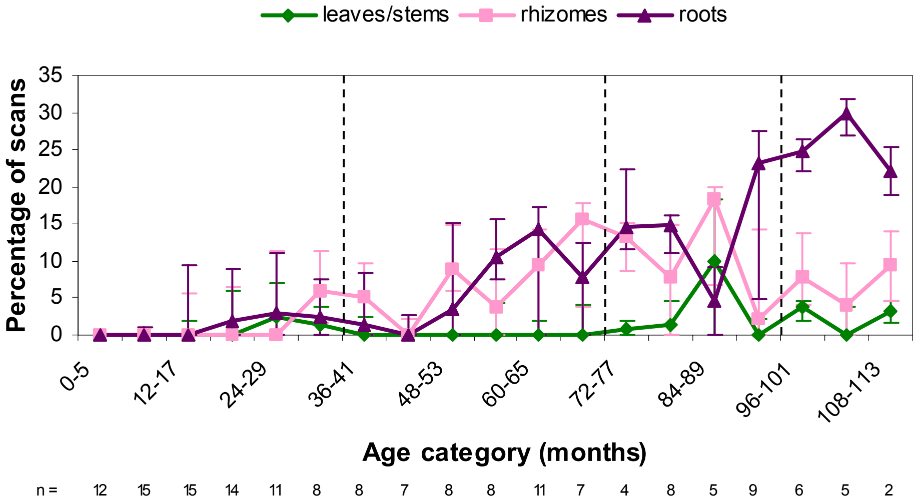


Figure 3.13. The percentage of feeding-related scans that study subjects of different ages spent feeding on *H. chevalieri* leaves and stems, rhizomes and roots. $N_{TOTAL} = 57$.

To assess the degree of variation in feeding behaviour between study subjects, the percentage of individuals observed to feed on each item was investigated. More study subjects fed on roots and rhizomes than fed on leaves and stems (**Figure 3.14**), with over 80% of juveniles, sub-adults and adults feeding on rhizomes and roots. Less than 50% of infants and juveniles fed on leaves and stems, despite it requiring no processing other than plucking stems from the bai matrix.

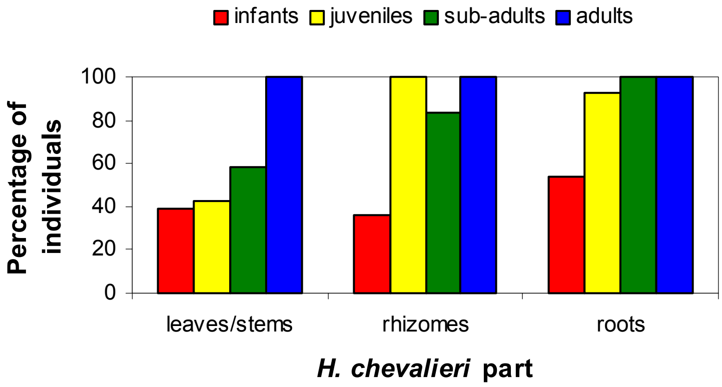


Figure 3.14. The percentage of infants, juveniles, sub-adults and adults who were observed to feed on *H. chevalieri* leaves and stems, rhizomes and roots. $N_{\text{infants}} = 28$, $N_{\text{juveniles}} = 14$, $N_{\text{sub-adults}} = 11$, $N_{\text{adults}} = 4$.

Since male and female gorillas experience different energetic costs as adults as a result of size, and also the demands of reproduction on females, an investigation was made as to whether differences existed in the feeding behaviour of male and female immatures. However, no significant differences were detected in the percentages of time that males and females fed on *H. chevalieri* leaves and stems ($Z = -0.237$, n = 15, $P = 0.813$), rhizomes ($Z = -0.549$, n = 15, $P = 0.583$) or roots ($Z = -0.237$, n = 15, $P = 0.813$).

3.7.7. Feeding on Other Species

The amount of time spent feeding on *Cyperus* sp., *R. corymbosa* and *Fimbristylis* sp. by immatures was very low, and fewer individuals fed on them than on *H. chevalieri* (**Figure 3.15**). Low frequencies of feeding and low levels of participation of feeding on these species suggested that they were of less value to study subjects than *H. chevalieri*.

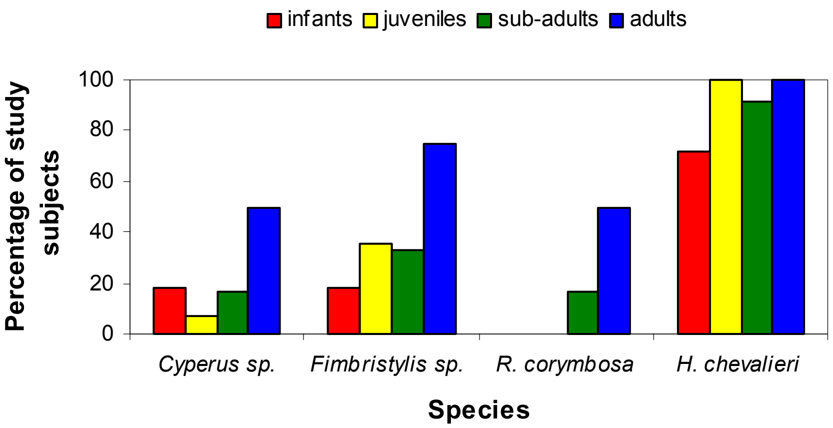


Figure 3.15. The percentage of study subjects observed to feed on *Cyperus* sp., *R. corymbosa* and *Fimbristylis* sp., compared with the percentages that fed on *H. chevalieri*. $N_{\text{infants}} = 28$, $N_{\text{juveniles}} = 14$, $N_{\text{sub-adults}} = 11$, $N_{\text{adults}} = 4$.

3.7.8. The Ontogeny of Processing Behaviour

When feeding on *H. chevalieri*, adult gorillas consistently show a series of processing elements (**Figure 3.16, Plate 3.5**). Gorillas "dredged" plants from the swampy water, by pulling the plants towards them. Plant parts were then separated from each other, and often washed to remove a sediment residue by sweeping the plant back and forth under water prior to ingestion (Parnell, 2001). Only leaves and stems were eaten with no processing involved. **Table 3.5** provides details on the first appearance of processing behaviours.

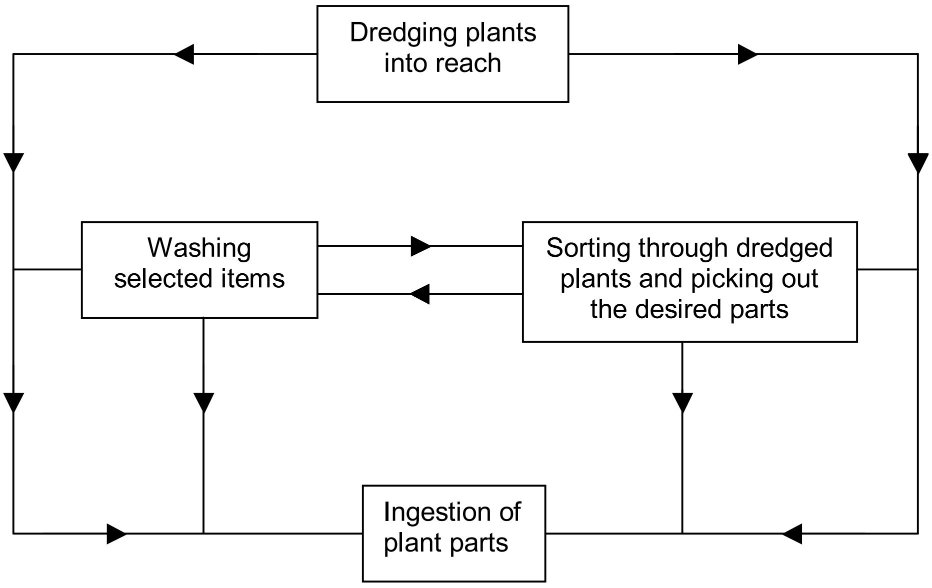


Figure 3.16. Simple flowchart showing the steps involved in processing *Hydrocharis chevalieri*.

Plate 3.5. Silverback, Mosombo dredging *H. chevalieri* (top left); black back, Bayleaf sorting *H. chevalieri* (top right) (photos taken by Emma Stokes); and blackback, Coriander washing *H. chevalieri.*

Table 3.5. Ages at which processing behaviours were first observed, and the individuals involved in them.

Behaviour	***Age range (months)***	***Number of individuals***	***Number of observations***
Dredging	4 – 110	47	719
Sorting	12 – 100	33	142
Washing	31 – 108	13	27

The total amount of food processing (the total of dredging, sorting and washing elements), calculated as a percentage of feeding-related scans, showed an increase with age category across the whole of the population (r_s = 0.590, n = 19, P = 0.008), although the majority of changes took place during infancy. All individual elements also increased in frequency with increasing study subject age (**Figure 3.17**: washing: r_s = 0.508, n = 19, P = 0.008; sorting: r_s = 0.471, n = 19, P = 0.042; dredging: r_s = 0.624, n = 19, P = 0.004). However, most development in processing skills seemed to occur during infancy, with the frequency of dredging showing a significant increase (r_s = 0.941, n = 6, P = 0.005), and sorting showing a tendency to increase with age although no significant correlation was found (r_s = 0.655, n = 6, P = 0.158). Only two infants were recorded to wash *H. chevalieri* before feeding on it. The frequency of dredging, sorting and washing fluctuated during the juvenile period, sub-adulthood and early adulthood, but generally, all elements of processing were observed more frequently than during infancy.

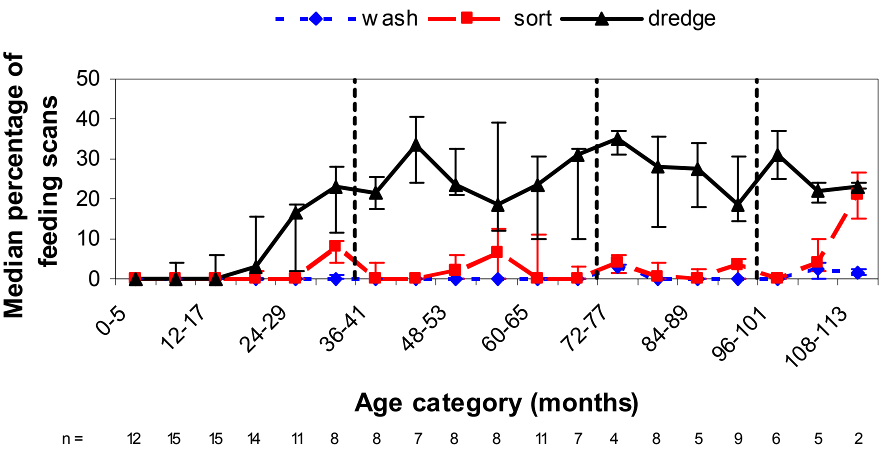


Figure 3.17. The percentage of feeding-related scans that study subjects of different ages spent washing, sorting and dredging roots and rhizomes of *H. chevalieri*. NTOTAL = 57.

Although the frequency of washing remained low, it was a reasonably widespread behaviour, with approximately 30% of juvenile and sub-adult, and 75% of adult study subjects observed to wash their food (**Figure 3.18**). Washing was usually a very brief activity, with overall median washing bout lengths (calculated from all age category medians) equalling 2.8 seconds, compared to 3.5 seconds for sorting and 6.9 seconds for dredging. Additionally, in individuals of sub-adult age and older, each dredged handful of *H. chevalieri* was often only washed once, but a common processing sequence was dredge, wash, sort, feed, sort, feed, etc. Consequently, regardless of whether data from scan focal samples were used, washing would be observed with a lower frequency than sorting and dredging, and this was exaggerated by the use of median values.

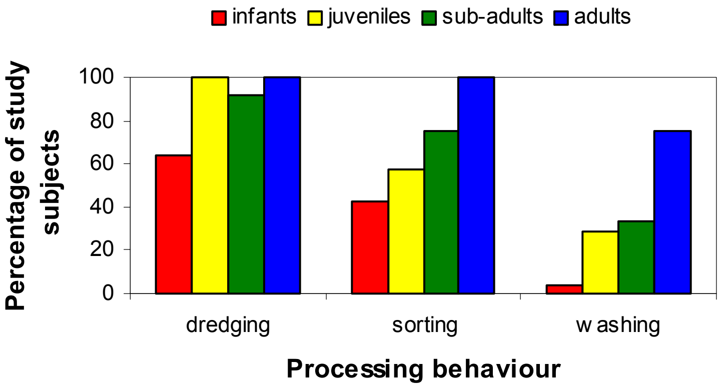


Figure 3.18. The percentage of available study subjects observed to dredge, sort and wash the roots and rhizomes of *H. chevalieri*. $N_{\text{infants}} = 28$, $N_{\text{juveniles}} = 14$, $N_{\text{sub-adults}} = 11$, $N_{\text{adults}} = 4$.

Tests matched for age were conducted to determine whether male and female study subjects differed in the extent that *H. chevalieri* roots and rhizomes were processed before consumption. The real function of processing food before feeding on it is unknown although it is assumed to be simply to remove debris and inedible items from edible plant parts before eating them (Parnell, 2001), therefore, no differences between the sexes were expected, or detected (washing: $Z = -0.730$, n = 15, $P = 0.465$; sorting: $Z = -0.059$, n = 15, $P = 0.953$; dredging: $Z = -0.314$, n = 15, $P = 0.754$).

3.7.9. Feeding:Processing Ratios

In order to further understand the development of feeding behaviour, an attempt to identify optimum feeding behaviour was made. Processing *H. chevalieri* before consumption is assumed to be beneficial, despite the fact that processing food reduces the time spent actually consuming food, given the frequency with which it is observed at Mbeli Bai (Parnell, 2001; Parnell, 2002b). Therefore, processing was assumed to be necessary to some extent, in order to gain the maximum benefit from the plant part that gorillas were feeding on, or to remove potentially harmful items entangled with edible parts. Because processing seemed so central to feeding behaviour, it was expected that an optimum balance between time spent processing and ingesting *H. chevalieri* would be achieved, and that little variation between individuals would be found (*sensu* Byrne & Byrne, 1993).

Data from each focal sample were used to calculate a ratio of feeding (on parts of *H. chevalieri*) to processing (washing, sorting, dredging) behaviour, by dividing the time that an individual spent feeding by the time spent processing during a 15 minute focal sample. When the ratio is high, relatively more feeding took place during a focal sample than processing, and vice versa. A ratio of less than 1 would indicate that more actual time was spent processing food than consuming it. The ratios from each focal sample were used to create individual medians within age categories, and then to calculate age category medians.

Data from subjects aged 0-5 months were removed as a result of very little processing or feeding behaviour performed. There was a significant negative correlation between the feeding:processing ratio and age category (**Figure 3.19**: r_s = -0.488, n = 18, P = 0.04).

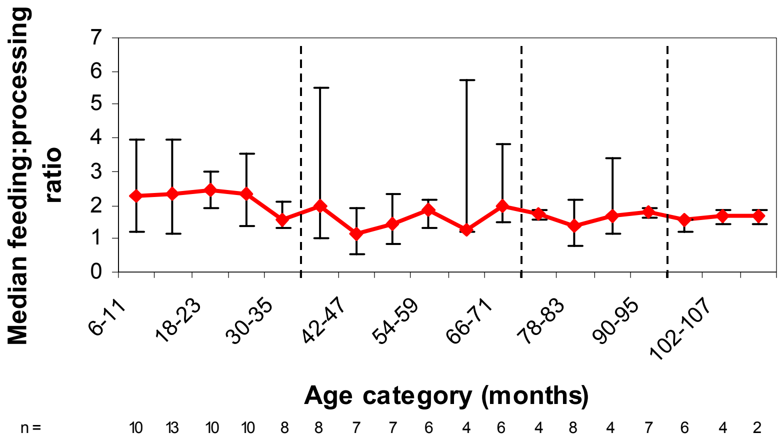


Figure 3.19. Median feeding:processing ratios and changes with increasing immature age. N_{TOTAL} = 50.

There was no indication that study subjects spent more time processing than actually feeding on parts of *H. chevalieri* (no median values were less than 1). During infancy, study subjects processed less, and actually spent more time feeding than older individuals did, as indicated by the higher values of the ratio during infancy. This may have been due to the infants feeding on more leaves and stems than other age classes, which require less processing, although provide lower quantities of minerals than do the roots and rhizomes (Nishihara, 1995). The feeding:processing ratio was variable during the juvenile period, with variation between individuals as well as between age categories. During sub-adulthood and the early stages of adulthood, this variation decreased, as individuals incorporated more processing into their feeding behaviour, which presumably also reflected the greater incorporation of roots and rhizomes into the diet, items that required a greater degree of processing (Parnell, 2001).

The attainment of optimum feeding behaviour was hypothesised to be linked with age at weaning: as the mother withdraws investment in her offspring, it becomes essential that the offspring obtains its resources elsewhere. To test this, median feeding:processing ratios from individuals, who were also observed to suckle during the study period were used. The median percentage of suckling bouts that were terminated by the mother (Chapter Four contains full details on the termination of suckling bouts) was calculated for each individual within each age category. It was only after infancy, when the level of processing began to increase relative to consumption of *H. chevalieri*, and feeding:processing ratios began to resemble those of older individuals, that mothers started to terminate suckling bouts (**Figure 3.20**).

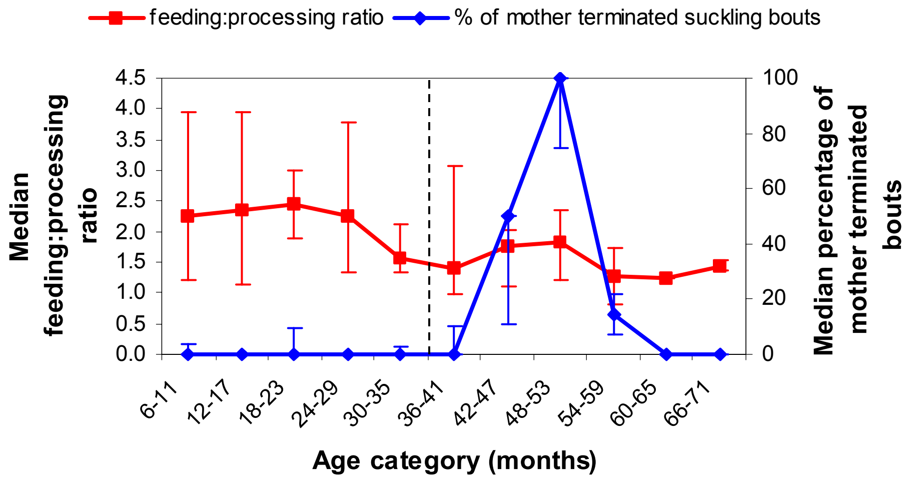


Figure 3.20. Comparison of the median percentage of suckling bouts that were terminated by the mother, and median feeding:processing ratios. $N_{TOTAL} = 32$.

3.8. DISCUSSION

3.8.1. Sex and Group Differences

This chapter has investigated the distribution of time between different activities, and the development of arboreal and feeding skills – all of which are essential for the survival of western lowland gorillas. Investigation of the apportioning of time has shown:

- No detected sex differences in activity budgets, arboreal locomotion and feeding behaviours, suggesting that no sex-specific costs (e.g., gestation and lactation (Lee, 1996), and defence of the social group (Sicotte, 1993)) exerted effects at young ages, or alternatively, that any sex-specific costs were equal.
- Differences between groups in relation to activity budgets and arboreal locomotion, which were related to the age of study subjects in the bai, and characteristics of particular groups. No differences between groups were found in their feeding behaviour in the bai, suggesting that the composition and size of groups does not influence the behaviour of groups when feeding on the abundant and evenly distributed resources in the bai.

The absence of group differences in feeding behaviours in this study suggested that these were not affected by group size or composition while in the bai environment; however, this does not mean that competition is absent outside the bai. There was no relationship between group size and the frequency of bai visits, so although larger groups would be expected to experience increased within-group competition in the forest (Chapman & Chapman, 2000), they did not visit the bai, an area with very little feeding competition, any more frequently than smaller groups. The effect of group size and composition on feeding competition was difficult to determine in the bai, as resources were abundant.

3.8.2. Activity Budgets

Appropriate partitioning of time between activities is necessary to ensure that individuals meet nutritional demands. Consequently, activity budgets of infants should show a transition from predominantly sedentary behaviour when very young, to increasingly incorporating elements of adult life. Results from this study showed that:

- During infancy, an increase was seen in the percentage of time spent feeding, and a concurrent decrease in other behaviours, particularly resting, while in the bai. This continued until the end of infancy, when no further changes in independent feeding were recorded.

The transition in behaviour from predominantly resting to actively feeding is necessary if an infant is to survive (Watts & Pusey, 1993; Hanya, 2003). Gorillas are relatively helpless for the first few months of life, and infant mountain gorillas appeared to spend approximately 75% of their time asleep (Fossey, 1979). At young ages, all the necessary requirements (food, warmth, transport) required by primates are provided by the mother (Fossey, 1979; Lee, 1995), from which infants must balance the demands of body growth, fat storage and energy expenditure (Lee, 1996). Increasing activity levels require more energy (Altmann, 1980), so an efficient method of maximising growth may be to remain inactive for large periods of time; exactly what infant gorillas do by appearing to spend the majority of their first 18 months resting. The transition from resting to feeding behaviour occurred after 18 months of age, and terrestrial locomotion also increased throughout infancy. Coinciding with the rise in activity levels, play-feed behaviour first appeared in infants' behavioural repertoires, before being replaced by the efficient processing and ingestion of food items.

In western lowland gorillas, a large amount of time is invested in locating sufficient quantities of food (Doran et al., 2004). Bais are considered valuable resources, providing large quantities of vegetation that meets the mineral requirements of gorillas, while also providing sources of carbohydrates during periods of fruit scarcity (Nishihara, 1995; Magliocca & Gautier-Hion, 2002; Doran et al., 2004). Therefore, when the overall activity budget of gorillas is considered, they should be expected to spend a great deal of time feeding there. Patch size and food availability are not limiting factors, however, units visited Mbeli Bai for an average of only 115 ± 75 minutes. There was little seasonal variation in bai use by gorillas (with the exception of periods of high use coinciding with the fruiting of *Nauclea vanderguchtii* trees found on the perimeter of the bai (Parnell, 2002b)), and therefore, no evidence that visits to Mbeli Bai were linked with fruit availability in the forest. One explanation for the relatively short and uniform visit lengths is that the high water content (94%: Parnell, 2002b) of *H. chevalieri* makes it difficult to consume in large quantities, and gorillas become satiated (see Parnell, 2002b). The smaller size and fewer requirements of immature gorillas predicts that a lesser quantity is required to satiate them (Lydersen et al., 1997; Parnell, 2002b), and although it was impossible to test how much food was actually consumed, immature gorillas often stopped feeding earlier in a bai visit than adults, probably as a result of earlier satiation (Parnell, 2002b; pers. obs.).

3.8.3. The Presence of Social Behaviours

Significant levels of play, grooming and other social interactions have been documented for immature gorillas both in the wild (mountain gorillas: Watts & Pusey, 1993; Fletcher, 2001; Stewart, 2001) and in captivity (western lowland gorillas: Hoff et al., 1981b; Hoff et al., 1994; Enciso et al., 1999; Maestripieri et al., 2002). Active social behaviour between individuals was the least frequently observed class of behaviour in the bai, but was more likely to be seen in those less than 4 years of age. Grooming, play and other social interactions tended to be performed during group rest periods in mountain gorillas (Harcourt, 1978a; Fletcher, 1994), and given that the predominant activity of gorillas in the bai was feeding (Magliocca & Gautier-Hion, 2002; Parnell, 2002b), this helps to explain this anomaly. Similarly, a second bai study has shown that only 0.5% of time was devoted to social behaviour by non-infant gorillas (Magliocca & Gautier-Hion, 2002). However, results from the current study have shown that resting behaviour was the most common activity in infants up to the age of 30 months of age, which overlaps with the start of the period during which play and other social behaviours are often the most prevalent in primate species (e.g., van Lawick-Goodall, 1968; Owens, 1975; Stewart & Harcourt, 1987; Fagen, 1993). Therefore, activity patterns do not fully explain the absence of social behaviours.

Firstly, it is possible that the physical nature of the bai limited social behaviour. The swampy ground makes locomotion difficult for small individuals (Parnell, 2002b; pers. obs.), thus potentially limiting aspects of social play such as chasing and rough and tumble play. Secondly, unrelated immature gorillas may be reluctant to approach a conspecific who is in close proximity to its mother in order to play (Nowell, 2001). Chapter Four shows that a long period of time was spent in proximity to the mother by immatures in this study, potentially reducing the opportunities an individual has to interact with others. Finally, if the play behaviour of immatures disturbs the feeding behaviour of nearby adults, adults may intervene and prematurely terminate play sessions (e.g., Stewart, 1981; Pereira & Altmann, 1985), although little evidence of this was seen.

In addition to the swampy bai environment and the presence of the mother, the high levels of frugivory in western lowland gorillas and its associated costs may contribute towards the low levels of social behaviour observed during this study. A recent study on howler monkeys showed that during periods where the diet was composed predominantly of fruit rather than leaves, levels of social behaviour were significantly decreased, suggesting that the costs of feeding on fruit result in a decrease in the time available for social interactions (Pavelka & Knopff, in press). Levels of social play in gelada baboons decreased during periods when food quality was poor and longer had to be spent feeding to gain the same amount of nutrition (Barrett et al., 1992), again suggesting that costs are associated with frugivory, and the availability of fruit can affect activity budgets of primates. Western lowland gorillas are predominantly frugivorous when fruit is available (Williamson et al., 1987; Remis, 1997b; Doran et al., 2002), and although data were not available to correlate behaviour with fruit abundance, overall, it may be expected that they would show less frequent active social interaction than do folivorous (Watts, 1984) mountain gorillas.

The low levels of social behaviour recorded in this study may be a true reflection of wild western lowland gorilla behaviour. Social grooming in many primates provides an important means by which bonds between individuals (particularly the philopatric sex) are maintained, strengthened and reaffirmed (e.g., Seyfarth & Cheney, 1984; Henzi & Barrett, 1999; Di Bitetti, 2000; Watts, 2000a; Barrett & Henzi, 2002). However, in western lowland gorillas, the eventual emigration of most individuals from the natal group (Stokes et al., 2003; Robbins et al., 2004), and the frequency of secondary transfer (Doran & McNeilage, 1998; Stokes et al., 2003) reduces the importance of establishing and investing in such relationships for future benefit. The nutritional demands on immature gorillas, and the discontinuous and ephemeral distribution of the majority of items constituting their diet may be such that limited time is available for activities other than feeding, thus providing an example of how the ecology of gorillas influences the development of behaviour. In the bai, where resources are abundant, exploitation of these resources may be more important than investing in relationships with individuals who are likely to be unavailable in the future.

3.8.4. The Presence of Solitary Behaviours

Solitary behaviours, such as vigilance, self-grooming, and solitary play were expected to increase in frequency as individuals mature, receive less attention from the mother, and take a greater interest in their surroundings (Fossey, 1979). In this study, however, these behaviours were observed infrequently at an age where exploration of the environment is expected to be high (Fossey, 1983; Byrne & Suomi, 1995). Low observed levels of vigilance perhaps indicated the low levels of predation (Robbins et al., 2004) and hunting (Stokes et al., 2003) experienced by gorillas in the study area, and the level of protection offered by the group silverback against infanticidal males (e.g., Watts, 1989; Stokes et al., 2003). Low levels of vigilance in immature gorillas while in the bai suggest that neither predation or infanticide posed a serious threat that required their vigilance, compared with juvenile baboons who do display vigilance behaviour when threat from predation is present (Alberts, 1994).

3.8.5. The Development of Arboreal Skills

Competence in independent arboreal locomotion in western lowland gorillas is essential, since the majority of fruit is gathered from trees (Williamson et al., 1990) (although fallen fruits are also harvested from the forest floor (pers. obs.)). Additionally, arboreal nests are constructed by weaned western lowland gorillas up to 35% of the time, often in response to predation or disturbance during the night, e.g., from elephants, and adaptations relating to diet (Tutin et al., 1995; Fruth & Hohman, 1996; Mehlman & Doran, 2002). Immature gorillas must, therefore, develop competence in independent arboreal locomotion, and in this study:

- Tree use was observed in all immature age classes, but was most common in juveniles.

The frequency of tree use by juveniles contrasted with Doran's (1997b) findings in wild mountain gorillas that arboreal behaviour was most frequent during infancy. The need of western lowland gorillas to travel competently within the canopies of trees, for the reasons above, is clear, compared with mountain gorillas, who use trees infrequently. The decline in arboreal behaviour by sub-adult and adult study subjects, compared with juveniles may have reflected the increased nutritional demands, and a longer time to satiety in older, larger gorillas. If bai visits serve to meet nutritional requirements (Magliocca & Gautier-Hion, 2002), then differential times to satiety will afford younger individuals with more opportunity to engage in non-feeding activities (Parnell, 2002b). Infants were more likely to be constrained in their levels of tree use by increased dependence on the mother, and a lack of confidence in arboreal locomotion: on several occasions, an infant moving or playing in a tree on the bai edge fell, and was “rescued” by the mother, suggesting that arboreal locomotion is a skill that improves with practise (Dunbar & Badam, 1998).

In this study, trees were not used only in the predicted way (i.e., for feeding or nesting), therefore, the motivation of different age classes for tree use may have been altered. The more playful nature of juveniles, in addition to their lower nutritional requirements was likely to inflate the frequency with which trees were used. They tended to use trees for feeding, nesting, entry/exit and resting, reflecting their increasing independence, both nutritionally and physically. Weaned juveniles build their own night nests (Tutin et al., 1995; Mehlman & Doran, 2002), and the instances recorded in this study showed no elements of play behaviour, and suggested that juveniles were preparing to, or already did sleep alone at night. The high frequencies of quadrupedal locomotion and play in trees by infants may have reflected their increasing confidence and familiarity with arboreal locomotion (e.g., Dunbar & Badam, 1998; Wells & Turnquist, 2001).

Despite their great size, silverbacks still often feed arboreally (Williamson et al., 1990; pers. obs.), although they are more likely to nest terrestrially (Brugiere & Sakom, 2001; Mehlman & Doran, 2002), and the lack of sex differences in tree use in this study suggests that skilled arboreal locomotion is equally important for both sexes. Differences between groups in tree use did not appear to be related to group composition, and instead, suggested differences between groups. Some groups had long visit lengths, and in these cases, the high use of trees was likely to result from immatures becoming satiated before adults, and spending the remainder of the visit resting, playing or locomoting in trees on the forest edge. Alternatively, frequent use of trees on the bai edge may have occurred in response to uncertainty about the open, bai environment in immatures who were newcomers to the Mbeli population.

However, it must be stressed that the tree use investigated in this study may not be representative of how trees are more commonly used in the forest. In this study, tree use seemed very much to represent a time-filling exercise, rather than as a means to obtaining sufficient food, so limited conclusions about the development of arboreal competence can be drawn.

3.8.6. The Ontogeny of Feeding and Processing Behaviour

Immature primates must learn both what and how to eat (Byrne & Byrne, 1993), in order for them to survive without assistance from the mother. In the current study, the development of feeding skills showed the following patterns:

- The distance between mother and offspring increased with immature age, and therefore, no conclusions could be reached as to what extent close proximity between mother and infant occurred to facilitate observational learning about diet and food choice.
- Play-feeding behaviour appeared to act as a precursor to the development of feeding skills, and its decline soon followed its appearance, as it was replaced by higher incidences of food preparation and ingestion.
- Initiators of food transfers were most often infants when the target of the initiation was the mother. Outside mother-infant dyads, older individuals were more likely to initiate food transfers, with younger individuals as targets. Items gained by food transfer were unlikely to contribute nutritionally to receiving individuals, but may have conveyed information on diet choice.
- *Hydrocharis chevalieri* roots were the preferred food item of immature gorillas visiting Mbeli Bai, and the frequency with which *H. chevalieri* leaves and stems were fed on decreased after infancy.
- The ratio of feeding to processing *H. chevalieri* initially increased, showing that infants spent relatively more time feeding than processing than older individuals. The ratio fell during the juvenile period, before becoming stable during sub-adult and adulthood. The attainment of the stable value, which was suspected to represent the optimum balance between processing and feeding on bai foods, was reached before mothers began to terminate suckling bouts.

This study was limited in what it could conclude about the acquisition of feeding skills by observational learning, but shorter mother-juvenile distances during feeding than during non-feeding behaviour may provide insights on potential levels of agonism directed from adults towards juveniles. Although feeding competition in the bai is assumed to be low due to the abundance of food, agonistic behaviour and feeding displacements between adults do occur (Stokes, 2004; pers. obs.). Juveniles may seek the proximity of the mother when feeding to buffer against any possible agonistic behaviour directed towards them by other group members, as mothers are more likely than other group members to tolerate the close proximity of their offspring during feeding periods (Pereira & Altmann, 1985).

During infancy and the juvenile period, study subjects tended to be closer to the mother than to any other individual, so if observational learning did occur, it was most likely to be from the mother. In order to fully test the hypothesis that acquisition of feeding skills occurs by social learning in western lowland gorillas, as in mountain (Watts, 1985a; Byrne & Byrne, 1993), and captive western lowland gorillas (Zimbler-De Lorenzo et al., 2001), more data on the synchronicity of behaviours between mothers and offspring are needed. As mother-offspring distance increased with offspring age (see Chapter Four, also Stewart, 1981; Fletcher, 2001)), it was impossible to determine to what extent the close proximity of infants to the mother occurred in order to learn feeding skills from her by means of observational learning. Infants tended to be found at closer distances to the mother when engaged in non-feeding activities, but seemed to require a degree of physical independence from the mother in order to manipulate food items. Mothers were usually intolerant of infants leaning down from a dorsal position to gather food items, and then manipulating and feeding on them while still dorsal. In response, mothers often pulled the infant from her back or removed the food item (pers. obs.).

Infants present at close distances to their mothers while feeding also showed interest in the items that she was feeding on by attempting to take them from her. Items gained in this manner were unlikely to significantly contribute towards their diet, contrary other primate species such as tamarins (Ruiz-Miranda et al., 1998; Roush & Snowdon, 2001) and titi monkeys (Starin, 1978). However, handling food items taken from the mother may still have provided information about food choice, regardless of whether items were eaten.

Play-feed behaviour represented the first manipulation of food items by infants, seeming to act as a precursor to actual feeding, given its decrease as individuals matured, and the concurrent increase in actual feeding behaviour. Exploration of food items was also the first feeding behaviour recorded in infant rhesus macaques (Wells & Turnquist, 2001), and it is suggested that infants progress from exploration and manipulation, to ingestion of food items. It was possible that play-feed may simply have been a form of object play, which in humans, has been linked with foraging activities (Pellegrini & Bjorklund, 2004). If play-feed did represent object play, its decrease in frequency may have resulted from increasing familiarity with the object, in this case, food. However, the “object” continued to be a source of attraction even when individuals had become familiar with it through continued exposure, and instead of manipulating these items, they were fed on. Very few observations of object play were recorded during this study, possibly due to the lack of objects with which to interact in the relatively uniform bai habitat. *H. chevalieri*, the preferred food item of gorillas at Mbeli, was the most frequent species to be used by infants in play feed behaviour, despite the availability of many others (Mbeli Bai Study, unpublished data) in the vicinity. This further suggests the role of play-feed behaviour in the development of feeding and food processing skills. Play-feed behaviour incorporated elements of dredging, sorting and washing (Parnell, 2001), and may have represented initial attempts at processing. However, infants lacked the finer motor skills necessary to control movement (Fossey, 1979), and they perhaps also lacked an understanding of the purpose and the end stage (i.e., consumption of food item, without attached debris) of the movements. All elements of processing behaviour increased in frequency with age, and more individuals participated in these behaviours as they matured. The combination of processing and consumption reached what was assumed to represent the optimum balance towards the end of infancy, and consequently, immature feeding behaviour began to resemble that of adults. Normally, this would be expected to be the point at which offspring are weaned, but this was not the case in this study (see Chapter Four), with mothers only beginning to terminate suckling bouts after the end of infancy.

The main hypothesis explaining the consumption of swamp vegetation by gorillas is the search for mineral salts (Nishihara, 1995; Magliocca & Gautier-Hion, 2002; Doran et al., 2004). From a young age, the species and parts of plants eaten by immatures reflected those eaten by adults, despite other species being available. All individuals spent the majority of their time feeding on *H. chevalieri*, as is also the case in adult gorillas (Stokes et al., 2003; T. Breuer, pers. comm.). *H. chevalieri*, particularly the roots and rhizomes, contains high levels of iron and sodium, which are not present to such an extent in at least some of the items fed upon in the surrounding forest (Nishihara, 1995). Although *H. chevalieri* was not the most abundant species in the bai, it is necessary to take into account the distribution of species within the bai before concluding that feeding on *H. chevalieri* indicates a degree of selectivity. In 2000, a preliminary bai vegetation study was carried out: the number of stems of different species were counted within $0.5m^2$ quadrats, which were contiguously placed on alternate sides of a transect line through a particular vegetation type (Mbeli Bai Study, unpublished data). The transect through *H. chevalieri* swamp (the usual location for feeding gorillas) measured 60m, and an average of 3.43 species in addition to *H. chevalieri* were present in each of the $0.5m^2$ quadrats. These species accounted for an average of 41.3% of each quadrat, compared to 57.3% for *H. chevalieri* (Mbeli Bai Study, unpublished data). *H. chevalieri* accounted for an average of only 0.2-1.67% of stems in the other three transects, all of which were placed in areas where gorillas have been observed feeding. So although groups spent the majority of time in the bai feeding on *H. chevalieri*, there were a number of different species that could have been eaten, although nothing is known of the toxicity to gorillas of these items. Other species (sitatungas and elephants) were observed to feed on some other bai plants (pers. obs.), showing that they were not toxic to these species. The preference for *H. chevalieri* in immature gorillas indicated that food selectivity did occur and was established at an early age.

The percentage of time spent feeding on different parts of *H. chevalieri* seemed different during infancy than in other immature age classes, with a greater proportion of feeding time spent on the leaves and stems. The leaves and stems contain significantly less sodium and iron than the roots (Nishihara, 1995), but are also more easily obtainable, requiring no processing other than plucking them from the plant (Parnell, 2001). In order to be suitable weaning foods, leaves and stems should be more digestible than the roots or rhizomes, but unfortunately, there are no data available to indicate whether this may be the case.

No sex or group differences were evident in any feeding or processing behaviours, suggesting that eventual sex-specific costs, and group size and composition did not affect the development of these behaviours in immature gorillas. There was no evidence to suggest that larger groups experienced increased feeding competition during this study (*sensu* Sterck et al., 1997; Chapman & Chapman, 2000). *Rhynchospora corymbosa* was the second most commonly fed upon plant by adult gorillas at Mbeli (Parnell, 2002b; T. Breuer, pers. comm.), but during the study, only one female subject fed on it, compared to three males. All were over 5 years of age. *R. corymbosa* is difficult to uproot from the bai matrix, requiring considerable strength, and infants and young juveniles attempting to do so often broke the leaves off above the base of the stem; the part which is eaten (pers. obs.). Adult female gorillas did often consume *R. corymbosa* at a rate that appeared comparable to males and with no more apparent difficulty. However, it was possible that sexual dimorphism began to develop between males and females aged 5-8 years, although more likely, these results highlighted a lack of strength and technique to feed on *R. corymbosa* in the majority of immature gorillas, rather than pointing at differences between males and females.

3.8.7. Limitations and Forest Feeding

Clearly, this study is limited in what it can conclude about the overall development of activity budgets, arboreal locomotion and feeding behaviour in wild western lowland gorillas. For that, some insight must be gained into the behaviour of immature gorillas in the forest. With reference to feeding behaviour, preliminary data from faecal samples at Mbeli showed that 80% of immature dung samples (n = 14) contained the fruit remains of up to three different species (T. Breuer, pers. comm.), thus indicating the importance of fruit to young gorillas. Few studies that have investigated diet using faecal samples have analysed the dung of immature gorillas. However, a study in Central African Republic found that by the third year, the percentage of faecal samples containing fruit, the mean number of fruit species in the faeces, and the average percentage of faeces consisting of fruit was similar between one infant and the adult female and silverback in the same group (C. Cipolletta, pers. comm.). A preliminary study on fruit feeding on the bai edge at Mbeli suggested that infants and juveniles were wasteful of *N. vanderguchtii*, a highly favoured fruit found around the bai edge. They often plucked unripe fruits then dropped them, rather than appearing to test ripeness by sniffing the fruits before plucking them, as adult gorillas seemed to (R. Parnell, pers. comm.; pers. obs.), and was also observed in bonobos (Fruth & Hohman, 2002). Additionally, at Mondika Research Centre in Central African Republic, infants have been observed attempting to feed on *Klainedoxa sp*., a fruit that is extremely hard and difficult to process (D. Doran, pers. comm.). Feeding on fruit appears not to be a simple task, and fruit-feeding skills must be developed in order to maximise resources with minimal wastage.

From these small insights, it is apparent that from a relatively early age, fruit is incorporated into the diet of immature gorillas. However, it is uncertain whether fruit-feeding behaviour develop at the same rate as those observed in the bai, and if the diet of individuals entering the juvenile period does in fact resemble that of adults across all food types.

3.8.8. Conclusions

At Mbeli Bai, behaviours developed and resembled that of adults by the end of infancy, undergoing little significant change afterwards, despite the fact that some individuals had not yet been weaned (see Chapter Four). Although results pertain to only a small part of Mbeli gorillas' lives, it was clear that competence in many aspects of feeding behaviour and travelling behaviour was achieved. The collection of data in a bai environment allowed detailed investigation into behaviours, such as food transfers and details on food processing, which may be limited in the forest, even with well-habituated groups, due to constraints of the habitat. However, due to the very different habitat provided by bais, findings from studies such as these may not be extrapolated to behaviour in the forest. Exposure to risks, such as predation and infanticide, may differ between the bai and forest environment and the effect of having to travel and feed in an environment that is swampy and difficult for smaller individuals to negotiate is unknown. Currently, however, bai studies provide the only data available to investigate these processes in wild immature western lowland gorillas.

CHAPTER FOUR

MOTHER-OFFSPRING RELATIONSHIPS

4.1. INTRODUCTION

The relationship between mammalian mothers and their offspring is critical, and the actions that mothers take to shield their infant from the dangers of the external environment can contribute to its death or survival (Hinde, 1971; Peripato & Cheverud, 2002). Mothers provide infants with nourishment, warmth and transport, and she also acts as a mediator in infants' first interactions with other members of the species (e.g., Horvat & Kraemer, 1981; Nicolson, 1987; Fletcher, 2001). The mother's investment in her offspring allows development to proceed in an environment, which is to a certain extent, shielded from ecological constraints. Indeed, Galef (1981) suggested that mammalian offspring may be more properly viewed as "highly adapted parasites than as incompletely formed adults" (cited in (Stamps, 2003)).

Young primates do not achieve independence from the mother until they have matured sufficiently to allow them to deal with the demands that their environment makes of them, and ultimately, the availability of resources that immatures can access will determine the age at which individuals gain independence from the mother. When born, primates are relatively helpless, and spend a longer period of time growing and developing than in species of other mammalian orders with similar body sizes (Harvey & Clutton-Brock, 1985; Kappeler et al., 2003). Furthermore, in great apes, the period of time during which offspring are dependent on the mother is comparably longer than in other primate species (Watts & Pusey, 1993). This may reflect the effort required to learn the behavioural and social skills necessary to survive in their complex environment (Watts & Pusey, 1993). Even when nutritionally and physically independent of their mothers, juvenile apes often continue to remain in proximity to their mothers and return to them when distressed: the strong bond between mother and offspring diminishes only gradually (Stewart, 1981; Watts & Pusey, 1993; Fletcher, 2001).

4.1.1. A Source of Food

Mountain gorillas are weaned at approximately 3.5 years of age (Stewart, 1981; Fletcher, 2001). Before this, the mother's milk (or its equivalent in hand reared gorillas) is an essential element in an immature gorilla's diet (Stewart, 1988), and close proximity to the mother is maintained before weaning takes place (e.g., Hoff et al., 1981a; Stewart, 1981; Fletcher, 2001). The importance of suckling declines as offspring mature, and their feeding and processing skills resemble those of adults (see Chapter Three).

Primates wean their infants when they reach roughly one third of adult body weight, or four times the birth weight (Lee et al., 1991; Ross, 1998). With the exception of growth spurts, seen in many species at puberty (e.g., Taylor, 1997; Hamada et al., 1999; Setchell et al., 2001), the rate at which primates grow reflects food availability (Barrett & Henzi, 2000). Species that feed on perennially available abundant resources, such as mountain gorillas, are predicted to have faster overall growth rates than those facing greater feeding challenges (Ross, 1998), for example, the sparsely distributed and seasonal resources of western lowland gorillas. Thus, variation in diet between mountain and western lowland gorillas predicts that important differences will also be present in suckling and weaning behaviour.

4.1.2. Parent-Offspring Conflict and Weaning

Weaning is the most obvious example of parent-offspring conflict, signifying the waning relationship between a mammalian mother and her offspring (Trivers, 1974; Lee et al., 1991; Barrett & Henzi, 2000; McDade, 2001). In many primates, including gorillas, the interbirth interval consists mainly of a period of postpartum lactational amenorrhoea, where continued suckling prevents a mother from resuming ovulation, and therefore, from conceiving and reallocating investment to her next offspring (Devinney et al., 2001). A reduction in the frequency of suckling by her current offspring is necessary before females can return to oestrus and conceive (Stewart, 1988; Sievert et al., 1991). Despite such an obvious conflict of interest, weaning in gorillas tends to be a relatively gentle process (Watts & Pusey, 1993). Infants seldom throw tantrums (Fossey, 1979; Stewart, 1981; Fletcher, 2001), and rejection by a mother most often takes the form of prevention of access to her nipples by simply crossing her arms in front of her breasts (Hoff et al., 1981a; Fletcher, 2001). However, in mountain gorillas, attempting to wean an infant at an early age can result in high levels of distress and tantrums (Fletcher, 2001).

Studies in rhesus monkeys and baboons have shown that instead of increased behavioural distress and parent-offspring conflict, as suggested by attachment (Bowlby, 1997) and parent-offspring conflict theories (Trivers, 1974), cooperation and compromise were more likely to result, as predicted by the Bateson's (1994) dynamic assessment theory. Offspring honestly signal their need, which mothers respond to (Bateson, 1994; Barrett & Henzi, 2000; Devinney et al., 2001). So, with regards to patterns of suckling and weaning and the development of feeding behaviour in this study:

- Infants are predicted to continue to suckle frequently and prevent the mother from resuming ovulation, until able to select, process and digest an adequate diet which resembles that of an adult, and that meets a maturing individual's nutritional needs.
- Mothers are expected to initiate weaning in their offspring by rejecting attempts to suckle. However, this is expected to be a gentle process, with little signs of extensive distress, and mothers responding to genuine needs of her offspring.

4.1.3. A Source of Transport

Detailed studies of maternal transport in wild western lowland gorillas have not yet been conducted, and consequently, information on various aspects of travelling behaviour are available only for wild mountain and captive western lowland gorillas (e.g., Fossey, 1979; Hoff et al., 1981a; Fletcher, 1994; Doran, 1997b; Maestripieri et al., 2002). These studies have found that gorillas maintain continuous contact with their mothers for the first few months, and the initial break of contact occurs around 4-5 months of age (Fossey, 1979; Hoff et al., 1981a; Fletcher, 2001). Very few cases have been observed of individuals other than the mother transporting immature gorillas (although see Warren & Williamson, 2001), but as a result of the low infant/maternal weight ratio, the transport of infants is unlikely to be very costly for females (Wright, 1990; Ruiz-Miranda et al., 1998).

No report has been published of infant apes being "parked", i.e., left unattended for long periods of time while the mother forages (Ross, 2001). Kappeler (1998) suggested that mothers might choose to carry their infants despite the costs, to allow her to range further without having to return to a parked infant to feed and protect it. In some species, avoidance of infanticidal males may provide an additional reason for carrying offspring (Watts, 1989; van Schaik & Kappeler, 1997; Weingrill, 2000). These factors must be taken into consideration when species are highly frugivorous, have widely dispersed resources, and infanticide operates in the population.

4.1.4. The Social Environment

The social group into which an infant is born can have a strong effect on development, and early social experiences may have long-lasting effects (Harcourt & Stewart, 1981; Brent et al., 1997). While infants are young and in continuous contact, a mother can control her infant's access to other group members. However, as offspring become increasingly independent, a mother is more likely to only intervene in her offspring's social activities if the infant is perceived to be at risk (Maestripieri et al., 2002). Such situations may take the form of the solicitous attentions of an adolescent female with little experience of mothering (Pereira & Altmann, 1985; Schino et al., 2003), or the rough play of older juveniles (Pereira & Altmann, 1985; Nowell, 2001). Bai studies have provided the first opportunities to observe all individuals concurrently within western lowland gorilla social groups (Magliocca et al., 1999; Parnell, 2002a; Gatti et al., 2004a), and as such, the present study can fully investigate the position of immature individuals within the group.

4.1.5. Influences on the Mother-Offspring Relationship

The parity, age or condition of the mother (van Lawick-Goodall, 1971b; Hooley & Simpson, 1981; Fletcher, 1994; Manson, 1999), the sex of the infant (Trivers, 1972; Hewison & Gaillard, 1999; Brown, 2001a), and the composition of the group in which individuals reside (Cheney, 1978; Fagen, 1993; Brent et al., 1997) are all factors that have been shown to influence the period of dependency of an infant on its mother in primates. In addition, ecological factors also influence when an immature individual can survive without the aid of the mother (see Barrett et al., in press).

Previous experience of motherhood can affect relationships between a mother and her offspring. Primiparous capuchin mothers have been shown to engage in more infant handling (Manson, 1999), and primiparous macaque mothers show more restrictive behaviours towards their offspring; therefore, their infants spend more time in close proximity to them than do offspring of multiparous females (Hooley & Simpson, 1981; Brown & Dixson, 2000). In addition, infants of primiparous mothers can be more vulnerable to neglect than those of experienced mothers, e.g., in rhesus macaques (Maestripieri & Carrol, 1998) and gorillas (Nakamichi et al., 2004). Even in elephant seals, pups produced by young, inexperienced mothers were less likely to survive their first year than pups of experienced mothers (McMahon & Bradshaw, 2004). Studies of baboons, chimpanzees and gorillas have discovered that mothers who did not begin to reject offspring until they were unusually old, were old mothers themselves, and therefore, nearing the end of their reproductive life (van Lawick-Goodall, 1971a; Nash, 1978; Fletcher, 1994). Old, multiparous mothers may be expected to invest heavily in their offspring, doing all they can to ensure that their potential final offspring survives. Therefore, with respect to the current study:

- Differences in mother-offspring relationships may arise as a result of the previous mothering experience of a female, with primiparous mothers either exhibiting more restrictive behaviours towards their offspring, or their offspring being more vulnerable to neglect.

Mothers are expected to invest more heavily in the sex that experiences the greatest variability in their reproductive success (Trivers, 1972; Boesch, 1997; Hewison & Gaillard, 1999; Brown, 2001a). Male gorillas often spend a period of time as a solitary male, with little opportunity for reproduction, and only some form a reproductive group and have access to all females within it. The sex ratio of 1:1 at birth (Watts, 1991b) is not reflected in the sex ratio of adults within reproductive groups, attesting to the more variable success of males compared with females, and the failure of some males to gain regular access to females and reproduce.

In polygynous mammals, reproductive success is influenced by body size and condition (Clutton-Brock et al., 1984), and by investing heavily in male infants, a mother may increase her son’s chances of gaining access to females, and thus producing a large number of offspring carrying her genes (Trivers & Willard, 1973; Boesch, 1997). Female reproductive success is limited by reproductive parameters, such as age at weaning of her infant, the duration of lactational amenorrhoea (Stewart, 1988; Sievert et al., 1991) and a general inability to care for any more than one offspring at a time (Matsumoto-Oda, 1995; Nowell et al., subm.): a mother may be limited in the difference she can make to the reproductive output of her daughters.

The fact that mothers are likely to make more difference to the success of sons by increasing their investment in them relative to females, and the likely eventual dispersal of both males and females from the natal group in western lowland gorillas (Parnell, 2002b; Stokes et al., 2003) make it reasonable to expect some degree of sex-biased maternal investment in favour of male gorillas post-birth. This study is the first to investigate relationships between wild western lowland gorilla mothers and male and female offspring to determine if sex-biased maternal investment does occur and predicts that:

- Mothers should invest more in male than female offspring, given the greater variability in male reproductive success. If apparent, this may manifest itself in males spending longer periods in contact or close proximity with the mother, and a later age at weaning.

The constraints and opportunities provided by other group members can affect the behaviour of mothers and infants (Berman et al., 1997), and consequently, the group size and composition potentially affects immatures' social development. Groups with a large number of conspecifics might promote earlier independence in infants as a consequence of the greater number of individuals with which they can interact (Cheney, 1978). Additionally, the presence of older siblings can also provide increased incentive to leave the proximity of the mother (Fagen, 1993; Fletcher, 1994; Brent et al., 1997). Preferred play partners of immature primates tend to be those who are similar in size and strength (Pereira & Altmann, 1985; Tomasello et al., 1990; Fairbanks, 1993), and if many individuals fitting these criteria are present, it might be reasonable to expect a decrease in the time spent associating with the mother earlier in development than is seen in groups with few immatures of similar ages. Therefore:

- Differences in mother-offspring relationships may arise as a result of group composition, with immatures in groups containing many conspecifics showing increased independence from the mother at early ages.

4.1.6. Changes in the Mother-Offspring Relationship with Increasing Offspring Age

As the intensity of the relationship between mother and offspring wanes, the following predictions were made with reference to the mother-offspring relationship:

- Infants are expected to show decreasing dependence on their mothers as they increase in age, manifested by infants spending less time in contact with the mother and more time at an increasing distance from her (e.g., Hinde & Atkinson, 1970; Fletcher, 2001).
- A gradual transition is expected in the modes of locomotion used by the offspring, from being entirely dependent on the mother for travel, to travelling independently (e.g., Fletcher, 1994; Doran, 1997b).
- An overall reduction is expected in the frequency of interaction with the mother, and an increase in the proportion of agonistic interactions as offspring begin to move out of the mother's immediate proximity, compete with her for food, approaches sexual maturity and reaches an age at which it is expected to emigrate from the natal group.

This study will be the first to make an in-depth analysis of the manner in which the ecology of western lowland gorillas affects the development of independence from the mother. Based on the predictions made, the nature of the relationship between mother and offspring will be investigated and interpreted with respect to the environmental and social constraints in which the development of the relationship proceeds.

RESULTS

4.2. CONTACT WITH THE MOTHER

A decline in contact rates is a clear indication of the decreasing relationship between mother and offspring, and the data used to demonstrate this were taken from scan samples (see Chapter Two: data were used in analysis as described, but median values were calculated for each month, rather than 6 month categories).

In addition to the percentage of time spent in contact with the mother, and the age at first break of contact, it was an aim of the study to investigate responsibility for the maintenance of contact. However, only six study subjects were recorded to make or break contact with the mother on more than ten occasions, thus, data were considered insufficient to provide useful information on the maintenance of contact between mother and offspring.

4.2.1. Effect of Age on Contact Behaviour

Contact between a mother and her offspring was not observed during scan samples in any offspring over the age of 55 months. There was a significant negative correlation between offspring age in months and the median percentage of scans spent in contact with the mother (**Figure 4.1**: $r_s = -0.926$, n = 59, $P < 0.0001$).

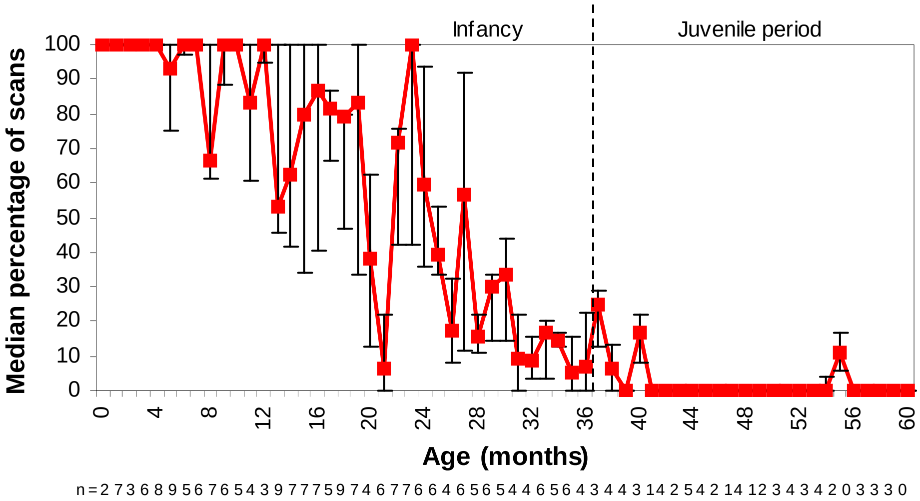


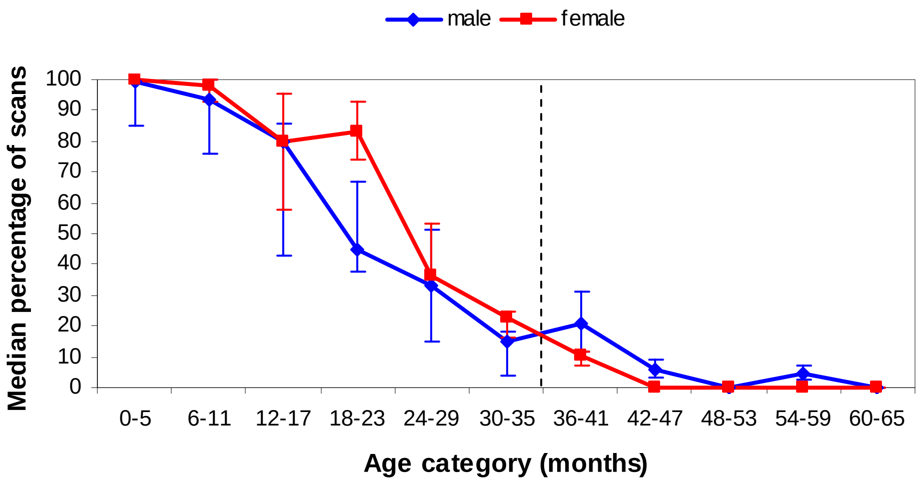
Figure 4.1. The median percentage of scans in which offspring of different ages were in contact with the mother. $N_{TOTAL} = 39$.

Between the ages of 1 and 3 years there was a great deal of variation (both within and between individuals) in the percentage of time spent in contact with the mother (**Figure 4.1**). The low value seen at 21 months was the result of five of the six individuals spending 25% of their time or less, in contact with the mother, while the 6th individual, Sage, spent over 80% of time in contact. Of the seven individuals who contributed values towards the high median score at 23 months, four of them spent all their time in contact with the mother at this age. No reason was evident for the high degree of variation in the percentage of scans in which offspring were in contact with their mothers between the ages of 21 and 23 months: different cohorts of individuals contributed towards the values of each of these months. Perhaps simply enough individual variation was present to influence the values in this way.

There was a clearly significant difference between infants and juveniles in the median percentage of time spent in contact with the mother ($U = 2.0$, $N_{\text{infants, juveniles}} = 27, 11$, $P < 0.0001$), with a median of 90% of scans (IQR: 46.5-100%) in contact with the mother for infants, compared to 0% (IQR: 0%) for juveniles.

4.2.2. Effect of Offspring Sex on Contact

The possibility of sex-biased investment in offspring was investigated by comparing time spent in contact with the mother for males and females. There were no significant sex differences for either infants or juveniles in the percentage of scans spent in contact with the mother (**Figure 4.2**: infants: $U = 51.5$, $N_{\text{males, females}} = 20, 7$, $P = 0.277$; juveniles: $U = 6.0$, $N_{\text{males, females}} = 4, 5$, $P = 0.180$).



males	11	12	11	7	5	4	2	4	2	2	1
females	3	3	4	4	3	4	1	2	2	1	1

Figure 4.2. Comparison between sexes in the median percentage of scans spent in contact with the mother. $N_{\text{TOTAL}} = 35$.

There appeared to be some effect of sex on contact with the mother between the ages of 18 and 23 months, however, the difference in this age category was not significant ($Z = -1.095$, $N_{\text{males, females}} = 10, 4$, $P = 0.273$). Males in this category showed a much greater range of values in their median scores – from 0% to 100% of time in contact with their mothers, but female values ranged only from 44.4% to 100%. Again, results suggest that individual differences existed, but there was no evidence that these resulted from significant differences between the sexes.

4.2.3. Effect of the Group on Maternal Contact

In order to examine the effect of group composition on the extent to which offspring were found in contact with their mothers, tests were carried out on infants. Juveniles were not included in the analysis, as median values for the percentage of time spent in contact with the mother equalled zero. There were no differences between groups on the time that infants spent in contact with their mothers (**Figure 4.3**: $\chi^2 = 6.452$, $N_{groups} = 10$, $P = 0.694$), however, the number of infants in each group was small.

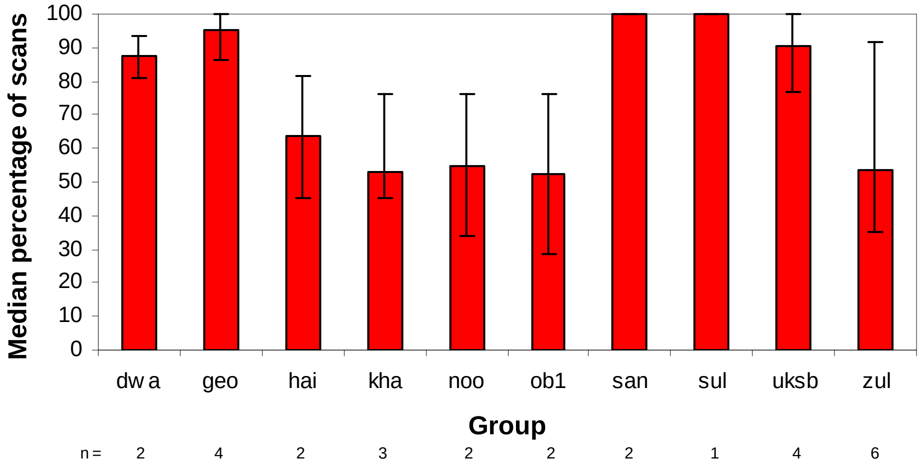


Figure 4.3. Median percentage of scans spent in contact with the mother for infants in each group. $N_{TOTAL} = 28$.

It was difficult to separate the effects of differently aged infants within the age class, and insufficient numbers of infants were present in each group to test for differences within age category. The high values of 100% of time in contact with the mother were found in groups with the fewest number of older infants, such as Sul, with only one infant born during the study period; San, with two infants born during the study, and Geo, with four infants, all under 1 year of age at the start of the study. Groups were split into two categories: those containing "older" infants (over 18 months) for at least half the study period (Dwa, Kha, Noo, Zul; 13 infants overall), and those not (Geo, Hai, OB1, San, Sul, UKSB; 15 infants overall). Eighteen months was chosen since infants seemed to show the first big decrease in time spent in contact with the mother shortly after this age (see **Figures 4.1** and **4.2**). The median percentage of time that infants spent in contact with the mother was then compared between the two categories of groups, but no significant results were found ($U = 65.0$, $N_{older\ infants}$,

$_{\text{no older infants}}$ = 13, 15, *P* = 0.120), although in groups without older infants, slightly more time was spent in contact with the mother. Thus, it appeared that the group composition, and the presence or absence of increasingly independent infants did not affect the percentage of time which infants spent in contact with the mother.

4.2.4. Parity of the Mother

The previous maternal experience of the mother has been found to influence the maternal behaviour of primates in a number of studies (e.g., Hooley & Simpson, 1981; Brown & Dixson, 2000; Maestripieri & Carrol, 1998; Nakamichi et al., 2004). In this study, there were no known primiparous mothers of juveniles, so analyses are limited to infants. Ten infants had mothers who were impossible to assign as primiparous or multiparous: this section does not deal with these infants. Fourteen mothers in the population were known to be multiparous. In some cases, previous infants had died before becoming juvenile (n = 6), and in others, the previous offspring was still alive (n = 8). The loss of an infant may have affected a mother's treatment of her next offspring, for example, she may have shown more attentive and restrictive behaviours to increase its likelihood of survival (e.g., Brown & Dixson, 2000), and consequently, mother-offspring contact may have been prolonged. The percentage of time spent in contact with the mother was compared between infants of mothers whose previous infants had died, and infants of mothers whose previous infants had survived. No difference was found (*U* = 20.0, n = 14, *P* = 0.604). Consequently, infants were divided into two categories: multiparous (n = 14) and primiparous (n = 4) mothers. Although there was a slight tendency for infants of multiparous mothers to spend less time in contact with the mother, no significant effect of parity on the amount of contact between mothers and infants was found (**Figure 4.4**: *U* = 17.0 n = 18, *P* = 0.238). The reproductive history of a mother was therefore not found to influence contact between mothers and infants.

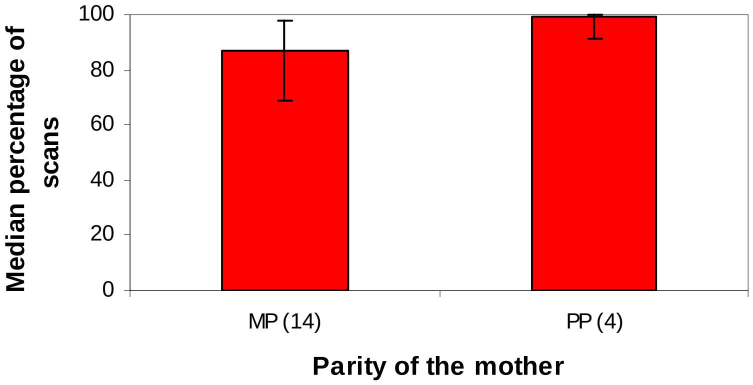


Figure 4.4. Influence of the parity of the mother on the percentage of scans that infants spent in contact with their mother. MP = multiparous, PP = primiparous. Numbers in parentheses indicate the sample sizes.

4.2.5. Break Of Contact

Ten individuals were observed to break contact with their mothers for the first time in the bai during the study. Of these ten, nine were males, and only one was female, therefore, data must be interpreted cautiously as the effects of sex could not be ruled out. The first break of contact between a mother and her offspring was observed in the bai at a median age of 164.5 days (5.9 months): n = 10, range: 3.7-10.2 months (**Figure 4.5**).

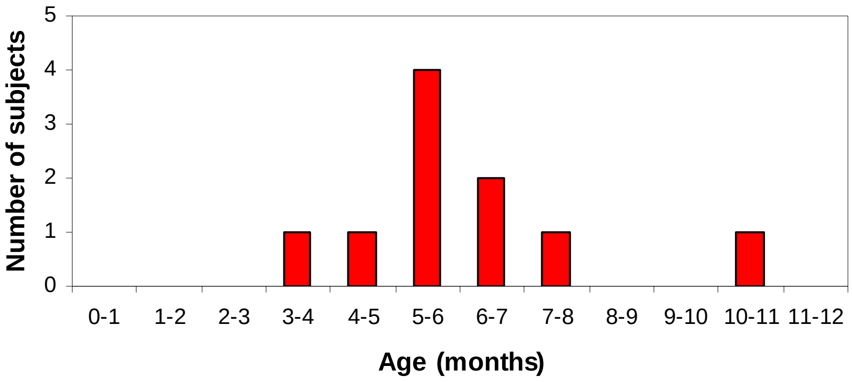


Figure 4.5. Ages at which study subjects first broke contact with their mothers in the bai.

The individual (Kojak) observed first breaking contact at 286 days was considerably older than the others. Kojak was observed in the bai when aged 149 days, but then not again until the age of 286 days. It was assumed that the first break of contact would have been recorded earlier had Kojak been observed during this interval. The median age calculated without the value of 286 days was 164 days, or 5.5 months (range: 3.7 – 6.5 months), so this outlier had very little effect on the median value. The limitations of a bai study in determining dates with accuracy are apparent here – in most cases, the first break of contact between a mother and her offspring would have almost certainly been recorded at an earlier age had visits to the bai been more frequent or longer. **Table 4.1** presents the age of infants on the last full contact day and the first break of contact day to estimate how large any potential errors may be. 63.6% of all ages obtained for the first break of contact fell within one month of each other, and the majority of individuals in this section were not absent from the bai for more than 2 months. Five and a half to six months of age seemed, therefore, a good representation of the age at which contact between a mother and her offspring was first broken in a bai environment. This age was slightly older than the values obtained previously for mountain gorillas by Stewart (1981) (5 months), and Fletcher (2001) (4 to 5 months), but was likely to be a consequence of the bai environment.

It was not possible to test the effect of parity on the age at first break of contact due to small sample sizes. There were no differences between groups (seven groups with one to three individuals in each) in the age at which infants were observed to break contact with their mothers ($\chi^2 = 5.030$, d.f. = 6, $P = 0.540$). Only one female infant (Jola) was observed to break contact with her mother for the first time (at the age of 182 days, compared to a median of 163.5 days for males) so analyses could not be conducted on the effects of sex on the age at first break of contact.

Table 4.1. Ages on last full day of contact with the mother in the bai, first day where break of contact was observed in the bai, and length of the intervening period for each individual.

Individual	*Age on last full contact day (months)*	*Age on first break day (months)*	*Interval in days (months)*
Lando	3.5	3.7	6 (0.2)
Piment	5.4	5.9	13 (0.5)
Howsa	5.4	5.9	15 (0.5)
Hathi	4.7	5.3	16 (0.6)
Custer	4.9	5.6	18 (0.6)
Columbus	5.6	6.4	24 (0.9)
Jola	5.5	6.5	28 (1.0)
Fang	2.8	4.3	42 (1.5)
Kojak	5.0	10.2	147 (5.3)
Clyde	-	5.8	-
Hitchcock*	0.5	7.3	190 (6.8)
Sherlock*	5.6	12.4	190 (6.8)
Marple*	6.8	13.5	190 (6.8)
DO(Agatha)**	3.4	-	-
Toomai §	6.7	-	-
Likouala §§	9.4	-	-

* Data not used for calculating median values given the long absence between observations.

** DO(Agatha) last observed aged 3.4 months

§ Toomai was a surviving twin who appeared under-developed for his age, and has since died (Nowell et al., subm.)

§§ Likouala was seen independent in the forest, but not in the bai.

4.2.6. Latency to Independence

The latency to independence was the period of time taken by offspring who entered the bai in contact with their mothers, to break contact and move independently from them. Again, this was thought to reflect the increasing independence of offspring, with individuals moving independently more quickly after entry to the bai as they increased in age. Before the age of 12 months, the majority of offspring entering in contact with their mothers remained in contact throughout the visit (see also **Figure 4.1**), therefore, no median latency values were calculated below this age. After this age, there was a significant negative correlation between age category and the latency to independence (**Figure 4.6**: $r_s = -0.933$, n = 10, $P = 0.0001$).

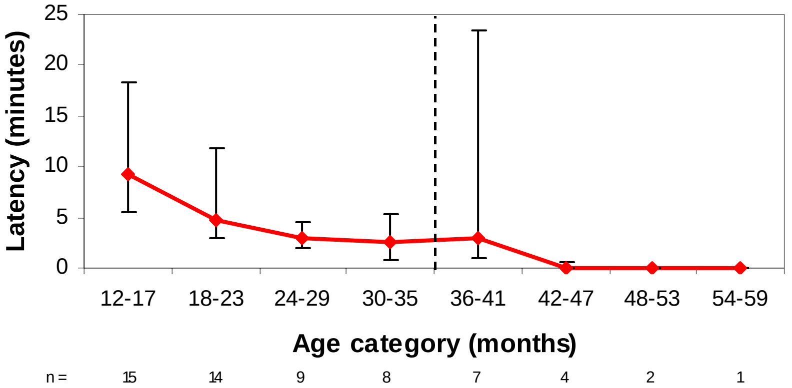


Figure 4.6. Median latency to independence and its relationship with increasing study subject age. $N_{\mathrm{TOTAL}} = 27$.

When gorillas entered the bai during rain, or after a storm, infants often seemed to take longer to break contact with their mothers. To test this, all occurrences on which offspring entered the bai when the weather was cold and rainy and then broke contact with the mother were extracted from the data. A median latency to independence was calculated for each of the individuals in whom this occurred (n = 11). These medians were then tested against medians from normal weather from the same individuals over the same age range (9 to 45 months) in which they had experienced the cold, wet weather. Results showed that offspring did spend longer in contact with the mother after entering the bai in cold, wet weather than they did in warm weather (**Figure 4.7**: $Z = -2.803$, n = 11, $P = 0.005$), suggesting the importance of the mother in helping offspring, even those who were juveniles, to maintain a constant body temperature.

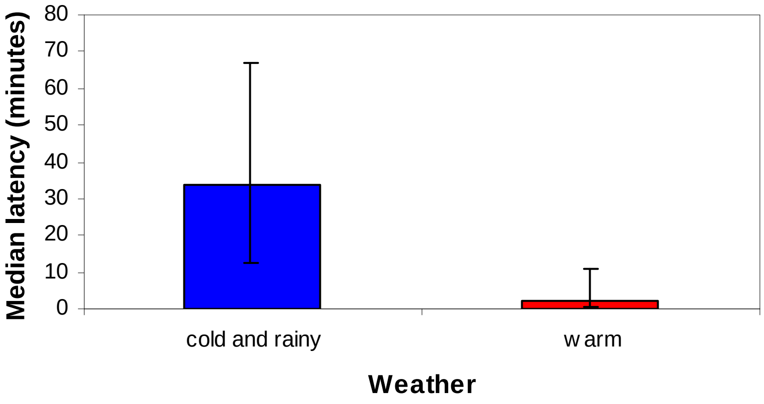


Figure 4.7. Differences in the median latency to independence for subjects observed to break contact with their mother in cold and wet conditions and in normal, warm conditions. $N_{TOTAL} = 11$.

4.3. SPATIAL PROXIMITY TO THE MOTHER

As infants moved out of contact with the mother, more time was spent at further distances from her (within 2m of the mother, 2-5m, 5-10, or 10m plus). As with contact between a mother and her offspring, the data for this section were taken from the scan samples and medians calculated for age categories as described previously.

Although it was desirable to analyse patterns of proximity maintenance between mothers and offspring, only five study subjects were observed to move to within, or further than 5m from the mother during the study, resulting in too few data to provide meaningful analyses.

4.3.1. Effect of Age on Proximity

There were significant positive correlations between age category and the median percentage of scan samples that study subjects spent 2-5m, 5-10m and 10m plus from the mother, but not for the percentage of scans within 2m, which initially increased during infancy before decreasing throughout the rest of the immature period (**Figure 4.8**, **Table 4.2**). Time in contact with the mother was gradually replaced by time spent within 2m. Juveniles and sub-adults then moved to distances of further than 2m from the mother as their independence increased.

The relationship between age category and the percentage of scans spent in each proximity category was investigated within age classes (infant, juvenile or sub-adult) to determine when changes in proximity patterns took place. During infancy, there were significant positive correlations with age category in the median percentage of scans spent within 2m of the mother ($r_s = 0.943$, n = 6, $P = 0.005$), 2-5m of the mother ($r_s = 0.941$, n = 6, $P = 0.005$), and at 5-10m from the mother ($r_s = 0.845$, n = 6, $P = 0.034$). After infancy, proximity to the mother did not change: no significant correlations between age category and the percentage of scans spent at any of the distance categories from the mother were found, and juveniles and sub-adults spent most of their time further from the mother than they did during infancy. Time spent at a distance of greater than 10m from the mother was very variable during the juvenile period, with individual medians for the 6-month age categories ranging from 0 to 66% of time. During sub-adulthood, time spent in all proximity classes showed little variance with age category, and most time was spent at a distance of more than 10m from the mother.

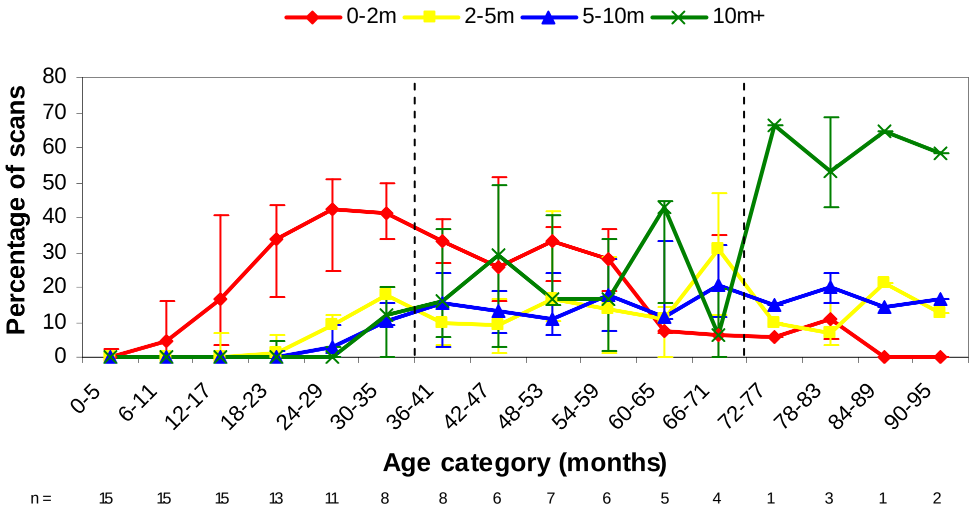


Figure 4.8. Spatial proximity between offspring and their mothers. $N_{TOTAL} = 42$.

Table 4.2. Results of Spearman rank correlations between age category and spatial proximity to the mother.

Distance	r_s	***N***	***P***
0-2m	-0.339	16	0.198
2-5m	0.646	16	0.007
5-10m	0.830	16	< 0.0001
10m+	0.892	16	< 0.0001

4.3.2. Effect of Sex on Proximity

There was no effect of sex on the proximity of infants or juveniles to their mother in any of the age categories (**Figure 4.9**). In some age categories there seemed to be difference between the sexes, but these were probably attributable to small sample sizes. Insufficient data were available to test for differences in proximity to the mother with sex for sub-adults.

4.3.3. Effect of Group on Spatial Proximity

Tests were conducted to determine whether differences existed between the groups in spatial patterning with the mother. There were between one and six subjects in each group. Data were analysed using Kruskal-Wallis tests to investigate differences between groups in the percentage of time that infants and juveniles spent in each proximity class from their mother, but no differences were found. Insufficient data were available to test for differences among sub-adults.

4.3.4. Parity of the Mother

Analyses investigating the effect of the mother's parity on spatial patterning were limited to infants, but no differences were found in the median percentage of time that infants spent at any of the distance categories to the mother as a result of the mother's reproductive history.

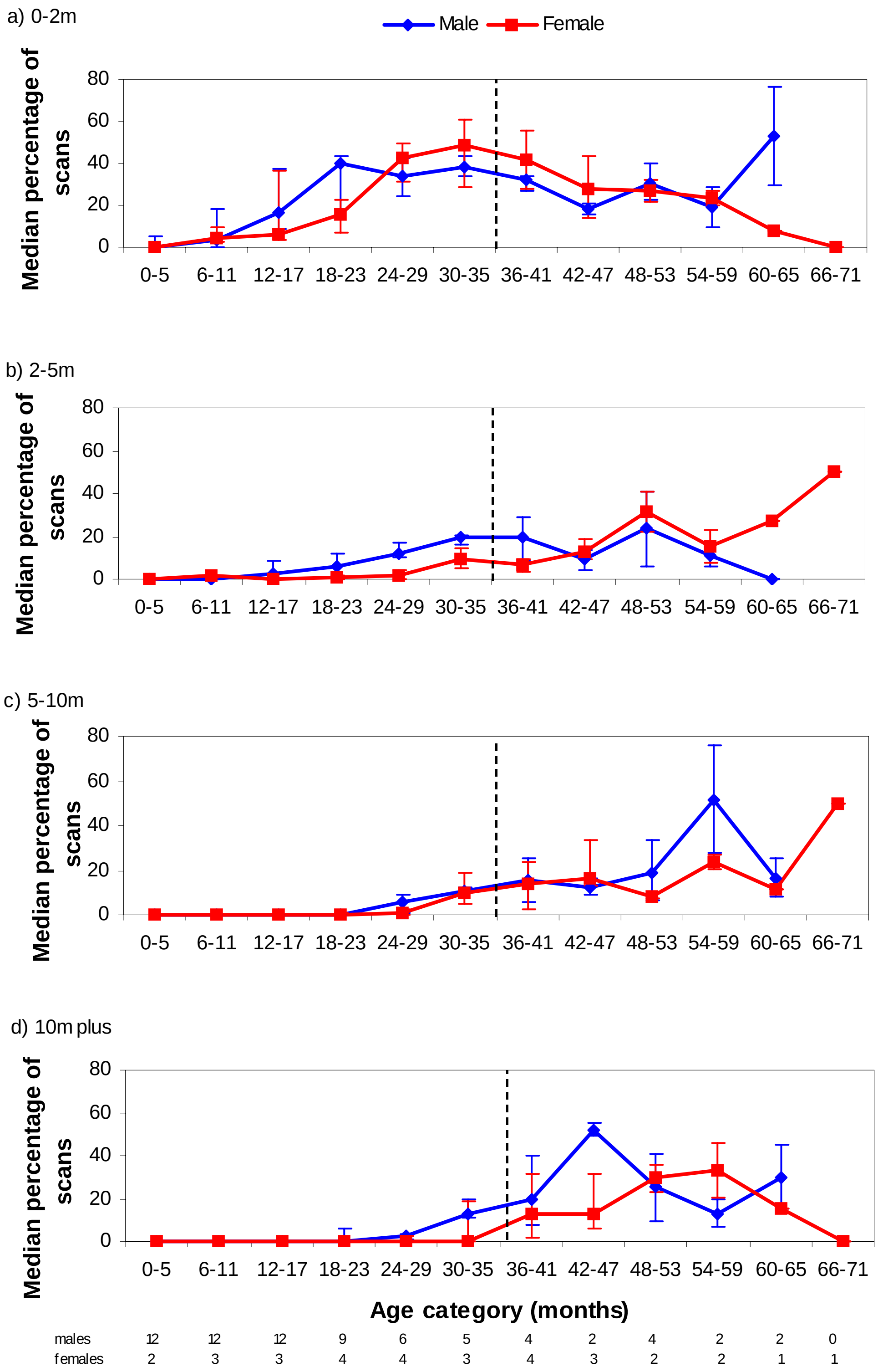


Figure 4.9. Comparisons between the sexes in the percentage of scans spent within a) 2m, b) 2-5m, c) 5-10m, and d) 10m plus from the mother. $N_{\text{males, females}} = 25, 11$.

4.4. SUCKLING AND WEANING

In addition to changes in spatial relationships between mother and offspring, patterns of suckling, and weaning also provide clear signs of increasing independence from the mother (Stewart, 1988; Fletcher, 2001). Data used in this section were collected using all-occurrence sampling, and 578 suckling bouts were recorded. Where possible, all positions of the offspring during the suckling bout were recorded, as were the start and end time of the bout to the nearest second. Not all data were available for all suckling bouts, e.g., it was not always possible to observe initiations and terminations of bouts due to the mother blocking the view or subjects entering or exiting during bouts. Such suckling bouts contributed data towards the calculation of suckling rate (bouts per hour), but not duration of suckling or bout length.

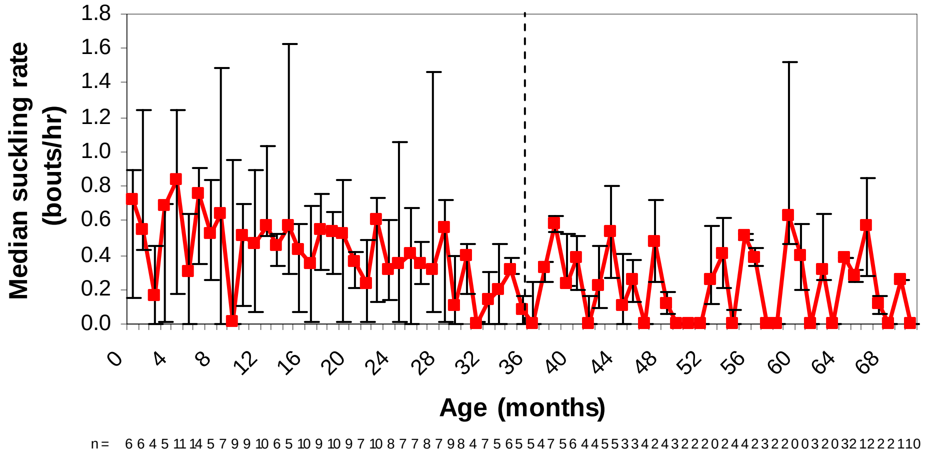
The rate of suckling was calculated for each individual by dividing the number of suckling bouts by the number of hours they were observed during each age. If subjects visited the bai more than once at a certain age, then a median rate was calculated from the different visits to give a value for that age. A median value was calculated for each age from these individual values. The duration of suckling per hour was calculated for each individual by taking the total time an individual was observed suckling at each age and dividing by the time spent in the bai. Medians were then calculated from these individual values to obtain a value for each age category. Data were used only from individuals when accurate durations were recorded of all suckling bouts at each age. Bout lengths were calculated by taking a median value from each subject at each age, and then a median from those values to give a representative figure for each age.

Only individuals who were observed to suckle during the study period were included in analyses. No suckling was observed after 69 months of age, therefore, analyses did not continue past this age.

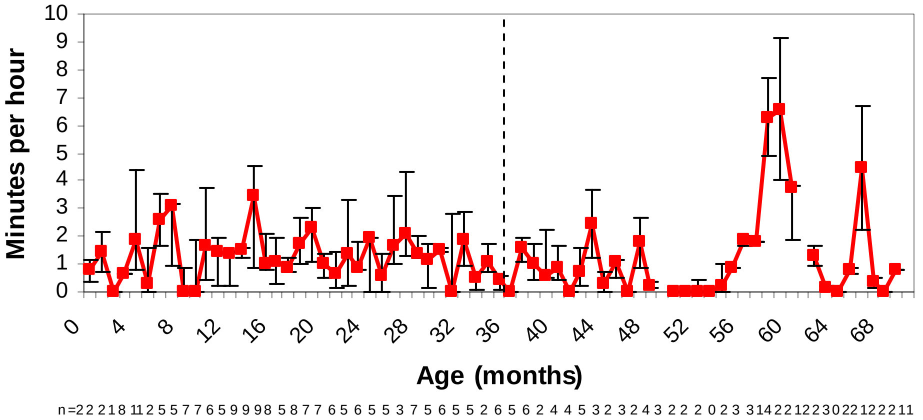
4.4.1. Effect of Age on Suckling

Suckling rate was significantly negatively correlated with age (**Figure 4.10a**: $r_s = -0.446$, n = 66, $P < 0.0001$), although there was much variation in the data, particularly during the juvenile period. Neither the duration of suckling per hour (**Figure 4.10b**: $r_s = -0.203$, n = 66, $P = 0.102$) nor the bout length (**Figure 4.10c**: $r_s = -0.093$, n = 62, $P = 0.471$) was significantly correlated with age, and again, much variation was evident. In both cases, the highest values were recorded towards the end of the juvenile period. The major change in the nature of suckling occurred in the frequency of bouts, and occurred during infancy ($r_s = -0.556$, n = 36, $P < 0.0001$).

a) Rate of suckling (bouts per hour). $N_{TOTAL} = 39$



b) Duration of suckling (minutes per hour). $N_{TOTAL} = 39$



c) Bout length (seconds). $N_{TOTAL} = 35$

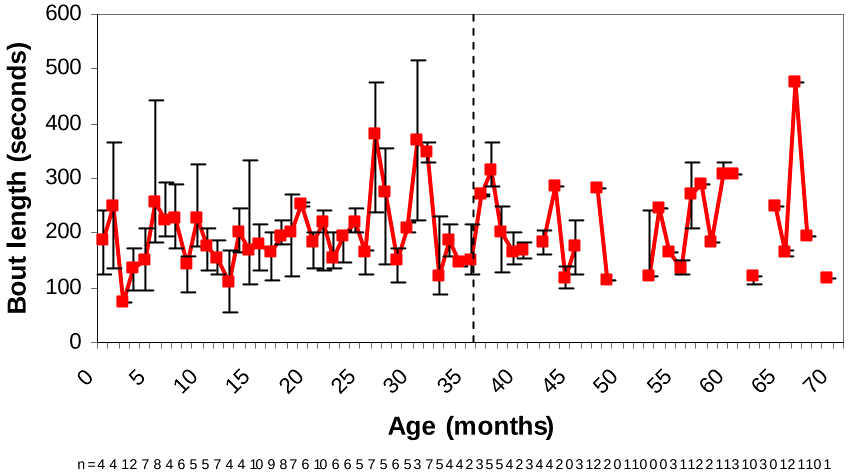
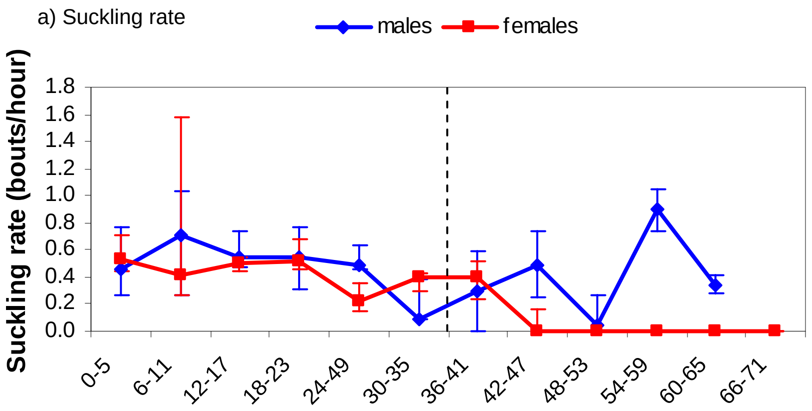


Figure 4.10. a) Suckling rate, b) duration of suckling per hour, and c) bout length for immature study subjects, and changes with increasing age.

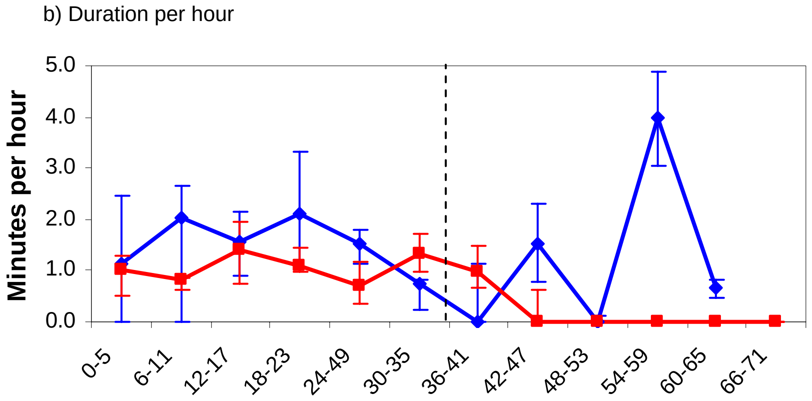
4.4.2. Effects of Offspring Sex, Group and Parity of the Mother on Suckling

Offspring sex, group and parity of the mother did not affect the rate, duration or bout length of suckling. Tests compared values within age classes, and matched for age category to combat the effects of age within an age class, given the significant correlation of age with suckling rate during infancy. Although non-significant results of tests between males and females showed that rate, duration and length of suckling bouts was similar between the sexes (**Figure 4.11**), midway through the juvenile period, both males sampled between 4.5 – 5 years of age showed marked peaks in all suckling parameters that were not present in females. In general, suckling decreased to zero at an earlier age in females than in males. Due to a smaller numbers of females than males, results must be interpreted with caution, however, these results were interesting since they were consistent with the theory that mothers may invest more heavily in male offspring in an attempt to increase their own inclusive fitness (e.g., Trivers, 1972; Hewison & Gaillard, 1999).

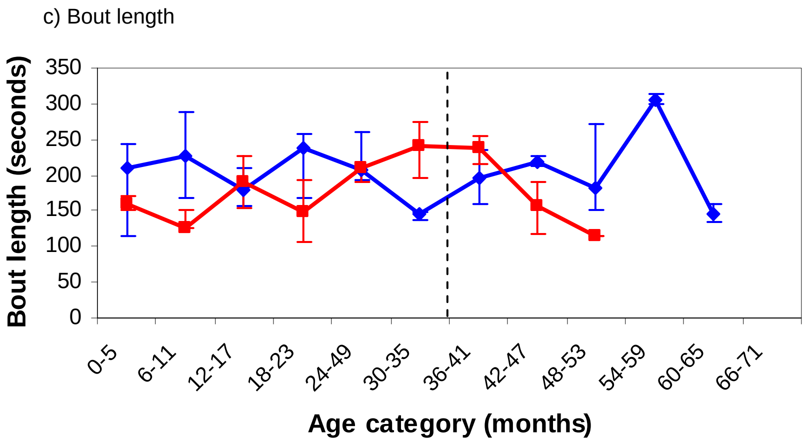
Considerable variation existed between groups in suckling rate, duration and bout length (**Figure 4.12**). Sample sizes are too small for statistical testing, and apparent differences probably highlight individual variation rather than real differences between groups.


a) Suckling rate

males:	12	12	11	10	6	5	4	2	4	2	2	0
females:	3	4	4	4	4	3	4	3	2	2	2	1


b) Duration per hour

males:	9	9	11	10	6	5	3	2	4	2	2	0
females:	3	3	4	4	3	3	4	3	2	2	1	1


c) Bout length

males:	11	11	11	10	6	5	3	2	3	2	2	0
females:	2	3	4	4	3	3	4	3	1	0	0	0

Figure 4.11. Comparisons between males and females in a) suckling rate, b) duration per hour, and c) bout length.

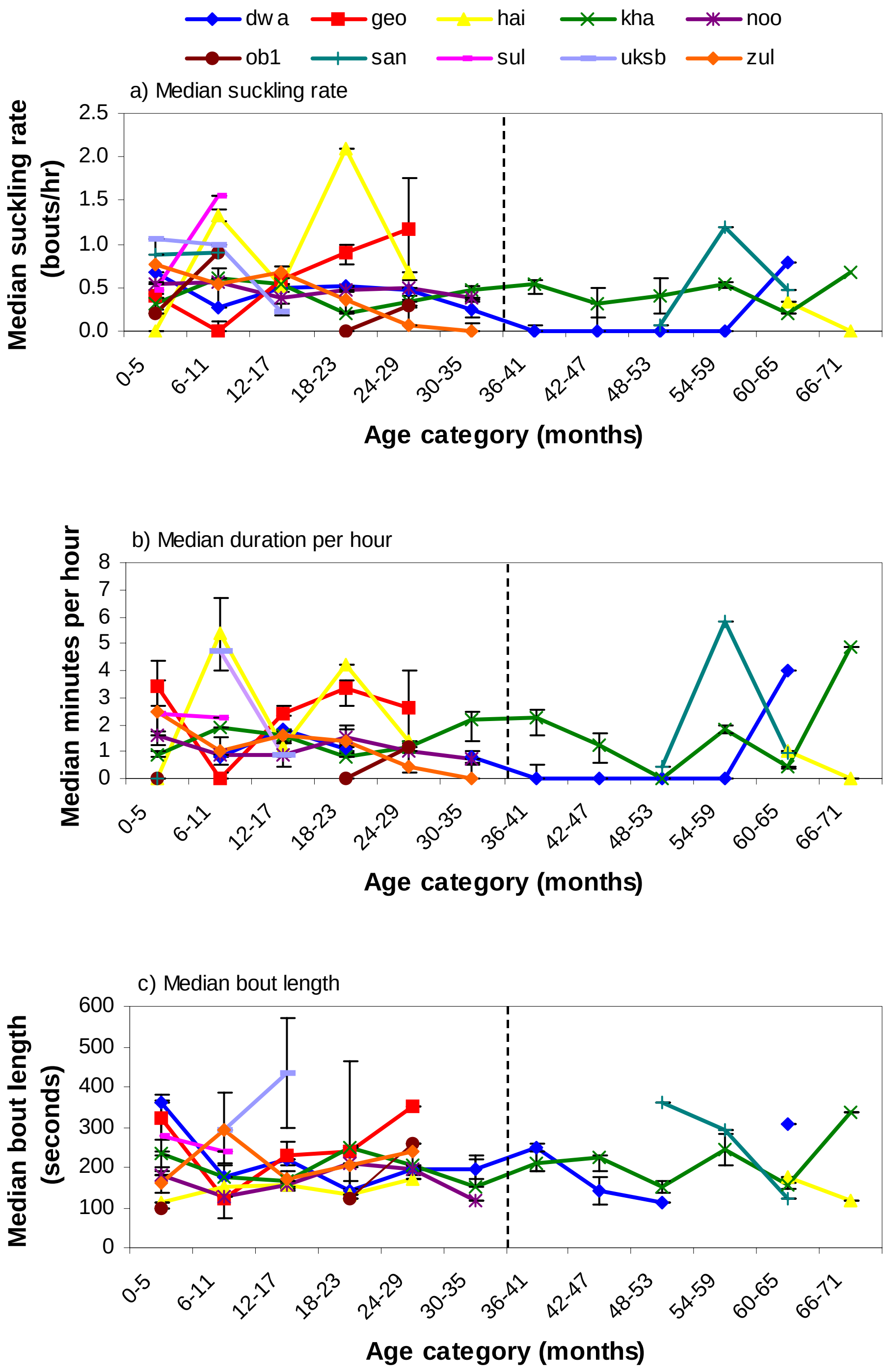
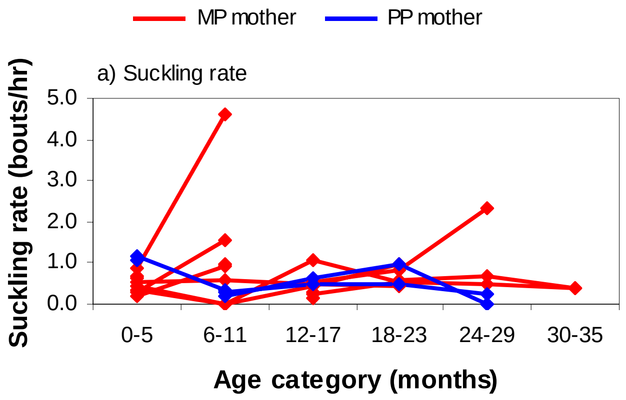
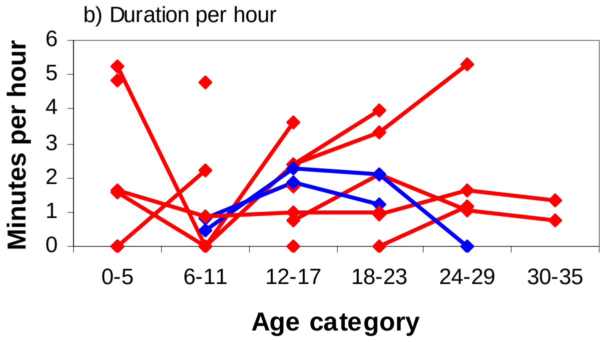


Figure 4.12. Comparisons between groups in a) median suckling rate, b) median duration per hour, and c) median bout length.

Parity of the mother had no effect on an infant's rate, duration or bout length of suckling (**Figure 4.13**), with infants of primiparous mothers (three infants of primiparous mothers were observed to suckle) falling, for the most part, well within the range of those for infants of multiparous mothers. The more extreme outliers were contributed by offspring of multiparous mothers, but none of whom were considered to be particularly old or young mothers.


a) Suckling rate


b) Duration per hour

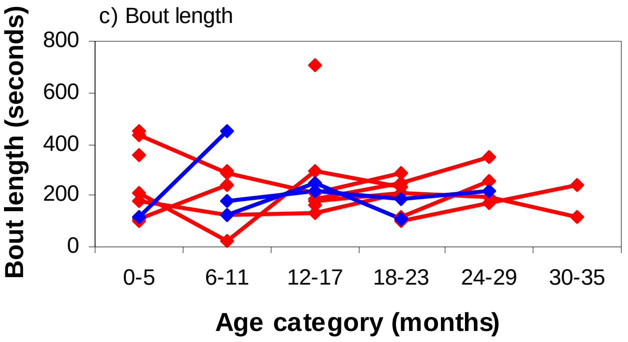

c) Bout length

Figure 4.13. Influence of mother's parity on a) median suckling rate, b) median duration per hour, and c) median bout length. Each series represents one individual. MP = multiparous, N = 14; PP = primiparous, N = 3.

4.4.3. Termination of Suckling Bouts

Parent-offspring conflict theory states that offspring are selected to demand more than parents are selected to provide (Trivers, 1974), therefore, mothers were predicted to be responsible for weaning, and begin to terminate or reject their offspring's attempts to suckle to allow investment in subsequent offspring (e.g., Trivers, 1974; Stewart, 1981; Fletcher, 2001). The following analyses considered all suckling bouts when the individual terminating the bout could be identified with confidence. Of these bouts (78.5% of the total suckling bouts), only 10.4% were clearly terminated by the mother, mainly as a result of the mother changing position while her offspring suckled or attempted to, crossing her arms in front of her so that her breasts were no longer accessible to the offspring, or by biting or pushing the offspring away from her or onto her back, and was sometimes accompanied by cough grunts from the mother. One temper tantrum was observed in response to the termination of a suckling bout by the mother. The median percentage of bouts in which the mother clearly terminated a suckling bout was calculated for each individual in each age category, and these individual values were then used to give an age category median (**Figure 4.14**). It was clear that mothers began to terminate suckling bouts with increasing frequency as their offspring reached 42 months (3.5 years) of age. Termination of bouts was most common at 48-53 months (4 – 4.5 years) of age. After this age, the frequency with which mother terminated suckling bouts decreased to 0 at 60-65 months (5 – 5.5 years), as fewer and eventually no subjects suckled past the age of 69 months. In addition, there was little evidence that high rates of suckling terminations during the juvenile period were attributable to particular mother-offspring dyads, as the majority of mothers terminated suckling bouts during this period (**Figure 4.15**).

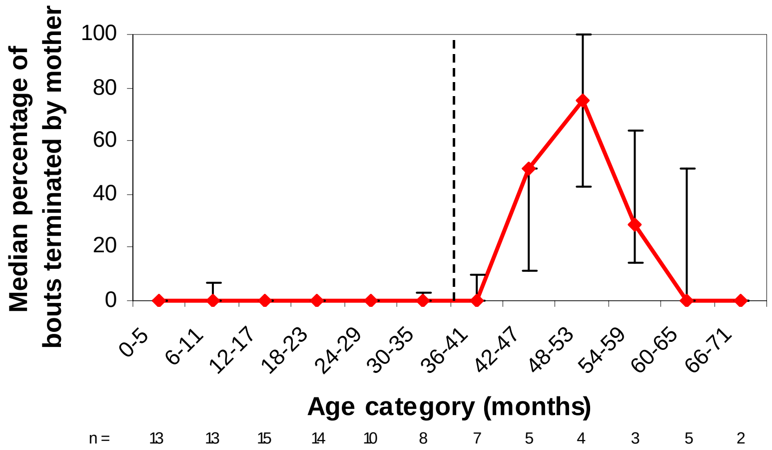


Figure 4.14. The median percentage of suckling bouts terminated by the mother in each age category. N_{TOTAL} = 37.

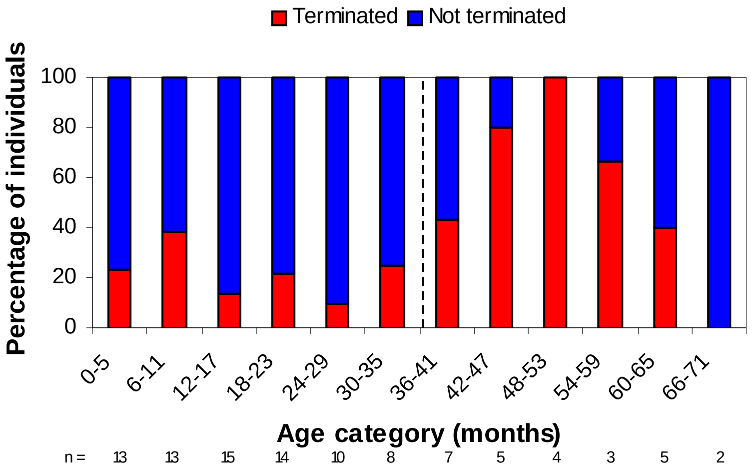


Figure 4.15. The percentage of individuals who suckled and had bouts terminated by the mother in each age category. N_{TOTAL} = 37.

Prior to weaning, all but one (Ike) of the six subjects who were observed to suckle for the last time, had at least half of his/her suckling bouts terminated by the mother during the age category, or the previous age category to the one in which they were weaned (**Figure 4.16**). The mother of Ike appeared old, and this was suggested as the reason for her tolerance of Ike's suckling (see van Lawick-Goodall, 1971a).

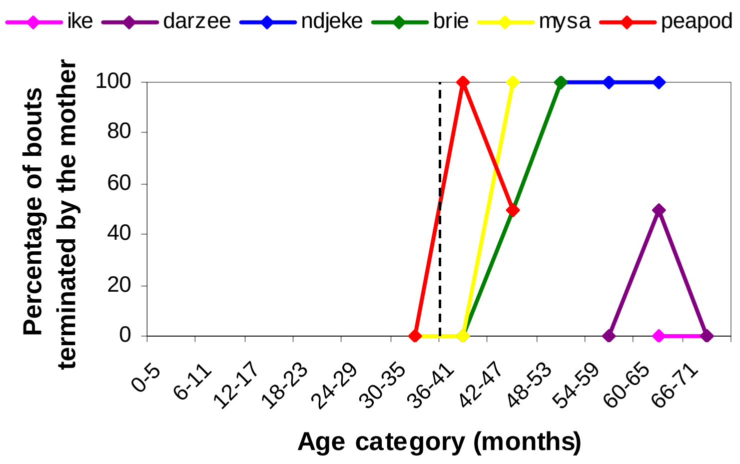


Figure 4.16. Termination of suckling bouts by the mother, prior to weaning. The end point of each series was the age category in which an individual was last observed to suckle.

When the percentage of terminated suckling bouts of subjects who were weaned during the study was compared to those who were not weaned (**Figure 4.17**) there was a clear difference, although high rates of terminations were also seen in three infants. An overall median 20% of suckling bouts were terminated for those who were weaned; 0% for those not weaned. Subjects who were weaned during the study had significantly more suckling bouts terminated ($U = 39.5$, $N_{\text{unweaned, weaned}} = 30, 6$, $P = 0.019$). This analysis does not account for differences in age, and sample sizes were too small to perform matched tests within age categories, however, the figure suggests that in most cases, weaning was preceded by a high rate of suckling terminations by the mother.

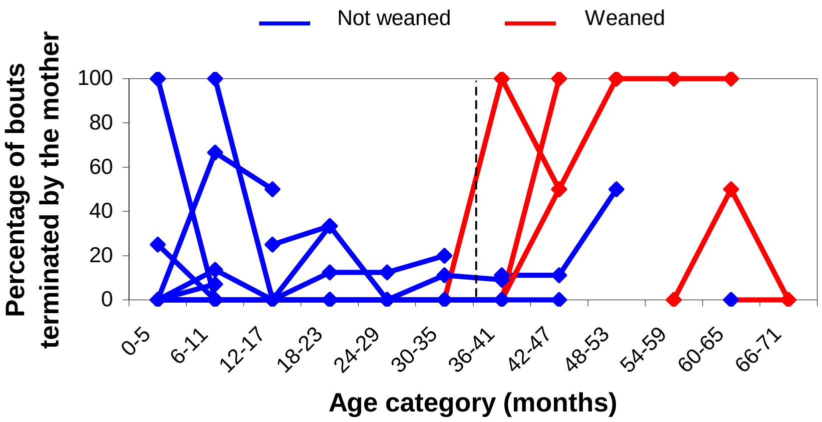


Figure 4.17. Comparison of the percentage of suckling bouts terminated by the mother for study subjects that were weaned during the study and those that were not. $N_{\text{unweaned, weaned}} = 30, 6$.

4.4.4. Weaned Individuals

Individuals who were not observed to suckle (n = 5) during the course of the study were assumed to already be weaned, and were aged between 44 and 86 months. Those observed to suckle for the last time were aged between 44 and 69 months when last seen suckling. Of these latter six subjects, all were subsequently observed (within two and a half months) in the bai and did not suckle. **Table 4.3** represents the pattern of suckling in the six individuals assumed to have been weaned during the study.

Table 4.3. Patterns of suckling and bai visitation in individuals weaned during the study. Each symbol represents a visit, and cells should be read from left to right. Note that the age column is not continuous.

● Previous visit observed suckling ▲ Visits not observed suckling
■ Final visit seen suckling

Age (months)	Mysa	Peapod	Brie	Ndjeke	Darzee	Ike
42	●	● ▲				
43						
44	■ ▲	▲ ▲				
45	▲	▲ ■				
46	▲	▲	●			
47		▲ ▲				
48			▲ ■			
49						
50						
51			▲ ▲			
52			▲			
59				●		
60						
61						
62				■		
63						
64				▲		
65						
66						
67					● ■	● ▲ ▲
68					▲	▲ ▲
69						▲ ■
70						
71						▲
72						▲
76						▲

4.4.5. Suckling Positions

The position in which individuals suckled was predicted to reflect their stage of development, and also give an indication to the extent to which a mother modified her behaviour in order to accommodate suckling by her offspring. Positions were categorised as:

- Supported ventral: mother supports her offspring with one or both arms while it suckles. The mother may be seated or standing.
- Cling ventral: the offspring clings to the mother's ventrum, unaided, while she stands quadrupedally.
- Sit: the offspring sits unsupported in the lap of the mother to suckle (**Plate 4.1**).
- Stand: the offspring stands quadrapedally or bipedally in front of the mothers' ventrum to suckle. The mother may be seated or standing.

Offspring suckled in more than one position in 153 out of 575 suckling bouts (26.6%). These bouts were removed from the sample, as the duration of suckling in each position was not recorded. A modal suckling position was calculated for each 6 month age category (calculated from individual modal positions). In all age categories up to and including 24-29 months, cling ventral was the most common suckling position. After this age, standing was the most commonly observed suckling position.

For each subject, the percentage of suckling bouts in each position was calculated, and then used to create a median percentage of suckling bouts in each position for each age category (**Figure 4.18**). The percentage of ventrally supported suckling bouts resulted in a median value greater than 0 only in the 0-5 month age category, and was recorded in only four individuals on five occasions in subjects older than 5 months. The percentage of suckling bouts in which subjects suckled while clinging ventrally was negatively correlated with age category ($r_s = -0.885$, $n = 12$, $P < 0.0001$). Bouts in which subjects sat in the mother's lap to suckle were also negatively correlated with age category ($r_s = -0.785$, $n = 12$, $P = 0.002$), although this category was most likely to be influenced by maternal behaviour and position. Finally, the percentage of standing suckling bouts was positively correlated with age ($r_s = 0.905$, $n = 12$, $P < 0.0001$), suggesting that as offspring increase in age, mothers are less likely to modify their behaviour in order to accommodate suckling.

Plate 4.1. Billie suckling while sitting in the mother's lap (photo by Richard Parnell).

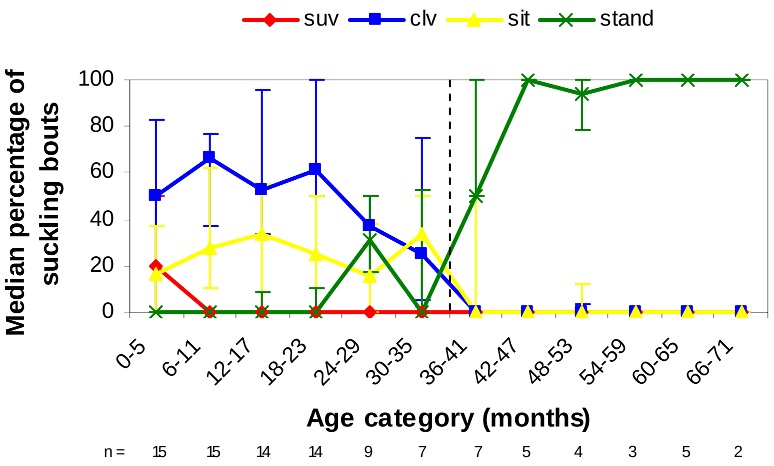


Figure 4.18. The median percentage of suckling bouts in which each position was observed in differently aged individuals. Suv = supported ventrally, clv – clinging ventrally. N_{TOTAL} = 38.

4.5. THE DEVELOPMENT OF TRAVELLING BEHAVIOUR

In this section, "travel behaviour" included all movement by immatures, regardless of whether it was dependent or independent from the mother. As with suckling position, the mode of travel used by immatures was predicted to reflect the physical development and increasing dependence of offspring, and give an indication of the extent to which mothers invested in their offspring (i.e., supporting infants ventrally requires a higher level of investment and greater behavioural modification by the mother than when infants cling ventrally).

4.5.1. The Ontogeny of Travelling Behaviour

The positions in which immatures travelled included supported ventral and cling ventral, both of which were used previously to describe suckling positions. In addition, the following were also used (**Plate 4.2**):

- Arm cling: clinging to the arm of the mother, with legs and arms wrapped around the mother's arm.
- Dorsal: sitting on, or clinging to the mother's back.
- Rump cling: grasping the rump of the mother and walking bipedally.
- Independent: out of contact with the mother.

Arm and rump clinging were observed infrequently and rarely recorded in focal or scan samples, so were not included in the analyses in this section. **Table 4.4** provides details on the ontogeny of travel behaviour for each of the other four methods of travel, and the percentages of individuals who engaged in each type of travel behaviour are illustrated in **Figure 4.19**. Data were taken from scan samples.

Table 4.4. Details of the age at which each travelling method was first and last observed, and the modal age of individuals using the method. Ages are in months. The number of individuals observed to travel during scan samples = 56.

Position	***Age first observed***	***Age last observed***	***Modal age***	***No. individuals involved***
Supported ventral	0	25	1	4
Cling ventral	1	21	4	11
Dorsal	3	44	18	21
Independent	11	-	80	42

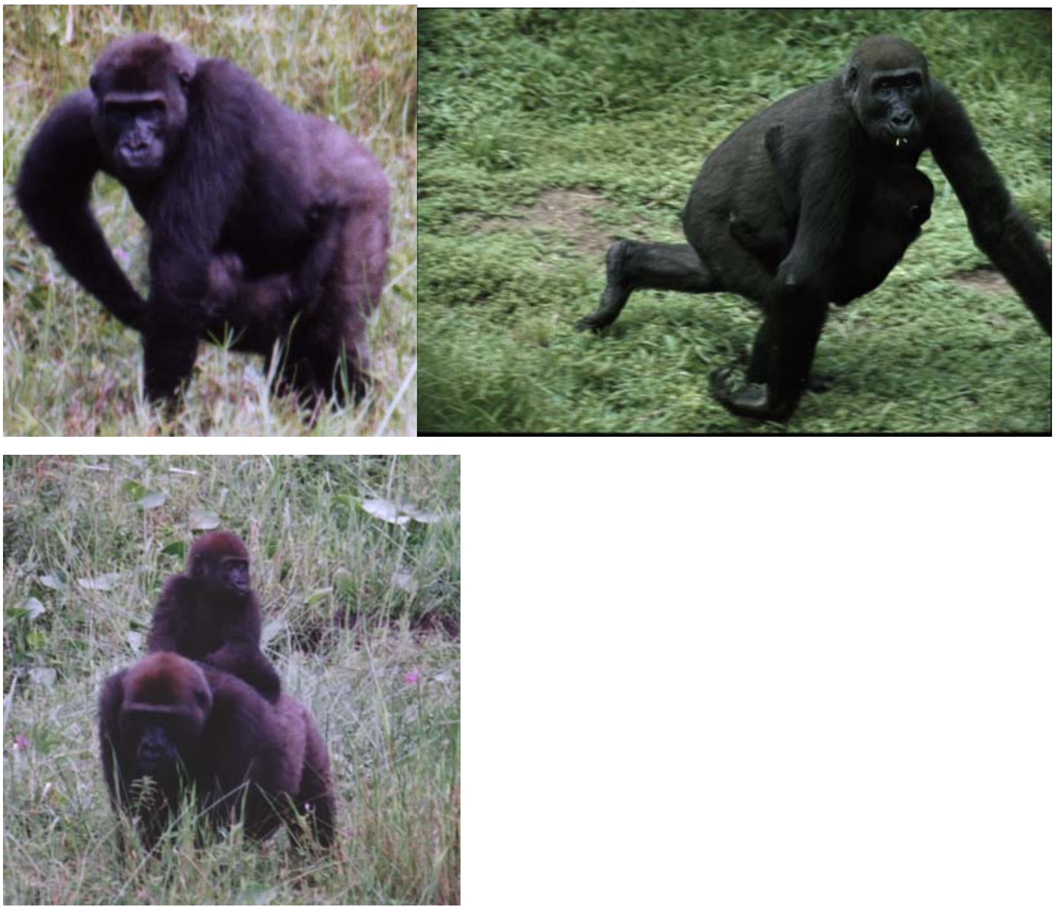


Plate 4.2. Fleur supporting Fig ventrally (top left), an adult female with infant clinging ventrally (top right, photo by Nick Nichols, taken at Maya Nord, Odzala National Park), and Sage dorsal on Salmonberry (bottom).

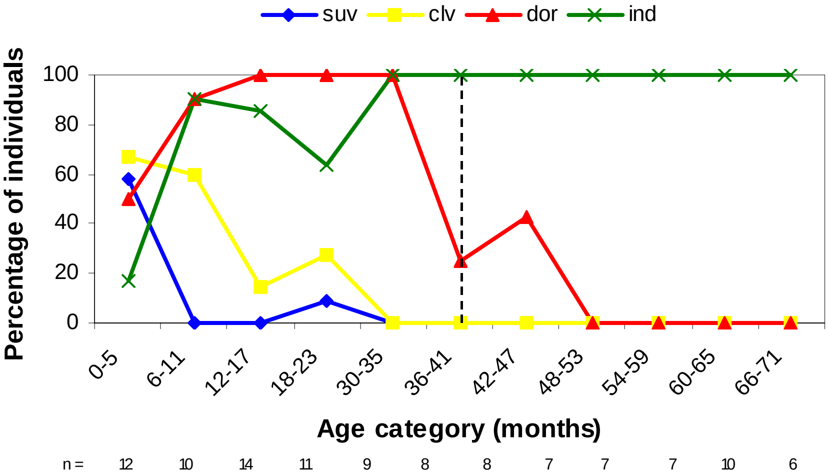


Figure 4.19. Percentage of individuals participating in each type of locomotion. N_{TOTAL} = 56.

All infants were present in the same group as the mother, so had the potential to travel dependently. Four out of 15 juveniles did not have mothers present in the same group, and one had a sibling born during the study period, resulting in 66.7% of juveniles being able to engage in dependent travel, however, only three individuals (20% of those that could) did so, the rest travelled independently.

When considering only individuals who were observed to travel during scan samples and who had mothers present in the same group (n = 36), there was a significant positive correlation between the median percentage of independent travelling bouts and age category (**Figure 4.20**: $r_s = 0.889$, n = 14, $P < 0.0001$). There was a transition period between the ages of 1 and 3 years where travel was as likely to be dependent as it was independent (although great variability between individuals was present between 12 and 24 months of age).

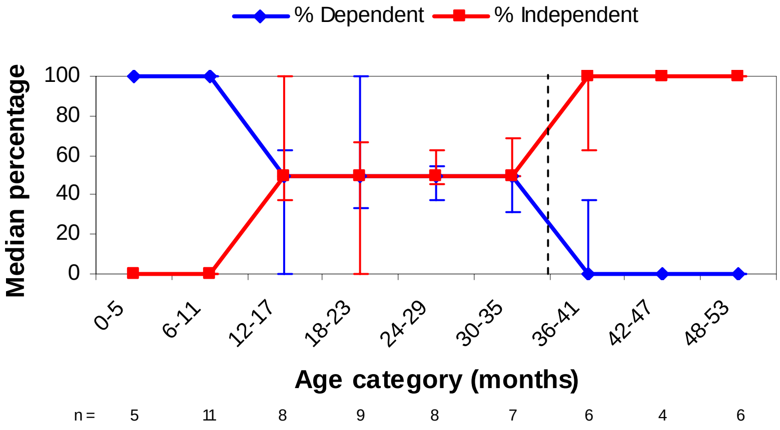


Figure 4.20. The median percentage of travel by individuals in each age category that was dependent or independent of the mother. $N_{TOTAL} = 36$.

4.5.2. Entry and Exit Positions

The effect of entering the bai and entering the forest on the travelling behaviour of study subjects was investigated to explore whether the bai was viewed as a threatening environment, as a result of its openness and potential for encountering other gorilla units. Mbeli Bai was a minor habitat type for the gorillas that visited it, and its unfamiliarity may have prompted a return to increased dependence on the mother when entering. If this was the case, it was hypothesised that subjects would adopt a less "mature" or more dependent method of travel when entering the bai than when exiting and returning to the more familiar forest environment. Locomotion during entry to and exit from the bai was similar to the ontogeny of travelling behaviour, with arm and rump clinging seen infrequently, and only when entering the bai.

Travel methods were ranked (in order of increasing maturity) as: supported ventrally, clinging ventrally, dorsal travel, and finally independent travel, based on results from analyses in the previous section, and also from results found in other studies on wild mountain gorillas (Fossey, 1979; Fletcher, 2004) and captive western lowland gorillas (Hoff et al., 1981a). Visits in which subjects entered the bai by arm or rump clinging were discarded, due to their infrequency and the difficulty with which these travel methods could accurately be ranked. Data were only used when the methods of travel used by study subjects for both entry to and exit from the bai were available. Additionally, only individuals who contributed entry and exit data from more than five visits during a 6 month age category were included to ensure that travel positions were not influenced by any unusual events. Consequently, data from 19 infants were used in this analysis.

An index was devised to conduct this analysis. Each visit in which a study subject entered using a more mature method of travel than they did upon exiting was given a score of +1; and each visit in which they entered using a less mature method of than they did upon exiting was given a score of –1. Visits where subjects entered and exited using the same method of travel was scored as 0. These scores were then added together for each individual in each age category, and then divided by the number of visits made during that age category in which entries and exits were recorded to give the final value. A negative index indicated that an individual was more likely to enter using a less mature method of travel than they did when exiting; a positive index indicated they entered more maturely than they exited. For example, Fang visited the bai ten times aged 0-5 months. On four occasions he exited more maturely than he entered, once he entered more maturely than he entered, and on the remaining five occasions he entered and exited using the same method of travel. Therefore, for Fang's index of travel maturity, aged 0-5 months, was calculated as follows:

$$\frac{1+1+1+1-1+0+0+0+0+0}{10} = \frac{3}{10} = 0.3$$

The positive value indicated that Fang was more likely to enter using a more mature travel method (e.g., dorsally) than he was upon exiting the bai (e.g., clinging ventrally) between the ages of 0-5 months, suggesting that the bai was not viewed as a more threatening habitat than the forest.

For each age category, a median index was calculated from the individual indices, and then correlated with age category (**Figure 4.21**), resulting in a significant negative correlation during infancy ($r_s = -0.880$, n = 6, $P = 0.021$). During the early part of infancy, study subjects were more likely to *enter* the bai using a more mature method of travel, whereas towards the end of infancy they were more likely to *exit* using a more mature method of travel. Of the subjects that entered either dorsally or independently and exited clinging ventrally, i.e., those exiting in a less mature way, and who tended to be younger, 58% of them (n = 11) were observed to suckle as they exited the bai. Of the subjects who entered travelling dorsally and exited independently, i.e., those exiting in a more mature way, and tending to be older, on 63% of visits, they (n = 12) exited into a tree on the bai edge at least 5 minutes before the mother departed. There was a great deal of variation and lack of consistency in the direction of index scores between individuals in each age category, as indicated by the interquartile ranges, and even within individuals' scores. It appeared as if the travel method used by study subjects when entering or exiting the bai was more a factor of subject age, rather than the bai. Younger subjects seemed constrained by their need to suckle, and older subjects exited before the mother, often into trees, made possible by their increasing independence. If, for example, the bai was a threatening place for study subjects to enter, a consistent index would have been expected, at least within individuals in each 6 month age category. Of the 15 individual indices that equalled 0 in various age categories, eight (53.3%) of the indices did so as a result of equal numbers of positive and negative values contributing to the final index score for the individual.

Figure 4.21. Median index of travel maturity for entry to and exit from the bai during infancy. $N_{TOTAL} = 19$.

4.6. INTERACTIONS BETWEEN MOTHERS AND OFFSPRING

4.6.1. Interaction Type: Frequency and the Effects of Age

An interaction was defined as any kind of *active behaviour directed from one individual to another*. A reaction from the recipient was not necessary for an interaction to be recorded. All interactions were recorded between mother and offspring dyads, and were divided into eight categories (**Table 4.5**).

Eight of the 43 study subjects (19 %) who were present in the same group as their mother did not engage in any active interaction with the mother throughout the study. The youngest subject observed to actively interact with its mother was 1 month of age, and the oldest, 80 months (median age at which interactions occurred with the mother: 18 months).

Table 4.5. Definitions of interaction types between mothers and offspring.

Interaction Type	***Definition***
Positive interactions	
Proximity seeking	One individual establishes contact with, or seeks the proximity of another, moving to within 2m of them without feeding or initiating agonism
Grooming	Manipulation of the hair of another individual using hands, teeth or lips
Play	Chasing, wrestling or slapping of an individual by another, with no apparent agonistic elements, and often accompanied by a play face
Other	Interactions which occurred too infrequently to merit a separate category (socio-sexual behaviours, and one intervention)
Negative interactions	
Agonistic	Instances of hitting, slapping, cough grunting (aggressive vocalisations (Harcourt et al., 1993)), biting, pushing, and displacement interactions (the approach of one individual followed within 10 seconds by the departure of the approached individual. The individual who approached occupied the vacated position.)
Suckling termination	Termination or refusal of a suckling bout
Other interactions	
Food transfer	The movement of solid food between individuals
Maternal restraint	The mother prevents her offspring from leaving her immediate proximity, or brings her offspring back into physical contact with her by clutching it to her, or grabbing an arm or leg to stop her offspring from moving away

Maternal restraint was the most commonly observed interaction type, with 62% of study subjects receiving this type of interaction (**Figure 4.22**). This was followed by proximity seeking (55% of subjects), food transfer (40%), suckling terminations

(43%), grooming (33.3%), agonistic (19%), play (9.5%) and then finally, other interactions (9.5%). There was a significant difference in the overall frequency with which different interaction types were observed (Chi-square goodness of fit test: $\chi^2 = 185.21$, d.f. = 4, $P < 0.0001$). The median age of each individual contributing to an interaction type was calculated, and then used to calculate a median age for the interaction type. There was a significant different in the median ages of subjects involved in different interaction types (**Figure 4.22**: $\chi^2 = 20.045$, d.f. = 7, $P = 0.005$). Post hoc multiple comparison tests revealed only that those participating in grooming interactions were significantly younger than those participating in proximity seeking interactions.

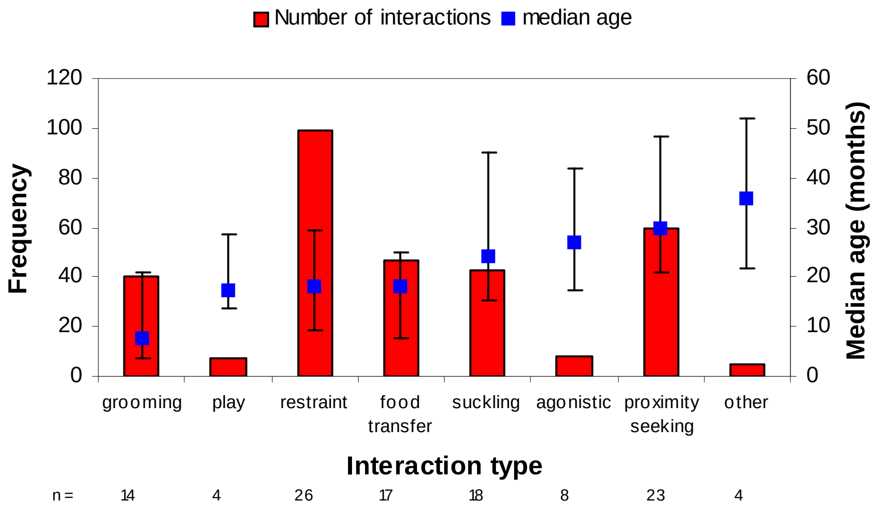


Figure 4.22. The frequency of occasions on which different interaction types between offspring and the mother were observed, and the median age of offspring when participating in each type, in order of increasing median age. $N_{\mathrm{TOTAL}} = 35$.

The frequency of each interaction type was also investigated with reference to age category over the whole of immaturity to determine the type of interactions that were prevalent at particular stages of development (**Figure 4.23**). Since rates of interaction were low during sub-adulthood, and many of these interactions, e.g., maternal restraint, would not be expected to occur during this period, correlations were carried out only over infancy and the juvenile period. The frequency of food transfers, grooming, and maternal restraint interactions with the mother significantly decreased with increasing age of the offspring (**Table 4.6**). For most of these interaction types, however, frequencies were low during the early stages of infancy, and then increased in frequency, as infants were involved in more active interactions with the mother. As they moved away from the mother, reflecting their increasing independence, rates of these interactions then decreased.

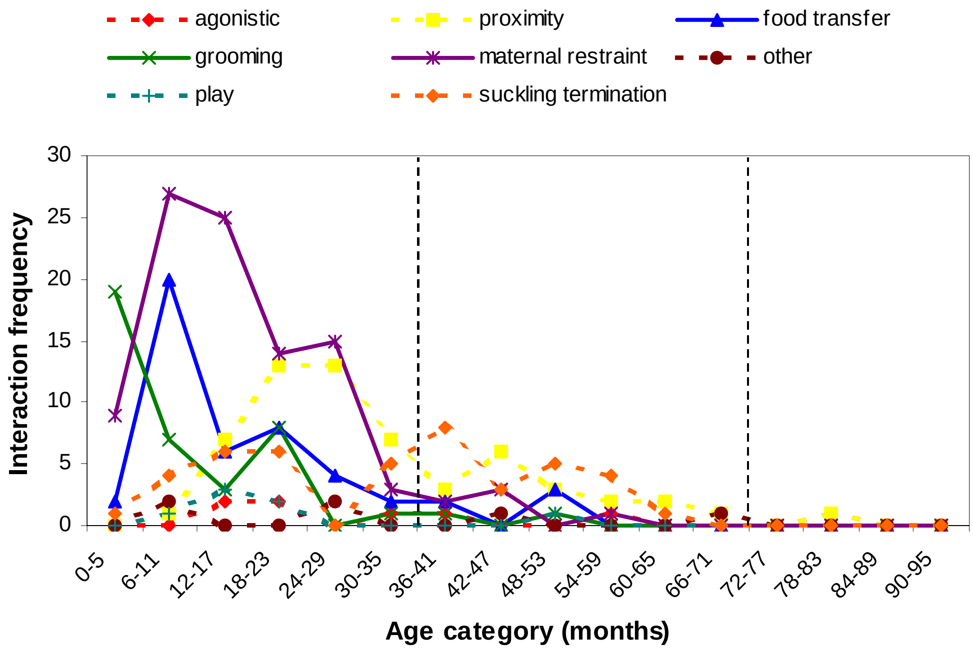


Figure 4.23. The frequency of each interaction type in individuals of different ages. Solid lines indicate a significant correlation between interaction frequency and age category. $N_{TOTAL} = 35$.

Table 4.6. Correlations between the frequency of each interaction type and age category over the immature period.

Interaction Type	r_s	***N***	***P***
Proximity seeking	-0.132	12	0.683
Food transfer	-0.757	12	0.004
Grooming	-0.818	12	0.001
Maternal restraint	-0.917	12	< 0.0001
Play	-0.438	12	0.154
Suckling termination	-0.258	12	0.419
Agonistic	-0.217	12	0.498
Other	-0.059	12	0.857

Median rates of each type of interaction were calculated for each subject by dividing the number of interactions for each subject by the number of hours that the subject spent with the mother in the bai during each age category. A median was calculated from these individual values to give a median age category value for each interaction type. Correlations were conducted over infancy and the juvenile period (**Figure 4.24**), and negative correlations were found between age category and the median rate of food transfer interactions between mother and offspring ($r_s = -0.751$, n = 12, $P = 0.005$), grooming interactions ($r_s = -0.653$, n = 12, $P = 0.021$), and maternal restraint interactions ($r_s = -0.852$, n = 12, $P < 0.0001$). No correlations between interaction rate and age category were significant within infant and juvenile age classes, only over the whole immature period.

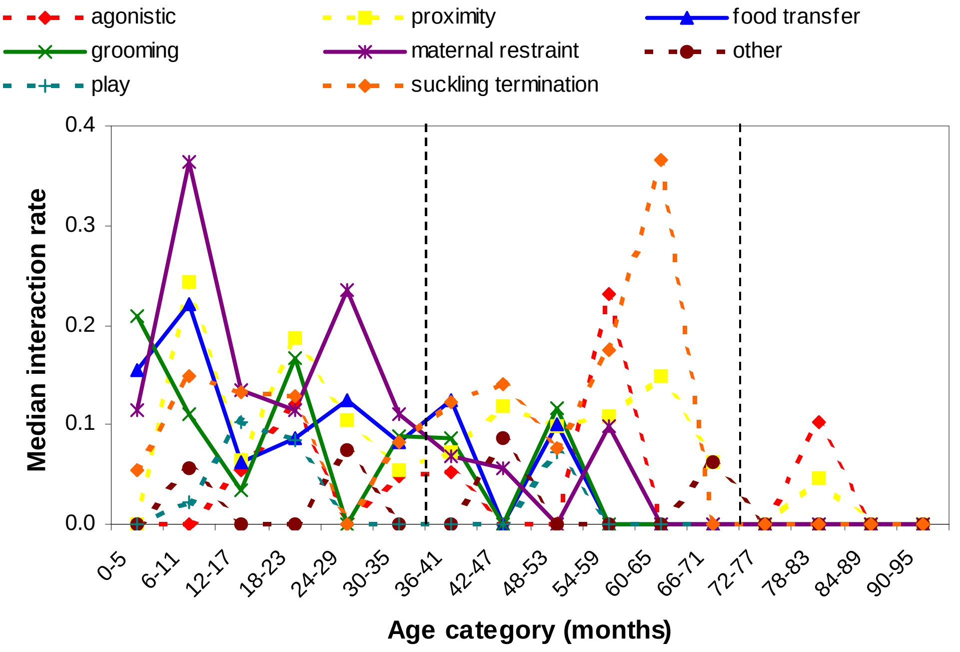


Figure 4.24. Median rates of interaction for each type in individuals of different ages. Solid lines indicate a significant correlation between median interaction rate and age category. $N_{TOTAL} = 35$.

4.6.2. "Negative" Interactions Between Mother and Offspring

Agonism and suckling termination interactions between mothers and offspring were termed "negative" interactions. Suckling terminations were not classed as "weaning" interactions, given the very young age of some of the participants. While it is advantageous for the mother to wean offspring as early as possible (Trivers, 1974), offspring must be capable of surviving without the mother's milk for early weaning to be beneficial. Cases involving young infants were thought to occur as a result of the mother simply moving position, rather than actual attempts to prevent suckling. Suckling terminations between older offspring and the mother were thought to represent a conflict between them regarding the age at which the offspring was weaned, but it was impossible, for the most part, to identify interactions that truly represented weaning behaviour and those occurring as a result of the mother's movement. Suckling terminations were classed as negative as actions of the mother and commonly caused distress to the offspring, or they contained elements of agonistic behaviour, such as biting or pushing by the mother.

Agonistic Interactions

Very few instances of agonism between mother and offspring were recorded during this study. Eight interactions were recorded, each involving a different mother-offspring dyad (**Table 4.7**). Subjects ranged in age from 14 to 80 months, with a median age of 27 months. Four (50%) of the subjects involved in agonistic interactions with the mother were female, three (37.5%) were male and one (12.5%) was of unknown sex. In three cases, the offspring initiated the interaction, and in the remaining five, the mother initiated the interaction.

Table 4.7. Names, ages, sex and group of study subjects involved in agonistic interactions with the mother, and details of the interaction. Ages are given in months.

Name	*Age*	*Sex*	*Group*	*Initiator*	*Details*
Hathi	14	Male	Kha	Hathi	Hathi bites Bagheera when trying to move ventral
Fig	15	Female	Dwa	Fig	Fig hits at Fleur's heel as Fleur stops play between Fig and Brie
Sage	18	Female	Noo	Mother	Salmonberry displaces Sage and feeds in the vacated spot

Name	***Age***	***Sex***	***Group***	***Initiator***	***Details***
Luther	21	Male	Geo	Luther	Luther bites Hilary's hand while she grooms him
Whisky	33	Male	Noo	Mother	Winona moves towards Whisky and pushes past him, almost knocking him over
Clover	38	Female	Dwa	Mother	Pansy cough grunting towards Clover as she tries to climb dorsal
Brie	54	Female	Dwa	Mother	Bluebell pushes Brie into the ground as she moves past her
Ike	80	Unknown	Hai	Mother	Tina displaces Ike and feeds in the vacated spot

A greater number of agonistic interactions between mother and offspring were recorded in the most frequently visiting groups, which would be expected when recording infrequently seen events such as these. Of the groups in which agonistic interactions were not observed, Zul and Sul groups both contained only infants, the majority of whom were less than 27 months of age, the median age for agonistic interactions, for the duration of the study.

From these few cases, offspring appeared to direct more intensive forms of agonism towards the mother (biting and hitting) than the mother did towards the offspring (pushing, displacements and cough grunting). Offspring directing agonism towards the mother tended to be younger than those receiving agonism. Additionally, offspring-initiated agonism appeared more directed at an action or response of the mother, whereas mother-initiated agonism seemed to occur mostly as a result of the offspring being in the way of the mother, or of something that the mother wanted.

Suckling Terminations

Eighteen of 39 (41.9%) subjects who were observed to suckle during the study were involved in suckling termination interactions, the general nature of which has been described on p. 134. Their median age at the time of the interactions was 24.3

months, with a range of 3 to 62 months. The frequency of suckling terminations decreased with increasing age (**Figure 4.23**).

Six of the 18 subjects involved were female (33.3%), 11 were male (61.1%), and one was of unknown sex (5.6%). There was a significant difference in the relative frequency with which males and females were involved in suckling terminations ($\chi^2 = 9.75$, d.f. = 1, $P < 0.01$), with females being involved more than expected and males less (expected values were calculated based on the presence of each sex in the population). One out of four (25%) primiparous mothers, and six out of 16 (37.5%) multiparous mothers were involved in suckling terminations: this did not represent a departure from the expected frequency with which primiparous and multiparous mothers should terminate or prevent suckling ($\chi^2 = 0.14$, d.f. = 1, n.s.)

Although females were involved more often than expected in suckling termination interactions with the mother, this did not appear to be the case for the rate of suckling terminations (**Figure 4.25**). Results were not statistically tested due to small sample sizes. In addition, males continued to be involved in suckling termination interactions for a year after this interaction type was no longer recorded in females, although fewer females of this age were available for comparison. This corresponded with **Figure 4.9** in which males continued to suckle for longer than females did. Similar to the peak recorded in male suckling rate and duration (**Figure 4.9**; although suckling rate and duration peaked at 54-59 months), the rate of suckling terminations peaked in males at 60-65 months of age.

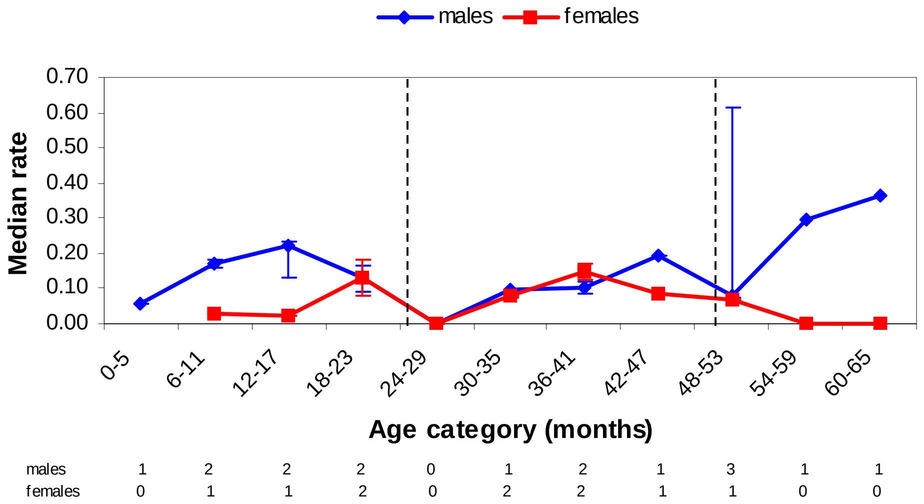


Figure 4.25. Median rate of suckling termination interactions between male and female offspring and the mother. The high interquartile range seen in males at 48-53 months resulted from one individual's rate of 1.15 interactions per hour, the highest value recorded, and over three times that of the next highest value (0.37 interactions per hour). $N_{males,\ females} = 11, 6$.

By definition, the mother initiated all suckling termination interactions. In 23% of cases the response of the offspring was to scream or whimper, and in 80% of cases where the offspring vocalised its protest, the offspring was then allowed to suckle. Of all 43 suckling terminations, the offspring was allowed to suckle after the interaction in 30% of cases (eight individuals, ranging in age from 8 to 59 months). That offspring were frequently allowed to suckle after the termination of a bout or an attempt was refused may suggest that a proportion of these interactions did not represent a conflict between mother and offspring. Instead, a suckling bout may simply have been terminated as a result of the mother shifting position, and after the offspring adapted to the new position, suckling continued. Alternatively, this could represent the gentle nature of weaning in western lowland gorillas.

4.6.3. "Positive" Interactions Between Mother and Offspring

Interactions included in this category were play, grooming, proximity seeking and "other" interactions, all of which were thought to be beneficial to offspring, most likely in terms of immediate protection or stimulation (play, grooming, proximity seeking), rather than behaviours that will be required in the future.

Play Interactions

Play between mother and offspring occurred very infrequently, on only seven occasions and involving four mother-offspring dyads (**Table 4.8**). The median age of offspring playing with the mother was 17.5 months (range: 7-51 months), the offspring was the initiator in all instances, and the mother never reciprocated with play behaviour. With so few instances it was impossible to predict the effects of sex and group on the incidence of play interactions between mother and offspring.

Table 4.8. Details of play interactions between mother and offspring.

Subject Name	*Age (months)*	*Number of Interactions*	*Sex*	*Group*	*Details*
Fig	13	3	Female	Dwa	Fig grabbed at Fleur's face, Fig patted and stroked Fleur's back (x2)
Sage	7, 21	2	Female	Noo	Sage patted Salmonberry's head; Sage spun directly in front of Salmonberry and patted her head
Kung	21	1	Male	Zul	Kung patted Khoisan's back
Louis	51	1	Male	Kha	Louis grabbed Jakala's head in both his hands and shook it

Grooming Interactions

Forty grooming interactions were recorded between mother and offspring during the study, involving 14 subjects aged between 1 and 53 months (median age: 17.5 months). Almost half of all grooming interactions were directed towards infants less than 6 months of age. The frequency and median rate of grooming interactions decreased with increasing offspring age (**Figures 4.23** and **4.24**). In the majority of grooming interactions (82.5%), the mother was the initiator. Offspring-initiated interactions tended to involve older offspring (**Figure 4.26**). Nine males, five females and one individual of unknown sex was involved in grooming interactions, and for males and females, was not a departure from the expected sex ratio (χ^2 = 0.21, d.f. = 1, n.s.). Subjects from eight of the ten possible groups were involved in grooming interactions, three of which had primiparous mothers, and eleven had multiparous mothers, again, not a significant departure from the frequencies expected (χ^2 = 0.02, d.f. = 1, n.s.).

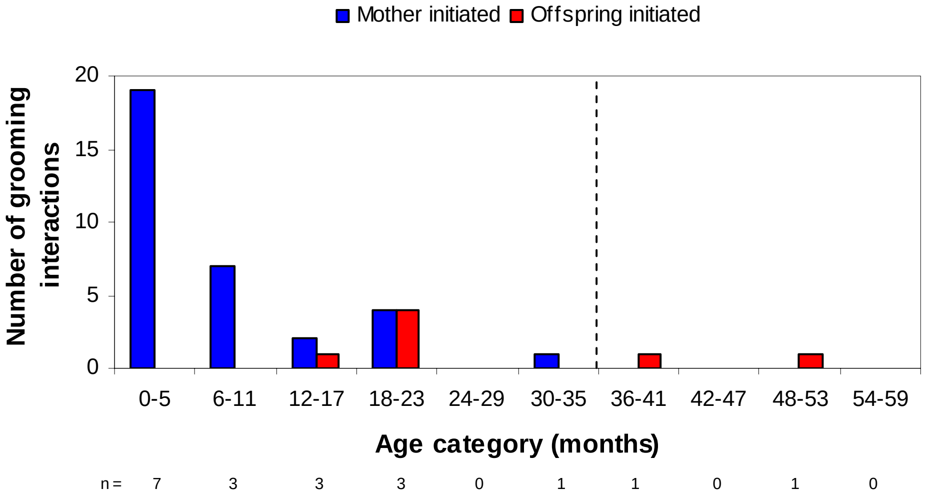


Figure 4.26. Initiators and frequency of grooming interactions between mothers and offspring. N_{TOTAL} = 14.

Proximity Seeking

Proximity seeking was the second most frequently observed interaction between mothers and offspring. Sixty proximity seeking interactions were observed between mother and offspring during the study, involving 23 study subjects ranging in age from 9 – 80 months, with a median age of 30 months. Subjects represented eight of the ten possible groups. Four females and 14 males were involved, which did not differ from the expected sex ratio (χ^2 = 0.52, d.f. = 1, n.s.), and also five individuals of unknown sex.

In 30 out of 60 cases (n = 15 subjects) the interaction was initiated by the offspring, and twenty eight proximity seeking incidents were initiated by the mother (n = 15 subjects). In no cases did primiparous mothers initiate proximity seeking, despite being predicted to show restrictive behaviours towards their infants. In two cases, it was impossible to distinguish the initiator of an embrace (n = 2 mother-offspring pairs). These interactions were generally initiated in one of four ways

(**Figure 4.27**): offspring either moved towards and *embraced*, or put one arm around the mother for no apparent reason, or the interaction followed some kind of *distress* experienced by the offspring, for example, falling out of a tree or the mother crossing a stream too deep for the offspring to follow independently. In a small number of cases, offspring appeared to *seek reassurance* from the mother, often in response to the approach of a sitatunga, or by reaching out and touching the mother as she shifted position slightly while feeding. "*Beckoning*" was the final context in which offspring and mother sought one another's proximity. A mother, before or just after her initial departure from a feeding location, turned towards her offspring and reached out a hand to assist the offspring in climbing dorsal before continuing to travel. In the one offspring-initiated instance of beckoning, Fig moved away from her mother, turned and looked at her. The mother then moved towards Fig who climbed dorsal and they continued travelling. Beckoning was always recorded within the 5 minutes prior to exiting the bai.

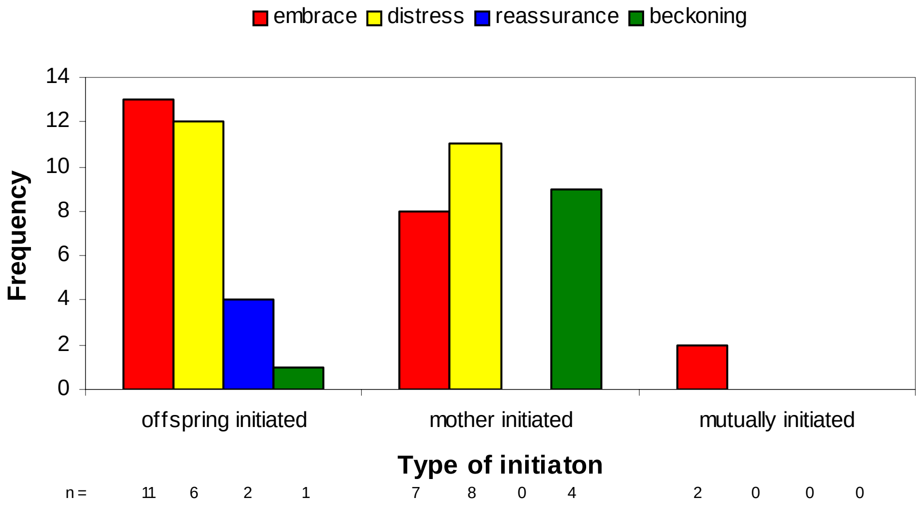


Figure 4.27. Initiators of different types of proximity seeking. $N_{TOTAL} = 23$.

Proximity seeking between mother and offspring became less frequent as offspring matured (**Figure 4.23**). The median rate appeared to be slightly lower in females than in males (**Figure 4.28**), but unfortunately, data were insufficient to allow statistical testing.

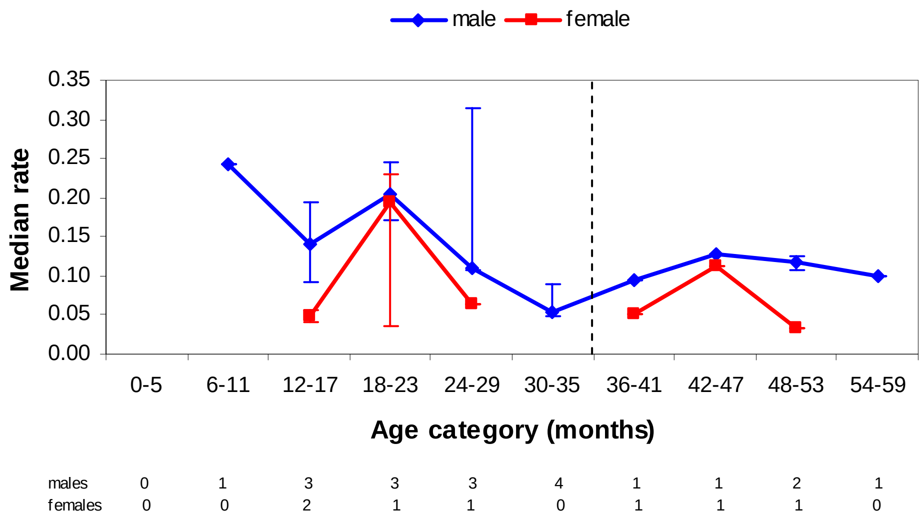


Figure 4.28. Comparison of the rates at which proximity seeking took place in males and females. $N_{\text{males, females}} = 14, 4$.

Other Interactions

An additional five interactions took place, which were not appropriate for any of the previous categories but did show elements of affiliation. Eighty percent of these interactions took the form of interest in the reproductive status of the mother, where the offspring touched or sniffed the ano-genital region of the mother. In no case did the mother react, and no behavioural indications of oestrus in the mother, such as presenting to the silverback (Watts, 1991b; Robbins, 1999) were observed.

The final interaction in this category took the form of the retrieval of a 9-month-old infant by the mother, but in response to the approach of the group silverback. This was not classed as proximity seeking, because no instances in that category occurred as a result of the behaviour of an individual outside the mother-offspring dyad. Additionally, it was not termed maternal restraint because the offspring was not attempting to increase the distance between herself and the mother, neither was the mother gathering the offspring to herself as a means of keeping the offspring close to her while she moved away. By placing the infant dorsal, the mother removed the possibility of an interaction between her infant and the silverback, which would not be expected to cause harm to the infant, but was consistent with the general avoidance of infants by silverbacks that is described in Chapter Five.

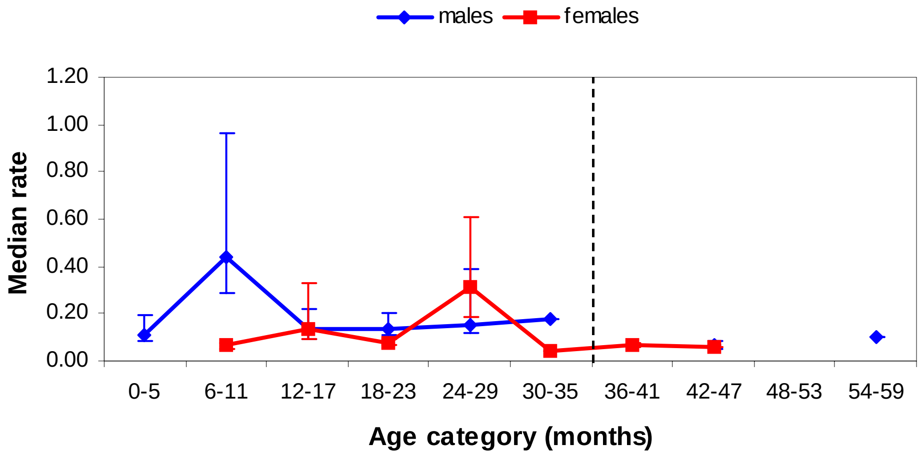
4.6.4. Other Interaction Types Between Mother and Offspring

Some interactions between mother and offspring were difficult to term as either negative or positive, and in the case of food transfers, depended on which individual initiated the interaction. Although restraint allowed the mother to control or limit the behaviour or movements of her offspring, in many cases, it caused distress to the offspring.

Maternal Restraint

Maternal restraint interactions were the most common type between mother and offspring. They were observed on 99 occasions involving 26 study subjects, ranging in age from 2 to 56 months, with a median age of 18 months. Eight females and 18 males were involved; again this did not depart from the expected sex ratio (χ^2 = 0.007, d.f. = 1, n.s.). Subjects from eight of the ten possible groups were involved.

Although both proximity seeking and maternal restraint interactions resulted in proximity or contact between mother and offspring, they were fundamentally different. Proximity was achieved through the actions of both mother and offspring during proximity seeking interactions, whereas the offspring attempted to break contact or decrease proximity to the mother in maternal restraint interactions, but was unable to as a result of the mother's behaviour. Consequently, all maternal restraint interactions were mother-initiated. Both the frequency and median rate of maternal restraint interactions declined with increasing offspring age (**Figures 4.23** and **4.24**). The median rate of maternal restraint interactions appeared similar in males and females (**Figure 4.29**), although the male rate peaked earlier than the female rate, at 24-29 months. Again, data could not be statistically tested due to small sample sizes. Both of these peaks preceded peaks in the median percentage of time spent at 0-2m from the mother (see **Figure 4.7**) by 6 months to 1 year. Consequently, it is possible that the mother prevented offspring from moving out of their immediate proximity at an early age by actively restricting their movements.



	0-5	6-11	12-17	18-23	24-29	30-35	36-41	42-47	48-53	54-59
males	4	7	8	5	3	1	0	2	0	1
females	0	2	4	3	3	1	2	1	0	0

Figure 4.29. Comparison of the rates at which maternal restraint took place in males and females. $N_{males, females} = 18, 8$.

In two different dyads, within 5 minutes of previously restraining the offspring, mothers were observed to tuck their infant's hand under their chin, thus physically ensuring that offspring could not break contact. In one case, the infant removed its hand after a few minutes, and no further maternal restraint interactions were observed during the remainder of the visit (15 minutes). In the other case, the infant removed its hand and moved away from the mother 2 minutes later, causing his mother to follow and restrain him in the same way. Although offspring often struggled after being restrained by the mother or prevented from travelling independently, it was thought that the mother initiated these interactions to ensure that her offspring was protected while she continued her activities, usually feeding, or travelling to another feeding location or out of the bai.

Previous studies have suggested that primiparous mothers are more restrictive of their infant's behaviour (e.g., Hooley & Simpson, 1981; Fletcher, 1994; Brown & Dixson, 2000). In this study, 75% of primiparous mothers and 62.5% of multiparous mothers restricted their infant's movements. This did not depart from the expected ratio ($\chi^2 = 0.007$, d.f. = 1, n.s.). There was no difference in the median number of restrictions performed by primiparous and multiparous mothers ($U = 13.5$, $N_{MP, PP} = 13, 3$, $P = 0.794$). However, sample sizes were small, so results are inconclusive, but in the bai, there was no evidence that primiparous mothers were more restrictive of their infant's behaviour.

Food Transfer Interactions

Interactions between mother and offspring involving the transfer of food items were recorded on 47 occasions, involving 17 subjects aged between 4 and 53 months, with a median age of 18 months. The offspring (n = 14) was the initiator of the interaction in 37 cases (79%), i.e., the offspring took food from the mother. The mother (n = 7) initiated the interaction in ten cases (21%). The frequency and median rate of food transfer interactions both decreased with increasing offspring age (**Figures 4.23** and **4.24**). A full analysis of food transfer interactions was provided in Chapter Three.

4.6.5. Frequencies of Negative and Positive Interactions with the Mother

Just under half (48%) of all interactions between mother and offspring could not easily be categorised as negative or positive. Thirty six percent of interactions between mother and offspring were positive, showing elements of affiliation, close contact between mother and offspring and the mother acting to ensure the safety of her offspring. Only 16% of interactions showed elements of agonism between mother and offspring, and occurred mainly as disagreements over suckling behaviour, which as the offspring grew older, became an indication of the weaning process. The frequency of both positive and negative interactions were significantly negatively correlated with offspring age category (**Figure 4.30**: positive: $r_s = -0.930$, n = 16, $P < 0.0001$, negative: $r_s = -0.567$, n = 16, $P = 0.022$), although within age classes, the only significant correlation was between juvenile age category and the frequency of negative interactions ($r_s = -0.812$, n = 6, $P = 0.05$).

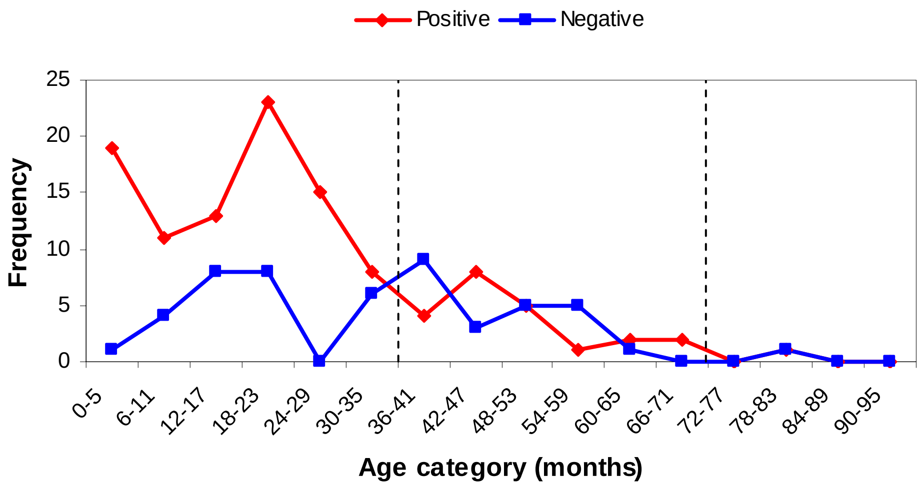


Figure 4.30. The frequency of positive and negative interactions between mothers and offspring of different ages. $N_{TOTAL} = 35$.

4.7. EFFECT OF SIBLING BIRTH

After giving birth, a mother invests in her new offspring, thus changing the dynamics of her relationship with her previous offspring (Brent et al., 1997; Devinney et al., 2001). Only two siblings were born during the study period, so results are preliminary and inconclusive, but it was suspected that the birth of a sibling might affect the relationship between a mother and her older offspring. No other infants had older siblings in the same group.

Lando and Piment were born, when their older siblings, Sunbeam and Pepper, were 60 and 76 months old respectively. In the period before the birth of their siblings, the modal distance categories between Sunbeam and Pepper and their respective mothers showed a gradual increase (one modal distance category was recorded for each month of age). After the birth of Piment, the modal distance between Pepper and mother Primrose was consistently recorded as 10m plus, the farthest recorded category, which had been the modal distance between them only during the two months recorded prior to the birth of Piment. After Lando's birth, the modal distance between Sunbeam and her mother decreased from 10m plus (recorded in the last two months prior to Lando's birth) to 2-5m (**Figure 4.31**). The modal distance then increased again to 10m plus in the last month that Sunbeam and Lando were observed. For Sunbeam, the difference in modal distance category to the mother before and after the birth of a sibling was not significant (*U* = 6.5, n = 6, 3, *P* = 0.480). For Pepper, the difference was significant (*U* = 5.0, n = 6, 5, *P* = 0.034), but it was difficult to determine to what extent this resulted from a general increase in independence from the mother, or occurred as a result of the birth of the younger sibling. Data in other categories were too few to analyse the effect of the birth of a sibling, so here, it can only be stated that proximity between older offspring and the mother may or may not be affected by the birth of a younger sibling.

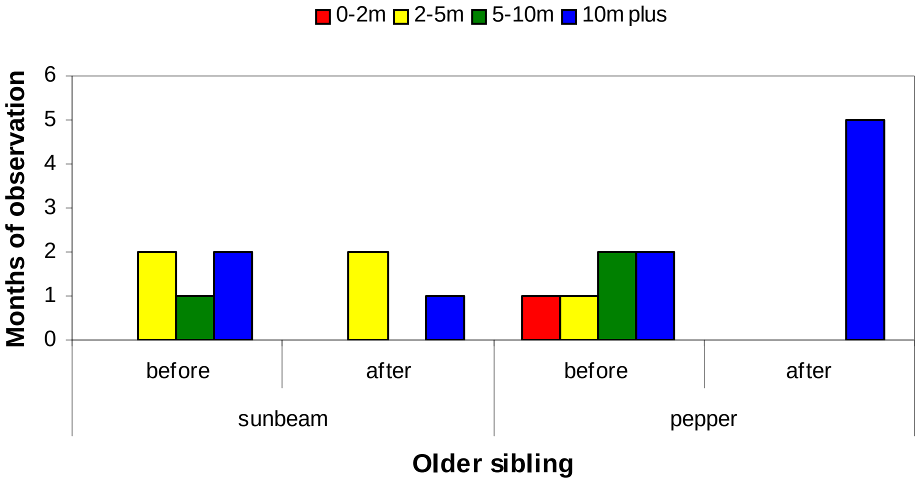


Figure 4.31. Monthly modal distance categories for Sunbeam and Pepper and their mothers before and after the birth of their siblings.

4.8. DISCUSSION

A number of predictions were made in the introduction to this chapter regarding the nature of the relationship between mother and offspring, and the changes that occur as offspring mature. Predictions relating directly to spatial relationships, suckling, the development of travelling behaviour and interactions are discussed below in the relevant sections. In terms of general predictions:

- No significant differences were apparent between males and females with regards to their relationship with the mother. However, males showed peaks in various behaviours (close proximity to the mother, suckling variables) not evident in females, which may suggest greater tolerance of sons, who were close to being completely weaned, than daughters, and is consistent with the theory that mothers invest more in the sex that experiences greater variation in their reproductive success (Trivers, 1972). Further research is needed to evaluate whether these apparent differences between males and females are real.

- No differences between groups were detected in the nature of the mother-offspring relationships, suggesting that in a bai environment, the presence of conspecifics, nor any factors relating to feeding competition as a consequence of group size, do not influence the development of independence from the mother in gorillas.
- No evidence was found to suggest that primiparous and multiparous mothers behave differently towards their offspring. However, sample sizes were small, so results remain inconclusive.

4.8.1. Spatial Relationships Between Mothers and Offspring

The pattern of gradually increasing distance from the mother as offspring mature is common among primates (e.g., Nash, 1978; Altmann, 1980; Pereira & Altmann, 1985; Fletcher, 2001; Maestripieri, 2002), and was mirrored in the current study:

- The distance between mothers and offspring gradually increased as offspring matured, and changes in spatial patterns were most pronounced during infancy.

Immature gorillas are expected to invest in relationships with individuals that are likely to be available and of benefit in the future (Fairbanks, 1993). For western lowland gorillas, dispersal rates from the natal group are high (Parnell, 2002b; Stokes et al., 2003), and therefore, the majority of individuals with whom immatures interact in the natal group, including the mother, are unlikely to be available in the future. The finding that western lowland gorilla females do not disperse far from the natal group, and therefore, might immigrate into the same group as female relatives (Jeffery et al., 2004), might provided a limited benefit to both males and females of continuing to invest heavily in a relationship with the mother (c.f. Watts, 1996a).

Body contact and close proximity provides warmth, security and protection, and if mothers invest more in male offspring than females (due to the more variable reproductive success of males (Boesch, 1997; Hewison & Gaillard, 1999)), differences would be expected in proximity between mothers and daughters, and mothers and sons. In this study, males and females appeared similar with regards to time spent in contact with the mother, and although differences were suggested between males and females in other measures of proximity, they did not reach significance. There was no evidence that mothers invested more in sons than daughters, with respect to spatial relationships, suggesting that continued proximity to the mother does not confer any real advantage to offspring.

Continued close proximity to the mother for males may be expected in species such as chimpanzees (Pusey, 1983; Watts & Pusey, 1993) and muriquis (Strier, 1993), where males tend to remain in the natal group, and may benefit from prolonged association with the mother. However, since male western lowland gorillas do not tend to remain in the natal group (Parnell, 2002a), the late increase in time spent in close proximity at around 5 years of age, and the mother's tolerance towards this and of suckling until later ages, may reflect preferential investment in sons by at least some mothers. This then provides the potential to lead to higher growth rates and body sizes that may be helpful in terms of attracting females with whom to breed (Hewison & Gaillard, 1999). More data are needed to produce conclusive results, particularly due to the small number of juvenile females in the current study.

The social group to which a study subject belonged was hypothesised to play a role in the nature of the spatial relationship between a mother and her offspring (*sensu* Berman et al., 1997). Groups with many youngsters of a similar age, or the presence of older siblings often provide more incentive for a young primate to leave the proximity of the mother and interact with peers (e.g., Pereira & Altmann, 1985; Fagen, 1993; Fairbanks, 1993; Fletcher, 1994). In chimpanzees, infants with regular access to older siblings have been shown to break contact with, and leave the close proximity of their mother earlier than infants with no access to older siblings (van Lawick-Goodall, 1971b; van de Rijt-Plooij & Plooij, 1987). In this study, however, no differences between groups were apparent with reference to spatial patterning between mothers and offspring, despite differences in group size and composition. Subjects present in groups with five other similarly aged infants were no more likely to leave the proximity of the mothers earlier than those in a group with only older juveniles and sub-adults in addition to adult members. Therefore, in a bai environment, the availability, or attractiveness of other individuals with whom to interact, did not influence spatial patterning between mother and offspring. In studies where the presence of conspecifics or siblings accelerated the development of independence from the mother, immature individuals often left the proximity of the mother to engage in play behaviour (van Lawick-Goodall, 1971b; Fagen, 1993). During bai visits, however, the percentage of time spent playing by immature gorillas was low (see Chapter Three). So, in the relative absence of play behaviour between conspecifics, potential differences between groups in the development of independence from the mother may have been masked.

In primate species, the birth of a younger sibling has been suggested to prove stressful for the older sibling, as the mother shifts her investment from the older offspring to the younger (Devinney et al., 2001; Schino & Troisi, 2001; Devinney et al., 2003). Increases in dependent behaviour and indications of stress in the older offspring have been documented after the birth of a sibling (Devinney et al., 2001; Schino & Troisi, 2001), but were not observed in this study, presumably since the older siblings were already weaned and spatially independent. In one case, the presence of a younger sibling appeared to change the spatial relationship between a juvenile female and her mother, with time in proximity between the older offspring and mother increasing after the birth of the sibling. In the other case, sibling birth had no effect on the older sibling's (who was of unknown sex) spatial relationship with the mother. Young females are generally more interested in infants than males (Hrdy, 1976; Nishida, 1983; Brent et al., 1997), but Pepper's apparent lack of interest in the new infant, cannot be suggested to be sex-related until the sex of Pepper is confirmed.

Previous studies have shown that experienced, multiparous mothers are less restrictive of offspring (e.g., Hooley & Simpson, 1981; Brown & Dixson, 2000). Additionally, primiparous mothers are often more controlling of the spatial relationship with their offspring, resulting in later breaks of contact and more time spent in close proximity, or being more likely to neglect or abuse her infant (Hooley & Simpson, 1981; Maestripieri, 1998; Nakamichi et al., 2004). Although data were limited, with only four primiparous mothers in this study, no differences in spatial relationships between mothers and offspring were found to be as a result of the reproductive history of the mother. The bai environment may have increased the restrictiveness of all mothers due to the perceived dangers facing offspring who move out of the proximity of their mothers in the swampy bai (Parnell, 2002b).

Previous studies in baboons and macaques have shown that in wet or cold conditions, infants show increased proximity to, and contact with the mother (Bernstein, 1980; Schino & Troisi, 1990; Schino & Troisi, 1998; Brent et al., 2003). The time between entering the bai in maternal contact and breaking contact with the mother was considered indicative of developmental stage. This period, the latency to independence, gradually decreased with increasing offspring age, until the offspring consistently entered the bai independently, and weather was found to affect latency to independence. When cold and rainy, the latency to independence significantly increased. Although western lowland gorillas do not occupy the colder end of gorillas' range, where mountain gorilla infants have been known to die from pneumonia (Watts & Hess, 1988), the mother is important for the maintenance of body temperature by contact with her offspring, and this continues well into the fourth year.

4.8.2. Suckling and Weaning

Results from this study, relating to suckling and weaning behaviour are similar to those reported in studies of other primates (e.g., Pusey, 1983; Lee et al., 1991; Fletcher, 1994):

- The rate with which offspring suckled decreased as they matured, however, the duration and length of suckling bouts was not influenced by age. Three out of four juveniles who were weaned later than others had mothers who were considered old, suggesting older mothers invested more in what was potentially their last offspring.
- As offspring increased in age, mothers increased the frequency with which they terminated suckling bouts, although individuals were permitted to suckle until well into the juvenile period. Only one temper tantrum was thrown in response to the termination of a suckling bout.

Stewart (1988) found that one suckling bout every two hours prevented mountain gorilla females from resuming oestrus cycles, so suckling frequency must fall to low levels before females can begin investment in their next offspring (Stewart, 1988; Sievert et al., 1991). Consequently, offspring are selected to demand more than the mother is prepared to give (Trivers, 1974; Bateson, 1994; Barrett & Henzi, 2000).

All three suckling variables that were investigated (rate, duration and bout length) showed increases in males as they approached the end of the juvenile period and were close to being weaned. These increases were not observed in females, and although data sets were small and significant differences not detected, they might suggest a trend towards increased maternal investment in males over females, consistent with Trivers' (1972) parental investment theory.

The increase in the frequency with which the mother terminated suckling bouts when offspring reached 3 years of age was consistent with the hypothesis that mothers reduced investment in their current offspring to begin investment in the next. Suckling terminations increased throughout the next two years, until offspring were weaned, and probably reflected the parent-offspring conflict. Age at weaning in this study was later than reported in mountain gorillas (although sample sizes were small), and differences in suckling patterns between western lowland and mountain gorillas will be discussed more fully in Chapter Seven. Prior to weaning, the percentage of suckling bouts that were terminated by the mother was significantly increased in a number of individuals, suggesting that although weaning appears gentle in gorillas (see Stewart, 1981; Fletcher, 2001), the mother controls the process. However, on many occasions, subjects who were initially denied suckling were often later permitted to suckle if they persisted in their attempts. The dynamic assessment theory predicts that mother and offspring monitor each other closely, and the mother responds to genuine need in her offspring (Bateson, 1994; Devinney et al., 2001), so these persistent attempts to suckle by offspring were thought to represent an honest need. Rather than open conflict between mother and offspring over the extent to which maternal investment continued, these results suggest that dynamic assessment theory may more accurately describe weaning behaviour between mothers and offspring in gorillas (*sensu* Bateson, 1994; Devinney et al., 2001).

Few studies have considered the position of the infant while suckling. In this study, suckling while clinging ventrally or sitting was negatively correlated with increasing offspring age, and only young infants were supported by the mother while suckling ventrally. When offspring suckled in a ventral position, either supported or unsupported, or sat to suckle, the behaviour of the mother seemed affected to some extent, whether by allowing only one hand to be used for feeding or travelling (in supported ventral suckling), or by appearing to restrict her range of movement (when suckling while sitting or clinging ventrally), and these positions were thought to represent a greater cost to the mother by impeding her feeding behaviour. As offspring increased in age and began to ingest solid food items, the relative contribution of milk to their diet decreased, and it was no longer necessary for mothers to facilitate suckling offspring to the same extent. The increasing frequency of standing suckling bouts indicates that mothers ceased to modify their behaviour to accommodate suckling offspring. When younger offspring suckled while ventral or sitting, the mother often ceased her activity, and waited for suckling to stop. No such behavioural modifications were seen when offspring suckled while standing, and likewise, in a study on baboons, mothers also made no alterations to their behaviour to increase the ease with which their maturing offspring could suckle (Altmann, 1980). The decreasing frequency with which mothers modified their behaviour to accommodate suckling suggested a decreased willingness to invest in the current offspring by the mother.

4.8.3. The Development of Travelling Behaviour

The ontogeny of travelling behaviour was similar to that described for wild mountain (Stewart, 1981; Fletcher, 1994; Doran, 1997b) and captive western gorillas (Hoff et al., 1981a; Hoff et al., 1983):

- Infants became physically independent during infancy, with a transition period between dependent and independent travel occurring between 18 months and 3 years.
- The increase in independent locomotion was achieved through a gradual progression of travelling behaviour that reflected the increasing size of immatures, and possibly their strength.

Gorilla infants travelling supported or clinging ventrally can limit the speed with which a mother can travel, and also hinder her in climbing trees to search for fruit, much in the same way as Wrangham (2000) described for female chimpanzees. In particular, the age and size of an infant gorilla, and its mother can determine the point at which an infant can begin to travel dorsally (see Fossey, 1979; Hoff et al., 1981a; Hoff et al., 1983): the offspring of large female gorillas in this study appeared to have difficulty in maintaining a good grip on their mothers' broad backs, when first observed travelling dorsally. The similarity in the development of travelling behaviour between this and other studies was unsurprising, since to a certain extent, the method of travel used reflects the size of an offspring. Newborns are not physically strong enough to support their own body weight when grasping the mother's ventrum (Fossey, 1979; Doran, 1997b), and this is true regardless of sub-species and the immediate environment (i.e., wild or captive). Likewise, the period during which offspring can travel dorsally will also be limited by their size, as they eventually become too big and heavy to be economically transported by the mother (Wright, 1990).

The perceived safety of the environment is a factor which has been shown to influence travelling behaviour in baboons: vulnerable individuals tended to be surrounded by adult males when entering a dangerous environment (Rhine & Owens, 1972), illustrating how the potential dangers of a non-captive environment can delay the development of independence in certain situations. In captivity, the surroundings remain constant, so familiarity and complacency within an environment may prompt the development of new skills, such as independent locomotion, accounting for the earlier appearance of independent travel in captive gorillas. A study which compared the behaviour of a juvenile gorilla before and after transfer to a new, more naturalistic environment showed decreased levels of activity, particularly play behaviours after the move (Goerke et al., 1987), suggesting that unfamiliarity with an environment (such as the infrequently visited bai) may limit the performance of new behaviours, prompting a return to increased dependence on the mother, as previously suggested. Therefore, although the ages at which individuals in this study showed transitions between different travel types was fairly consistent, they may not be representative of the speed with which these transitions take place in the forest environment.

4.8.4. Entry and Exit Positions

Travelling positions used by immature gorillas during entry and exit to the bai could provide information on the perceived danger of entering an unfamiliar area of the habitat. A study on baboons (Rhine & Owens, 1972) indicated that the order of movement of group members into a clearing reflected the potential danger of predation in the clearing, with adult males entering first more than was expected, and females with young infants occupying the middle of the progression. Following similar logic, if Mbeli Bai was perceived to be potentially dangerous, young infants would be expected to travel into the bai in a way that was most likely to ensure their safety. However, there was no consistency in whether immatures left or entered the bai using a more mature method of locomotion. This suggests that neither entering nor exiting the bai was perceived to present a threat to young individuals, or otherwise, that entrance to both the bai and the forest were equally "dangerous". These possibilities were further suggested by the lack of consistency in the order of group members entering and exiting the bai. The pattern of adult males entering the clearing first by Rhine and Owens (1972) was not replicated at Mbeli Bai; it was not unusual for adult females with young infants to be the first individuals to enter, or the last to leave the clearing (pers. obs.). Both bai and forest environments have their potential dangers: the bai has swampy, unfamiliar terrain, while the forest affords lower levels of visibility that may increase vulnerability to predation and infanticidal males. There was a tendency for younger infants to enter the bai more maturely than when they exited, whereas this trend was reversed in older infants. Due to the length of average bai visits, this was thought to be as a result of the need to suckle in younger infants (and indeed, they often suckled just prior to or during exit from the bai, resulting in their more dependent travelling behaviour), whereas older infants often left the bai to play on the forest edge before their mothers had finished feeding in the bai.

4.8.5. Mother-Offspring Interactions

The nature of interactions between mother and offspring provided more information on the type of relationship that existed between them, and was predicted to reflect decreasing levels of investment in the offspring by the mother. It was found that:

- Overall, rates of social interaction declined with increasing offspring age, but interaction types that contained elements of agonism were more prevalent in older offspring. The frequency of positive interactions with the mother decreased more quickly during immaturity than the frequency of negative interactions.

During the first 6 months, there were relatively few active interactions between mother and offspring, and the passivity of offspring in initiating interactions was presumably due to the general inactivity and unawareness of surroundings found in very young animals (Fossey, 1979). Interactions between mother and offspring increased towards the end of the second year, and this period was one in which infants began to explore and interact with their immediate environment, resulting in an increase in behaviour directed towards the mother, as has been recorded in other studies (e.g., Hoff et al., 1981b; Fagen, 1993; Spinka et al., 2001). Interaction rates then fell to low levels when offspring reached the age of five years, perhaps representing the reduced necessity for maintenance of the maternal relationship in individuals who are likely to disperse from the natal group.

The frequency of affiliative interactions between mother and offspring, showing elements of affiliation, or instances in which the mother restrained her offspring, indicated high levels of investment in offspring. Interactions that were unrelated to suckling behaviour, and in which offspring directed aggression towards the mother were rare, as is also the case in mountain gorillas (Stewart, 1981; Fletcher, 2001), and in this study, occurred in response to the mother’s actions. Weaning behaviour should not begin to be seen until immature individuals approach the age at which they can nutritionally survive the death of the mother (Trivers, 1974), and therefore, suckling termination interactions involving only older offspring were thought to represent the process of weaning. Those observed early in infancy were thought to result simply from the mother’s movements, rather than a rejection of suckling. As subjects increased in age, the mother was more likely to respond negatively to her offspring, with agonism and interactions leading towards weaning her offspring becoming more prevalent, as also shown by Maestripieri & Carrol (1998).

There was no observed effect of the parity of the mother on the nature and frequency of interactions between mother and offspring, which was surprising, given the number of other studies that have found the parity of the mother to influence the relationship between mother and offspring (e.g., Hooley & Simpson, 1981; Maestripieri, 1998; Brown & Dixson, 2000). It was certainly possible that the bai environment masked any differences. All mothers seemed to show a high level of restraint towards their offspring in this environment, and the small number of primiparous females may have been insufficient to detect a difference between the behaviour of multiparous and primiparous mothers towards their offspring in this particular environment. The possibility of a difference between multiparous and primiparous mothers in the forest cannot be ruled out.

Additionally, no clear effects of offspring sex or group on the nature of mother-offspring interactions were detected, although in many cases, data could not be tested statistically. Certain factors, mainly relating to suckling behaviour may have indicated that mothers invested for a longer period in male rather than female offspring, at least in terms of nutrition. The infrequency of grooming, a generally accepted form of investing in relationships in primates (Silk, 1982; Henzi & Barrett, 1999; Di Bitetti, 2000) between mother and offspring in the bai environment increase the difficulty with which conclusions can be drawn regarding preferential investment by the mother in one sex or the other.

Overall, the patterning of interactions between mother and offspring were indicative of the waning relationship between them. Although the possibility of offspring and mothers transferring independently into the same group exists (Jeffery et al., 2004), there may be little benefit to immatures of continuing to invest in relationships with the mother in a group where they have no future (Fairbanks, 1993), since both sexes are likely to disperse from the natal group in western lowland gorillas (Stokes et al., 2003). It is proposed that this limited benefit is reflected in the paucity of grooming, play and general affiliative interactions seen between mothers and older offspring. The increase in agonistic interactions may be indicative of the parent-offspring conflict, as offspring continue to demand more than mothers are prepared to give (Trivers, 1974). However, the effect of the bai on the frequency and nature of interactions between mother and offspring cannot be determined, particularly as all interactions occurred at very low rates. Many primates tend to interact more frequently during rest periods (Harcourt, 1978a; Altmann, 1980; Robinson & van Schaik, 1987; Robinson et al., 1987), and therefore, it was not surprising that interactions, particularly play and grooming which are those most frequently performed during rest periods in other species (Robinson & van Schaik, 1987; Robinson et al., 1987) should occur at low levels in this environment, where the predominant activity of gorillas is feeding (Magliocca & Gautier-Hion, 2002; Parnell, 2002a). However, levels of investment in offspring are highest when infants are young, in terms of contact and proximity, suckling and affiliative interactions, when mothers can make the biggest difference to the survival of her offspring.

4.9. CONCLUSIONS

The relationship between mothers and offspring in this study followed a predictable pattern based on other studies of mother-offspring relationships in primates (e.g., gorillas (Fossey, 1979; Hoff et al., 1981a; Fletcher, 2001; Maestripieri et al., 2002), baboons (Nash, 1978; Altmann, 1980) and vervet monkeys (Fairbanks, 1993)), with the mother continuing to invest in offspring until it develops the skills that are likely to promote its survival. It is suggested that in western lowland gorillas, the unpredictable dispersal of resources results in mothers continuing to invest in offspring, even after locomotor and feeding skills (Chapter Three) have developed. The nature of the relationship between mother and offspring displayed aspects of, if not openly affiliative behaviour, then tolerance and familiarity between mother and offspring. Examples of this include suckling well into the juvenile period and the infrequency of agonistic interactions between within mother-offspring dyads. Interactions that did cause distress to the offspring tended to be those in which the mother restrained her infant, presumably with the purpose of providing protection. The relatively gentle nature of weaning which had been suggested in studies of mountain gorillas (Fossey, 1979; Stewart, 1981; Fletcher, 2001) also seemed in evidence in this population of western lowland gorillas.

No evidence suggested that offspring sex or group, or parity of the mother influenced the way in which independence developed in immature gorillas, although such differences may have been difficult to detect given the nature of the bai environment. Differences were suggested between the sexes in the percentage of time spent in close contact, age at weaning and the mother's tolerance to suckling, but further research, preferably in the more usual forest habitat may help to establish whether such sex differences do exist. Results from this study must be interpreted with the proviso that the bai habitat may have affected which behaviours were performed, and also that their frequencies and rates might be altered from the usual forest environment. It is becoming clear that the ecology of a species affects the development of independence from the mother: in species where resources are widely dispersed, both in space and in time, it follows that a longer period of growth and development will be necessary before development of independence from the mother is likely to be followed by a successful transition to adulthood. This idea is developed further in Chapter Seven.

CHAPTER FIVE

RELATIONSHIPS OF IMMATURES WITH ADULT GROUP MEMBERS, AND WITH OTHER GROUPS

5.1. INTRODUCTION

Most young gorillas live in a dynamic and socially complex environment (Stewart & Harcourt, 1987; Tutin, 1996; Yamagiwa & Kahekwa, 2001), and as with other group-living primates, young gorillas' associations and interactions with related and unrelated individuals facilitate their assimilation into the social group (Fairbanks, 1993; Berman et al., 1997; Brent et al., 1997). Primate mothers and infants influence, and are influenced by, other group members; a mother's sociability and her response to the social milieu can have long term effects on her infant's social networks (Horvat & Kraemer, 1981; Tomasello et al., 1990; Berman et al., 1997).

Immature primates are predicted to form relationships with individuals who are useful current social partners (Nikolei & Borries, 1997), as well as those likely to influence their competitive ability as adults (Fairbanks, 1993). However, if both sexes disperse from the natal group, current group members will be of limited future benefit (Fairbanks, 1993). In eastern lowland and mountain gorillas, individuals have been known to transfer together, or into groups which contain previous members of their natal group, so in these cases, there may be some future benefit of investing in relationships with natal group members (Watts, 1991a; Yamagiwa & Kahekwa, 2001). One western lowland gorilla study has shown high levels of relatedness between females from neighbouring groups, suggesting in that region, females did not disperse far from their natal group (Jeffery et al., 2004). Therefore, benefits may also exist for western lowland gorillas of investing in relationships within the natal group.

Relationships, characterised by spatial proximity and interactions, between immature gorillas and adult group members are expected to differ according to the age and sex of those involved (e.g., Stewart, 1981; Fletcher, 1994). Other factors influencing these relationships may include relatedness (Watts, 1994c), the size of the social group and, therefore, levels of competition (Watts, 1985b), and the presence or absence of the mother (Stewart, 1981; Fletcher, 1994). Relationships are expected to change as immatures increase in age, become independent members of the group, and become involved in group dynamics.

In this chapter, the role played by adult group members (which in this study, are silverbacks, adult females and blackbacks) in the development of immatures will be investigated, first by considering proximity between individuals. Spatial patterning provides information on the nature of the relationship between individuals, with closer proximity representing a stronger relationship (e.g., Harcourt, 1979b; Watts, 1994c; Brown, 2001b; Nakamichi & Kato, 2001; Stewart, 2001). Second, the nature and frequency of interactions involving immatures will be considered to provide information on the social position of immatures, relative to adults, within the social group.

5.2. RELATIONSHIPS BETWEEN IMMATURES AND SILVERBACKS

In gorillas, the cost to the mother of transporting a single infant is relatively low, as a result of the low infant/maternal weight ratio (Wright, 1990), and male contribution to care of the offspring appears to be limited to protection from predation and infanticidal males (Palombit, 1999; Stewart, 2001). Infanticide can occur when female mate selection leads to the exclusion of some males from the mating process (van Schaik & Kappeler, 1997; Watts, 1989), as is the case in gorillas (Sicotte, 2001). In order for males to act as protectors against infanticide, a degree of paternity certainty is a prerequisite (Wright, 1990; van Schaik & Kappeler, 1997; Borries et al., 1999). In groups with more than one adult male, the past sexual relationship with the mother is used to assess the likelihood of paternity (Enciso et al., 1999; Buchan et al., 2003), and “phenotype matching” may also be involved (Alberts, 1999; Buchan et al., 2003). In the single-male groups at Mbeli, paternity certainty is expected to be high, and:

- Higher levels of investment (indicated by proximity and the nature of interactions) by the silverback are predicted to be directed towards related offspring rather than unrelated immature group members.

Male primates’ reactions towards immature group members are often simply tolerance, with immatures playing the greater role in the initiation and maintenance of affiliative interactions. This suggests that the immature individual benefits more from the association (Fairbanks, 1993; Stewart, 2001), and that a silverback provides a novel stimulus to which young gorillas are drawn. Studies regarding relationships between silverbacks and offspring in wild mountain gorillas describe an increase in association with the silverback with increasing offspring age, a general preference for the dominant silverback where more than one is present within a group, and relatively infrequent grooming, intervention and aggressive interactions, and transport of infants by silverbacks (see Stewart, 1981; Fletcher, 1994; Stewart, 2001; Warren & Williamson, 2001). Therefore, as a result of the attractiveness of the silverback to immature group members, and to allow him to protect his offspring successfully:

- Proximity between immature individuals and the silverback male is expected to increase, as immatures mature.
- An active relationship is not expected to increase the effectiveness with which silverbacks can protect infants from infanticide, therefore, interactions between immature gorillas and silverback males are predicted to be mostly initiated by the immature, but rare. Silverbacks are expected to respond to offspring with indifference, but with a degree of tolerance.

Silverbacks have been found to differ in their propensity for interaction with immature group members; for example, in Stewart's (2001) study, one silverback performed the majority of grooming with immatures, whereas other silverbacks tended to primarily receive grooming. Therefore:

- Any differences between groups in the nature of the immature-silverback relationship may represent individual silverback differences in the attitude and tolerance towards immature within his social group, or, to an extent, the genetic relationship between silverbacks and immatures.

In both mountain and captive western lowland gorillas, the silverback has been described as providing a spatial focus for immatures within the group, with young individuals often leaving the proximity of the mother to be closer to him (Fletcher, 1994; Enciso et al., 1999; Stewart, 2001). Silverbacks have acted as attachment figures for maternal orphans in mountain gorillas, which can increase the likelihood of an orphaned individual surviving (Fossey, 1983; Stewart, 2001). Similar findings have resulted from studies on chimpanzees, but with older siblings usually taking over the care of young orphans (Goodall, 1986). Close association between mother and offspring and suckling persists well into the juvenile period in gorillas, suggesting that older offspring continue to benefit from the relationship with the mother. Although few of the orphaned immatures in this study were the offspring of the silverback, and all were nutritionally and physically independent of the mother:

- Immatures without a mother present in the social group were predicted to show a stronger relationship with the silverback, if the silverback acts as an attachment figure in the case of the death or disappearance of the mother.

For adult male and female gorillas the relationship between them is the most important in the social group (Harcourt, 1979b; Stokes, 2004). As a result, differences between males and females in the relationship with the silverback may appear during immaturity. Immature females may be expected to have more affiliative relations with the silverback: if they are not related to him, they are potential mates, and if they are related, young females can still gain experience in male-female interaction for the future, which may indirectly increase a silverback's success as well as their own (Stewart & Harcourt, 1987; Fairbanks, 1993; Watts & Pusey, 1993). Conversely, immature males may be viewed as potential competitors and be more likely to receive aggression. Although in mountain gorillas, the relationship between immatures and the silverback may influence whether males will remain in the natal group to breed (Harcourt & Stewart, 1981), the majority of western lowland gorilla males leaving the natal group (Parnell, 2002b; Stokes et al., 2003), suggest that relationships between immature males and silverbacks will be fairly uniform. The nature of relationships between immature males and the silverback may be unlikely to effect *whether* males emigrate, but may influence the age at which they do so. Therefore:

- Relationships between immature females and silverbacks may be stronger than those between immature males and silverbacks, if the investment in a relationship with the silverback can increase a female's reproductive success. However, the likely eventual dispersal of both sexes from the natal group predicts that any differences between males and females in their relationship with the silverback are likely to be minimal.

Only preliminary investigations into silverback-immature behaviour in western lowland gorillas have previously been conducted in the wild (Nowell, 2001). The predictions that have been outlined are tested in the following section to determine how, in western lowland gorillas, aspects of socioecology, such as the likely eventual dispersal from the natal group, the protection required from silverbacks against infanticide, and individual differences between silverbacks influence the development of relationships between group silverbacks and immatures.

RESULTS

5.2.1. SPATIAL RELATIONSHIPS WITH THE SILVERBACK

In this and the following chapter, both the percentage of time that study subjects spent within 2m, 2-5m, 5-10m, and more than 10m from other individuals, in this section, the silverback, and the modal distance category to other age-sex classes are used to quantify the spatial relationships of study subjects. In analyses where infant, juvenile, sub-adult and adult age classes are compared, study subjects contributed data to only one age class if the range of ages during which they were observed crossed an age class transition, thereby providing independence of age classes.

Six study subjects did not contribute data to the analysis of the immature relationship with the group silverback, as they were never, or very infrequently observed in the bai with the silverback. All groups (with the exception of the UKSB - Unknown Silverback group) were known to contain only one fully adult silverback male.

5.2.1.1. Contact with the Group Silverback

Contact between immatures and the group silverback was rare, and not a feature of the relationship between them. Contact was recorded *ad libitum* on seven occasions, involving five study subjects. On five occasions, immatures reached out to touch the silverback, which the silverback ignored. One instance recorded an infant and juvenile lying resting in contact in the bai with the silverback. A final instance saw an infant make contact with the silverback when trying to move past the silverback on a submerged log. This was the only occasion on which a silverback directed attention towards an immature of any age: he attempted to let the infant past him on the log by adjusting his stance.

5.2.1.2. Influence of Immature Age on Proximity to the Silverback

As young primates increase in age and become more independent, they are expected to increase proximity to all group members (Nakamichi, 1989; Berman et al., 1997; Nikolei & Borries, 1997), including, in gorillas, the silverback male. Data in this section are taken from scan samples, and analyses are performed on the median percentage of scan samples immatures and silverbacks spent in each distance category from one another, and the modal distance category between them.

There was no change over immaturity in the percentage of time that immatures spent in any of the distance categories to the silverback (**Figure 5.1**: 0-2m: r_s = 0.385, n = 19, *P* = 0.104; 2-5m: r_s = -0.027, n = 19, *P* = 0.912; 5-10m: r_s = 0.003, n = 19, *P* = 0.991; 10m plus: r_s = 0.182, n = 19, *P* = 0.457).

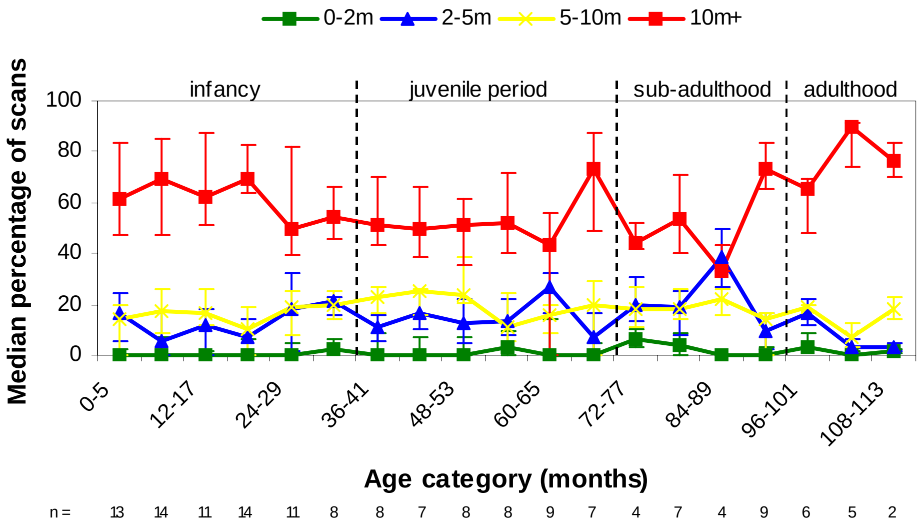


Figure 5.1. The median percentage of time spent at each distance category from the silverback by study subjects. N_{TOTAL} = 52.

There were no differences between age classes in the percentages of time that individuals spent 0-2m, 2-5m or 5-10m from the silverback (**Figure 5.2**: 0-2: χ^2 = 2.976, d.f. = 3, *P* = 0.395; 2-5m: χ^2 = 6.097, d.f. = 3, *P* = 0.107; 5-10m: χ^2 = 5.058, d.f. = 3, *P* = 0.168). However, a significant difference was found between age classes in the percentage of time spent more than 10m from the silverback (χ^2 = 8.680, d.f. = 3, *P* = 0.034). Post hoc multiple comparison tests could not determine where the differences lay, but juveniles and sub-adults seemed to spend less time at this distance to the silverback than infants and adults did. There were no differences between age classes in the modal distance category to the group silverback (χ^2 = 4.806, d.f. = 3, *P* = 0.187).

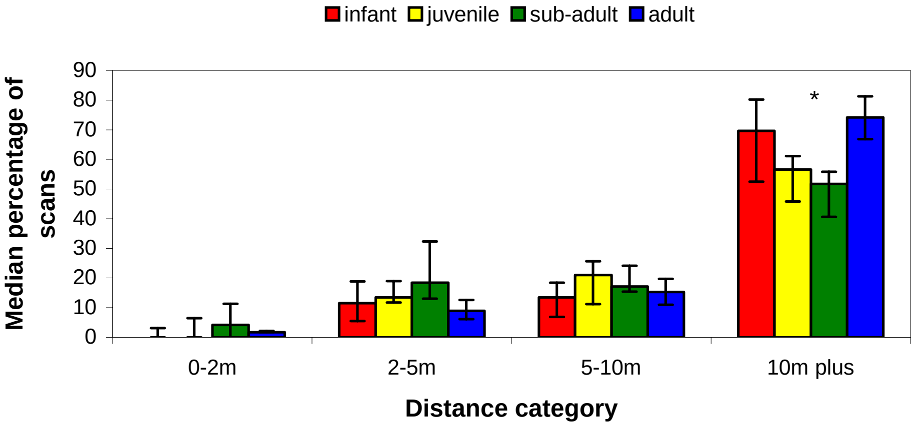


Figure 5.2. Comparisons of the percentages of time spent at each distance category to the silverback by infants, juveniles, sub-adults and adults. * indicates a significant different at the 0.05 level. $N_{infants}$ = 24, $N_{juveniles}$ = 14, $N_{sub\text{-}adults}$ = 10, N_{adults} = 4.

5.2.1.3. Effect of Immature Sex on Proximity to the Silverback

If differences exist between males and females in their relationship with the silverback, females were predicted to be more likely to benefit more from a stronger relationship with the silverback, by either providing them with potential mating opportunities, or by gaining experience in male-female interaction (Watts & Pusey, 1993).

As predicted, the median percentage of scans in which male infants were found further than 10m from the silverback tended to be greater than for females (**Figure 5.3**: infants: U = 19.0, $N_{males,\ females}$ = 18, 5, P = 0.053). However, no differences were detected between males and females when tests matched for age were carried out (0-2m: Z = -0.524, n = 15, P = 0.600; 2-5m: Z = -0.341, n = 15, P = 0.733; 5-10m: Z = -1.250, n = 15, P = 0.211; 10m plus: Z = -0.568, n = 15, P = 0.570). Additionally, tests matched for age showed no difference between males and females in the modal distance category to the group silverback (Z = -1.000, n = 15, P = 0.317).

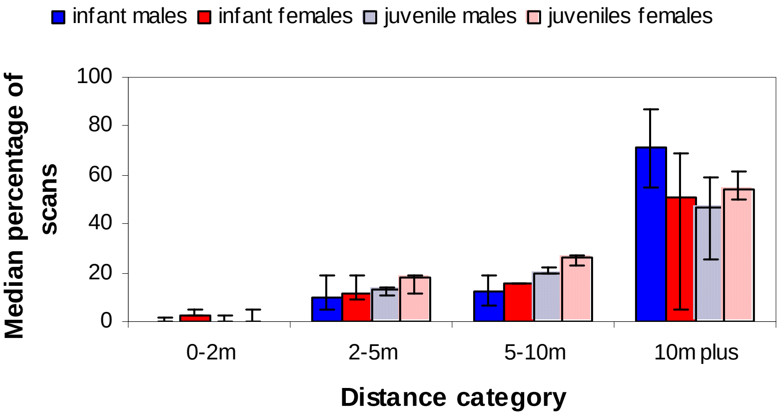


Figure 5.3. Comparison of the median percentage of scan samples spent in each distance category from the silverback for males and females. Infants: $N_{\text{males, females}} = 17, 4$; juveniles: $N_{\text{males, females}} = 4, 5$.

5.2.1.4. Effect of the Social Group on Proximity to the Silverback

An investigation of differences between groups was conducted to elucidate the effect of group size and composition on immature-silverback spatial proximity, individual differences between silverbacks in their tolerance of immature group members, or the relatedness between silverbacks and immatures. Due to small sample sizes, modal distance categories were calculated from all study subjects within the group regardless of age. The previous section showed that the effects of age on silverback proximity were minimal: therefore, any group differences should not be obscured.

The social group did affect the percentage of time that immatures spent within 2m, 2-5m, and 10m plus from the silverback, but not the percentage of scans spent 5-10m from the silverback (**Table 5.1**). Post hoc multiple comparison tests revealed only that immatures in Kha group spent significantly less time within 2m of the group silverback than did individuals in Bea and Dwa groups.

Table 5.1. Results of Kruskal-Wallis tests to investigate the effect of immature group on the proximity between immatures and the group silverback.

	0-2m	*2-5m*	*5-10m*	*10m plus*
X^2	29.141	20.427	9.304	19.276
d.f.	10	10	10	10
P	0.001	0.025	0.503	0.037

A significant difference between groups in the modal distance to the silverback was found (**Figure 5.4**: $\chi^2 = 31.625$, $N_{groups} = 11$, $P < 0.0001$). Immatures in Bea group showed clearly different patterns to the others, with both individuals being most commonly found at distances less than 10m from the silverback. Of the groups considered in this section, Bea group experienced some of the most major demographic changes during the study, with four individuals (including the two immatures) joining the previously solitary silverback, Bear, after being observed without a silverback in the bai.

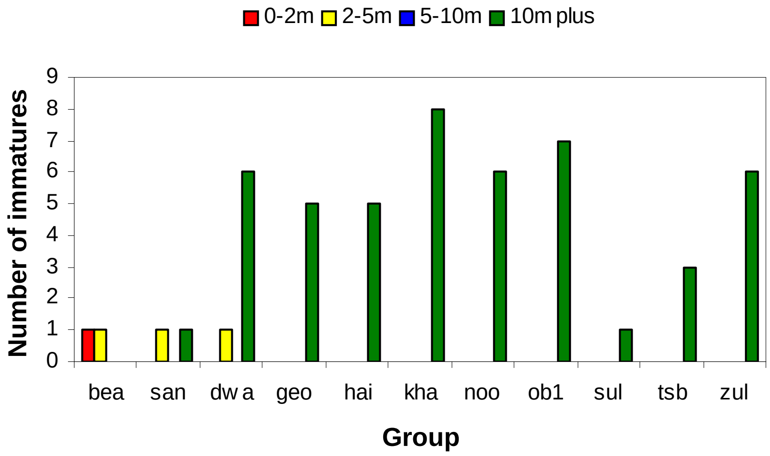


Figure 5.4. Differences between groups in the modal distance category between study subjects and the silverback.

5.2.1.5. Presence of the Mother and Distance to the Silverback

Immature gorillas remain close to the mother even when physically and nutritionally independent (Stewart, 1981; Fletcher, 1994; Nowell, 2001), Chapter Four). The mother may act as a buffer against the potential of aggression from other group members (Stewart, 1981), and so maternal orphans may instead seek the silverback as an attachment figure, or to intervene in any cases of aggression directed towards them (Stewart, 2001).

In most cases (n = 11) where the mother of a study subject was not present in the group, the study subject was not the offspring of the group silverback. Three other individuals had no mother in their current group due to her death or emigration, but were the offspring of the silverback. Two subjects who were not the offspring of the group silverback did have a mother present. However, the presence of the mother had no effect on the distance at which juveniles and sub-adults (there were no infants without mothers present, and no adult with mothers present) were found from the silverback, with a test matching for age categories showing no significant differences in their modal distance to the silverback ($Z = -1.342$, n = 8, $P = 0.180$). Thus, there was no evidence that the silverback acted as an attachment figure for orphans.

5.2.1.6. Paternity Confidence

In 13 cases, the silverback was known to be unrelated to immatures within the group. These individuals had either been previously observed in the known natal group, and following its disintegration, had immigrated into another group (n = 5), or had immigrated into a study group from outside the Mbeli population (n = 8). The 39 remaining study subjects were assumed to be the offspring of the silverback of the current group, having been observed in these groups from an early age, usually in the presence of the mother. Paternity certainty is predicted to influence the degree of paternal care (Wright, 1990), so proximity to the silverback for offspring and non-offspring were investigated to determine whether silverbacks invest preferentially (by maintaining closer distances, and thus being able to better protect) in their own offspring.

The modal distances between putative offspring and non-offspring of the group silverback were compared, and results of tests matched for age showed no differences in their modal distance categories to the silverback ($Z = -0.816$, n = 16, $P = 0.414$). Sample sizes for non-offspring were very small, so results should be interpreted cautiously, but suggest that no preferential investment in offspring was made.

5.2.2. INTERACTIONS WITH SILVERBACKS

As a result of the increase in independence from the mother (see Chapter Four), immatures' social position in the group should change as they begin to encounter other group members more frequently (Altmann, 1980; Pereira & Altmann, 1985; Brent et al., 1997). The nature and frequency of different interaction types (**Table 5.2**) between study subjects and other group members provide an indication of the influence of adults on social development, but due to low frequencies of many interaction types, actual frequencies do not take into consideration differences between individuals.

Table 5.2. Definitions of all interaction types in which study subjects were involved with group members other than the mother.

Interaction Type	***Definitions***
§* Food transfer	The movement of solid food between individuals
§* Intervention	Where the behaviour of an individual prevents the possibility of interaction between two other individuals
Positive interactions	
Affiliation	Instances of touching, embraces and "kissing"
Alloparental	Care (usually transport) of an infant by an individual other than the mother
Grooming	One individual manipulates the hair of another using hands, teeth or lips
Play	Chasing and wrestling, or mock biting of an individual by another, with no apparent agonistic elements, and often accompanied by a play face
* Proximity seeking	One individual establishes contact with, or seeks the proximity of another and moves to within 2m of them without feeding. No other interaction type follows.
* Socio-sexual	Mounting behaviour, sniffing or touching of the ano-genital region of one individual by another

Negative interactions	
Agonistic	Instances of aggressive displays, hitting, slapping, cough grunting, biting and pushing
Displacement	The approach of one individual results in another individual moving away from their previous position
Play agonism	Mock display behaviour, wrestling, and chasing which was unlikely to escalate into serious aggression that could cause injury. Usually ignored by silverbacks

§ Category could not be defined as positive or negative

*Observed infrequently, so not considered in great detail in this chapter.

Previous studies in wild mountain gorillas have described silverbacks as being an attractive group member with whom to interact, increasingly so as immatures increase in age (Stewart, 1981; Fletcher, 1994). The nature of interactions between immatures and silverbacks are investigated here to further test the hypothesis that silverbacks are attractive to immature group members.

Of the 52 immatures present in a group with the silverback, only 19 (36.5%) interacted with the silverback in a total of 55 interactions, consisting of agonism, displacements (negative interactions), affiliation and proximity seeking (positive interactions). The median age (53 months: range: 8 - 107 months) of those that did interact with the silverback was significantly greater ($U = 207.5$, n = 19, 35, $P = 0.024$) than those who did not (median: 29 months).

Interactions between immatures and silverbacks were not evenly distributed by type (**Figure 5.5**: $\chi^2 = 24.0$, d.f. = 3, $P < 0.001$), with displacements being most common, followed by agonistic interactions. Immatures who were involved in displacement interactions were significantly older than those involved in other interaction types (**Figure 5.5**: $U = 75.0$, n = 14, 20, $P = 0.023$); however, no significant difference between ages was detected when interactions were divided into positive and negative types ($U = 57.5$, n = 23, 8, $P = 0.119$). Negative interactions (n = 40) occurred approximately four times as frequently as positive interactions (n = 12), and were almost exclusively initiated by the silverback. Conversely, positive interaction types tended to be initiated by immatures (**Figure 5.5**), suggesting that immatures were drawn to the silverback, but he was likely to be intolerant of them.

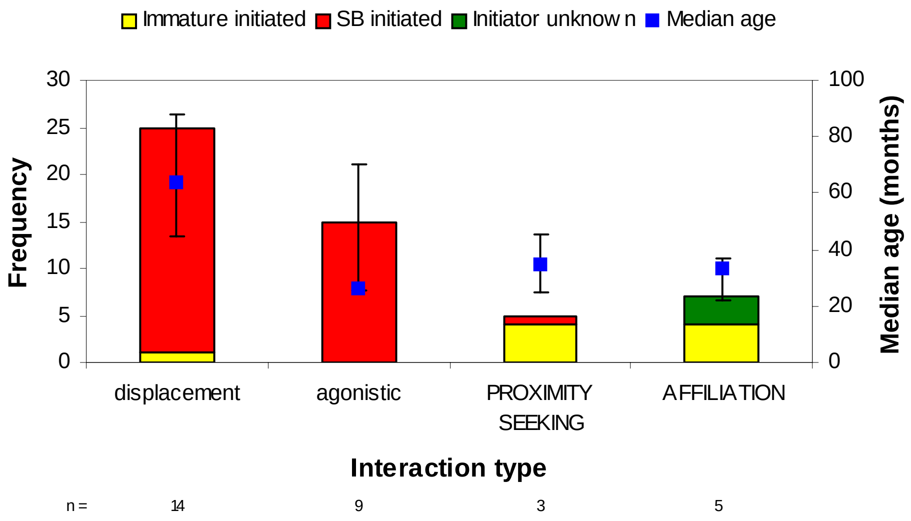


Figure 5.5. The frequency and initiators of different interaction types with the silverback, and the median ages of immatures who engaged in them. Negative (lower case) and positive (upper case) interaction types are grouped. $N_{TOTAL} = 19$.

5.2.2.1. Negative **i***nteractions*

Displacements

Juveniles and sub-adults were the most frequent recipients of displacements by the silverback, receiving nine and ten displacements respectively, with infants receiving three and young adults, two. The median rate of displacements received by immatures from silverbacks was calculated by dividing the frequency of displacements per age category by the number of hours spent in the bai for each age category for each study subject, allowing an age category median to be calculated. Only one infant was recorded to “displace” a silverback, as per the definition, but the motivation of the displacing infant was unlikely to be the same as that of displacing silverbacks, and was not considered further. There was no correlation between the rate of displacements received from the silverback and age category, either overall ($r_s = 0.002$, n = 19, $P = 0.993$), or within age classes (infants: $r_s = 0.101$, n = 6, $P = 0.846$; juveniles: $r_s = 0.698$, n = 6, $P = 0.123$; sub-adults: $r_s = 0.211$, n = 4, $P = 0.789$; adults: all medians = 0).

There were too few displacement interactions to warrant further statistical analysis, but **Figure 5.6** presents the data for displacements received from silverbacks, broken down by social group. The highest rates of displacements were received from the silverback during the juvenile period, with all silverbacks but one

(OB1 silverback) observed to displace a juvenile at some point. Again, the data were insufficient to allow testing for differences between the sexes, with only six males (12%) and three females (27.3%) involved in displacement interactions, although these numbers suggest that females may be the more frequent recipients.

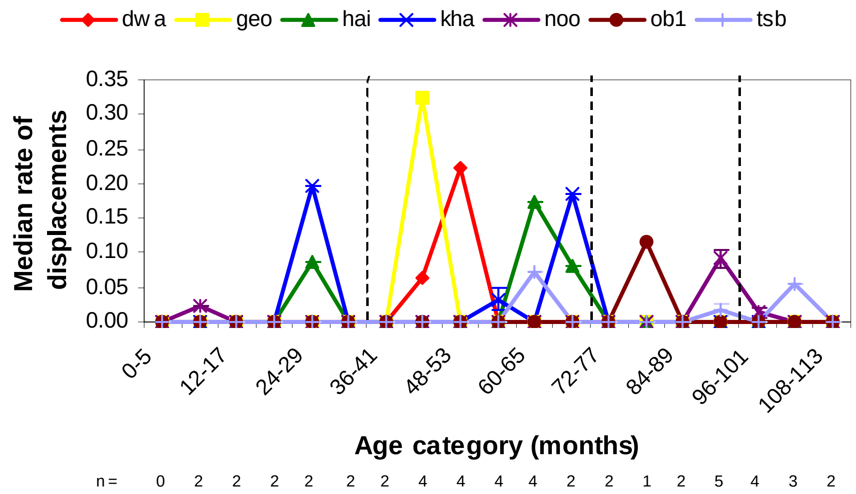


Figure 5.6. Distribution of displacements received from the silverback in each group. $N_{dwa} = 1$, $N_{geo} = 1$, $N_{hai} = 2$, $N_{kha} = 3$, $N_{noo} = 3$, $N_{OB1} = 1$, $N_{TSB} = 3$.

Agonistic Interactions

Agonism between immatures and silverbacks was performed solely by silverbacks on only 15 occasions, and took the form of cough grunts (46.7% of all agonism) and displays (53.3%). The only discernable cause was proximity-related, accounting for 40% of agonistic interactions. Agonism was directed towards five infants, two juveniles, two sub-adults, and one adult. The rate of agonistic interactions (calculated in the same way as for displacements) was not correlated with immature age category ($r_s = 0.125$, n = 17, $P = 0.623$). Too few data were available to analyse the effects of immature sex and social group on agonistic interactions. However, in study subjects of known sex, three (of 25) males and four (of 11) females were involved, again implying that levels of agonism from silverbacks towards females were greater than towards males. Of the fifteen agonistic interactions, seven were directed towards the four females, and five towards the three males, so at least for certain females, rates of received agonism seemed higher. This corresponds with adult behaviour, where silverbacks assert dominance over females in an attempt to retain mates within the social group (Harcourt, 1979b; Watts, 1992; Stokes, 2004), but when females are infants and the offspring of the silverback, the underlying motivation of the silverback is likely to be different. Two of the females (one young adult and one infant) to which agonism was directed by silverbacks were unrelated to the silverback.

5.2.2.2. Positive Interactions

Affiliation

Affiliation between immatures and silverbacks was recorded on seven different occasions, involving three silverbacks and five immatures. Its infrequency suggested affiliation was not an important part of the immature-silverback relationship. Affiliation was more common between infants (n = 6) and silverbacks than juveniles and silverbacks (n = 1). When initiators could be determined, silverbacks never initiated an affiliative interaction, whereas immatures were the initiators on four occasions (n = 3). The majority of affiliation (85.7%) took the form of immatures touching or embracing the silverback, but grooming of the silverback was recorded on one occasion. In only one instance did the silverback respond to an immature in response to affiliative contact being made: Dwayne turned to look at Peapod, but then continued feeding.

Proximity Seeking

Five instances of proximity seeking were observed between immatures and the group silverback, involving two infants and one juvenile (who had no mother present in the group). All instances were initiated by the immature, and took the form of moving to within 2m of the silverback without feeding, and in the majority of cases, seemed to be for reassurance.

5.2.3. DISCUSSION OF IMMATURE-SILVERBACK RELATIONSHIPS

Obvious forms of paternal care that are seen in species that engage in communal care of offspring (for example, carriage of offspring, provision of food (Goldizen, 1987;

Wright, 1990)), do not occur in gorillas, and paternal care instead seems limited to protection from predation and infanticide (Watts, 1989; Stewart, 2001). To be effective, the silverback must remain vigilant and react to the presence of potential predators or infanticidal males (e.g., Watts, 1989; Reichard & Sommer, 1997; Palombit, 1999), but simply the presence of a silverback may provide a deterrent to initiating aggression towards his offspring. At Mbeli, paternity certainty was assumed to be high, with only one adult silverback present in each group, although the potential for "extra-pair" copulations is presumed to exist. Genetic analysis of faecal samples from Mbeli is underway to confirm relatedness between individuals. In circumstances where immatures were not the offspring of the group silverback, a different relationship to that between father and offspring was expected. In this study, unrelated immatures immigrated into groups, and therefore, silverbacks should be aware that these individuals were not their own offspring. However, results did show that:

- Paternity was not found to affect proximity between immatures and silverbacks, perhaps because the type of paternal care provided by the silverback cannot be easily divided to benefit genetic offspring and avoid investment in non-related individuals. Silverbacks appeared to show little active investment in their own offspring, so it was unsurprising that unrelated individuals did not receive less.

Individuals immigrating into groups were predominantly of an age when the maternal relationship (in terms of proximity) still was of importance, but having already successfully transferred between groups on their own, they must gain acceptance from members of the new group to avoid being targets of aggression. The silverback is clearly the most dominant individual within a social group (Stewart & Harcourt, 1987; Watts, 1996b; Parnell, 2002b), and therefore, his acceptance is essential to enable newly immigrated individuals to remain (Watts, 1990c). This is likely to be more important for males than for females, since the latter should be welcomed as they represent future breeding opportunities, but data were insufficient to test this. Although more common in younger individuals who are unable to survive without the mother, previous studies in mountain gorillas have found that the absence of the mother can lead to the silverback acting as a maternal attachment figure (Fossey, 1983; Stewart, 2001). However, in this study:

- The absence of the mother of study subjects did not appear to affect the relationship between immature and silverback. There was no evidence that maternal orphans used the silverback as an attachment figure in the absence of the mother.

Seemingly without exception, previous studies on mountain and captive western lowland gorillas have shown that immature individuals are attracted to, and increasingly seek the proximity of the group silverback as they increase in age (e.g., Tilford & Nadler, 1978; Fletcher, 1994; Enciso et al., 1999; Stewart, 2001). However, in this study, the most noticeable feature of the relationship between immatures and the silverback was that:

- Proximity to the silverback did not increase as immatures increased in age and began to move away from the mother, but instead remained at low levels throughout the immature period. This suggests, at least in a bai environment, that close proximity to the silverback is not necessary in order to receive protection from infanticidal males and predators.

Corresponding with the lack of close proximity observed between silverbacks and immature group members:

- Interactions between study subjects and group silverbacks occurred infrequently, and were more likely to be negative in nature, rather than positive.

Silverbacks were not observed to play an active role in the socialisation of their offspring, further suggesting that the type of paternal care provided by silverbacks does not require close association and affiliative interaction with immatures. Interactions initiated by study subjects were predominantly affiliative, showing that immatures were drawn to the silverback, but that the silverback inhibited more frequent interactions or closer proximity. Data from captive gorillas have shown silverbacks to pay great attention to offspring, and initiate interactions with particularly young infants (Tilford & Nadler, 1978; Hoff et al., 1982; Enciso et al., 1999). This interest in infants by the silverback may be a consequence of captivity, or only possible when resources are not constrained. In the current study, the reaction of the silverback in most interactions with immatures tended towards intolerance, such has been hinted at in studies of wild mountain gorillas, particularly during feeding periods (Stewart, 2001), and exemplified by the frequency of displacements.

Because of the great size of silverbacks, they require large quantities of food (Remis, 2000), and consequently, their tolerance of younger group members, regardless of relatedness, may have been affected by the collection of data during feeding periods (*sensu* Harcourt, 1978a). No data exist for the relationship between silverback and immature western lowland gorillas during non-feeding periods. It was impossible to determine if the results reported here were representative of the more general nature of the relationship between western lowland gorillas immatures and silverbacks in the wild or if they arose from the nutritional demands on a silverback and were limited to feeding periods.

An additional possible effect of the bai is that due to high levels of visibility, the need for close proximity between immatures and silverbacks to enable the silverback to protect individuals within his group may be reduced. However, studies conducted in the forest have documented very large group spreads (up to 500m) in western lowland gorillas groups (Tutin, 1996; Remis, 1997a; Bermejo, 2004), so in the forest, it does not appear that close proximity is always required to enable the silverback to protect offspring. Group spread in the bai is rarely more than 100m (pers. obs.), so groups may be more cohesive in the bai than in the forest, and consequently immature-silverback association (and potential for interaction) recorded here may be greater than in the normal forest, ultimately due to the abundance of resources in the bai.

As with mother-offspring relationships, it would have been useful to investigate the maintenance of proximity between silverbacks and immature group members, but too few data were available to provide meaningful analyses. Using approaches and leaves to within 5m, and Brown’s index (Brown, 2001b), which measures the percentage of *changes* in proximity that an individual is responsible for, available data suggested that immatures tended to be more responsible than silverbacks for changes in their proximity to one another, again, suggesting that immatures were drawn to the silverback. More data are needed to confirm these preliminary findings.

Stewart (2001) described individual differences between silverbacks in relation to interactions with immatures. Results from the present study showed:

- Differences between groups were found in immature proximity to the silverback. The individuals in the majority of groups had modal distances of greater than 10m to the silverback, but individuals in three groups were found at closer distances.

It was impossible to determine the extent to which immatures or silverbacks were responsible for these differences, and with the exception of demographic changes influencing spatial patterning in Bea group (which will be discussed with relation to both adult females and blackbacks in the relevant sections in this chapter), individual differences between immatures seemed more likely to account for these differences.

In addition:

- No *significant* differences between immature males and females were found in any aspect of the immature-silverback relationship, with neither sex appearing to invest heavily in the formation of a strong relationship with the silverback. There was a tendency for females to receive more agonism from silverbacks than males, which may have reflected a male mating tactic to retain females within the group.

Since paternity, social group and sex of the immature had limited effects on proximity to the silverback, other factors were assumed to be involved in determining spatial proximity between immatures and silverbacks. Interestingly, in the two groups with closer proximity between silverback and study subjects, none of the study subjects (three in TSB group, two in Bea group) were the offspring of the silverback, and both had immigrated into the groups either during or shortly before the start of the study. Recent changes in demography may, therefore, influence spatial relationships within groups, but more evidence is needed to confirm this.

When the presence of an unrelated suckling infant prevents a male from increasing his own reproductive success by conceiving offspring with its mother, infanticide can result (Watts, 1989; van Schaik & Kappeler, 1997; Palombit, 1999). Mbeli Bai Study long term records suggest that older silverbacks may be more tolerant of transferring, unrelated immatures, perhaps since they were unlikely to father more offspring. Consequently, groups led by older silverbacks may provide a safe “holding ground” for immature individuals old enough to survive without the mother, but not yet capable of surviving alone (males only), and for females with suckling infants.

In mountain gorillas, immature males often immigrate into a bachelor group following the disintegration of their natal group (Robbins, 2001). Immatures in the Mbeli population seem, instead (given the lack of bachelor groups in the visiting Mbeli population, and the frequency with which unknown immature individuals immigrate into known Mbeli groups), to join a reproductive group with an older silverback following group disintegration. Many immature individuals immigrating into groups remain to be sexed before this can be shown to be an alternative to joining bachelor groups, but preliminary data from Lokoué Bai in Congo (F. Levrero, pers. comm.) also suggest that joining a reproductive group as a juvenile might provide an alternative to joining an available (Gatti et al., 2004b) bachelor group.

In multi-male mountain gorilla groups, male-male competition is assumed to exist (Sicotte, 1993; Robbins, 2001), and in captivity, the female-silverback relationship is the factor most likely to influence whether mating will occur (Tilford & Nadler, 1978). If this also applies to wild western lowland gorillas, then males spending more time in association with females can expect to gain matings (see Smuts, 1983). It may also be the case that by investing in relationships with immature gorillas, a silverback can increase the chance that he will gain future matings with the mother of the immature (see Smuts, 1983; Stewart, 2001). However, at Mbeli with only one adult male present in each group, within-group male competition was negligible (see Jack & Fedigan, 2004b). Therefore, in the absence of within-group competition, the silverback-offspring relationship may carry less weight in determining the mating success of males, and less effort needs to be invested by silverbacks to maintain relationships with the offspring of potential future mates.

So, silverbacks were observed to make minimal active contributions to immatures within their group, regardless of relatedness. This was in spite of occasional attraction of immatures to the silverback, which resulted in displacement and agonism received by immatures. The collection of data during feeding periods may be the overriding reason for this, or the large size and uneven resource distribution may result in a limited tolerance of immatures by western lowland silverbacks, whose primary concern is the acquisition of sufficient resources. The lack of close proximity and affiliative interactions between immatures and silverbacks observed in this study contrasts with the tolerance of immatures by silverbacks in mountain and captive gorillas, and provides new insight into the relationship that exists between immature and silverback western lowland gorillas, living within the constraints of an unpredictable environment.

5.3. RELATIONSHIPS BETWEEN IMMATURES AND ADULT FEMALES

Immature gorillas are unlikely to be related to adult females other than the mother within the social unit, given the absence of female philopatry as a common tactic in gorillas (Watts, 1996b; Doran & McNeilage, 1998). Consequently, relationships with adult females are predicted to be weak, as has previously been observed in mountain gorillas (Fossey, 1979; Stewart, 1981; Fletcher, 1994). High rates of natal dispersal by both males and females in western lowland gorillas, (Stokes et al., 2003; Robbins et al., 2004) suggests that investment in strong relationships with adult females will have limited future benefit (*sensu* Fairbanks, 1993), except where individuals transfer together, or into groups that female relatives have already transferred into (see Jeffery et al., 2004).

Studies of mountain gorillas have shown the silverback to be particularly attractive to new mothers, resulting in a gathering point for mothers and infants (Harcourt, 1979b). The previous section failed to find evidence that during bai visits, silverback provide a spatial focus, however, a possibility exists that mountain gorilla females with new infants were also attracted to each other, as well as to the silverback. Therefore, in this study:

- Spatial proximity between immature individuals and unrelated adult females is expected to remain low throughout the immature period, with the possible exception of an initial period during infancy when new mothers are attracted to one another.

Previous mountain gorilla studies have shown adult females to be the age-sex class most likely to direct aggression towards immature group members (Stewart, 1981; Fletcher, 1994). Unrelated immatures, regardless of their sex, provide competition for a female's offspring, and as they mature, for the female herself (Pereira & Altmann, 1985; Nicolson, 1987), in terms of both feeding (more so when resources are limited) and receiving protection from the silverback. Mothers are expected to act to improve their offspring's competitive ability, and chances of survival and reproductive success (Pereira, 1995). Consequently:

- Any interactions between immatures and unrelated adult females are likely to be agonistic, and directed from adult females towards immatures.

- Females are not predicted to differentiate between unrelated male and female immatures, and therefore, adult female-immature relationships are expected to be constant regardless of immature sex.
- In larger groups (therefore, with higher levels of competition between group members (see Watts, 1985b; Chapman & Chapman, 2000), unrelated immatures are predicted to be the recipients of more agonism from adult females than those in smaller groups.

The parity of a female may influence relationships with immatures, with nulliparous females likely to show less aggression towards unrelated immatures given they have no infant for whom unrelated immatures provide competition. Young nulliparous females are also the age-class most likely to be involved in alloparental behaviour (Lancaster, 1971; Hrdy, 1976; Hiraiwa, 1981; Nishida, 1983; Silk, 1999), and generally have a relatively more playful nature (e.g., Fletcher, 1994) than older females do. This leads to the prediction:

- Female parity is the factor most likely to influence the relationship between adult females and immatures, with younger, nulliparous females expected to engage in less agonistic behaviour with immatures than do parous females.

Overall, indifference is expected to characterise relationships between immatures and unrelated adults, but when interactions occur, they are more likely to be agonistic, particularly when females are parous or the group is large. The following section tests these predictions in order to elucidate the nature of relationships between immature gorillas and unrelated females, and the effect of female competition.

RESULTS

5.3.1. SPATIAL RELATIONSHIPS WITH ADULT FEMALES

As in the previous section, the percentage of time spent within each distance category (contact, 0-2m, 2-5m 5-10m and 10m plus) from other individuals was calculated for each study subject at each age category. When there was more than one individual of the age-sex class under investigation (e.g., if four adult females were present in the group), percentages for each distance category were obtained by:

a) Calculating dyad medians for all distance categories between each study subject and each adult female in each age category
b) Calculating individual medians from the dyad medians for all distance categories for each study subject in each age category
c) Calculating age category medians from individual medians for all distances in each age category.

The same protocol was followed when calculating the modal distance category between immatures and age-sex classes. All study subjects (n = 57) were present in the same group with at least one, and up to seven presumably unrelated (genetic testing is currently underway) adult females (49 adult females in total) at some point during the study.

5.3.1.1. Contact with Unrelated Adult Females

As with silverbacks, contact between adult females and immatures was rare, and was not considered a feature of their relationship. Contact was recorded on only 21 separate occasions, involving six infants and four juveniles, and seven adult females, three of which were nulliparous. The majority of these instances were mostly initiated by the immature, and in the form of brief touches (n = 11), occasional play (n = 4), grooming (n = 2), and agonism (n = 4, directed only to juveniles).

5.3.1.2. Influence of Immature Age on Proximity to Adult Females

Correlations between immature age category and the median percentage of scans spent within each distance category to adult females were carried out to determine if proximity to adult females varied with immature age (**Figure 5.7**). Over the immature period, no correlations were found between age category and the percentage of time spent within any of the distance categories to adult females (0-2m: $r_s = 0.358$, n = 19, $P = 0.132$; 2-5m: $r_s = 0.179$, n = 19, $P = 0.464$; 5-10m: $r_s = 0.451$, n = 19, $P = 0.053$; 10m plus: $r_s = -0.018$, n = 19, $P = 0.943$). Distances between study subjects and adult females were at a maximum during the end of infancy and the beginning of the juvenile period (see **Figure 5.7**), and generally, the percentage of time spent further than 10m from adult females seemed higher in juvenile period than in other age classes. Adult females and infants spent more time at closer distances during the first two years of life, when infants are unlikely to be responsible for their spatial associations. There were no differences between age classes in the percentage of time that individuals spent at each distance to adult females (within 2m: $\chi^2 = 5.006$, d.f. = 3, $P = 0.171$; 2-5m: $\chi^2 = 7.161$, d.f. = 3, $P = 0.067$; 5-10m: $\chi^2 = 0.111$, d.f. = 3, $P = 0.990$; 10m plus: $\chi^2 = 3.030$, d.f. = 3, $P = 0.387$).

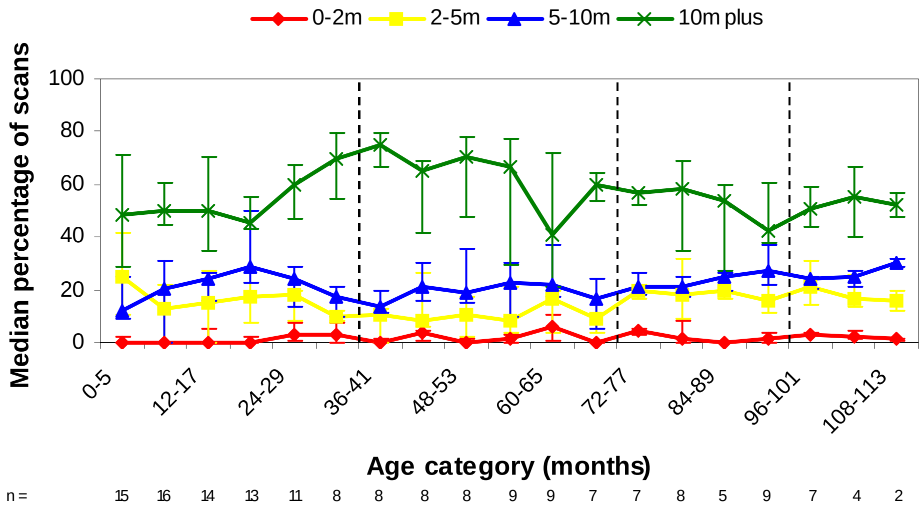


Figure 5.7. The median percentage of time spent at each distance category from adult females by study subjects. $N_{TOTAL} = 57$.

5.3.1.3. Effect of Immature Sex on Proximity to Adult Females

No statistically significant results emerged from tests that investigated differences between male and female study infants in the modal distance category between them and adult females (**Figure 5.8**: $U = 39.5$, $N_{males, females} = 18, 6$, $P = 0.225$) or juveniles ($U = 10.0$, $N_{males, females} = 5, 4$, $P = 1.000$), providing no evidence that females differentiate between unrelated immature males and females. A greater proportion of males (77.8%) had modal distances of greater than 10m to adult females compared with only 50% of females, however, this apparent difference was not significant.

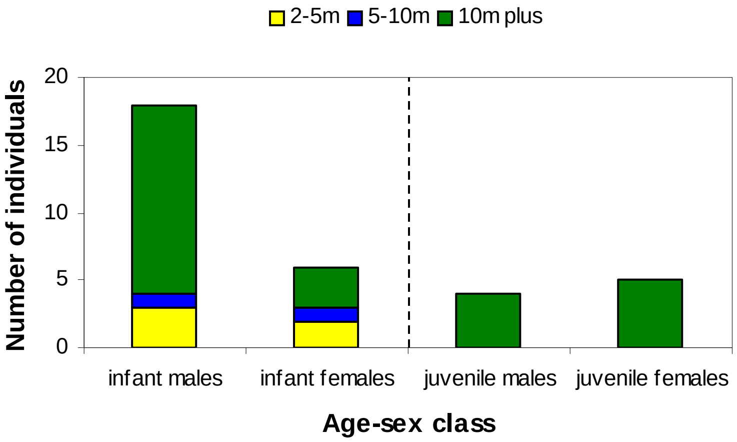


Figure 5.8. Comparison between the sexes of individual modal distance categories to adult females.

5.3.1.4. Influence of the Social Group on Immature-Adult Female Proximity

The social group to which study subjects belonged did affect the modal distance between them and adult females (**Figure 5.9**: $\chi^2 = 36.264$, d.f. = 10, $P < 0.0001$), with individuals in Bea, UKSB and Geo groups more likely to be found at closer distances to adult females. In UKSB, the close distances between adult females and their infants can be related to the absence of a group silverback: overall group spread generally seemed reduced in response to the absence of the silverback (pers. obs,). This may also have resulted in the shorter distances between immatures and adult females in Geo group. Although data used in this analysis were recorded only when all group members were present in the bai, there was a tendency in Geo group for individuals, including the silverback, to move in and out of the bai during a visit. A smaller group spread, and hence closer distances between immatures and adult females were the probable result. The previous section showed that individuals in Bea group were also found at closer distances to the silverback than individuals in other groups. Close proximity with the adult female in Bea group probably resulted for similar reasons: data were collected shortly after the study subjects (and the adult female) joined Bea, and consequently, spatial patterning within the group was affected. The behaviour of group members during bai visits of all other groups was unremarkable, and it is suggested that in the absence of recent demographic change, or the group silverback, immature group members are not usually found in close proximity to unrelated adult females.

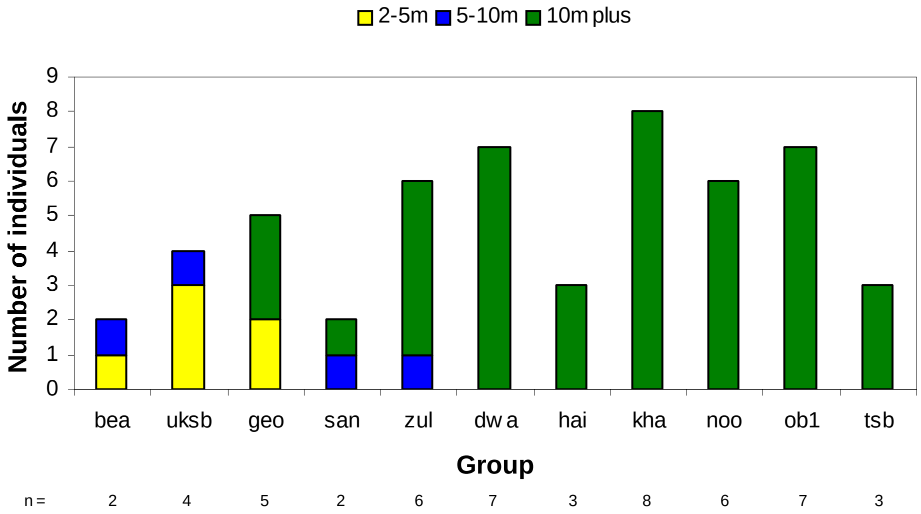


Figure 5.9. Differences between groups in individual modal distance categories between study subjects and unrelated adult females. $N_{TOTAL} = 53$.

5.3.1.5. Influence of Infants on Proximity to Adult Females

In many species, the presence of a young infant attracts others, making its mother more likely to be close to other group members (Hrdy, 1976; Small, 1990; MatisooSmith et al., 1997; Silk, 1999). Therefore, females were divided into the following categories to investigate the effect of reproductive status on proximity between study subjects and adult females:

1. Females with infants less than 6 months old
2. Females with offspring older than 6 months of age
3. Parous females but with no offspring in the current group
4. Nulliparous females

Ten females made a transition between categories during the course of the study, either by giving birth (and changing from category 2, 3 or 4 to 1), or by infants passing the cut-off age of 6 months (and changing from category 1 to 2). For these females, the modal distance category between them and group immatures was calculated before and after the transition (**Figure 5.10**). There were no significant differences in the modal distance categories between these ten females and immatures when they had an infant less than 6 months old, and when they did not (*Z* = -1.633, n = 10, *P* = 0.102). However, three females had a closer modal distance to immature group members when with a young infant, suggesting that in some cases, the presence of a young infant increased the attractiveness of females to immature group members.

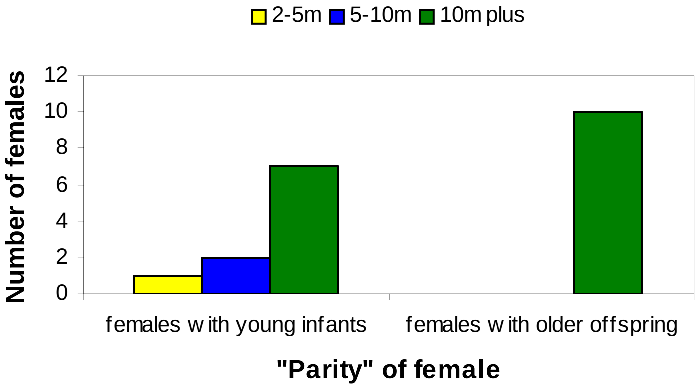


Figure 5.10. Modal distance categories between immatures and unrelated adult females who made a transition between "parity" categories, as described in the text.

When all adult females were considered rather than just those who changed category, and only two categories of female were used (with or without infants under 6 months), there was still no effect of the presence of a young infant on the distance between study subjects and adult females (*Z* = -1.732, n = 15, *P* = 0.083), although there was a tendency for study subjects to be slightly closer to adult females with young infants, as predicted. Only six study subjects had access to all four categories of females, and a matched test failed to detect differences in the modal distances to females in each of the four categories (χ^2 = 4.0, d.f. = 3, n = 6, *P* = 0.261).

Tests carried out within age classes did not reveal any significant differences in the modal distance category to females as a result of their parity, using the four categories previously described (infants: χ^2 = 2.391, d.f. = 3, *P* = 0.402; juveniles: χ^2 = 2.893, d.f. = 3, *P* = 0.408; sub-adults: χ^2 = 2.778, d.f. = 3, *P* = 0.427; adults: χ^2 = 0.000, d.f. = 2, *P* = 1.000). However, **Figure 5.11** suggests that infants were most likely to show a tendency to be closer to adult females in general, but particularly those with young infants. This may simply have been as a result of the mother's tendency to associate with other females. Infants also seemed relatively closer to nulliparous females; an age class that in other studies has been implicated in high frequencies of alloparental behaviour (e.g., Hrdy, 1976). It appeared that while study subjects remained close to their mother (i.e., during infancy, and to a lesser extent, during the juvenile period), they were generally more likely than older study subjects to be closer to other unrelated adult females. However, results are preliminary, and no significant results were found: more data are needed to produce conclusive results.

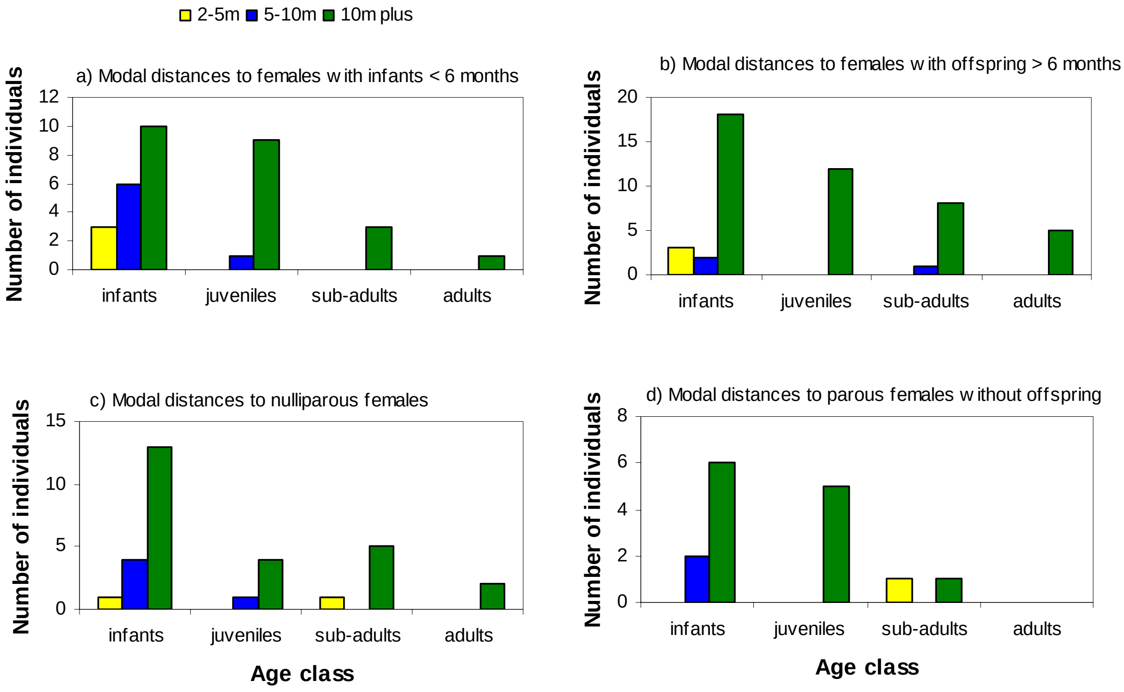


Figure 5.11. Individual modal distance categories between infant, juvenile, sub-adult and adult study subjects to a) adult females with infants less than 6 months, b) adult females with offspring older than 6 months, c) nulliparous females, and d) parous females without offspring in the current group.

5.3.1.6. Maintenance of Proximity Between Immatures and Adult Females

Problems were encountered in calculating indices of proximity maintenance for each immature and adult female dyad, due to the small number of approaches and departures within 5m. Data were too few for analysis, but the available data, using

Brown's index (Brown, 2001b)[1], suggested an increase in the role of the study subjects in changing the proximity between them and adult females, until becoming responsible for the majority of changes in proximity between themselves and adult females during the juvenile period. Further data collection is required before tests can provide useful results on the maintenance of proximity between immatures and adult females.

5.3.2. INTERACTIONS BETWEEN IMMATURES AND ADULT FEMALES

Previous studies on wild mountain gorillas (Stewart, 1981; Fletcher, 1994) have described adult females as the age-sex class most likely to direct aggression towards unrelated immatures. This section deals with interactions between immatures and adult females in an attempt to investigate whether this is also true for wild western lowland gorillas.

Of 58 immatures who could, only 23 (40.4%) were observed to engage in active interactions (of which there were 84) with adult females during the study period. Immatures interacting with adult females were significantly older than those who did not interact (**Figure 5.12**: $U = 246.5$, n = 23, 35, $P = 0.013$).

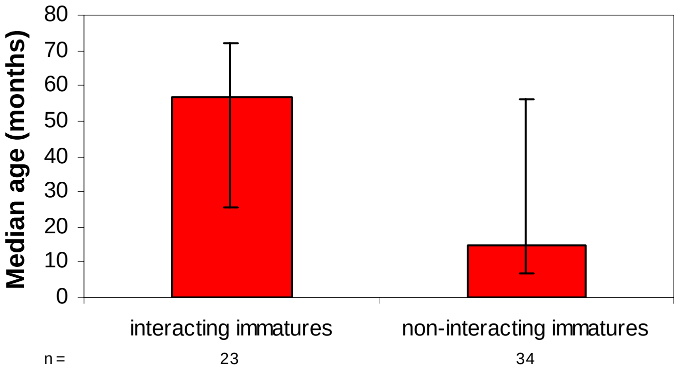


Figure 5.12. Median ages of study subjects who did, and did not engage in active interactions with adult females during the study. $N_{TOTAL} = 57$.

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[1] (IM + IB)/(IM + OM + IB + OB) * 100, where IM = immature makes contact/moves into proximity; OM = "other" makes contact/moves into proximity; IB = immature breaks contact/moves out of proximity; and OB = other breaks contact/ moves out of proximity

Immatures and adult females engaged in agonistic and displacement (negative), and affiliative, alloparental and play (positive) interactions (see **Table 5.2** for definitions). Negative interactions (n = 44) with adult females occurred more frequently than positive interactions (n = 34), and immatures who were involved in negative interactions with adult females were significantly older than those involved in positive interactions (**Figure 5.13**: $U = 88.0$, $N_{\text{positive, negative}} = 15, 21$, $P = 0.026$). When an initiator could be determined, adult females were predominantly responsible for initiating negative interactions, and positive interactions were mostly initiated by immatures (**Figure 5.13**).

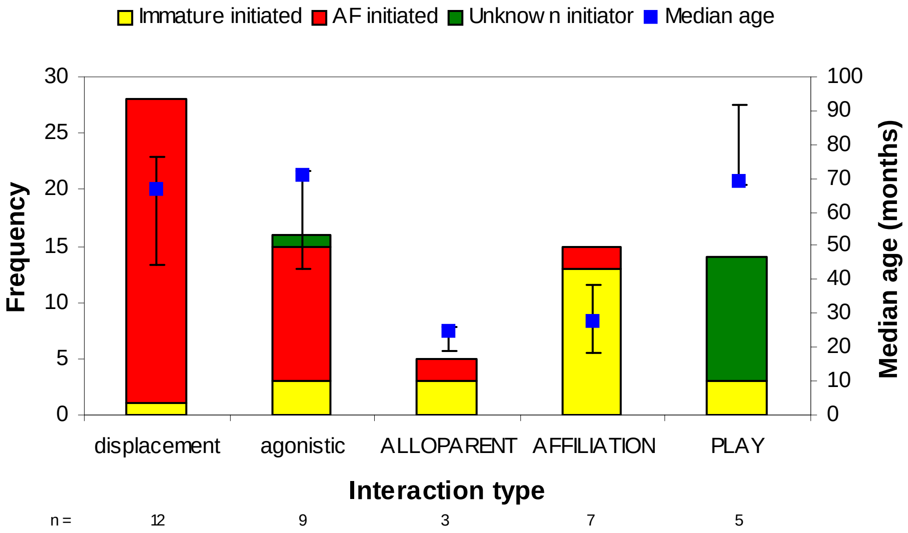


Figure 5.13. The frequency and initiators of interaction types with adult females, and the median ages of immatures who engaged in them. Negative (lower case) and positive (upper case) interaction types are grouped. $N_{\text{TOTAL}} = 23$.

5.3.2.1. Negative Interactions

Agonism

Agonism between immatures and adult females occurred infrequently, was relatively mild in form, and was observed to escalate beyond displays and vocalisations only once. Sixteen agonistic interactions between adult females and immatures were observed, involving seven adult females and two infant, three juvenile, one juvenile/sub-adult, two sub-adult and one adult study subjects. One adult female, Fleur, accounted for ten (62.5%) of these interactions, of which she initiated 80%.

Although Fleur had been part of Dwa group for approximately 2.5 years, she was the newest and presumed youngest adult member in the group and was perhaps still establishing herself. A newly immigrant female was previously found to be involved in a high number of agonistic interactions (Nowell, 2001; Stokes, 2004), however, she was the recipient of most of them. In this study, the majority of agonism with adult females took the form of cough grunts (56.25%), and displays accounted for 37.5% of agonism. Only one case of contact aggression (6.25%) was observed, and consisted of Fleur pinning Brie (juvenile female) to the ground after play stopped between Brie and Fig (infant daughter of Fleur). Agonism was reciprocated in only two cases: a charge made by sub-adult Djino was reciprocated with a tight-lipped display from the adult female to whom it was directed; and Fleur and Pepper mutually engaged in a cough grunting bout. In seven of the observed cases, agonism altered the behaviour of the individual to whom it was directed (usually the immature), either by stopping the approach of an individual, or resulting in one individual moving away from another, thus providing a useful, if infrequent means of regulating relationships.

Displacements

Displacements between immatures and adult females were more common than agonistic interactions, with 28 cases observed during the study, involving twelve immatures (only two of whom were infants) and thirteen adult females. An immature was observed to displace an adult female on only one occasion, but although this interaction was consistent with the definition for displacement interactions, it may be more correctly termed “avoidance” since the interaction occurred during the first visit that the “displaced” female was observed with a new infant. The rate at which displacements were received by immatures was variable, with no correlations between age category and the rate of displacements detected ($r_s = 0.166$, n = 18, $P = 0.509$). (Rates were calculated in the same way as for silverbacks.) As with silverbacks, juveniles and sub-adults were the most frequent recipients of displacements from adult females, receiving fourteen, and nine respectively, while infants and adult study subjects both received only two.

5.3.2.2. Positive Interactions

Affiliation

Affiliation occurred on fifteen occasions involving seven immatures (five infants and two juveniles) and seven adult females, four of whom were nulliparous. Almost all (86.7%) interactions were initiated by the immature, and in no case did the adult female recipient of the interaction respond except to look towards the immature. Affiliation between immatures and adult females took the form of touches, sniffs, or “kisses”.

Alloparenting

Five cases of alloparental interactions were observed during the study involving three infants and three adult females, one of whom was also a study subject (and nulliparous), and a second nulliparous female. The four cases involving these two individuals are included in the section on alloparenting in Chapter Six. A further case of alloparenting by an adult female may have occurred in error, and although it falls under the definition of alloparenting, was qualitatively different. After reacting to a noise in the forest, Fulani moved past Kung (unrelated infant) and picked him up, placing him dorsal. Kung and his mother, Khoisan both screamed, and Khoisan tried to pull Kung from Fulani’s grasp. Fulani resisted, while Khoisan bit and cough grunted towards her, and after the silverback intervened by cough grunting towards them, Kung managed to climb out of Fulani’s grasp and onto his mother. Fulani then moved away and located her own infant.

Play

Fourteen play interactions involved adult females and immatures, and all but one involved Muffin (a study subject and nulliparous). Four individuals played with Muffin, one was an infant, and the other three were aged between 69 and 104 months. The analyses involving Muffin are included in the section of play among immatures in Chapter Six. The other instance involved Fleur, a young primiparous female, who was the recipient of an unsuccessful attempt at play initiation by a sub-adult of unknown sex. No parous adult females were observed to engage in play with unrelated immatures at any point during the study.

5.3.3. DISCUSSION OF IMMATURE-ADULT FEMALE RELATIONSHIPS

In female-bonded species it is important for young females to integrate into the social group. This seems to be achieved primarily through nurturing affiliative relationships with older females in the group (Perry, 1996a; Henzi & Barrett, 1999; Cords, 2002). The high degree of relatedness and familiarity between females (Wrangham, 1980), probably aids in the formation of relationships between females and immature group members in species where females are philopatric. In gorillas, the absence of this matrilineal link, in conjunction with low levels of association among adult female gorillas (Harcourt, 1979a; Stokes et al., 2003; Stokes, 2004) and the high probability of dispersal from the natal group (Stokes et al., 2003), suggests that there may be little reason to invest in relationships with adult females who can provide little or no future benefit. With reference to the spatial relationship between immatures and adult females in this study:

- Very little time was spent in close proximity to adult females during the study. Distance between immatures and adult females was at a maximum towards the end of infancy, coinciding with the period during which immature associations were being made independently of the mother.

The decrease in proximity seen towards the end of infancy may not represent an avoidance of adult females (immatures did attempt affiliative interactions with adult females), but could be related to increasing independence from the mother. In captive western lowland gorillas, adult females do not associate with the silverback preferentially (Nakamichi & Kato, 2001; Stoinski et al., 2003), and instead, association with other females is relatively common (particularly by those with young infants). This contrasts with the situation in mountain gorillas, where rates of male-female association are much greater than female-female association (Harcourt, 1979b). A reduced need for protection from the silverback in captive situations was thought to be the main factor accounting for this disparity (Nakamichi & Kato, 2001; Stoinski et al., 2003). In this study, young infant (and therefore, mother) association with silverbacks was low, and instead it appeared that young infants and their mothers were more likely to associate with other adult females, particularly during the first two years. Subsequently, as infants began to move out of proximity to the mother, they also moved out of proximity of the adult females with whom she associated.

Differences between groups in the nature of the relationship between immatures and adult females were predicted as a consequence of the effects of feeding competition on differently sized groups. Data were too few to investigate the distribution of agonistic behaviours between adult females and immatures among groups, but:

- Differences between groups were found in the modal distances categories between adult females and immature study subjects.

However, there was no clear connection between the size of the group (and therefore, levels of feeding competition (see Watts, 1985b)) and the spatial relationships that existed. The differences found between groups seemed more likely to result from demographic factors, such as individuals' familiarity with the bai, and the presence of a group silverback, which both served to increase group spread and distances between all group members.

Groups such as Geo, Bea and UKSB, in which closer proximity of immatures to adult females was found, all also had adult females with young infants, or nulliparous females, and with reference to the parity of the adult females:

- The parity of the adult female did appear to have some influence on relationships with immatures. There was preliminary evidence that infants were more likely to be near adult females who also had young infants than other adult females. In some groups, nulliparous females were also found at closer distances to study subjects, particularly infants and juveniles, than other adult females.

In Geo, Bea and UKSB groups the presence of nulliparous females and those with young infants resulted in overall shorter modal distances between study subjects and adult females, and added to the influence of unfamiliarity with the bai, and the absence of silverbacks. However, the presence of females with young infants or nulliparous females did not always result in shorter modal distances to females. All six groups in which study subjects were consistently found at a distance of more than 10m from adult females contained both females with young infants and nulliparous females during the study. Although the silverback was not a focal point for immatures in the current study, results suggested that females with young offspring were still attracted to one another, and the presence of the silverback was not necessary for the attraction to occur.

One variable that failed to affect proximity between adult females and immatures was the sex of the immatures:

- No differences between male and female study subjects were detected in any aspect of the immature-adult female relationship, suggesting that adult females did not differentiate between males and females, either as social partners, or potential competitors for food, protection and potential mating opportunities from the silverback for their own offspring.

Beyond the first two years, when infants were beginning to move about independently, levels of spatial association between adult females and immatures were generally low. Correspondingly:

- Interactions between adult females and immatures occurred rarely, and the majority took the form of agonism or displacements, mostly initiated by adult females. This was possibly a consequence of the competition unrelated immatures provide for an adult female and her offspring. Positive interactions were also observed, but at a lower frequency, and were predominantly initiated by immatures, showing that immatures do not universally avoid adult females.

Immatures interacting with adult females tended to be older than those who did not, and preliminary data on the maintenance of proximity between individuals suggested that an increase in responsibility by immatures to change proximity to adult females occurred at a similar age to the increase in frequency of displacements of immatures by adult females. Contact aggression is rare between adult western lowland gorillas (Stokes, 2004; Parnell & Nowell, in prep.), and although adult females in the current study directed predominantly aggressive interactions towards immatures (consistent with the hypothesis that they were viewed as competitors (Pereira, 1995)), aggression rarely escalated past mild forms: cough grunting and displacements. It may not be worthwhile for a female to escalate aggression towards an immature, particularly in the bai environment where feeding competition is assumed to be low as a result of unlimited resources. Silverbacks are known to intervene in cases of serious aggression between adult females, often showing clear support for one of the participants (Watts, 1997; Parnell, 2002b; Stokes, 2004). The majority of immatures within a group are expected to be the offspring of the silverback, particularly in the single-male groups at Mbeli, and there may be a greater likelihood, therefore, of the silverback supporting his offspring, rather than an unrelated female should cases of serious aggression arise (*sensu* Watts, 1992; Chapais, 2001). On the other hand, a female is always a potential mate, so a silverback may not always support offspring against females (although see Watts, 1992).

Although rare, the majority of immature-initiated interactions with adult females were positive, consisting of affiliation, alloparental behaviours or play. These behaviours were directed mainly to young, nulliparous females, again showing indications of a preference for these females by immatures, and possibly attesting to the more playful nature of young nulliparous females. Young females may benefit from interactions with immatures by gaining maternal experience (Hrdy, 1976), and there may also be other benefits to interacting with immatures. For example, young females that engage in play behaviour with males gain experience of male behaviour, and such knowledge is likely to be of great importance during their adult life (Maestripieri & Ross, 2004).

Overall, the relationships between immatures and adult females appeared weak and were not invested in heavily by either immatures or females. It is suggested that these relationships were not strongly developed as a result of the eventual dispersal from the natal group (Fairbanks, 1993), and levels of competition between unrelated individuals, for food, and for protection by the silverback.

5.4. RELATIONSHIPS BETWEEN IMMATURES AND BLACKBACKS

No detailed investigation of the relationship between immature and blackback gorillas (8 to 12 year old males: Watts, 1990b) has so far been conducted, despite the frequent presence of blackback males in social groups. The presence of males in groups who are assumed to be physically capable of breeding but do not do so is limited to the great apes, and probably reflects the long period of immaturity and the length of time it takes to acquire social skills (Watts & Pusey, 1993). In other species, individuals often transfer from the natal group at puberty, and are afterwards classed as "adults" (e.g., Pusey & Packer, 1987; Wimmer & Kappeler, 2002; Korstjens & Schippers, 2003; Jack & Fedigan, 2004a), with no intermediate stage. Chimpanzee males, who tend to remain and breed in the natal group (Goodall, 1986; Mitani et al., 2002; Nishida et al., 2003) experience a life stage comparable to "blackbacks" in gorillas, termed adolescence (Mitani et al., 2002; Nishida et al., 2003). During this period, males are still growing and attempting to integrate into the social world of adults (Mitani et al., 2002), and interactions of both adolescent chimpanzees and blackback gorillas, seem to be characterised by play agonism, harassment and teasing (Adang, 1984; Mendoza-Granados & Sommer, 1995; Spijkerman et al., 1997; Nishida, 2003; Parnell & Nowell, in prep.). This behaviour consists of "seemingly bothering actions, often with a bluff-like appearance but without the elements characteristic of agonistic behaviour", and is rarely reciprocated (Spijkerman et al., 1997). Play agonism for blackbacks seems to act as a form of social exploration, allowing them to assess the responses that result from their actions, revealing the limit of their authority (Spijkerman et al., 1997), which is of considerable importance during this stage of their lives, since they are expected to soon disperse from the natal group and attempt to acquire females of their own, or attempt to gain matings within the natal group. Therefore, as preparation for this:

- Interactions between blackbacks and immature group members were expected to consist mainly of teasing and play agonism, and be predominantly initiated by blackbacks.

Immature, but independent male mountain gorillas have been known to join bachelor groups (containing blackbacks) following departure from, or disintegration of the natal group (Yamagiwa, 1987; Robbins, 1996; Robbins, 2001). These groups are thought to provide males with an appropriate setting in which to gain experience of affiliative and aggressive social interactions (Robbins, 2001). All-male groups occur infrequently in western lowland gorillas (Magliocca et al., 1999; Parnell, 2002a; Gatti et al., 2004a, although see Gatti et al., 2004b), so the presence of blackbacks in a heterosexual natal group and inter-unit encounters may be the only situations in which western lowland gorillas are exposed to blackbacks during immaturity. In the absence of all-male groups, blackbacks must gain experience of social interactions within the natal group. Primate mothers are known to intervene in situations where they perceive their offspring to be at risk (Stewart, 1981; Pereira & Altmann, 1985; Maestripieri, 2002; Schino et al., 2003), so are unlikely to allow blackbacks access to young infants, given their apparent propensity for play agonism and teasing (Parnell, 2002b; Parnell & Nowell, in prep.). In much the same way, female baboons with young infants avoid the approach of unrelated juveniles and sub-adults (Cheney, 1978). Mothers might be more tolerant of familiar blackbacks (those born in the same natal group and therefore, potential half-siblings in cases where groups have only one silverback) than blackbacks who have not matured in the mother's social group. Additionally, immatures with no mother in the current group may be more comfortable with, and more likely to associate with blackbacks with whom they have matured rather than blackbacks present in a group into which immatures have immigrated. As immatures begin to move away from the mother, they are likely to become more involved in social interactions with blackbacks as blackbacks use individuals within the natal group to refine their social repertoire Therefore, interactions and association with blackbacks are expected to change with increasing immature age, and:

- Association between young infants and blackbacks was expected to be rare, but then predicted to increase as maturing individuals began to move away from the mother and integrate into the social group.
- Mothers are predicted to be more tolerant of, and immatures more confident with familiar blackbacks, and therefore, association and interactions between immatures and blackbacks with whom they have matured is expected to be greater than with unfamiliar blackbacks.

With increasing age, interactions with blackbacks may prove beneficial to immatures, providing males with experience of the male-male competition that will be experienced during adulthood (Sicotte, 1993), and providing females with experience of male behaviour, also important for adulthood (Stewart & Harcourt, 1987; Fairbanks, 1993). Male-male, and male-female relationships in adulthood have a very different nature (see Harcourt, 1979b; Sicotte, 1993; Stokes, 2004), and consequently:

- Sex differences in interactions with blackbacks are expected, and would serve to prepare both immatures and blackbacks for male-male competition and important male-female relationships in adulthood.

Finally, differences between groups in the nature of social relationships were originally predicted to occur as a direct result of group size and composition, and the associated effects on feeding competition. However, previous sections have shown that any differences between groups were more likely to occur as a result of demographic changes within groups, and therefore:

- Demographic changes within social groups are predicted to change the nature of immature-blackback relationships.

Using the predictions outlined in this section, the nature of the relationship between blackbacks and immature western lowland gorillas is investigated.

RESULTS

5.4.1. SPATIAL RELATIONSHIPS WITH BLACKBACKS

Due to group compositions, eighteen study subjects had access to thirteen blackbacks that were present in five groups (Noo, OB1, TSB, Mos and Bea). There was an additional observation of one juvenile male briefly visiting the bai with a previously solitary blackback. No scan or focal data were collected during this visit but *ad libitum* observations were made.

5.4.1.1. Contact Between Immatures and Blackback Males

Contact between immatures and blackbacks occurred infrequently, and was not considered important in immature-blackback relationships. *Ad libitum* observations recorded twenty-six instances of contact between two infant, one juvenile, three sub-adult and three adult study subjects and blackbacks. Play and affiliative contact was more frequent (n = 18) with blackbacks less than 10 years of age, whereas with older blackbacks, contact was more likely to occur in agonistic contexts (n = 8).

5.4.1.2. Effect of Immature Age on Proximity to Blackback Males

There were no significant correlations between age category and the median percentage of time that immatures spent within any of the distance categories to blackbacks within their social group (**Figure 5.14**: 0-2m: r_s = -0.010, n = 18, P = 0.967; 2-5m: r_s = -0.040, n = 18, P = 0.874; 5-10m: r_s = -0.276, n = 18, P = 0.268; 10m plus: r_s = 0.189, n = 18, P = 0.453). There was a slight tendency for juveniles to be present at closer distances to blackbacks than sub-adults and adults, who spent very little time in proximity to blackbacks, however, no differences between age classes in the percentage of scans spent within any of the distance categories were detected.

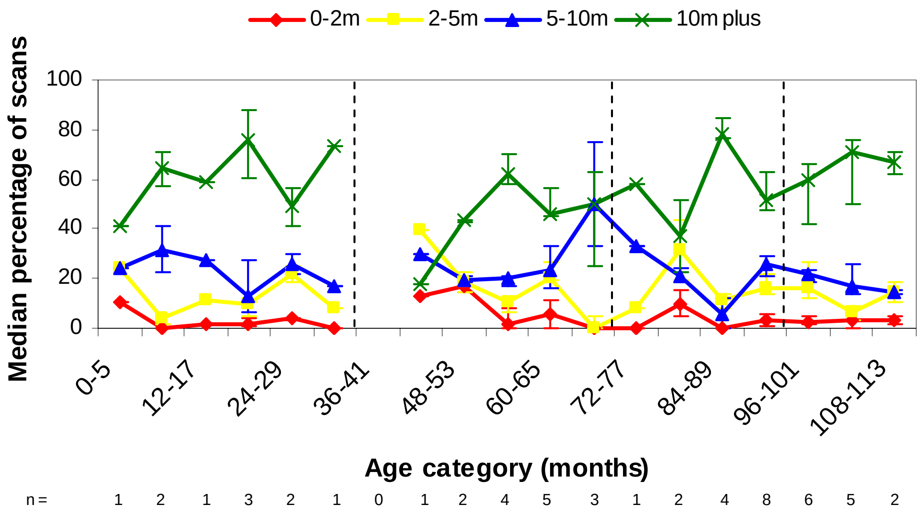


Figure 5.14. The median percentage of time spent at each distance category from blackbacks by study subjects. N_{TOTAL} = 18.

In other sections when the modal distance categories were calculated, study subjects have only contributed to one age-class. However, for Iook and Lyle, both were present in Mos group in a different age class before transferring to Noo group, and consequently, are represented in two age classes in **Figure 5.15**, which shows the distribution of modal distance categories between each immature-blackback dyad. Although no differences between age classes in the modal distance category were detected ($\chi^2 = 3.295$, d.f. = 3, $P = 0.348$), proximity patterns can be explained through knowledge of the population demographics. In four of the six dyads with a modal distance less than 10m, a major demographic change (either the death of the silverback, or emigration into a new group) had recently occurred. The two remaining dyads involved the same blackback, Moses, who had immigrated alone into TSB group as a young juvenile, and has consistently maintained close proximity (within 5m) to at least one other group member since his immigration.

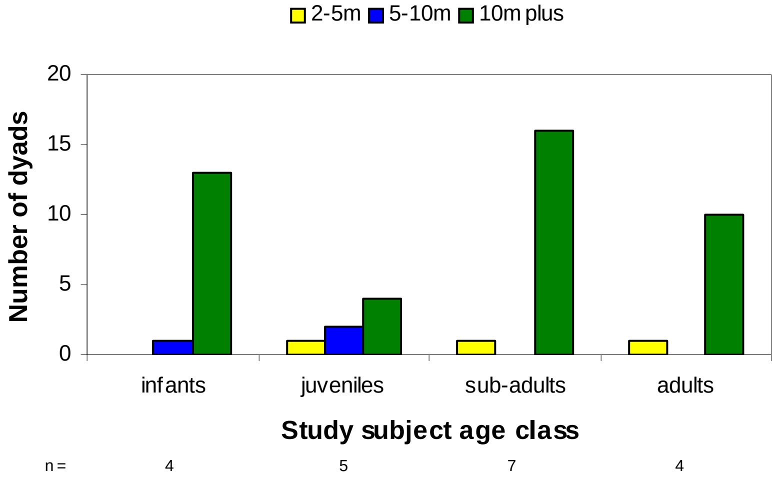


Figure 5.15. Number of immature-blackback dyads at different modal distances. $N_{TOTAL} = 18$

There were limitations to the analyses that could be carried out with regards to spatial patterning between immatures and blackbacks, due to the small numbers of blackbacks and study subjects with access to them. Only nine immatures of known sex were available (six males and three females), and only in two immature male-blackback dyads was the modal distance between them less than 10m. These datasets are far too small to perform analyses on, and more are needed before meaningful analyses of the effect of immature sex on the spatial relationships with blackbacks can be made.

Significant differences between groups were found in the median percentage of scans spent within 2m, 2-5m, and 10m plus, although not at 5-10m (**Table 5.3**). Post hoc multiple comparison tests revealed only significant differences between immatures in Noo group and TSB group, and Noo group and Bea group, with those from Noo spending more time distant (10m plus) from blackbacks than those in other groups. By investigating modal distance categories of immature-blackback dyads, the same groups showed shorter distances between individuals following change (**Figure 5.16**), and reinforcing the effect of changing demographics on spatial proximity within groups.

Table 5.3. Results of Kruskal-Wallis tests to investigate differences between groups in the proximity between immatures and blackbacks.

	0-2m	***2-5m***	***5-10m***	***10m plus***
X^2	10.182	11.502	7.545	16.769
d.f.	4	4	4	4
P	0.037	0.021	0.110	0.002

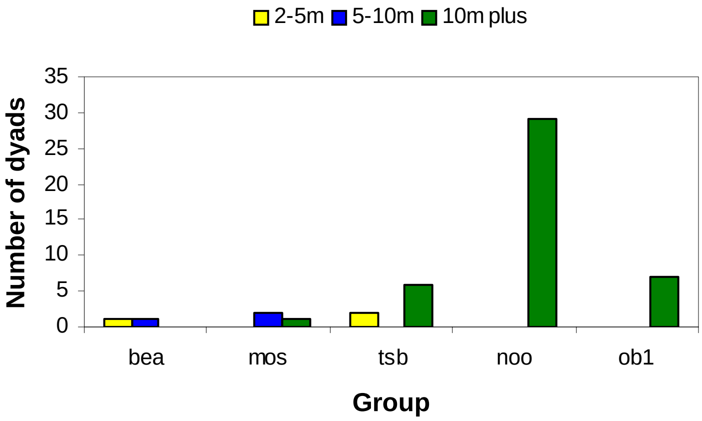


Figure 5.16. The distribution of modal distance categories between immature-blackback dyads in different groups.

The experience that subjects had with particular blackbacks may have influenced their spatial relationships: immatures familiar with blackbacks (judged as being present in the same group for at least one year) may have been more likely to associate with them than immatures with unfamiliar blackbacks. However, no significant differences were found in modal distances between familiar and unfamiliar dyads ($U = 55.0$, $N_{\text{familiar, unfamiliar}} = 13, 11$, $P = 0.096$), although all five dyads whose modal distance category was less than 10m were familiar with one another, suggesting that in some cases, familiarity with blackbacks may have played a small role.

5.4.2. INTERACTIONS WITH BLACKBACKS

Interactions between blackbacks and immature study subjects were predicted to be dominated by "teasing" behaviour of blackbacks, who used these relationships as a form of social exploration before leaving the social group (e.g., Spijkerman et al., 1997). This section investigates the nature of interactions between immatures and blackback males in wild western lowland gorillas to test this hypothesis.

Of 18 immatures in a group with blackbacks, 12 (66.67%) of them actively interacted with blackbacks during the study on a total of 101 occasions (more frequently than with silverbacks or adult females). Immatures who did interact with blackbacks were significantly older than those who did not interact with blackbacks (**Figure 5.17**: $U = 14.5$, n = 12, 6, $P = 0.044$). It was impossible to test the effects of immature sex on the frequency with which interactions between blackbacks and immatures occurred, as only three females were present in groups with blackbacks.

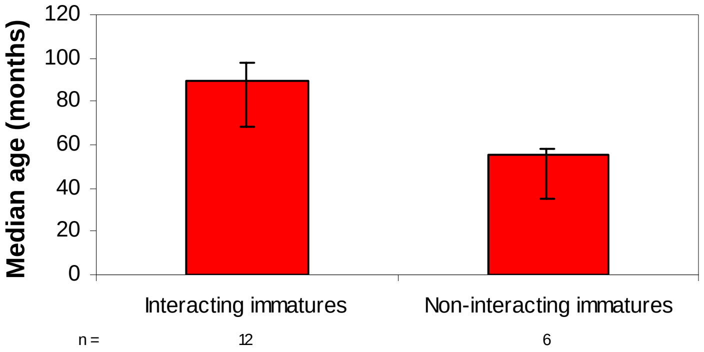


Figure 5.17. Median ages of immatures who engaged and did not engage in active interactions with blackbacks during the study. $N_{TOTAL} = 18$.

Immatures were involved in agonistic, displacement, play agonism (negative), affiliative, alloparental, grooming, and play (positive) interactions with blackbacks (see **Table 5.2** for definitions). Negative interactions (n = 68) were more than twice as frequent as positive interactions (n = 33) (**Figure 5.18**). There was no difference between the ages of individuals who were involved in positive, and those involved in negative interactions with blackbacks (**Figure 5.18**: $U = 96.0$, $N_{positive, negative} = 11, 20$, $P = 0.563$), although negative interactions very rarely involved infants (n = 2). Displacements (and grooming, although n = 1) were exclusively blackback initiated, and agonism and play agonism were largely blackback initiated. Affiliation was mostly immature initiated, and alloparental exclusively immature-initiated, although sample sizes were very small (**Figure 5.18**). Where the initiator of play could be determined, there was an equal division of immature and blackback-initiated bouts.

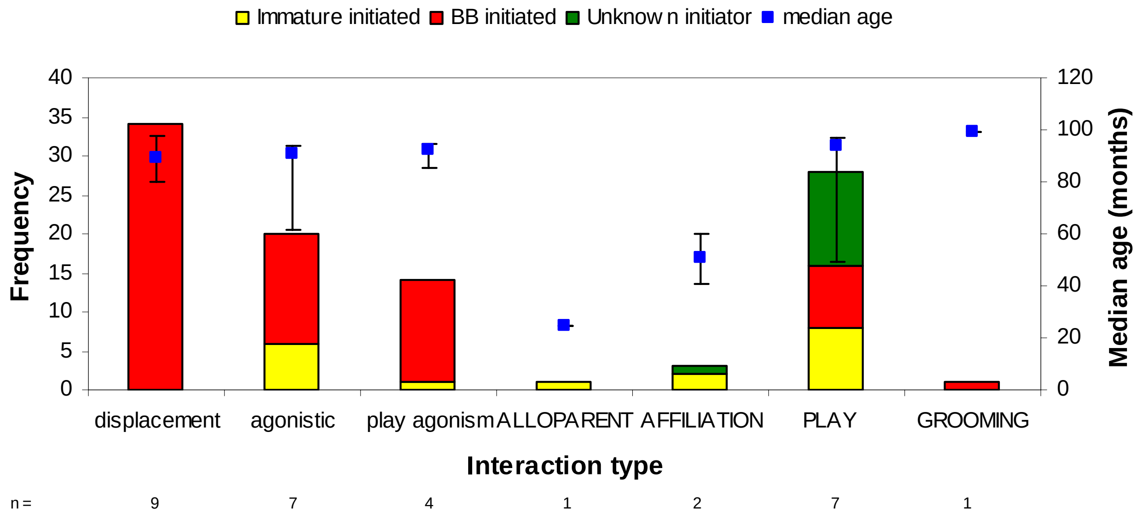


Figure 5.18. The frequency and initiators of interaction types with blackbacks, and the median ages of immatures who engaged in them. Negative (lower case) and positive (upper case) interactions are grouped. $N_{TOTAL} = 12$.

Demographic changes appeared to directly influence the rates at which negative interactions between immature and blackbacks were observed. Rates of interaction in Mos and Noo groups were higher than in the other groups, and the majority of negative interactions in OB1 group involved a recently immigrated sub-adult (**Figure 5.19**). The highest interaction rate per hour was recorded during one visit in which a juvenile of the recently disintegrated Mos group joined with a previously solitary blackback (Vid). Although only one agonistic interaction was observed in Vid, the calculated rate of interactions was high as a result of the short visit length.

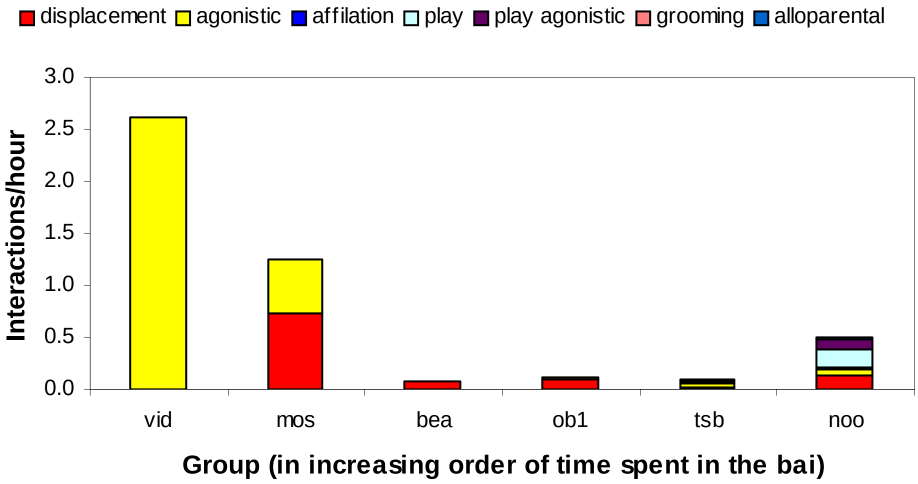


Figure 5.19. The rate (interactions per hour) of each type of interaction between immatures and blackbacks per group. $N_{TOTAL} = 12$.

5.4.2.1. Negative Interactions

Displacements

Displacements between immatures and blackbacks were the most commonly observed interaction. All were directed from the blackback towards the immature. There was no correlation between age category and the rate of displacements received from blackbacks ($r_s = 0.051$, n = 18, $P = 0.841$). Displacements were more commonly directed towards sub-adults than any other age class (19 displacements, and six sub-adults, compared with one displacement of an infant, and seven each for juvenile and adult study subjects), although significant differences were not detected between age classes in the rate of displacements received ($\chi^2 = 4.302$, d.f. = 3, $P = 0.231$). High rates of displacements tended to follow demographic changes: at the end of the juvenile period, high rates were contributed by Lyle, and were received from blackback Homer before Lyle emigrated from Mos group after the death of the silverback. The rate of displacements was also relatively high between 90-95 months of age, with Picard, who had recently immigrated into OB1 group, contributing the highest rate.

Agonism

Agonism between immatures and blackbacks was observed on 20 occasions, involving eight blackbacks and seven immatures. Agonism involved an infant only once, juveniles three times, and sub-adults and young adults were each involved on eight occasions. Immatures directed agonism towards a blackback on six occasions: on three occasions it was ignored, and on one occasion, the blackback retaliated by hitting the immature and ending the interaction. Two instances, involving the same immature-blackback dyad (who were at least half-brother and sister) occurred on the same day. The final instance of a study subject directing agonism towards a blackback involved the same dyad.

Display was the most frequent element used by blackbacks when they directed agonism towards immatures, constituting 50% of agonistic interactions (including the only case directed towards an infant. Cough grunting was the second most common element (28.6%) and contact was observed on 21.4% of occasions. The less frequent use of contact aggression (despite it being observed between blackbacks) perhaps suggested that blackbacks curbed their strength when interacting with immatures.

Play Agonism

Play agonism was observed relatively infrequently overall during the study period: subjects were involved in 15 interactions, 14 involving blackbacks. The interaction not involving a blackback, and instead involving Ike (74 months, unknown sex) and Axel (an infant male) was included in this section as the nature of the interaction was indistinguishable from other play agonism interactions. Dill and Bogplant (young blackbacks less than 10 years of age) were both involved on one occasion, and Coriander (old blackback) was involved in 12 instances. All but one act of play agonism was directed from an older to a younger individual, and on the occasion where this was not true, those involved were similar in age, with 7 months separating them. With the exception of Axel, immature recipients of play agonism were old juveniles (n = 1) or old sub-adults (n = 2), none of which had a mother present in the current social group.

Play agonism involving Coriander was investigated in more detail. All 12 interactions occurred during two visits by Noo group over a period of eight days in August 2002. Since play agonism appeared to be directed mainly from blackbacks towards older immatures, there were potentially four individuals to whom he could direct his behaviour: Lyle, Jaica, Iook and Muffin. Noo group averaged 5.2 visits to the bai per month, and since Iook and Lyle had joined the group in May and June 2002 respectively, the visits on which these interactions took place represented their 15th and 16th, and 9th and 10th bai visits with Noo group. There was a significant departure from the expected frequency with which Coriander directed play agonism towards familiar individuals, Jaica and Muffin, and towards "new" individuals, Iook and Lyle, (**Figure 5.20**: $\chi^2 = 5.3$, d.f. = 1, $P < 0.05$). However, not all blackbacks targeted immatures, new or otherwise with play agonism as a means of social exploration. Immatures immigrated into OB1 group without receiving play agonism from Skywalker (although he did direct agonism and displacements towards them). Results presented here may be heavily skewed by the behaviour of Coriander towards two individuals.

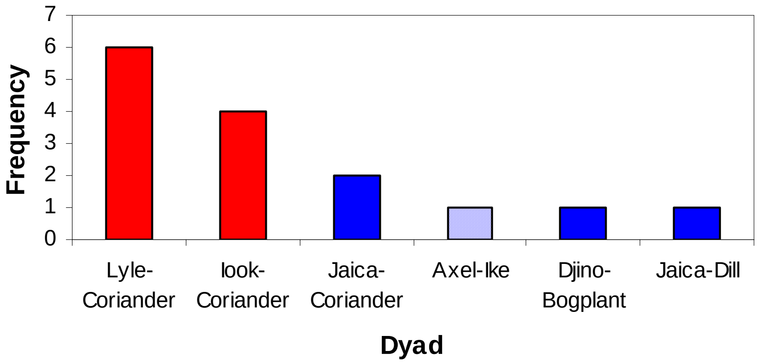


Figure 5.20. Frequency of play agonism involving study subjects. Red bars indicate "new" immatures, and blue bars indicate familiarity between dyads. The hatched bar represents the non-blackback dyad.

Play agonism was, therefore, not a ubiquitous feature of immature-blackback relationships, and for blackbacks, its frequency may be affected by the arrival of new individuals in the group. Not all blackbacks used play agonism as a means of social exploration, but the relatively higher frequencies of agonism and displacements may have been used instead to assert their position within the social group.

5.4.2.2. Positive Interactions

With the exception of play, other positive interactions were observed rarely, and did not appear to contribute to immature-blackback relationships. All three cases of affiliation involved young blackbacks and took the form of an embrace or touch initiated by the immature, or mutually. An alloparental interaction involved a young blackback, and is included in the later analyses of alloparental interactions. The single recorded instance of grooming with a blackback involved a young blackback, and a young adult study subject. The blackback spent some minutes grooming Jaica's back, to which Jaica did not respond.

Play

Play between immatures and blackbacks occurred on 28 occasions, and was the second most commonly observed interaction type. It involved mostly young blackbacks, with only three interactions involving a blackback over the age of 10 years. Details of blackback-immature play are included in the fuller analysis of play between immatures.

5.4.3. DISCUSSION OF IMMATURE-BLACKBACK RELATIONSHIPS

Relatively few blackbacks were available to associate with immatures, and consequently, results obtained in this study must be interpreted with caution, as they were likely to have been affected by small sample sizes and individual differences. This study found that:

- In terms of spatial relationships, age had no significant effect on the proximity between immatures and blackbacks, although there was a tendency for juveniles and sub-adults to be closer to blackbacks than infants and adult study subjects.

It was not possible to test the effects of immature sex on the relationship between immatures and blackbacks due to small sample sizes, but:

- Differences between groups were found in the spatial patterning between immatures and blackbacks.

This difference was very much influenced by recent demographic changes that occurred within groups as has been described to account for differences between groups in immatures' proximity to silverbacks and adult females. Immatures remaining in groups that had lost the silverback, or those that had joined a new silverback together with a familiar blackback, tended to be closer to blackbacks than individuals in groups who had not experienced recent change. No significant differences were found as a result of familiarity with blackbacks, but sample sizes were small, and further data are needed to produce more conclusive results.

In groups without a silverback a familiar blackback may take over the leadership role, in groups with an unfamiliar silverback, blackbacks may provide reassurance for immature members of the group. This has been observed three times in the Mbeli population: following the death of the FFF group silverback, a female, her juvenile offspring, a sub-adult male and an increasingly peripheral blackback/young silverback ranged alone for 16 months (Parnell, 2002b). Following the death of the Noo group silverback, remaining members of the group ranged together for a number of months, seemingly led by an older blackback, before a new, unknown silverback "took over" the group (T. Breuer, pers. comm.). The individuals (a juvenile, sub-adult, adult female and blackback) who joined previously solitary silverback, Bear, to form his group were seen in the bai together, with the blackback appearing the take the role of the silverback, in that the other group members responded to his behaviour. Therefore, the "reliance" of immature study subjects on blackbacks during times of group instability was predicted to be the biggest influence on the nature of relationships between immatures and blackbacks, and was manifested most clearly in analyses that tested for differences in immature-blackback relationships between groups. In these situations, although the blackback appeared to take the role of the silverback in the group, the relationship between blackbacks and immatures showed differences to the relationship between silverbacks and immatures:

- Interactions between immatures and blackbacks occurred more frequently than with silverbacks, but similarly, negative interactions between immatures and blackbacks were more frequent than positive interactions, as was also the case with silverbacks. Positive interactions, predominantly play, were observed between immatures and mainly young blackbacks with a higher frequency than between immatures and silverbacks.

The main reason for the difference in the nature of immature-blackback and immature-silverback relationships is predicted to be a result of the younger age, and therefore, more playful nature of blackbacks in relation to silverbacks. Additionally, blackbacks have not yet reached full maturity, so may still gain behavioural experience from interacting with younger individuals that will be useful to them when attempting to acquire their own females if they emigrate, or protecting the natal group, or attempting to gain matings within it if they do not undergo natal transfer. Play agonism was observed between immatures and blackbacks, and for one blackback, was directed mainly towards immigrants. Other forms of negative interaction (agonism and displacements) were more frequent than play agonism, and it seemed to be through these means that blackbacks asserted their position within the social group, and prepared them for the male-male competition they will experience after emigration from the natal group. The situations allowed blackbacks to develop their abilities in agonistic situations where they are likely to “win”, with minimal risk to themselves. Therefore, these interactions may be equally as important to blackbacks as to immatures (who experience displacements and agonism from silverbacks and adult females), such that blackbacks without access to immatures may experience a larger gap in their social development than immatures without access to blackbacks. Given the evolution of group type, proposed by Parnell (2002b), from nascent groups with no young individuals, through infant, juvenile, mature, and finally senescent group types, the majority of blackbacks are likely to have access to younger individuals, but the same is not necessarily true for infants and juveniles and their access to blackbacks. Therefore, young individuals in infant and juvenile group types will miss the opportunities provided by blackbacks for the development of behaviour, so it seems more likely that immatures play an important role in the development of blackbacks.

Although interactions between immatures and blackbacks provide clear benefits for blackbacks, by allowing them to practise behaviours that will be necessary later in life, these types of interactions are likely also to ultimately prove beneficial for the immatures to whom they were directed. Through them, males gain experience of male aggression while in the relative safety of the natal group (Owens, 1975), while females would experience something of the aggression directed from silverbacks towards females as a mate-retention strategy (Watts, 1992; Stokes, 2004).

With the exception of play behaviour (which may also serve as preparation for male-male competition, and male-female relationship formation), positive interactions between immatures and blackbacks involved young immatures, who were responsible for initiating most of these interactions, and young blackbacks. Both partners in these interactions are predicted to gain benefits; immatures, by socialising with other members of the group, while young blackbacks develop an ability for, and tolerance of, gentle association with infants will eventually help them when protecting their own offspring (see Sommerfeld et al., 1998).

5.5. INTER-UNIT ENCOUNTERS

In addition to interacting with individuals within their immediate social group, opportunities may also arise for interactions with other social groups. The bai is an attractive resource for many different gorilla units, resulting in a relatively high rate of inter-group encounters (Magliocca, 2000; Parnell, 2002b; Doran et al., 2003; Parnell & Nowell, in prep.). Interactions between groups in primates can range from affiliation and play between individuals, peaceful feeding merges, proximity tolerance and indifference, to high levels of agonism, displays and lethal aggression between adult males (Tutin, 1996; Cipolletta, 2004), with more than one type of interaction often occurring during a single encounter (Sicotte, 1993; Parnell, 2002b; Bermejo, 2004; Parnell & Nowell, in prep.). Infanticide can also occur during inter-group interactions (Fossey, 1984; Watts, 1989). Consequently, females with young infants are not expected to become involved in inter-group interactions, and remain at a distance whenever possible (Fossey, 1979; Cheney, 1987a; Perry, 1996b; Steenbeek, 1999; Fashing, 2001). It is not unusual for immatures from different groups to engage in affiliative interactions, gaining valuable information about others from the surrounding population, even when adult group members are engaged in agonistic displays with one another nearby (Reichard & Sommer, 1997; Parnell, 2002b; Bartlett, 2003).

Inter-unit encounters may provide the only opportunities for female transfer to take place, since females rarely travel alone, and instead transfer directly into another social group (Harcourt, 1978b; Sicotte, 1993; Doran & McNeilage, 1998). Female eastern lowland gorillas seem to be the exception and are known to occasionally travel alone, but in the absence of observed infanticide in the population (Yamagiwa & Kahekwa, 2001). As a result of the potential that inter-unit encounters provide for female transfer:

- Sub-adult females are expected to express an interest in the presence of other social groups, and increase proximity to them. Any interactions are expected to show elements of affiliation or tolerance on the part of the sub-adult female to facilitate potential transfer.

Through play, inter-group encounters provide individuals with socialisation experience, and perhaps more relevant for males, allows them to test their skills and strength against unfamiliar and potential future competitors (Pereira & Altmann, 1985) while still within the safety of the natal group (Owens, 1975). Therefore:

- Sub-adult males are predicted to show elements of play agonism in the presence of other groups. Infants and juveniles of both sexes may engage in affiliative interactions with conspecifics from other groups when given the opportunity to improve their socialisation experience and gain information about other individuals in the population.

Interactions between groups of western lowland gorillas in the forest are more likely to occur in relation to access to food (Tutin, 1996; Bermejo, 2004), contrary to mountain gorilla inter-unit encounters, which tend to be related to the acquisition of females in the absence of high levels of feeding competition (Sicotte, 1993; Watts, 1996b). Consequently, in the bai environment, where feeding competition is thought to be minimal (Stokes, 2004), inter-unit encounters may be more similar to those observed in mountain gorillas than those of western lowland gorillas in the forest. Mountain gorilla reports focus mainly on the behaviour of adults during encounters, with little information given on the behaviour of immature group members. Herding of females has been considered an important behaviour during mountain gorilla interactions, in that it serves to prevent female transfer (Sicotte, 1993). However, when considering only the behaviour of immature group members during inter-unit encounters, herding was not expected to play a major role. In the vast majority of cases at Mbeli, immature females were the daughters of the single silverbacks in the group, therefore, it is in both the interests of the silverbacks and the females to transfer from the natal group. It was also thought unlikely that silverbacks would herd male offspring away from other groups, since ultimately, they will provide competition for the silverback within his group.

The behaviour of immature group members during inter-unit encounters is investigated here, from the immature perspective; and the opportunities that such interactions provide for wider social interaction, transfer from the natal group, and engaging in behaviours that are of future benefit.

RESULTS

5.5.1. BEHAVIOUR OF STUDY SUBJECTS DURING INTER-UNIT ENCOUNTERS

During the study, a study group shared the bai with another gorilla unit on 70 occasions. On 60.3% of these occasions the bai was shared with a solitary male, and on 39.7% of occasions, with another social group. Parnell (2002b) found the majority of inter-unit interactions took place when groups were within 200m of one another (range: 0 – 270m). On 36 occasions during the current study the shortest distance between units was less than 200m, and therefore, the encounter was judged to have the potential to develop into an interaction between units. These 36 encounters are considered below.

Twelve encounters (33.3%) were between groups, and 24 (66.6%) were between a group and a solitary silverback. Results were not significant ($\chi^2 = 2.94$, n = 1, $P < 0.1$), but immatures were more likely to react (by glancing, approaching, “clumping together”, or exiting the bai) to another group within 200m than to a solitary silverback (**Figure 5.21**). This may have resulted from groups being more visible in the bai than solitary silverbacks.

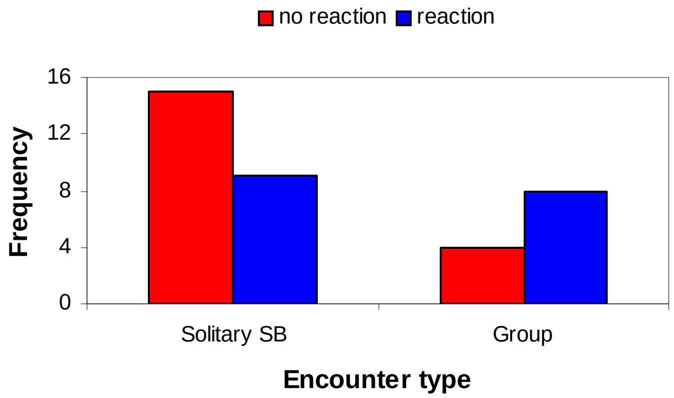


Figure 5.21. Comparison of the frequency with which study subjects reacted to groups and solitary silverbacks within 200m.

When a reaction occurred (n = 17, 47% of occasions on which there was considered to be potential for interaction), social groups and solitary silverbacks appeared to elicit different types of reaction (**Figure 5.22**). The most common reaction of immatures to solitary silverbacks was "vigilance", where they would monitor the position of the solitary silverback by intermittently glancing in his direction. Peaceful feeding merges, where individuals are as near to members of the other unit as they are to members of their own, occurred on just two occasions: once with a group and once with a solitary silverback. Nervousness (group members bunching together or moving away from another unit) was more common when sharing the bai with solitary silverbacks than with other groups. Study subjects approached a solitary silverback on only one occasion, compared with five approaches to groups.

The most common reaction of immatures towards another group was to approach them. Four sub-adults (three of unknown sex and one male) and two male juveniles were observed to approach another social group during the study. In none of these encounters did immatures spend more than 30 minutes with, or make physical contact with individuals from another group. Therefore, it was unlikely that males gained useful information regarding the strength of potential competitors, and no apparently serious attempts to transfer between groups, or gain information on its potential as a breeding group from a closer distance was made by any individual. So, if information is required before making transfer decisions, it seemed unlikely that it was gained during inter-unit encounters while in a bai environment.

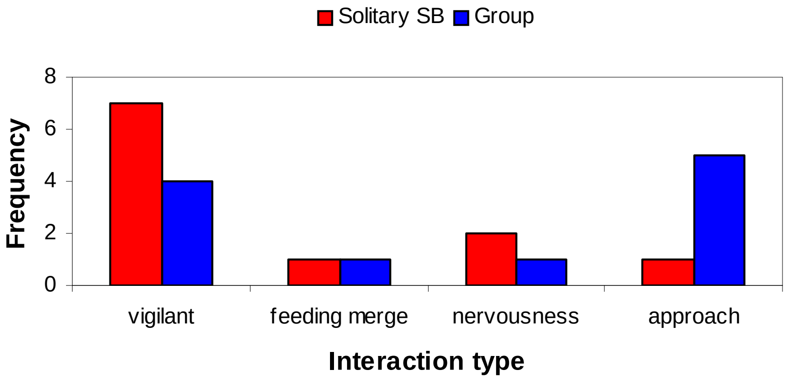


Figure 5.22. Types of interaction that study subjects were involved in when gorilla units encountered one another in the bai. Note that more than one interaction type could occur during each encounter.

5.5.2. DISCUSSION OF INTER-UNIT ENCOUNTERS

Encounters between units that had the potential to result in an interaction did not always do so. Immatures tended to react to groups more than to solitary silverbacks, but there was no evidence that females used these encounters to gain information on possible groups into which to transfer despite inter-unit encounters providing opportunities for transfer to take place (Harcourt, 1978b; Sicotte, 1993):

- No instances of immature females approaching other groups were recorded, although three of the individuals who did so were of unknown sex.
- Encounters with solitary silverbacks prompted higher levels of vigilance and nervousness from immatures, rather than interest or approaches from females.

Males do not transfer directly into another unit upon leaving the natal group (Harcourt, 1978b; Stokes et al., 2003), but often remain close to, if not within the home range of the natal group (Watts, 1991c; Watts, 1994b; Parnell, 2002b). Therefore, it seems important that they have some knowledge of the groups and other solitary males within the area when they do leave the natal group. There was little evidence that inter-unit encounters were useful in acquiring this knowledge, unless such knowledge can be gained from a distance. It may be more likely that males learn about others in the population as solitary silverbacks, which are known to track groups (Tutin, 1996; Bermejo, 2004).

Solitary silverbacks may pose a higher threat to groups than other groups do: they have no group members to lose, and with the exception of any injuries received, can only gain from an interaction with a group. For group silverbacks, the potential of gaining reproductive females must be greater than the risk of receiving injuries and/or losing valuable group members (transfer of reproductive females or loss of offspring through infanticide) for engagement in an aggressive interaction to be beneficial. Consequently, levels of aggression between two groups may be lower than between a group and a lone silverback, since a higher risk of engaging in an interaction is implicated. In mountain gorillas, silverbacks within groups carry out most cases of infanticide (Watts, 1989). However, there is also a lower percentage of solitary males in the population (Kalpers et al., 2003), compared with western lowland gorillas (Magliocca et al., 1999; Parnell, 2002a; Gatti et al., 2004a), and few solitary silverbacks in the Karisoke population of mountain gorillas is likely to increase the proportion of infanticide that is attributable to group silverbacks. Interactions between groups and solitary silverbacks were found to be more aggressive than interactions between groups in a study on western lowland gorillas (Parnell & Nowell, in prep.). The extent to which infanticide occurs in western lowland gorillas is still to be determined, but the higher frequency of solitary males in the population, and hence, high levels of male competition for females suggests that solitary silverbacks might be more likely to become infanticidal; hence, the greater vigilance and nervousness of immature group members in response to solitary silverbacks as reported in this study.

Although immatures have previously been recorded to approach and interact affiliatively with immatures in other groups (Parnell, 2002b; Mbeli Bai Study, unpublished data), the infrequency with which immature group members actively interacted with other units in the bai suggested that doing so had limited current benefits, few ramifications for transfer decisions and socialising experience and may involve potential risks. Actively interacting with other units may be of increased importance when immature gorillas travel without a group, following its disintegration. One of the encounters observed represented such a circumstance. For a brief period after the death of their silverback, and the disintegration of Mos group, Iook (sub-adult male) and Lyle (juvenile male) travelled with an adult female and her infant. Both Iook and Lyle were independent but were considered too young to survive without belonging to a group and benefiting from older individuals' knowledge of resource availability. All finally joined Noo group, but were observed to approach and interact with Hai group, with Iook and Lyle being the most active in this interaction. The silverback of Hai group was judged to be younger than the silverback of Noo group, and a young infant was present in Hai group at the time of the interaction. Immatures (and females with dependent infants) seem to prefer to transfer into the group of an older silverback because he is likely to be more tolerant of them (see discussion on p. 202-203), and this may explain why the interaction between Lyle and Iook with Hai group did not lead to them joining that group. In addition, Mos and Noo groups were both frequent visitors to the bai, and had shared it on many previous occasions over the years (Parnell, 2002b). In the case of the remaining individuals from Mos group, they appeared to seek a safe refuge, rather than a group in which they could increase their reproductive success, therefore, joining a familiar group was likely to involve less harassment from resident group members (see Watts, 1992).

5.6. OVERALL CONCLUSIONS

Proximity between group members differs during feeding and resting periods in mountain gorillas (Harcourt, 1978a; Fletcher, 2001). All observations in this study took place during feeding periods, and therefore, proximity data are limited in what can be imparted with regards to social relationships within a group. Only mothers (and possibly silverbacks) would be expected to tolerate the close proximity of immature group members while feeding (Pereira & Altmann, 1985), since a degree of competition (albeit low in a bai environment) exists between individuals. Therefore, proximity between immature and adult group members provided limited information on the relationships that existed between them, and instead, the nature of their interactions gave more details on how these individuals influenced behavioural development in immatures. In the bai, individuals feed in relatively close proximity compared with the large group spreads that have been recorded in the forest (Tutin, 1996; Bermejo, 2004), and probably experience lower levels of feeding competition as a result of abundant resources, and therefore, the nature of the interactions between individuals recorded in this study may illustrate the extreme of the relationships between individuals. The relationships between immatures and other group members recorded in this study have been broadly consistent with theories put forward: unrelated adults interacted with immatures either for their own gain by continuing to develop social skills with little risk to themselves (blackbacks) (e.g., Owens, 1975; Spijkerman et al., 1997), or by reducing competition for their own offspring by behaving agonistically towards other unrelated immatures (adult females) (e.g., Pereira & Altmann, 1985). Silverbacks associated and interacted infrequently with immatures, but this is not suggested to affect their ability to protect offspring from infanticide and predation (*sensu* Wright, 1990). The development of immatures' relationships with adult members of the group proceeded in a manner that reflected their likely eventual dispersal from the natal group, and the need for socialisation and experience in different social situations before doing so. Association and positive interactions with older group members were rare, and there was no evidence to show immatures invested in these relationships in order to gain future benefits, such as through coalition formation, as is seen in many other primate species (e.g., Seyfarth & Cheney, 1984; Silk et al., 2004). Finally, as immatures reach independence and are predicted to emigrate from the natal group, there was no indication that encounters with other gorilla units in the bai provided them with a substantial amount of useful information, either on the potential of groups or solitary silverbacks for mating purposes, or on the individuals present in the population with whom encounters were likely.

CHAPTER SIX

THE DEVELOPMENT OF RELATIONSHIPS BETWEEN IMMATURE GORILLAS

6.1. INTRODUCTION

Within most primate social groups, immature individuals have access to other similarly aged conspecifics or immature siblings with whom they can associate and interact, e.g., gorillas (Parnell, 2002a), bonobos (Furuichi et al., 1998), chimpanzees (Nishida et al., 2003), and baboons (Altmann, 1980; Swedell, 2002). Species that do not conform include orangutans and most of the nocturnal primates; the only exception being when different units come together to access abundant, valuable resources (Nash, 1993). Immature conspecifics in primate species experience similar costs, have similar time budgets and are of comparable strength, making them ideal association and interaction partners (Kummer, 1978; Fagen, 1993; Fairbanks, 1993; O'Brien & Robinson, 1993; de Oliveira et al., 2003). Infancy and the juvenile period tend to be characterised by high levels of play (Fagen, 1993), and alloparental behaviour is often performed by young, immature group members (Hrdy, 1976). In addition to spatial relationships among immatures, these interactions and others (see **Table 5.2** for definitions of interaction types) will be focussed on, to provide information on the social relationships between immature group members. This will allow the development of these relationships to be interpreted with respect to current and potential future benefits to study subjects.

6.1.1. Relationships Between Immatures

As primate infants begin to move out of the mother’s proximity, the frequency of association with peers increases (e.g., Fletcher, 1994; Berman et al., 1997; Brent et al., 1997). Consequently:

- Proximity between immature group members is expected to increase towards the end of infancy, as infants become more responsible for their own locomotion and move out of the mother’s proximity.

Association and interactions between conspecifics are predicted to serve two purposes: the development of skills that are likely to be useful later in life, and the development of relationships between individuals (Fairbanks, 1993). The *skills* that are learned, which include motor and maternal skills, and experience of interactions with immatures of the opposite sex *are* expected to be beneficial to immatures (Fairbanks, 1993), and consequently:

- The rate of interactions between immatures is expected to reflect the development of independence from the mother, showing increased levels towards the end of infancy.

Conversely, the individual *relationships* that develop through association and interactions between immature gorillas are unlikely to be useful in the future, since adult western lowland gorillas spend little time with individuals with whom they were immature (see Stokes et al., 2003; Robbins et al., 2004). This is a direct contrast to primate groups in which one species is philopatric, and particularly those with despotic dominance hierarchies and where dominance rank is inherited. In these species, the philopatric sex is likely to invest heavily in developing relationships with the offspring of high-ranking females, in an attempt to improve their own social position within the group (e.g., Pereira, 1995; Bentley-Condit & Smith, 1999; Silk et al., 1999; Range & Noe, 2002). In the absence of both philopatry (Stokes et al., 2003), and clear dominance hierarchies in wild western lowland gorillas (Stokes, 2004):

- Levels of association and interaction between individuals are predicted to decrease as individuals of both sexes approach the age at which they will leave the natal group.

Studies that have investigated relationships between immature conspecifics have often found that the number of peers with whom they can interact can influence the relationships that exist between them (e.g., Berman et al., 1997; Brent et al., 1997). Therefore, the differences in composition of the groups in this study may affect the levels of association and interaction between individuals recorded. In particular:

- Groups with more immature members are expected to have higher rates of association and interaction as a result of more available individuals.

6.1.2. Play Behaviour

Play is frequently expressed by immature individuals, is widespread among mammals, and has also been recorded in birds and some reptiles (Fagen, 1981; Bekoff & Byers, 1998). The distribution of play tends to mirror the evolution of brain size (Fagen, 1981; Iwaniuk et al., 2001), with orders containing larger brained species also containing more species that are playful (Iwaniuk et al., 2001). Play is hypothesised to serve two major purposes: motor training purposes, allowing immature individuals to practise behaviours that might later be used for hunting, avoiding predation or fighting with conspecifics (see Spinka et al., 2001); and as a means to develop social relationships that will prove useful in the future (e.g., Nakamichi, 1989; Fairbanks, 1993). Play tends to be most common towards the end of infancy and the beginning of the juvenile period before declining in frequency, thus coinciding with periods of rapid allometric growth (Barber, 1991; Pellis & Iwaniuk, 2000; Spinka et al., 2001), and when individuals begin to move out of the mother's proximity and regulate their own social relationships. Play, however, is not without its costs, which include energy expenditure, increases in the frequency of accidents (e.g., falling from a tree during arboreal play), and vulnerability to predation (Fagen, 1993; de Oliveira et al., 2003).

Sex differences are often apparent in the play behaviour of primates, concurrent with the hypothesis that play socially prepares immatures for adulthood. Females tend to engage in less rough play, have shorter play bouts, and are more likely to play with younger individuals, whereas males are often observed to play more roughly, employing wrestling, chasing and display elements more frequently than females (e.g., Brown, 1988; Nakamichi, 1989; Meder, 1990; Fagen, 1993; Maestripieri & Ross, 2004). With reference to this study:

- Play behaviour between males and females is expected to differ, with males playing more frequently and engaging in more rough play, to prepare them for competition with other males during adulthood. Females are predicted to engage in less frequent, and gentler play.
- Both males and females are expected to prefer male play partners, given that the relationship between adult males and females is the most important relationship that adult females invest in, with the exception of that with their offspring, and again, to prepare males for the competition that exists between them as adults.
- Females are expected to show a preference for younger individuals to gain maternal experience, while males should play with similarly aged peers since

these individuals provide the best training partners to help them develop competitive skills.

In many species, the presence of siblings provides additional opportunities for play (Fossey, 1979; Stewart, 1981; Fletcher, 1994; Brent et al., 1997), but the older sibling must self-handicap in order to avoid causing injury to the younger sibling and receiving castigation from the mother (Pereira & Preisser, 1998). However, in this study, the paucity of sibling pairs, and the very young age of infants in the available pairs precludes the possibility of drawing conclusions on the effect of siblings on play behaviour.

6.1.3. Allomothering

In primates, allomothering involves the handling, engagement in interactions with, and grooming of infants by individuals other than the mother (Lancaster, 1971; Hrdy, 1976; Hiraiwa, 1981; Nishida, 1983; Silk, 1999). Although not restricted to immature individuals (in capped langurs, allomothers are usually parous females: Stanford, 1992), allomothers are most commonly sub-adult or juvenile females (Lancaster, 1971; Hrdy, 1976; Hiraiwa, 1981; Nishida, 1983; Silk, 1999). Allomothering was recorded during this study, and it was predicted that:

- Instances of allomothering should involve juvenile or sub-adult females, to provide them with maternal experience, rather than for the purpose of contributing to the survival of infants.
- Consequently, allomothering was expected to consist of gentle handling by the allomother and to be monitored by the mother.

Allomothering in gorillas has not previously been documented, and studies in mountain gorillas have shown that interactions between older immatures and infants tend to consist of play and grooming (Stewart, 1981; Fletcher, 1994). Fletcher (1994) documented the low priority of infants as play partners for adolescent females in mountain gorillas, suggesting that adolescent females gained little experience in infant handling. In contrast, adolescent males in Fletcher's study (1994) showed a great interest in male infants as play partners. Sommerfeld et al. (1998) suggested that access to infants may be important for adolescent male chimpanzees to allow them to develop an ability for gentle play, protection and tolerance of infants, which will eventually help them to ensure the safety of immatures in their groups. This may also be important for gorillas: although active interaction between silverbacks and infants is uncommon (Stewart, 1977; Fletcher, 1994; Enciso et al., 1999). It is of importance, however, that the huge dichotomy in strength is minimised when they do interact (Pereira & Preisser, 1998), and by interacting with infants during immaturity, males can learn how this may be achieved.

The nature of spatial association and interactions of each immature age class will be investigated in this chapter to determine how other immature group members influence behaviour during each immature life stage.

RESULTS

6.2. SUB-ADULTS' RELATIONSHIPS WITH OTHER IMMATURES

Sub-adults are aged between 6-8 years, and it is during this life stage that behavioural differences between the sexes are more evident as social behaviour becomes more refined (e.g., Cords, 1987; Janson & van Schaik, 1993). Throughout the study period, there were 15 sub-adult individuals in eight different groups, and in total, 30 study subjects had access to at least one sub-adult. This section will deal with the spatial proximity of sub-adults to other immature group members, including proximity between sub-adults.

6.2.1. Sub-Adults' Contact With Other Immatures

Contact between sub-adults and others was rare, and recorded on only 32 occasions, mostly *ad libitum*. The majority (65%) of sub-adults' contact with others occurred in the context of play, and was most likely to involve infants (59.4% of all recorded cases), followed by juveniles (18.75%). Contact between sub-adults accounted for 12.5% of cases, and 9.4% occurred between sub-adults and adult study subjects.

6.2.2. Effect of Age on Sub-Adults' Proximity to Other Immatures

Sub-adults spent significantly more time within 2m of older study subjects that younger ones (**Figure 6.1**: $r_s = 0.526$, n = 19, $P = 0.021$), but there were no other correlations between the percentage of scans spent in any of the other distance categories by sub-adults and study subject age (2-5m: $r_s = -0.125$, n = 19, $P = 0.611$; 5-10m: $r_s = 0.296$, n = 19, $P = 0.218$; 10m plus: $r_s = -0.172$, n = 19, $P = 0.482$). Consequently, sub-adults spent little time in close proximity to infants. There were no correlations between immature age category and the percentage of scans spent at each distance category within any age class, and no differences were found between age classes in the percentage of time that sub-adults spent in each of the distance categories with them (0-2m: $\chi^2 = 6.867$, d.f. = 3, $P = 0.076$; 2-5m: $\chi^2 = 1.854$, d.f. = 3, $P = 0.603$; 5-10m: $\chi^2 = 1.562$, d.f. = 3, $P = 0.668$; 10m plus: $\chi^2 = 1.080$, d.f. = 3, $P = 0.782$).

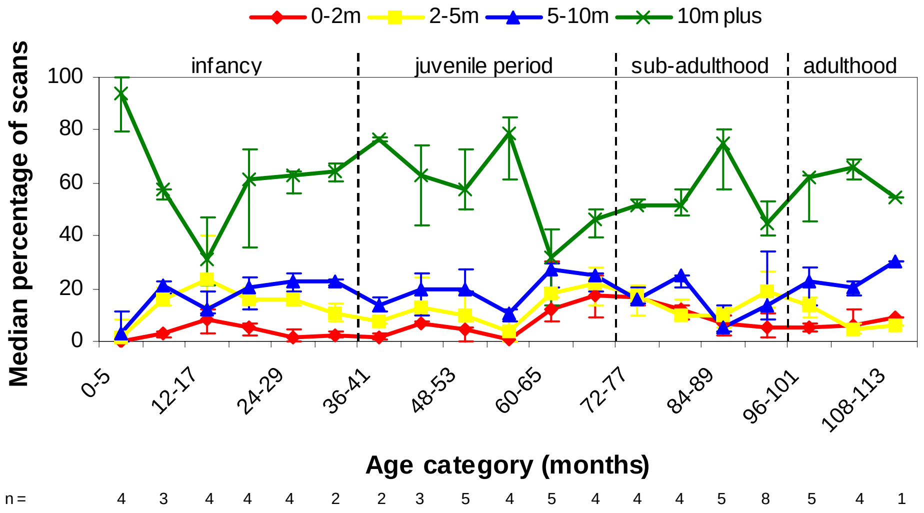


Figure 6.1. The median percentage of time that sub-adults spent at each distance category from other study subjects of differing ages. $N_{TOTAL} = 30$.

The percentage of time spent more than 10m from sub-adults appeared more variable than for any of the previously investigated age-sex classes and there was a significant difference between sub-adults in their modal distance categories to other immature group members (**Figure 6.2**: $\chi^2 = 40.145$, d.f. = 14, $P < 0.0001$) – although results must be interpreted cautiously due to small sample sizes. Of the sub-adults who tended to be found at closer distances to other immatures, Livingstone and Peter had experienced major demographic changes (emigrating into a new group, and the death of the group silverback – also applicable to Lyle, but when he was juvenile rather than sub-adult), so in these cases, the increased proximity between them and others may have represented an increased need for support and association with others (e.g., Meder, 1985; Meder, 1989; Spijkerman et al., 1997).

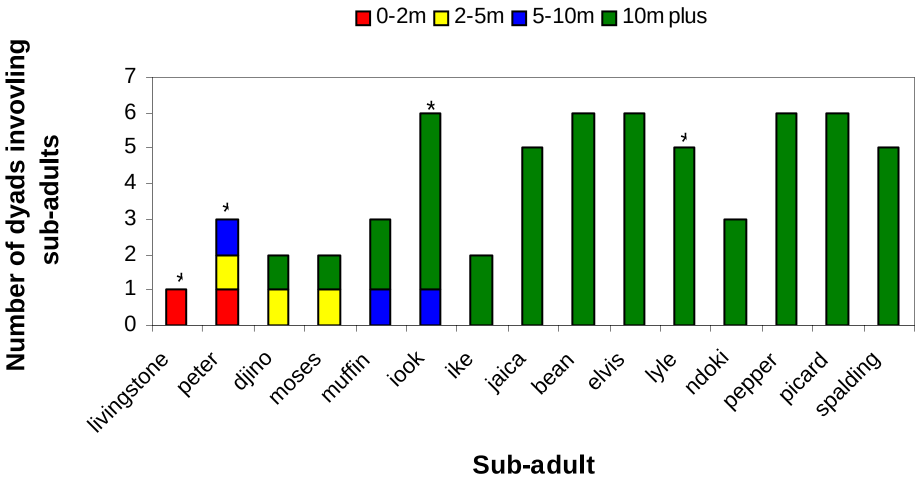


Figure 6.2. Modal distance categories between sub-adults and other immature group members. * indicates individuals who experienced major demographic changes during the study.

Sub-adults' modal distance categories to other immatures in the social group did not differ as a result of age class of the mother individual (**Figure 6.3**: $\chi^2 = 4.144$, d.f. = 3, $P = 0.246$), although sub-adults showed a tendency to be closer to juveniles than other age classes.

Figure 6.3. The distribution of modal distance categories for each sub-adult-study subject dyad. $N_{TOTAL} = 15$.

6.2.3. Effect of Sub-Adults' Sex on Proximity to Other Immatures

Only one sub-adult was known to be female, six were male, and eight were of unknown sex, therefore, very little can be said regarding the possible effects of sex on sub-adults' relationships with others.

6.2.4. Influence of the Social Group on Sub-Adults' Proximity to Other Immatures

The social group to which an immature belonged appeared to play a greater role than age in influencing the spatial patterning of sub-adults. There were significant differences between groups in the percentage of time that sub-adults spent in both the 2-5m and 10m plus distance categories with study subjects (**Table 6.1**), and results from the remaining distance categories approached significance.

Table 6.1. Results of Kruskal-Wallis tests to investigate the effect of immature group on the proximity sub-adults.

	0-2m	***2-5m***	***5-10m***	***10m plus***
χ^2	12.387	18.532	13.123	18.176
d.f.	7	7	7	7
P	0.089	0.010	0.069	0.011

Sub-adults in Bea, TSB and Mos groups were more likely than those in other groups to be found at distances of less than 10m from immature group members (**Figure 6.4**). In all instances when the individual modal distance between a sub-adult and another immature was less than 10m, one member of the dyad had recently experienced demographic change. The only exception to this involved Picard, in OB1 group. Picard emigrated into OB1 group together with a nulliparous adult female and juvenile, and unlike the other sub-adults, his distance to other immature group members was consistently over 10m. Picard was estimated to be the oldest individual to experience such demographic change, and consequently, his behaviour seemed less likely to be affected than younger individuals.

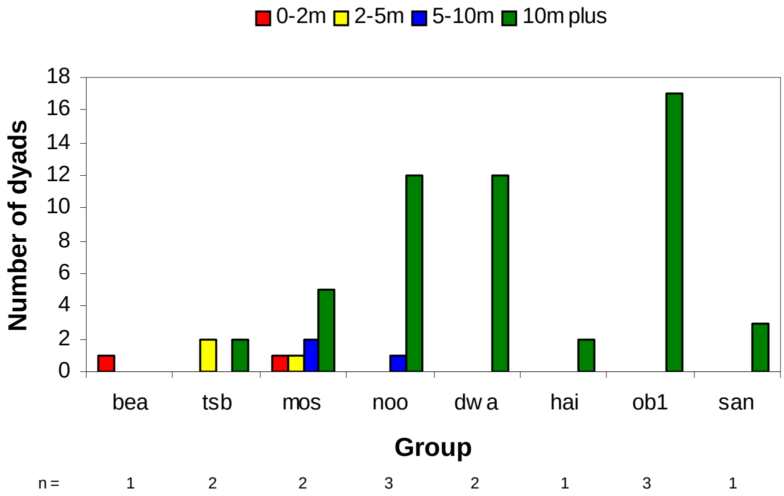


Figure 6.4. Comparison of sub-adults' modal distance categories with other immature members of each group. $N_{TOTAL} = 15$.

6.2.5. Sub-Adults' Distance to Siblings

Two sub-adults in the study population had maternal siblings born during the study period, and no other sub-adult-immature sibling pairs existed in the study population. There was no evidence of preferential spatial proximity between sub-adults and their young siblings, with both sub-adults having modal distances greater than 10m to all other immature group members, including their siblings. More sibling pairs are needed before meaningful analyses of the relationships between sub-adults and their siblings can be conducted.

6.2.6. Overview of Sub-Adults' Interactions with Other Immature Group Members

Of the fifteen sub-adult study subjects, eleven of them (73.3%) of them actively interacted with 19 (63.3% of the total possible) other immatures during the study. There were no differences in the ages of individuals whom sub-adults did and did not interact with ($U = 92.5$, n = 17, 12, $P = 0.674$), so partner age was unlikely to limit sub-adult interactions.

Sub-adults engaged in displacement, play agonism (negative), affiliative, alloparental, grooming, and play (positive) interactions (see **Table 5.2** for definitions) (**Figure 6.5**), although with the exception of play interactions, all occurred at a low frequency. There did not appear to be any significant differences in the ages of individuals with whom sub-adults engaged in particular interaction types, but small sample sizes meant that data could not be tested. Sub-adults were more likely to interact positively (n = 54) than negatively (n = 8), and initiated (n = 15) and received (n = 14) interactions with almost equal frequency (**Figure 6.5**). Interactions between sub-adults and infants were the most common (35.5% of the total), tending to consist of positive behaviours with the exception of low frequencies of play agonism and displacement. Displacements occurred mainly between sub-adults, and play behaviour was relatively evenly distributed between infants, juveniles, other sub-adults and adult study subjects. The involvement of sub-adults in the more frequent interaction types will be investigated in greater detail, but although relatively infrequent, sub-adults' interactions tended to be positive in nature, with negative interactions more likely to involve adult group members than other immatures (Chapter Five).

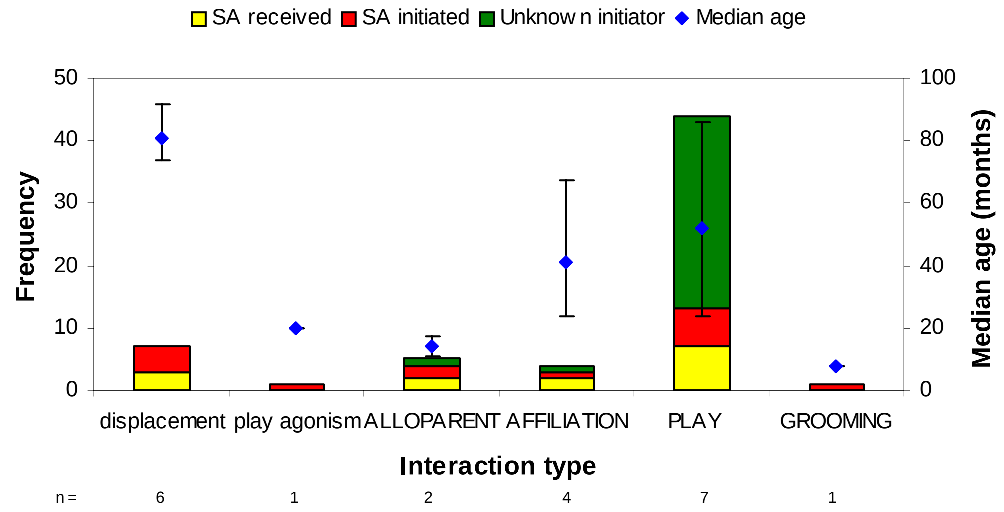


Figure 6.5. The distribution and initiators of sub-adults' interactions with other study subjects, and the median ages of those they interacted with for each interaction type. Positive (upper case) and negative (lower case) interactions are grouped. Note that some interactions involved two sub-adults, therefore, the sum of all interactions presented in the graph is greater than the actual number of interactions. $N_{TOTAL} = 11$ sub-adults.

6.3. JUVENILES' RELATIONSHIPS WITH OTHER IMMATURES

During the study period, there were 19 juvenile individuals, seven of whom were known to be male, and five female. Forty study subjects had access to juveniles at some point during the study. Juveniles were present in ten of the 13 different social groups.

6.3.1. Juveniles' Contact with Other Immatures

Juveniles were observed in contact with other immatures on 99 occasions. Juvenile-infant contact accounted for 42.7% of juveniles' contact with other immatures, and 9.4% was attributable to sub-adults. Contact between juveniles was the most common (47.9%). The vast majority of contact with juveniles arose during play behaviour (76%), with the rest resulting from affiliative touches, alloparental, grooming, and socio-sexual behaviour.

6.3.2. Effect of Age on Juveniles' Proximity to Other Immatures

Juveniles spent increasing amounts of time 2-5m ($r_s = 0.694$, n = 19, $P = 0.001$) and 5-10m ($r_s = 0.502$, n = 19, $P = 0.029$) from other study subjects as the study subjects increased in age (**Figure 6.6**). There was no correlation between study subject age and the percentage of scan samples in which juveniles were within 2m of other immatures ($r_s = 0.338$, n = 19, $P = 0.157$), or at more than 10m from them ($r_s = -0.293$, n = 19, $P = 0.223$). Correlations were not significant within age classes. There was a significant difference between age classes in the median percentage of scans which study subjects and juveniles spent within 0-2m of each other ($\chi^2 = 9.978$, d.f. = 3, $P = 0.019$), with post hoc tests showing that juveniles spent less time within 2m of infants than sub-adults and adults, and that juveniles spent less time than adults within 2m of other juveniles. So with the exception of a high frequency of time spent by juveniles 5-10m from 6-12 month old infants, juveniles tended to be found closest to sub-adult and adult study subjects.

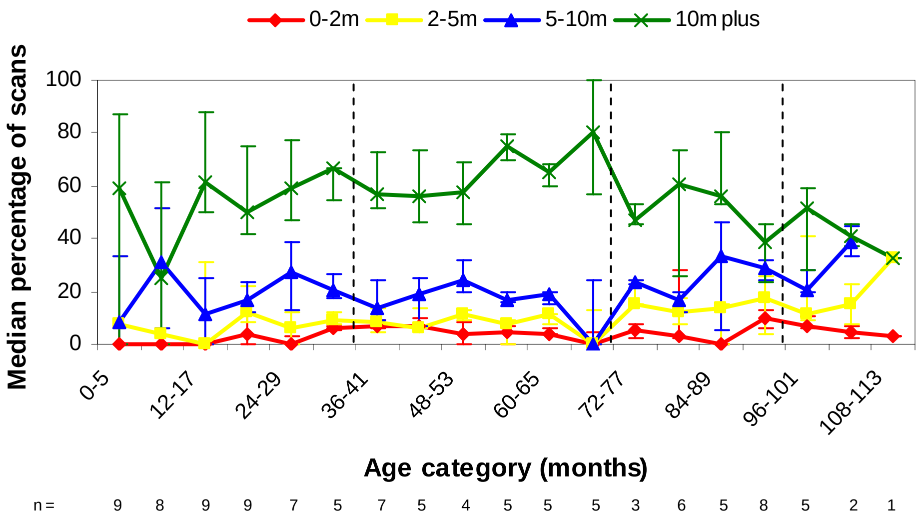


Figure 6.6. The median percentage of time that juveniles spent at each distance category from other study subjects of differing ages. $N_{TOTAL} = 40$.

6.3.3. Effect of Juveniles' Sex on Proximity to Other Immatures

To compare the modal distance category between male and female juveniles to other study subjects, tests matched for age were carried out, but no differences were found ($Z = -0.333$, n = 17, $P = 0.739$). All juvenile males and females both had modal distance categories of more than 10m to other study subjects, but when individual dyads were looked at, there was a slight tendency for juvenile females to be closer to other study subjects (**Figure 6.7**).

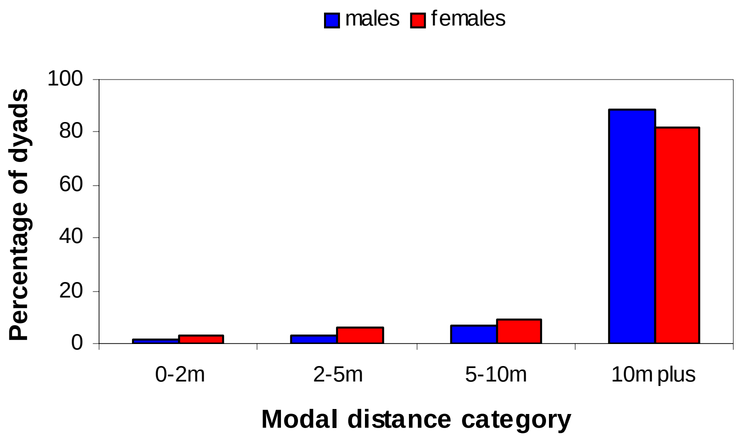


Figure 6.7. Comparison between juvenile males (n = 7) and females (n = 5) of their modal distance categories to study subjects. Number of dyads: males = 88, females = 66.

There was some evidence that juvenile females tended to be closer to infants than juvenile males: juvenile females spent significantly more time 2-5m (U = 1.0, $N_{males, females}$ = 4, 6, P = 0.019), and 5-10m (U = 1.0, $N_{males, females}$ = 4, 6, P = 0.019) from infants than did juvenile males. There were no differences between the sexes for juveniles at 0-2m (U = 4.0, $N_{males, females}$ = 4, 6, P = 0.055) (although again, there was a tendency for juvenile females to be closer to infants than males) or 10m plus (U = 7.0, $N_{males, females}$ = 4, 6, P = 0.285). Sample sizes were small, so should be interpreted with caution, but this finding is consistent with the theory that juvenile females are interested in and attracted to infants, which may provide the potential to develop maternal skills.

6.3.4. Effect of Social Group on Juveniles' Proximity to Other Immatures

There was a small difference between groups (using data from all individuals within a group) in the percentage of scans that juveniles spent more than 10m from immatures (10m plus: χ^2 = 17.052, d.f. = 9, P = 0.048), but not in the other distance categories. These differences were clearer when the modal distance categories of each juvenile with other immature group member was looked at (**Figure 6.8**). Stanley, in Bea group and Ulysses in TSB group were both consistently closer to other immature group members than juveniles in other groups. Betsy, in Geo group, was found within 5m of the two youngest infants in the group. Spatial patterns in Bea group have consistently been affected by the changes that had recently taken place in that group, and similarly, the immigration of Ulysses into TSB shortly before the start of the study seems to have affected spatial patterning within that group. As will be discussed in a subsequent section, Betsy was involved in allomothering interactions more frequently than the majority of other juveniles, and therefore, clearly showed an attraction towards the infants (all other immatures in Geo group were infants) in her group, which is reflected in her spatial patterning. Ike, in Hai group, accounted for the majority of alloparental behaviour observed, but tended to be found further than 10m from both other infants in the group. In Ike's case, the attraction to infants seemed limited to actively interacting with them, rather than a more general attraction. Alternatively, a smaller group spread in Geo group has been suggested as a result of the occasional absence of the silverback: closer distances between Betsy and two of the infants may simply have been a consequence of this.

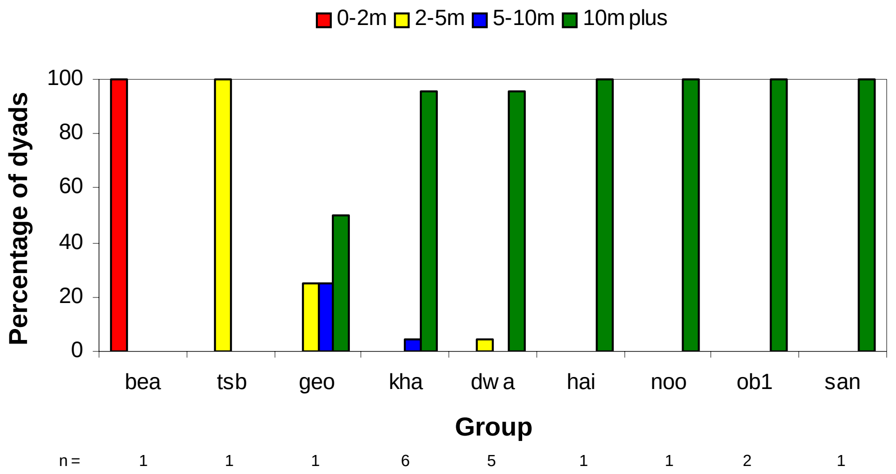


Figure 6.8. Comparison between groups of the modal distance categories of dyads involving a juvenile. Number of dyads: Bea = 1, Dwa = 22, Geo = 4, Hai = 1, Kha = 42, Noo = 5, OB1 = 12, San = 1, TSB = 2.

6.3.5. Juveniles' Distance to Siblings

One juvenile had a younger sibling born during the study period: Sunbeam (female), with younger sibling, Lando (male). Sunbeam's modal distance categories to all other study subjects in the group, including Lando, was 10m plus. When the percentage of scan samples that Sunbeam spent in each distance category to other study subjects in the group was investigated, the percentage of time spent within 2m and 2-5m from Lando was greater than for non-maternally related immatures. However, the data are too few to draw any conclusions regarding how relatedness may affect juveniles' spatial patterning.

6.3.6. Overview Of Juveniles' Interactions With Immature Group Members

Of the 19 juveniles that were present during the study, 18 (94.7%) actively engaged in interactions with 26 other study subjects (57.8% of those available to them within the social group). Despite close proximity between Ulysses and the two study subjects in his group, he was not observed to actively interact with them. Juveniles tended to interact with other juveniles and sub-adults, and the ages of individuals with whom juveniles did interact were significantly higher than the ages of those with whom they did not interact ($U = 154.5$, n = 19, 26, $P = 0.033$). Juveniles were involved in agonistic, displacement (negative), affiliative, alloparental, grooming, and play (positive) interactions – see **Table 5.2** for definitions. Play was the most common interaction type of juveniles, almost 20 times as frequent as the next most commonly observed interaction type (affiliation). Even when play was discounted (it will be discussed further in the subsequent section on play behaviour between study subjects), positive interactions involving juveniles (n = 17) outnumbered negative interactions (n = 9). Juveniles interacted positively with study subjects who were significantly younger than those with whom they interacted negatively (**Figure 6.9**: $U = 66.0$, $N_{\text{positive, negative}} = 34, 8$, $P = 0.025$). Overall, juveniles initiated slightly more (n = 15) interactions than they received (n = 10), and were more likely to initiate grooming, alloparental, and displacement interactions than to be the recipient.

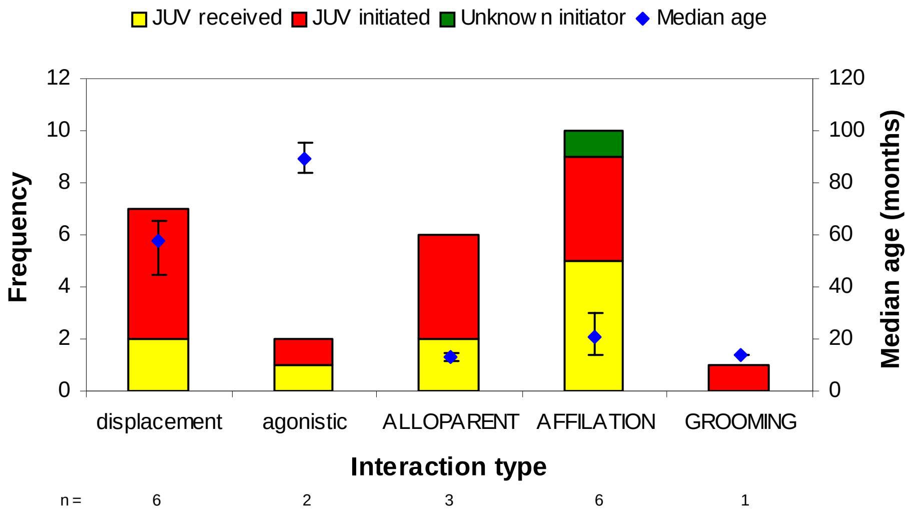


Figure 6.9. The frequency and initiators of each interaction type for juveniles, and the median ages of the individuals with whom juveniles interacted for each type. Positive (upper case) and negative (lower case) interactions are grouped. Note that some interactions involved two juveniles, therefore, the sum of all interactions presented in the graph is greater than the actual number of interactions. $N_{\text{TOTAL}} = 18$ juveniles.

6.4. INFANTS' RELATIONSHIPS WITH OTHER IMMATURES

A total of 29 infants were present during the study period, and 45 study subjects had access to them. Infants were present in nine groups, and 19 were known to be male and nine female. Much of infancy is spent close to the mother and under her close control (e.g., Fletcher, 2001), therefore, at younger ages, association and interactions involving infants were expected to be few, and show a gradual increase as infants become more independent.

6.4.1. Infants' Contact with Other Immatures

Contact was recorded between infants and other study subjects on 141 occasions in total. Contact between infants was most common, accounting for 46.1% of instances. 32.6% occurred between infants and juveniles, with contact between infants and sub-adults accounting for the remaining 21.3%. Two-thirds of the instances of contact took place during play sessions, with the rest resulting from brief touches or embraces, alloparental behaviour, grooming behaviour and only 2.1% arising from agonistic situations.

6.4.2. Effect of Age on Infants' Proximity to Other Immatures

An individual's age had no effect on the percentage of scans that infants spent within any of the distance categories to them (**Figure 6.10**: 0-2m: $r_s = 0.139$, n = 19, $P = 0.570$; 2-5m: $r_s = -0.154$, n = 19, $P = 0.528$; 5-10m: $r_s = 0.236$, n = 19, $P = 0.331$; 10m plus: $r_s = 0.237$, n = 19, $P = 0.328$). Likewise, there were no differences in infants' proximity to different age classes (0-2m: $\chi^2 = 4.055$, d.f. = 3, $P = 0.256$; 2-5m: $\chi^2 = 0.688$, d.f. = 3, $P = 0.876$; 5-10m: $\chi^2 = 2.196$, d.f. = 3, $P = 0.533$; 10m plus: $\chi^2 = 1.632$, d.f. = 3, $P = 0.652$). There was no difference between infants' modal distances to any of the age classes ($\chi^2 = 3.070$, d.f. = 3, $P = 0.381$), although there was a tendency for infants to be less than 10m from other one another and juveniles than they were sub-adults or adults.

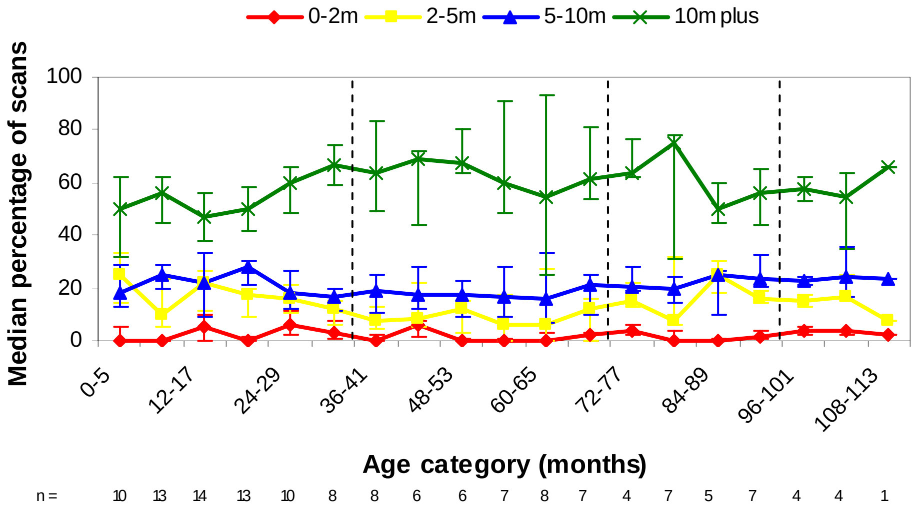


Figure 6.10. The median percentage of time that infants spent at each distance category from other study subjects of differing ages. $N_{TOTAL} = 47$.

6.4.3. Effect of Infants' Sex on Proximity to Other Immatures

To investigate the effect of infant sex on proximity to immatures, each infant's modal distance category to other immatures was used. No differences were found between males and females ($U = 84.5$, $N_{\text{males, females}} = 19, 9$, $P = 0.945$), suggesting that the sex of an infant does not influence its spatial patterning. Additionally, tests matched for age category failed to find a significant difference between the modal distance categories of males and females ($Z = 0.0$, n = 18, $P = 1.0$).

6.4.4. Influence of the Social Group on Infants' Proximity to Other Immatures

Consistent with results of previous analyses, there were significant differences between groups in the percentage of scan samples spent within each distance category to infants (**Table 6.2**).

Table 6.2. Results of Kruskal-Wallis tests investigating the effect of group on the percentage of scan samples infants and immatures spent in each distance category.

	0-2m	***2-5m***	***5-10m***	***10m plus***
χ^2	34.054	34.397	22.329	31.466
d.f.	9	9	9	9
P	0.000	0.000	0.008	0.000

Additionally, there was a significant difference between groups in infants' modal distance categories to other immatures (**Figure 6.11**: $\chi^2 = 19.062$, d.f. = 7, $P = 0.008$). The pattern reflected proximity seen between study subjects and adult females, with infants in UKSB and Geo groups being more likely to be near other immatures (presumably the offspring of the females they were previously found close to). Since UKSB group always lacked a silverback, and the silverback of Geo group was prone to moving in and out of the bai (although all data come from periods when he was in the bai), these data suggest that the lack of close proximity to the group silverback can result in decreased group spread, particularly between adult females with infants.

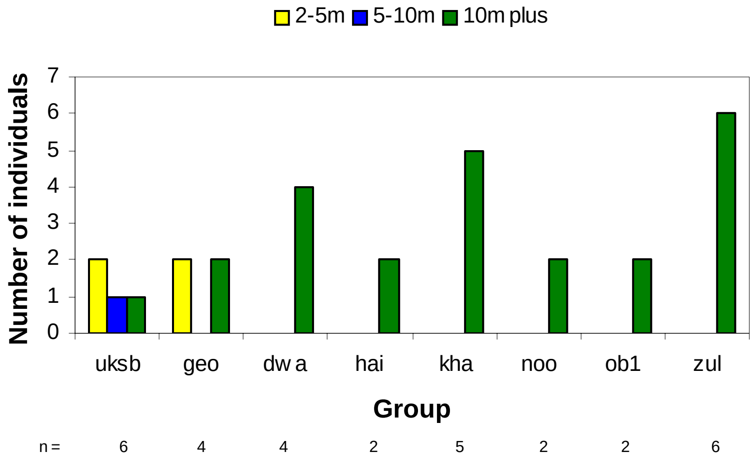


Figure 6.11. Differences between groups in infants' modal distances to immature group members.

6.4.5. Overview Of Infants' Interactions With Immature Group Members

Of 31 infants present during the study, 24 (77.4%) of them interacted with 34 other immature group members (72.3% of those available to them) over the course of the study. Infants were involved in agonistic, displacement (negative), affiliative, alloparental, grooming, and play (positive) interactions. There was no difference in the ages of study subjects with whom infants did and did not interact ($U = 236.0$, n = 34, 14, $P = 0.964$). There seemed to be a bimodal distribution in the ages of those who infants *did not* interact with: they were either very young, or older juveniles and sub-adults (**Figure 6.12**). Infants interacted with all individuals aged between 2 and 4.5 years of age that they had access to within the social group. As with juveniles and sub-adults, infants were more likely to engage in positive than negative interactions, and overall, infants were responsible for initiating almost equal frequencies of interactions as they received (**Figure 6.13**). Play interactions (which are discussed later) were the most common interaction type involving infants, occurring 2.5 times more frequently than the next most commonly observed interaction type.

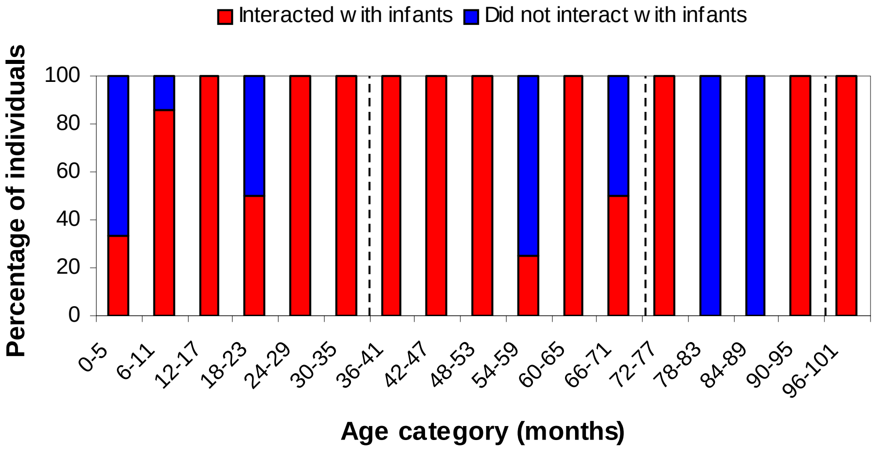


Figure 6.12. Age distribution of study subjects who did and did not interact with infants during the course of the study. $N_{TOTAL} = 58$.

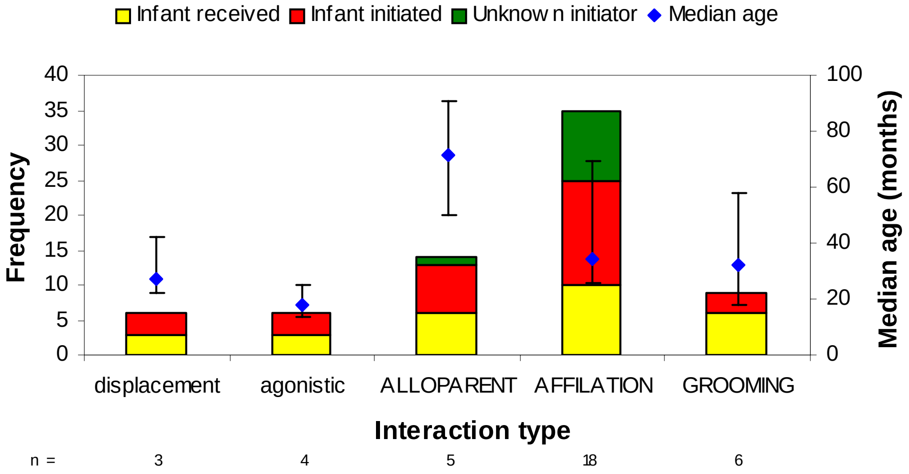


Figure 6.13. The frequency and initiators of infants' interaction types, and the median ages of individuals with whom infants interacted for each type. Positive (upper case) and negative (lower case) interactions are grouped. Some interactions involved two infants, therefore, the sum of interactions presented in the graph is greater than the actual number. $N_{TOTAL} = 24$.

6.5. INTERACTIONS BETWEEN IMMATURES

Infancy and the juvenile period are characterised by high levels of play in many primate species (Loizos, 1967; Fagen, 1993), and this study also found that the majority of interactions between immatures consisted of play behaviour. Alloparental behaviour also featured strongly in immature interactions. This section will give brief details of interactions other than play and alloparental interactions, which are then focussed on in separate sections. Only interaction types that were observed on more than five occasions (affiliation, grooming, agonism and displacements) are addressed.

6.5.1. NEGATIVE INTERACTIONS

6.5.1.1. Agonism

Agonism between study subjects was rare, occurring only on five separate occasions, involving seven individuals (**Table 6.3**). Agonistic interactions, which consisted of hitting and swiping, were most common between infants, although only three individuals were involved. On two occasions agonism was directed from an older to a younger individual. Agonism did not feature strongly in immatures' relationships with one another.

Table 6.3. *Distribution of agonistic interactions between immatures, and the initiators and receivers of such interactions.* $N_{TOTAL} = 7$.

AGONISM			***Receiver***		
Initiator	Infants	Juveniles	Sub-adults	Adults	TOTAL
Infants	3	-	-	-	3
Juveniles	-	-	1	-	1
Sub-adults	-	-	-	-	0
Adults	-	1	-	-	1
TOTAL	3	1	1	0	5

6.5.1.2. Displacements

Displacements were the more common element of negative interactions observed between study subjects, occurring on eleven occasions and involving 14 individuals (**Table 6.4**). Juveniles were the most frequent recipients of displacements. Sub-adults and infant study subjects displaced juveniles more than adult study subjects. In the majority of cases (81.8%), displacements were directed from older to younger individuals. In the remaining two instances, the Ike (juvenile) moved away from the boisterous approach of Axel (infant), and continued to feed.

Table 6.4. Distribution of displacements between immatures, and the initiators and receivers of such interactions. $N_{TOTAL} = 14$.

DISPLACEMENTS	***Receiver***				
Initiator	Infants	Juveniles	Sub-adults	Adults	TOTAL
Infants	2	2	-	-	4
Juveniles	-	2	-	-	2
Sub-adults	1	1	2	-	4
Adults	-	-	1	-	1
TOTAL	3	5	3	0	11

6.5.2. POSITIVE INTERACTIONS

6.5.2.1. Affiliation

Affiliation between immatures was observed on 22 occasions, involving 26 individuals (**Table 6.5**). Affiliation between infants was most common, and infants were also the more frequent initiators, and the only age class to initiate affiliation with sub-adult and adult study subjects. Infants were also the most frequent recipients of affiliative interactions. The majority of affiliation took the form of contact and embraces between individuals. Although more frequent than types of negative interaction, affiliation was still observed infrequently and did not involve all immature subjects. This suggests that general affiliative and friendly behaviour between immatures has limited benefits for immature western lowland gorillas in the bai.

Table 6.5. Distribution of affiliative interactions between immatures, and the initiators and receivers of such interactions. $N_{TOTAL} = 26$.

AFFILIATION	***Receiver***				
Initiator	Infants	Juveniles	Sub-adults	Adults	TOTAL
Infants	6	4	1	4	15
Juveniles	5	-	-	-	5
Sub-adults	-	1	-	-	1
Adults	1	-	-	-	1
TOTAL	12	5	1	4	22

6.5.2.2. Grooming

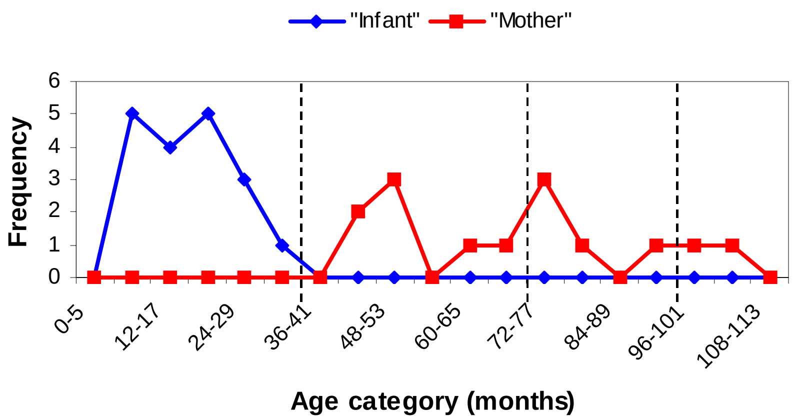
Grooming between study subjects was observed infrequently, on only six occasions and involving ten individuals. Initiators of grooming interactions were always the groomers; the groomee always received the interaction. On five of the six occasions, grooming was directed from an older individual to an infant; no other age class was groomed. Infants groomed other infants on three occasions, juveniles groomed infants twice, and sub-adults groomed infants only once during the study.

6.5.2.3. Alloparental Interactions

Alloparental interactions are hypothesised to serve the purpose of allowing the practise of mothering skills to improve maternal performance (Hrdy, 1976). Consequently, predominantly female, older individuals were predicted to play the role of the “mother”.

Nineteen distinct alloparental events were observed, involving twelve individuals, all of whom were older than 6 months. A small number of dyads were responsible for a large proportion of these interactions: Axel (infant male) and Ike (juvenile/sub-adult of unknown sex) contributed 37.5% of alloparental interactions, and Betsy (juvenile of unknown sex) and either Clyde or Luther (both infant males) accounted for 25%. Together, Sage (infant female) and Whisky (infant male) were involved in four distinct alloparental events and initiated all of them. Although only a few individuals were involved, and alloparenting was not a population-wide trait, an analysis was made of this behaviour to determine its nature, and if it was consistent with allomothering behaviour recorded in other species.

Alloparental interactions were divided by the role played by study subjects: that of the mother or the infant. When the frequencies of these two types were correlated with age category, a significant decrease in the frequency with which individuals played the "infant" role ($r_s = -0.664$, n = 19, $P = 0.002$), and a non-significant increase in the frequency with which individuals played the "mother" role ($r_s = 0.439$, n = 19, $P = 0.060$) was found (**Figure 6.14**). Although the general frequency with which immatures were involved as "mothers" in alloparental interactions showed an overall increase with immature age, this was not a steady increase, and peaks were seen during the juvenile period, and then again at the beginning of the sub-adulthood.



"Infant"	0	3	4	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0
"Mother"	0	0	0	0	0	0	0	2	1	0	1	1	1	1	0	1	1	1	0

Figure 6.14. The corrected frequency with which immatures of different ages took the role of the infant, or the mother in alloparental interactions. $N_{TOTAL} = 12$.

In no instance did an alloparental interaction result in distress to the infant (with the exception of the interaction discussed on p. 216, which was unlikely to represent a true alloparental interaction). A mother was never observed to retrieve her infant from an allomother. All interactions involved an infant, and either a juvenile, sub-adult, adult female or blackback. Infants were most likely to initiate alloparental interactions, most often by climbing onto another individual (**Table 6.6**).

Table 6.6. Distribution of allomothering between immatures, (including three occasions where the other individual was not a study subject) and the initiators and receivers of such interactions. $N_{TOTAL} = 12$

ALLOPARENTAL	***Receiver***				
Initiator	Infants	Juveniles	Sub-adults	Adults	TOTAL
Infants	-	4	5	4	13
Juveniles	3	-	-	-	3
Sub-adults	1	-	-	-	1
Adults	2	-	-	-	2
TOTAL	6	4	6	4	19

When investigating the effect of sex on participation in alloparental interactions, it was found that males were preferred as the younger partner, although this may have resulted from their increased availability. There was a slight tendency for females to be the older partner (**Figure 6.15**), and of course, the learning to mother hypothesis predicts that the "mothers" of unknown sex should be female.

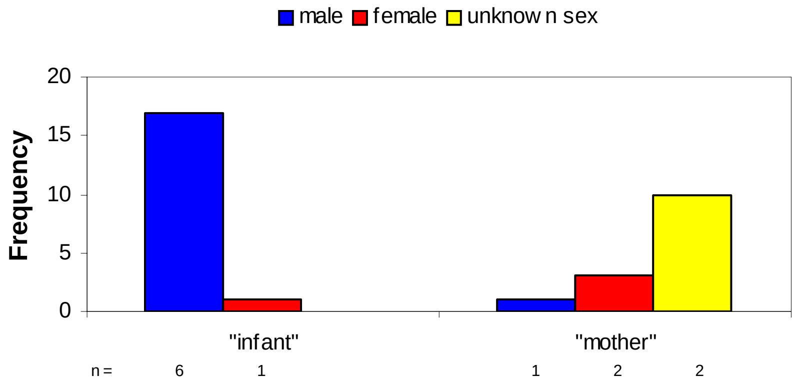


Figure 6.15. Comparison of the frequency with which males and females played the role of infant and mother in alloparental interactions.

Again, alloparenting was more common that agonism or displacement but still occurred at a low frequency and involved a small number of individuals. The cases that were observed were consistent with "learning to mother", and the need for males to interact gently with infants, so it was likely to serve a useful purpose for individuals that engaged in it.

6.5.2.4. Play Interactions: Frequency and Partners

Play has been widely described for many primate species, and trends, such as the ages at which play behaviour is most common, the types of play behaviour observed, and differences between the sexes in the manifestation of play behaviour (Loizos, 1967; Fagen, 1993; Spinka et al., 2001) often emerge, consistent with hypotheses of motor skill training (Spinka et al., 2001), and the development of social relationships (e.g., Maestripieri & Ross, 2004). The nature of play in this study is analysed to determine whether it was consistent with these hypotheses. Some interactions included here involve individuals who were not immatures, although the majority were young adults, and all females were nulliparous. These have been included in this section to give an overall presentation of play behaviour involving immature gorillas.

Play was the most common interaction between study subjects: 242 separate play sessions were recorded, with 80% of interactions involving only two individuals. The distribution of play between study subjects is presented in **Table 6.7**. Play between juveniles was most common, followed by play between infants. Overall, juveniles were most involved in play (145 interactions), followed by infants (124), sub-adults (43) and finally adult study subjects (21).

Table 6.7. Distribution of play behaviour between study subjects.

PLAY	Infants	Juveniles	Sub-adults	Adults	TOTAL
Infants	60	45	11	8	124
Juveniles	-	84	14	2	100
Sub-adults	-	-	7	11	18
Adults	-	-	-	-	0
TOTAL	60	129	32	21	242

The hourly rate of play behaviour was calculated for each individual in each category, and age category medians were calculated from individual median rates.

There was a significant increase during infancy in the rate of play behaviour (**Figure 6.16**: $r_s = 0.928$, n = 6, $P = 0.008$), but no correlations with age category were found in the other age classes (juveniles: $r_s = -0.086$, n = 6, $P = 0.872$; sub-adults: $r_s = -0.738$, n = 4, $P = 0.262$; adults: $r_s = -0.500$, n = 3, $P = 0.667$), although a gradual decrease occurred during each of these age classes as play reached very low levels in the early part of adulthood. Play rates peaked towards the end of infancy, and then again towards the end of the juvenile period.

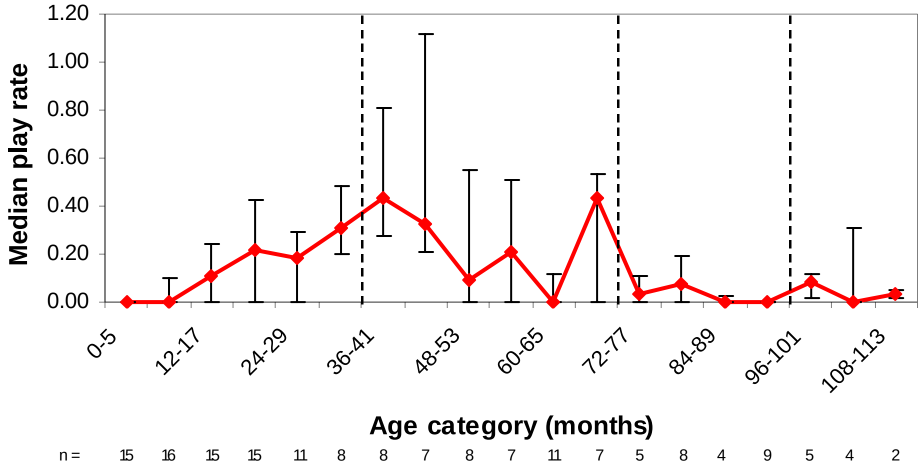


Figure 6.16. The rate of play interactions (interactions per hour) in study subjects of increasing age. $N_{TOTAL} = 39$.

During the juvenile period, males played more frequently than did females (**Figure 6.17**: $Z = -2.023$, n = 6, $P = 0.043$), although sample sizes were small, so cautious interpretation of results is required. No sex differences were evident during infancy ($Z = -0.730$, n = 6, $P = 0.465$), and sample sizes precluded other analyses.

The median age difference between individuals who engaged in dyadic play interactions was 21.5 months, and females were predicted to play more frequently with younger partners. However, there was no difference in the median ages of male and females' play partners (**Figure 6.18**: $U = 47.0$, $N_{\text{males, females}} = 16, 7$, $P = 0.548$), but the play partners of males showed a much wider age range than did those of females.

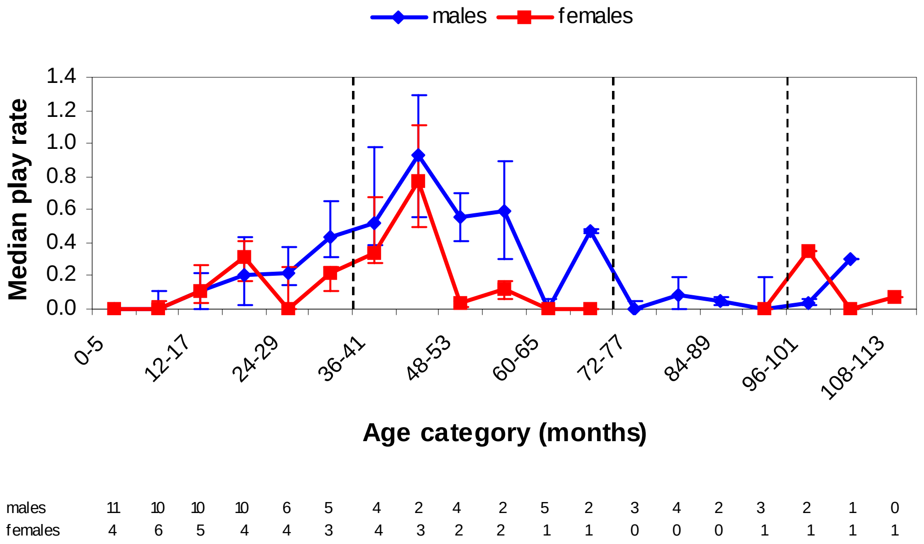


Figure 6.17. Comparison of the median play rates for males and females. $N_{\text{males, females}} = 21, 10$.

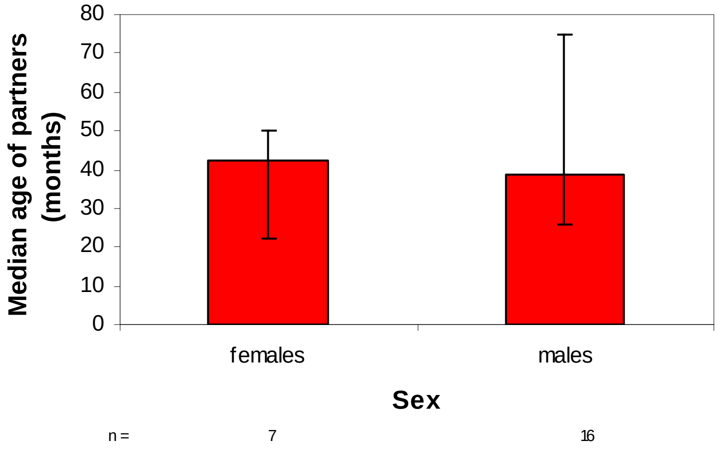


Figure 6.18. The median ages of male and females' play partners.

To investigate partner preferences, only dyadic play interactions were investigated. Females were involved in 50 dyadic play sessions, and only 10% occurred between females, with 90% occurring in mixed-sex dyads (**Figure 6.19**). Males were involved in 102 dyadic play sessions: 55.9% in same-sex dyads, and 44.1% in mixed-sex dyads, and the frequency with which individuals engaged in male-male, male-female and female-female play across the population did not different from the expected frequencies ($\chi^2 = 4.6$, d.f. = 2, $P > 0.1$).

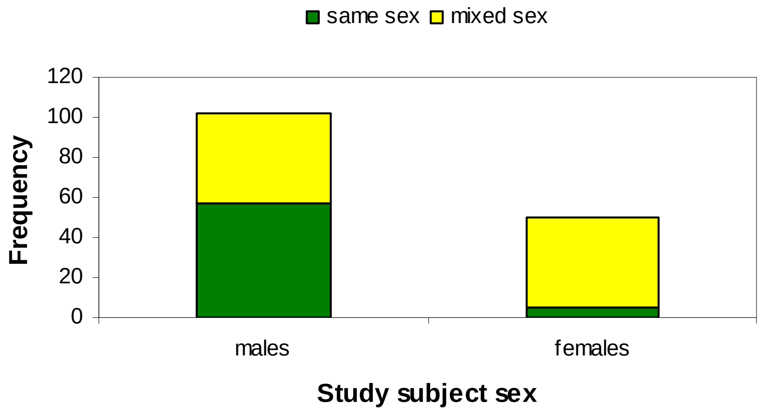


Figure 6.19. The frequency with which males and females engaged in same-sex and mixed sex dyadic play interactions.

The data presented in **Figure 6.19** suggests that both sexes preferred to play with males. However, more males were present in the population, so it was necessary to determine if apparent partner preferences simply reflected the availability of males and females within groups. Play interactions occurred with sufficient frequency in four groups (Kha, Dwa, Noo and Zul) that included both male and female study subjects to allow a preliminary analysis to be made of whether partner preferences were a result of the availability of each sex within a group. Although numbers were still too small to conduct chi-square goodness-of-fit tests (at least one expected number was less than 5 in each group), the distribution of play in male-male, male-female and female-female dyads can be seen in **Figure 6.20**. There were no consistent patterns in the distribution of play between the different types of dyads. Although males were expected to play preferentially with other males, observed levels exceeded the expected levels in only two of the groups. Likewise, females were predicted to play preferentially with males, but observed levels exceeded expected levels, again, in only two of the groups. It seemed that playful females in Dwa and Kha groups increased the frequency of male-female and reduced the frequency of male-male play. Female-female play was predicted to occur infrequently, and in only Dwa group did the frequency of female-female play exceed the expected frequency. Therefore, it appeared that although population-wide, patterns appeared to follow the predictions made with reference to partner choice, but this was largely due to more males in the population than females. When data were invested with reference to the interactions that could physically take place between individuals, results were much less clear and probably reflected differences in the playfulness of individuals.

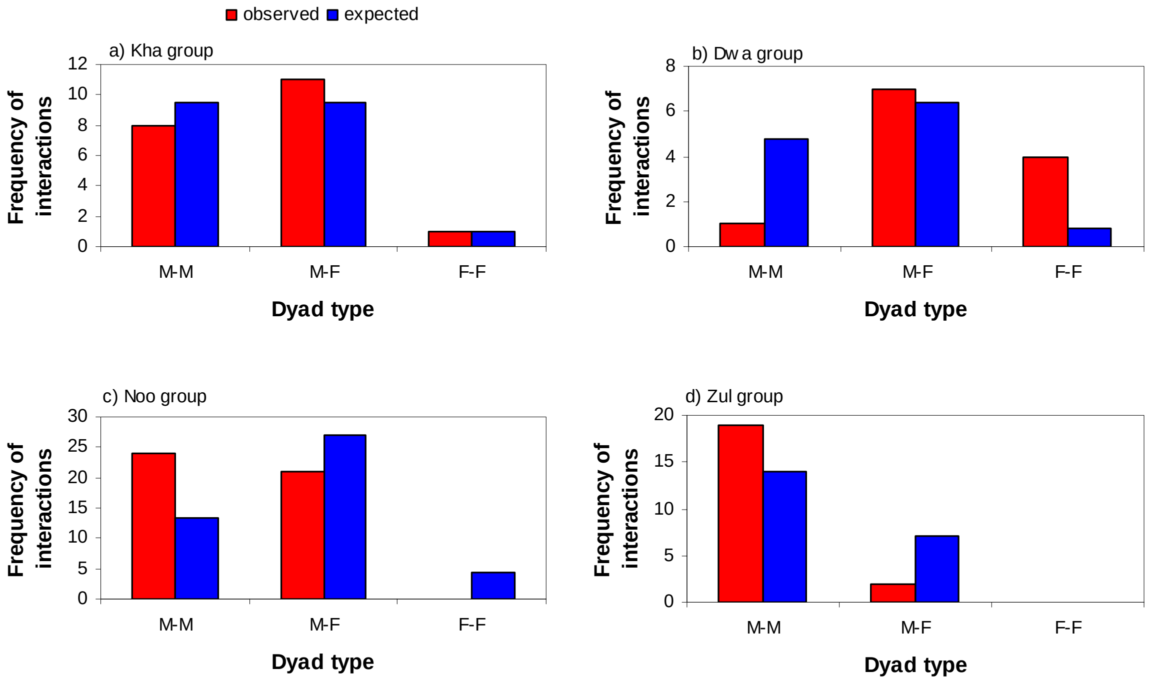


Figure 6.20. Distribution of play in male-male, male-female and female-female dyads in a) Kha, b) Dwa, c) Noo, and d) Zul groups. Expected frequencies were calculated based on the presence of males and females in each group.

Median group rates of play were calculated (from individual medians), and the largest group (which also had the largest number of study subjects) had a median play rate almost 2.5 times that of the group with the next highest play rates (**Figure 6.21**), suggesting an increased availability of partners may lead to increased rates of play. However, the median group rate of play interactions was not significantly correlated with the number of study subjects in a group ($r_s = 0.442$, n = 12, $P = 0.150$).

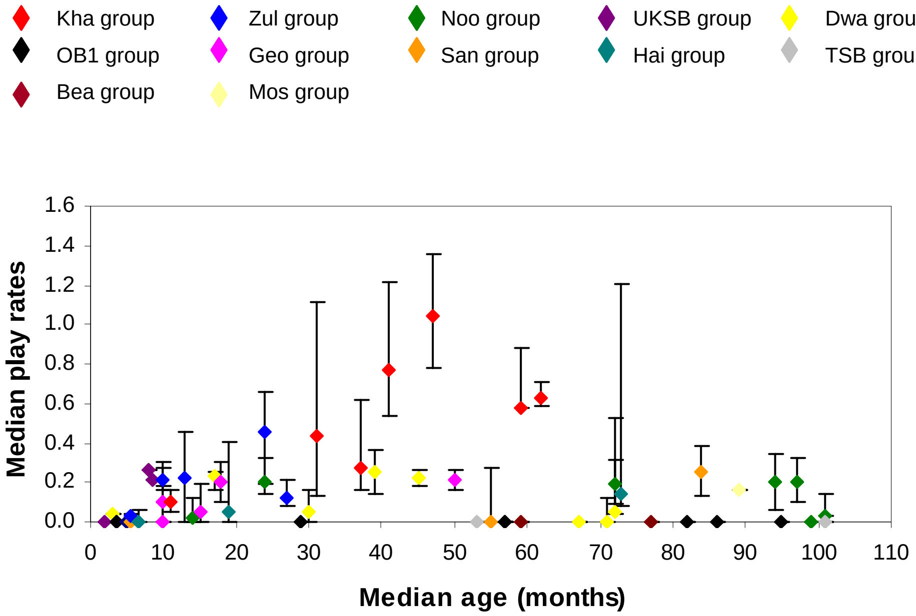


Figure 6.21. Median rates of play for immature individuals over the course of the study. Each point represents one individual, and their median rate of play during the study, and individuals in each group are indicated by a distinct colour code. $N_{TOTAL} = 55$.

Of all dyadic play sessions, 37.1% were clearly initiated by one of the participating individuals. In the remaining cases, it was either impossible to distinguish which individual initiated the bout, or the play session was already in progress when subjects entered the bai. There were no differences between the median ages of those initiating play or being the recipient ($U = 243.5$, n = 23, 24, $P = 0.489$). Of the sessions where the initiator could be determined, the younger individual initiated the interaction in 51.4%, the older in 48.6% of sessions.

6.5.2.5. Play Interactions: Play Types

Four distinct types of play interaction were defined (**Table 6.8**), but most commonly (34.9% of play interactions), play sessions involved a mix of different types of play behaviour. Rough play was the next most frequently observed type (28.1%), followed by chase (20.1%), gentle (13%) and display (3.8%).

Table 6.8. Play types and their definitions (see **Plate 6.1**).

Play Type	***Definition***
Rough play	Involved vigorous wrestling, grappling, and mouthing/biting
Chase play	One or more individuals running with a distinctive gait, behind one or more other individuals. Often included individuals twirling or spinning away from one another
Gentle play	Individuals patted each other, and explored each other's bodies. Also included parallel play – individuals engaged in solitary play but looked towards and maintained proximity to another individual who was engaged in similar movements
Display play	Chest beats, charging and strutting similar to adult behaviour, but sequences occurring in incomplete forms and often accompanied by a play face (lips pulled back exposing teeth)

Plate 6.1. Juvenile engaging in display play and showing a play face (top left, photo taken by Nick Nichols), two juveniles engaging in rough play (top right), three juveniles chasing each other (bottom).

There was no departure from the expected frequency (based on the presence of males and females within the population) with which male and female study subjects engaged in each type of play interaction (**Figure 6.22**), with the exception of gentle play, where females engaged more than expected ($\chi^2 = 15.15$, d.f. = 1, $P < 0.001$). There was a significant difference in the ages at which each play type was observed (**Figure 6.23**: $\chi^2 = 13.302$, d.f. = 4, $P = 0.010$). Multiple comparison post hoc tests found only that those engaging in display play were significantly older than those engaging in gentle play.

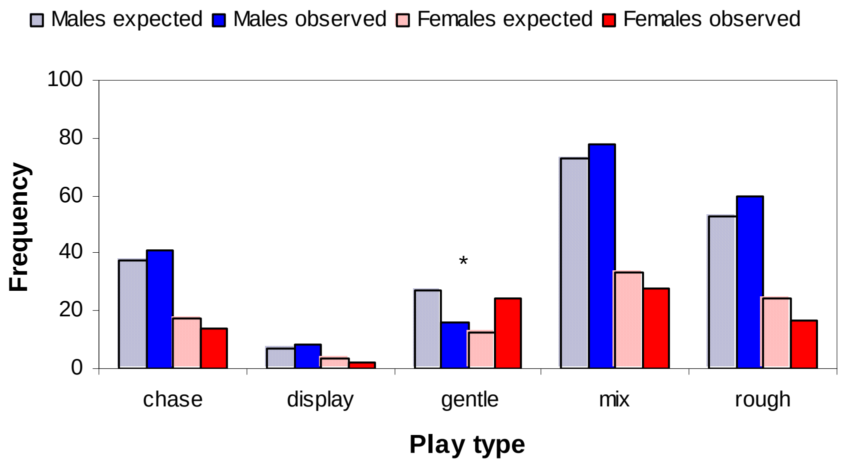


Figure 6.22. Expected and observed frequencies with which males and females engaged in each interaction type. * indicates a difference significant at the 0.01 level.

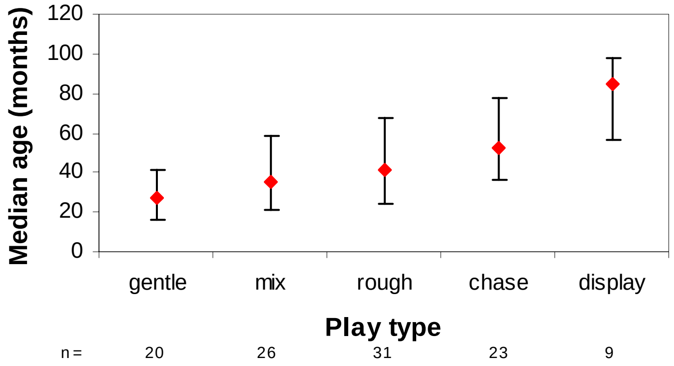


Figure 6.23. Differences between the median ages at which individuals engaged in different play types. $N_{TOTAL} = 39$.

Play was clearly the most frequent interaction type between immatures, and therefore, was likely to provide more benefits than other interaction types. Play observed in this study was consistent with the motor training and social skills hypotheses, pointing to clear benefits to immatures of engaging in this behaviour with conspecifics.

6.6. DISCUSSION OF RELATIONSHIPS BETWEEN IMMATURES

Spatial association may not be the best predictor of the relationships between immature group members, in particular, in only one of their possible environments, and while feeding. Instead, active interactions between them provide more information on the nature of their relationships and how immatures benefit from them. With regards to spatial relationships:

- Age and sex were found to have limited effects on immatures' proximity to conspecifics. Infants showed a tendency to associate with other infants (and their mothers, as shown in the previous chapter), and there were indications that juveniles and sub-adults were more likely to associate with one another than with infants, or young adult study subjects.

The tendency for close proximity between infants suggested that a variant of "creching" (involving infants *and* their mothers) might be in evidence with adult females with young infants remaining closer to one another than to other group members (Fossey, 1979; Harcourt, 1979a; see also Besnard et al., 2002). The proximity of mother-infant dyads to one another has been linked in mountain gorilla studies, with the spatial focus provided by the silverback (Harcourt, 1979b; Fletcher, 1994; Stewart, 2001). However, in this study, silverbacks were often the most distant individuals from infants. This results of this study differ from those obtained from mountain gorilla studies (Harcourt, 1979b), but are consistent with results from captive western lowland gorillas studies during the six months following birth (Stoinski et al., 2003). Closer association between mother-infant dyads than with the silverback was suggested to reflect the reduced risk of infanticide, and thus the reduced need for male protection in captivity (Stoinski et al., 2003). Although infanticide is suspected to occur in western lowland gorillas in the wild (Stokes et al., 2003), cases also exist in which females have successfully transferred with an infant (Stokes et al., 2003; pers. obs.). In conjunction with the potentially lower levels of infanticide than are seen in mountain gorillas, high levels of visibility in the bai may reduce the need for close proximity to the male to ensure his protection. Ultimately, this results in decreased infant-silverback proximity, while female-female (and infant) association continues in his absence, and infants still have access to others when they begin to develop independence from the mother.

Mothers of young infants are predicted to avoid the approaches of boisterous individuals (Pereira & Altmann, 1985), which are most often likely to be from juveniles, given the high rates of play expected from this age group (e.g., Brown, 1988; Fagen, 1993; Spinka et al., 2001). This may have contributed towards the infrequency of association between young infants and older immature study subjects. Juveniles and sub-adults did associate with each other. As they moved out of proximity with their mother (see Chapter Four, also Stewart, 1981; Fletcher, 2001), there was a tendency to increase levels of association with one another, which corresponded with increased play levels and rates of interactions, similar activity budgets and therefore, similar costs, or being tolerated to the same degree by other group members, ultimately resulting in them gravitating towards each other (see Kummer, 1978; Fagen, 1993; Fairbanks, 1993; de Oliveira et al., 2003).

The clearest influence on the spatial patterning of immatures, was a recent change in demography of the social group:

- Study subjects in groups that had recently experienced major demographic change, such as the death of the silverback, or integration into a new group, were the most likely to show closer association with conspecifics.

This reinforces findings from Chapter Five, suggesting that demographic changes affect the spatial patterning of all individuals, not just immatures. This is testament to the stability and confidence that the presence of a familiar silverback gives his group, even without being in close proximity to them. Without a familiar silverback, immature group members appear drawn to one another, showing higher levels of association than was normally observed. However, the high levels of association seen in immatures in groups without a stable, familiar leader does not translate into higher levels of interaction between them. Three of the five groups that experienced major demographic change during, or just prior to the start of the study had three of the lowest play rates. The subjective impression was also gained that when immatures were present in the bai without a silverback, that their levels of vigilance were higher than normal. However, vigilance occurred too infrequently to test for differences.

There was very little change in spatial relationships with age, so it was difficult to relate the frequency of interactions between immatures with their association with one another. In very general terms:

- Slightly higher rates of association amongst infants than with other immature age classes, may have resulted in a larger proportion of their interactions, particularly play, occurring with other infants. Similarly, the indications that juveniles and sub-adults preferred to associate with one another may have led to the relatively high frequency of play among and between juveniles and sub-adults.

Ultimately, spatial association among immature group members seemed a weak indicator of the likely frequency of interactions among them. A clearer predictor of the frequency of interactions between immature group members was the degree of independence from the mother (see Chapter Four). Individuals increased their proximity from the mother towards the end of infancy, coinciding with increased rates of interactions with other immature group members. This may be indicative of the control that a mother has over her infant's social relationships (see Pereira & Altmann, 1985; Fletcher, 1994), but as infants move beyond their mother's immediate proximity, they begin to develop and take responsibility for their own relationships.

Towards the end of the immature period:

- The frequency with which immatures interacted with one another slowly declined, reaching their lowest levels during the early parts of adulthood.

This was as predicted, and consistent with the hypothesis that involvement in particular relationships are less important in species where individuals are unlikely to live in the same group as others that they interacted with as immatures (see Maestripieri & Ross, 2004). Older immature individuals are likely to have already developed the skills (motor and social) that interactions with other immatures facilitated when they were younger and more active in interactions. With these skills in place, interacting with conspecifics may take on a lesser importance, allowing sub-adults and young adults to concentrate on feeding, and gain valuable resources for impending gestation and lactation, and continued body growth and competition among males.

Agonistic, displacement, affiliative, and grooming interactions were infrequently observed during the study. Agonism was directed both up and down the age gradient, but agonism directed up the age gradient was unlikely to influence relationships with others (apart from perhaps, those with other infants), given the frequency with which it was ignored or older individuals retaliated, the latter emerging as the “more dominant” individual. Displacements between study subjects were more commonly directed down the age gradient, as was also true for displacements involving other age-sex classes. This suggests that displacements may be the true means by which western lowland gorillas regulate their relationships (e.g., Scott & Lockard, 1999).

The observed cases of alloparenting were broadly consistent with the “learning to mother” hypothesis, whereby nulliparous females interact with and care for other females’ infants, becoming more adept at infant handling and increasing the chances that their first offspring will be raised successfully (Lancaster, 1971; Hrdy, 1976; Silk, 1999). In the case of “allomothers” being males, these interactions allow them to learn to interact gently with, and protect infants (e.g., Spijkerman et al., 1997). This study found that:

- When the sex of individuals was known, young females were the most frequent allomothers, and infant males the most frequent “infants”.
- No true alloparental interaction resulted in distress to the infant, and the mother never intervened or retrieved her infant from an allomother.

It was unfortunate that the sex of the two most active “allomothers” was unknown. If the learning to mother explanation for the presence of alloparental behaviour is correct, these two individuals are predicted to be female (Lancaster, 1971; Silk, 1999), particularly given the frequency with which they initiated interactions. Infants frequently initiated alloparental care, suggesting that they also gained from these interactions by widening their social circle and improving social skills (e.g., Lancaster, 1971; Small, 1990). The tolerance of alloparental behaviour by mothers also suggests a benefit for them, freeing them for foraging and resting in addition to providing socialisation for their infants (Hrdy, 1976; Hrdy, 1977)

Play is predicted to be at its most common during periods of rapid growth, allowing the development of motor skills (Spinka et al., 2001; Maestripieri & Ross, 2004), and during an increase in development from the mother, to provide social skills training for the future (Loizos, 1967; Brown, 1988; Fagen, 1993; Markus & Croft, 1995; Maestripieri & Ross, 2004). In gorillas, the strong relationships between adult males and females (Harcourt, 1979b; Stokes, 2004), mean that interacting with the opposite sex during immaturity will provide useful experience for the formation of relationships as adults. Differences in the life history variables of male and female gorillas predict that sex differences should exist between males and females in their play behaviour. This study found that:

- Females engaged in more gentle play than males did, and although a significant difference was not observed in the ages of individuals that males and females played with, males were more likely to play with older individuals than females.
- Males played at significantly higher rates than females during the juvenile period.
- Although the distribution of play partners did not differ significantly from the expected distribution, female-female play tended to occur less frequently than predicted. Partner choice was limited by the availability of males and females within each group, and individual differences may have accounted for the results observed in this study, since the number of immatures in any one group was small.

These findings suggested that in the Mbeli gorillas, play served as training for the future, most likely in the form of allowing males to develop physical and motor skills when engaging in rough play with one another. It was also likely that social skills were developed during play that are useful during adulthood (Spinka et al., 2001; Maestripieri & Ross, 2004).

In summary, associations between immatures did not always reflect the predictions that were made in this chapter, but interactions between immatures were more likely to proceed as predicted. Finally, it must be remembered that all observations took place during feeding periods: the time during which social interactions are often reduced in frequency (Harcourt, 1978a; Fletcher, 1994). It remains to be determined whether the nature of interactions among immatures is altered during feeding periods in the bai. This study provides a preliminary analysis of relationships that exist between immatures, and gives comprehensive data on the behaviours that are involved during interactions between immatures, which are likely to be difficult to collect from western lowland gorillas in the forest, even those that are well-habituated.

CHAPTER SEVEN

BEHAVIOURAL DEVELOPMENT IN WESTERN LOWLAND AND MOUNTAIN GORILLAS

7.1. INTRODUCTION

Variation in gorilla ecology is predicted to have implications for behavioural ecology theory (McNeilage, 2001; Doran-Sheehy & Boesch, 2004), and also for the development of behaviour (Fletcher, 2001). The availability and distribution of resources are expected to be fundamental to the rate at which behaviour develops, and to when independence from the mother can be achieved. This chapter compares the behavioural development of western lowland gorillas, as described in this study, with accounts from mountain gorillas to elucidate how the variation in socioecology influences behavioural development in gorillas. Mountain gorilla data are taken from studies that were conducted on the Karisoke population of mountain gorillas in the Virunga Volcanoes between the 1960’s and 1990’s: Fossey (1979), Stewart (1981, 1988, 2001) and Fletcher (1994, 2001). Data from captive studies on western lowland gorillas are also used for comparative purposes (Hoff et al., 1981a; Hoff et al., 1981b; Enciso et al., 1999; Maestripieri & Ross, 2004), and statistical analyses are carried out where possible.

The majority of knowledge concerning gorilla social behaviour comes from long-term studies on the Karisoke population of mountain gorillas, who represent one extreme of gorilla habitat, at the upper end of their altitudinal range (Doran & McNeilage, 2001; McNeilage, 2001). It is becoming clear that differences in gorilla socioecology exist, not only between different species, but also within species, and seem to result from habitat type. For example, differences in the amount of fruit incorporated into the diet exist between highland and lowland populations of eastern lowland gorillas (Yamagiwa et al., 2003); and ranging behaviour differs as a result of food density between the Karisoke study population and mountain gorilla groups ranging at lower altitudes (McNeilage, 2001). Ecological differences between *Gorilla* species and the resulting effects on social organisation are becoming clearer with the emergence of more comprehensive data from western lowland gorilla study sites (**Table 7.1**). Many differences in the behaviour of gorillas seem to result from levels of frugivory in the diet, with more frugivorous populations tending to have smaller group sizes, larger home ranges and daily path lengths, fewer multi-male groups and a greater percentage of natal dispersal.

Table 7.1. Socioecological features of gorillas, and variation between mountain (MG), eastern lowland (ELG) and western lowland (WLG) gorillas.

Feature	***MG***	***ELG***	***WLG***
Diet	[1]Folivorous	[2]Intermediate between MG and WLG; dependent on habitat	[3]Seasonally frugivorous
Mean daily path length	[4]500m, 918m (mean: 709m)	[2]716m	[5]2014m, [6]2083m (mean: 2048.5m)
Group size	Median: [7]24, [8]10; maximum: [11]47	[2]Median: 10, 7; maximum: 31	Median: [9]6-13.9; maximum: [10]32
Multi-male groups?	[11]59.2% of groups multi-male	[2]0 – 8% of groups multi-male	[9, 12]Vast majority of groups single-male
Percentage of individuals dispersing from natal group	[13]Males: 36%; females: 44%	[2]Males: 100%; females: 72%	[14,15]No individuals yet observed breeding in natal groups
Infanticide?	[16]Accounts for 37% of infant mortality in the first 3 years, [17]~10% of all births	[18]14 cases where infanticide was predicted, but did not occur	[15]May occur, although not universally

[1]Watts, 1984
[2]Yamagiwa et al., 2003
[3]Remis, 1997b
[4]Doran & McNeilage, 2001
[5]Doran et al., 2004
[6]Cipolletta, 2003
[7]Steklis & Gerald-Steklis, 2001
[8]McNeilage, 2001
[9]Parnell, 2002a
[10]Bermejo, 1997
[11]Kalpers et al., 2003
[12]Magliocca et al., 1999
[13]Watts, 1991b
[14]Parnell, 2002b
[15]Stokes et al., 2003
[16]Watts, 1989
[18]Yamagiwa & Kahekwa, 2001
[17]Robbins & Robbins, 2004

Morphological features are also predicted to influence the development of independence. **Table 7.2** summarises some of these, plus ecological factors, and their predicted effects on the development of independence in wild gorillas. The majority of these factors predict the later development of independence from the mother in western lowland gorillas

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Table 7.2. Features of mountain (MG) and western lowland gorilla (WLG) ecology and morphology, and their predicted effects on the development of independence.

Feature	***Predicted Effect on the Development of Independence***
Habitat	[1]MGs: Steep slopes/ravines are predicted to increase dependence on mother in areas where independent locomotion may be dangerous. WLGs: Swampy bais and poor visibility in the forest are predicted to increase dependence on mother in areas where independent locomotion may be dangerous.
Resource abundance[2]	MGs: Abundant resources should allow the earlier development of independence; immatures are less dependent on the mother for provision of resources. WLGs: Dispersed and seasonal resources predict increased dependence on the mother to a later age, as environmental resources cannot always be relied upon.
Ranging[3]	MGs: Shorter daily path lengths may result in young immatures being able to travel independently for more of the day. WLGs: Longer daily path lengths may result in greater infant fatigue, increasing the need for them to travel dependently.
Cranio-dental features [4]	MGs: Adaptations to folivory predict that young individuals are capable of processing fibrous items, leading to nutritional independence at a young age. WLGs: Lack of adaptations to a folivorous diet predicts that young individuals are less capable of processing fibrous items in times of fruit shortage; therefore, the length of nutritional dependence on the mother is predicted to be increased relative to MGs.

[1]A. Fletcher, pers. comm. [2]See Barrett et al., in press [3]L. Barrett, pers. comm. [4]Taylor, 1997

A rigorous analysis of these features would permit more conclusive suggestions to be made regarding the effects of ecological variables on the development of independence, but limited data are available for comparison. Using the available data, this chapter will investigate aspects of behavioural development in mountain and western lowland gorillas (few data are available on the development of behaviour in eastern lowland gorillas), with respect to:

- The ontogeny of feeding behaviour
- Contact and proximity between mother and offspring
- The development of independent travel
- Suckling, and age at weaning
- Relationships between silverbacks and immature group members
- The nature of relationships between immatures and unrelated adult group members
- Play behaviour between immatures.

Any differences between mountain and western lowland gorillas in development will be discussed in terms of ecological variables.

7.2. THE ONTOGENY OF FEEDING BEHAVIOUR

The diets of mountain and western lowland gorillas differ greatly, with mountain gorillas consuming considerably more herbaceous vegetation than frugivorous western lowland gorillas (Watts, 1984; Williamson et al., 1990; Watts, 1996b; Remis, 1997b), resulting in a less "risky" diet (Ross, 1998). Consequently, mountain gorillas have faster growth rates (Taylor, 1997; Ross, 1998), which should allow earlier nutritional dependence in mountain gorillas. But before nutritional independence can be reached, competence in feeding and processing behaviour must be developed. Complicating comparisons of the ontogeny of feeding behaviour, this study only investigated feeding behaviour in western lowland gorillas with reference to a particular resource (*Hydrocharis chevalieri* – see Chapter Three) that is abundant in Mbeli Bai, but is thought to contribute minimally to overall diet (Parnell, 2002b), whereas data from mountain gorillas relate to all items in the diet. Therefore, only limited conclusions can be drawn.

Both mountain gorillas (Byrne & Byrne, 1993) and western lowland gorillas (Parnell, 2001) must learn *how* to eat their food as well as *what* items to feed on, and Byrne & Byrne (1993) have suggested that in mountain gorillas, the former may be more demanding. The behaviours exhibited by gorillas at Mbeli feeding on *H. chevalieri* did not undergo any significant development after infancy, and therefore, almost complete forms of the adult feeding behaviours were achieved by this age. If other feeding behaviours develop at a similar rate, this suggests that by the end of infancy, western lowland gorillas to sustain themselves and become nutritionally independent from the mother. Similarly, immature mountain gorilla feeding resembles adult patterns in composition, processing skills and timescale by the end of infancy (Watts, 1985a; Watts, 1988; Byrne & Byrne, 1993; Watts & Pusey, 1993).

Adults visiting Mbeli Bai commonly fed on *Rhynchospora corymbosa*, particularly when entering or exiting the bai. However, very few immature individuals fed on it, and they appeared to lack the strength to uproot this species from the bai in order to feed on the stem bases. Limited observations of infants feeding on fruit (D. Doran, pers. comm.) suggest that infants lacked the strength they needed to manipulate hard, fibrous fruits, and in addition, their skill at feeding on fruit with minimal wastage needed development (pers. obs.). These few observations and preliminary data on faecal analysis (T. Breuer; C. Cipoletta, pers. comm.) suggest that infants do routinely feed, or attempt to feed on fruit in the forest. Succulent fruits are likely to be preferred weaning foods (see Altmann, 1980; Barrett & Henzi, 2000), but their availability tends to be more restricted than harder, fibrous fruits, one of which, *Duboscia macrocarpa*, fruits asynchronously and seems to act as a fallback for western lowland gorillas in times of fruit scarcity (Doran et al., 2002; T. Breuer, pers. comm.).

The feeding behaviour of western lowland juveniles could not quantitatively be distinguished from that of adults when feeding on *H. chevalieri* in the bai. Outside the bai, however, and when feeding on items other than *H. chevalieri*, it appears that all aspects of feeding behaviour in young gorillas do not fully resemble adult behaviour by the end of infancy in western lowland gorillas, however, consistent observations of immatures feeding in the forest are required before this can be concluded with certainty. The data from mountain gorillas concern all elements of mountain gorilla diet suggesting that, unlike western lowland gorillas, their feeding skills are fully developed by the end of infancy. The relatively high quality of items constituting mountain gorilla diet (items constituting the mountain gorilla diet are low in tannins and indigestible fibres (Byrne & Byrne, 1993)), the lack of seasonal variation in the availability of items constituting the diet (Watts, 1998b), and morphological adaptations to this diet (Taylor, 1997) appear to allow the development of nutritional independence from the mother around the end of infancy. In mountain gorillas, the length of time required to learn how and what to eat seems to constrain the development of nutritional independence, rather than the availability of appropriate resources in the environment.

7.3. ASPECTS OF THE MOTHER-OFFSPRING RELATIONSHIP

Infant mortality has two sources: care-dependent (those under female control, e.g., the amount of milk received from the mother) and care-independent (sources outside of parental control, e.g., disease) (Lycett et al., 1998). Mothers can contribute towards a reduction in mortality by increasing levels of care (*sensu* Barrett et al., in press), for example, by allowing offspring to suckle or remain in close proximity until a later age. In both eastern lowland and mountain gorillas, infant mortality is higher in the first year after birth than in later years (Yamagiwa & Kahekwa, 2001), suggesting that in the eastern species, the first year is more risky for infants than later years. However, infant mortality in western lowland gorillas is higher in later years of infancy than during the first year (where mortality rates fall between those of eastern lowland and mountain gorillas), suggesting that risks increase after the first year (**Table 7.3**). Although the causes of infant mortality are not always known, this suggests that western lowland gorilla mothers should continue to invest in offspring for longer than mountain and eastern lowland gorilla mothers, in an attempt to increase offspring's chances of surviving infancy. It would therefore be expected that continued investment by the mother (as seen in western lowland gorillas relative to mountain gorillas, and which will be discussed in this section) should result in reduced infant mortality at later ages, not the increased levels that have been recorded (Robbins et al., 2004). Given that the nature of weaning in western lowland gorillas appears to be relatively flexible, with mothers responding to genuine need in their offspring (Chapter Four; see also Bateson, 1994; Barrett & Henzi, 2000), increased probabilities of infant mortality may result when offspring embark on independent foraging trajectories that cannot be sustained during periods of fruit shortage (see Barrett et al., in press). In such circumstances, "remedial action" by the mother may not always be taken, resulting in the high levels of third year infant mortality. Remedial action, when the mother takes it, requires extra maternal investment (e.g., later ages at weaning, continued close proximity which might reduce costs to offspring of thermoregulation) if offspring are to survive.

Table 7.3. Rates of infant mortality in western and eastern lowland, and mountain gorillas.

	First year infant mortality	***Third year infant mortality***
Western lowland gorillas[1]	18.5% (n = 35 births)	26.1% (n = 24)
Eastern lowland gorillas[2]	19.6% (n = 46)	6.5% (n = 46)
Mountain gorillas[3]	26.2% (n = 65)	7.7% (n = 65)

[1] Median of data taken from two sites (Robbins et al., 2004)

[2] Data taken from the highland population (Yamagiwa & Kahekwa, 2001)

[3] Data taken from the Karisoke population (Watts, 1991)

7.3.1. Contact Between Mother and Offspring

In mammalian species that exhibit maternal care, a reduction in investment by the mother as offspring increase in age is usually characterised by a decrease in the time that mother and offspring spend in contact with one another (Stewart, 1981; Nicolson, 1987). Various factors, such as resource abundance and ranging behaviour, suggest that increased investment in offspring from western lowland gorilla mothers is necessary; therefore, the reduction in investment is predicted to occur later in western lowland compared with mountain gorillas, and one way in which this could be manifested is by mothers and infants spending longer in contact with one another, and be more commonly in contact until a later age, relative to mountain gorillas.

In gorillas (and other great apes), infants were continuously in contact with their mothers until at least the third month of life, but more usually, contact with the mother was not broken until the 5th month (**Table 7.4**). There was relatively little variation in the age at which mothers and infants first broke contact with one another, but infants at Mbeli were slightly older than those in other studies. However, due to the nature of data collection at Mbeli, this figure is less reliable than the others. More than a month often passed between group visits at Mbeli, so the potential error in observing the first break of contact was dependent on the amount of time between group visits. However, as discussed in Chapter Four, 5.9 months was thought to be a reasonably accurate estimate. It was likely, however, that limitations on data collection in a bai study, or as a result of observations in this study being carried out in a minority environment type for the gorillas were the cause of the slightly later break in contact between western lowland gorillas and the mother. The fact that some infants were seen independent on the forest edge before being seen independent in the bai further attests to this. However, no data are currently available for the first break in contact in the forest environment.

Table 7.4. Ages at first break of contact between mothers and offspring in mountain gorillas (MGs), and wild and captive western lowland gorillas (WLGs). First break of contact is the range of ages, or most commonly observed age at which contact was first broken, unless stated otherwise.

Species/Sub-species	***First break of contact***	***Source***
MG (wild)	5th month	Fossey (1979)
MG (wild)	4th – 5th month	Fletcher (2001)
MG (wild	5th month	Stewart (1981)
WLG (captive)	3rd – 5th month	Hoff et al. (1981a)
WLG (wild)	Median = 5.9 months	This study

Contact between mother and infant enables the mother to provide protection from predators (Fay et al., 1995), infanticidal males (Watts, 1989), and from the environmental elements (Watts & Hess, 1988; Tutin et al., 1995). In captivity, these threats are absent, or occur at negligible levels (e.g., indoor enclosures are often maintained at constant temperatures, hence the reduced need for thermoregulation by the mother (Maestripieri et al., 2002)). Consequently, the importance of mother-infant contact may be reduced for gorillas in captivity, and the earliest recorded break of maternal contact was observed in captive gorillas (Hoff et al., 1981a).

Data from Fletcher (2001) were used to compare the amount of time that infants in the Mbeli population spent in contact with the mother with wild mountain gorillas during feeding periods. Fletcher (2001, p.163) presented results on the median contact rate between mother and offspring per half hour, with a maximum contact rate of six scan samples per half hour in contact with the mother. Values were estimated from Figure 6.1 (Fletcher, 2001), and converted into percentages of time so as to be comparable with data collected during this study. Six scan samples in contact per half hour gave a value of 100%; five scan samples gave a value of 83.3%, and so on. Western lowland gorillas were found to spend a significantly greater percentage of time in contact with the mother than mountain gorillas (**Figure 7.1**: *Z* = -2.803, n = 12, *P* = 0.005). Contact between mothers and offspring was significantly greater in western lowland gorillas for all age categories between 15 and 27 months of age, and then again between the ages of 33-36 months.

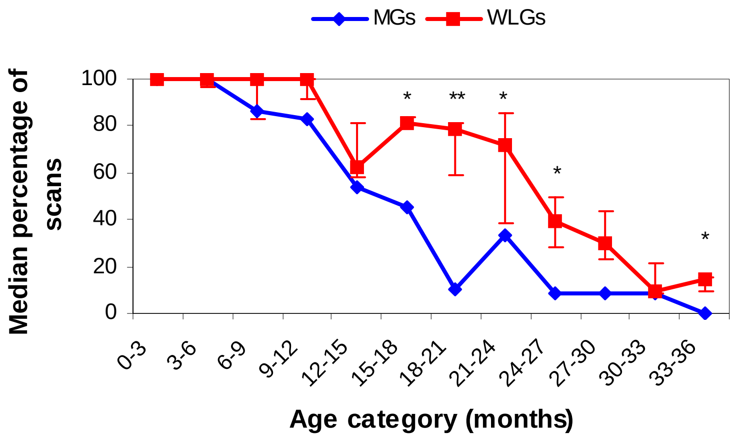

Figure 7.1. Differences between mountain gorilla (MGs) and western lowland gorilla (WLGs) infants in the median percentage of scan samples that were spent in contact with the mother. * indicates a difference at the 0.05 level; ** indicates a difference at the 0.01 level.

Infants in this study first broke contact with the mother at a slightly later age, and maintained higher levels of contact with the mother to a later age than in mountain or captive western lowland gorillas. However, the extent of the effect of the bai environment could not be determined. Areas of the bai, including those in which some groups often fed (**Plate 7.1**), have areas of standing water up to 1m in depth, and gorillas of juvenile and infant age were often observed to experience difficulties when moving through the thick mud, or across streams (Parnell, 2002b; pers. obs.). This provides one possible reason why Mbeli infants maintained contact with the mother until a later age than mountain gorillas, although the terrain of mountain gorillas could be demanding at times for immature individuals as a result of steep slopes and ravines (A. Fletcher, pers. comm.), the physical nature of the bai provides one possible reason why Mbeli infants maintained contact with the mother until a later age than in mountain gorillas.

7.3.2. Decreasing Mother-Offspring Proximity

Time spent out of contact with the mother is a useful indicator of developing independence, as it is likely to suffer less from effects of the immediate surroundings. Concurrent with the decrease in time that mother and offspring spend in contact, the distance between them increases reflecting the reduction of investment in offspring by the mother (Stewart, 1981; Watts & Pusey, 1993; Fletcher, 2001). If longer spent in contact with the mother did represent increased dependence at later ages on the mother in western lowland gorillas, they would also predicted to move out of the mother's close proximity at a later age than in mountain gorillas.

Fletcher (1994, p.54) measured the proportion of time that infants spent within 5m of the mother during feeding periods, and found that from the age of 27-30 months, mountain gorilla infants spent more than half their time at distances greater than 5m from the mother. In this study, this criterion was not reached until the age of 36-45 months (**Figure 7.2**).

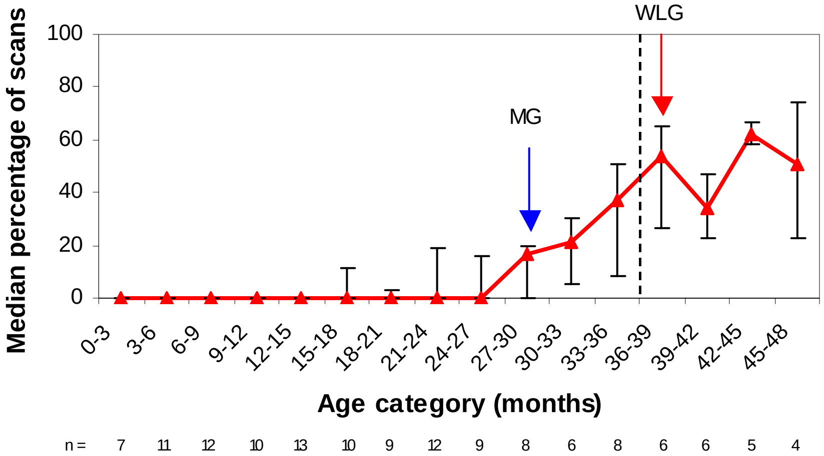

Figure 7.2. The median percentage of scans that western lowland gorillas spent at distances greater than 5m from the mother. Arrows indicate age at which western lowland (WLG) and mountain gorilla (MG) infants first spent more than 50% of their time beyond 5m of the mother. $N_{TOTAL} = 34$.

Plate 7.1. Silverback moving with difficulty through a swampy area of Mbeli Bai commonly used by gorillas for feeding. Photo by Nick Nichols.

Mountain gorillas, with an overall more abundant and evenly distributed diet may have more time available to invest in non-feeding activities, and a result of reduced foraging time: daily path lengths are lower in mountain gorillas (**Table 7.1**). Additionally, regular periods of rest (during which social interaction often takes place (Harcourt, 1978a)) may be necessary to allow mountain gorillas to digest the large quantities of vegetation that they consume (see Remis & Dierenfeld, 2004). Low levels of feeding competition for mountain gorillas (Watts, 1985b) and in the bai environment for western lowland gorillas (Stokes, 2004) may allow immatures to invest in relationships with individuals other than the mother as their reduced nutritional requirements may allow them more "free time" than adults. Immatures are expected to leave the proximity of the mother to socialise with other individuals, for example, in mountain gorillas immatures sometimes seek the proximity of the silverback rather than that of the mother (Fletcher, 1994). Although the bai environment must be taken into consideration: infants in an unfamiliar environment or situation are more likely to return to the close proximity of the mother (*sensu* Fossey, 1979), this was not thought to be the sole reason contributing towards continued close proximity between mother and offspring. By the age of 24 months, western gorilla infants in the current study spent more than half their time out of contact with the mother (see **Figure 7.1**), showing competence in travel in all but the swampiest parts of the bai. However, infants did not move further than 5m from the mother until another three months had passed.

The difficulty faced by smaller individuals in the bai undoubtedly resulted in infants spending longer in contact with the mother, but the effect of the bai on time

spent out of contact with the mother was less clear-cut. The area in which gorillas most often fed (the area encompassing zones 1, 5, 6 and 7 – see **Plate 2.3**) was at its deepest and swampiest in the centre of this area, a maximum strip width of around 20m. Few adults fed in the very deepest areas, so it was often necessary for infants to move only 5-10m from the mother to reach more solid ground that would facilitate easier locomotion, and remaining within 5m of the mother often presented greater locomotor challenges for infants. Despite this, infants tended to remain close to the mother. The choice, whether by infants or the mother (data on proximity and contact maintenance were inconclusive) to remain within 5m may have been affected by other features of the bai, such as its relative unfamiliarity, openness and occasional proximity to other species (sitatunga, elephants, buffalo) and other gorilla units.

7.3.4. The Development of Travelling Behaviour

The transition from dependent to independent travel tends to follow the same patterns in infant apes of supported ventro-ventral travel position, which is succeeded by unsupported ventro-ventral travel. Dorsal travel follows, and then finally, offspring travel independently (Fletcher, 1994; Doran, 1997b; Dunbar & Badam, 1998; this study). With western lowland gorillas seeming to gain independence from the mother more slowly than in mountain gorillas, the age at which transitions between travelling positions were made was predicted to be later than in mountain gorillas.

There was surprisingly little variation in the ages at which mountain, wild and captive western lowland gorillas were first observed to travel in each of the different travelling positions (**Table 7.5**), particularly in the ages at which infants were first observed to travel supported ventrally, ventrally without support and dorsally. Both mountain and wild western lowland gorillas travelled independently of the mother at a later age than did captive western lowland gorillas. This was unsurprising: captive gorilla infants they lived in a familiar, stable environment, and were exposed to very little additional risk by travelling independently. Captive individuals also have shorter distances to travel per day than their wild counterparts, and a study on chacma baboons has found that infants tended to travel dependently more on days with long journey lengths than those with shorter ones (L. Barrett, pers. comm.). Therefore, daily path lengths may affect the degree of dependent travel in immature individuals, and this also predicts that western lowland gorillas should travel dependently more than mountain gorillas, given their longer daily path lengths.

There was little difference in the age at which mountain and wild western lowland gorillas were last observed to travel supported ventrally, and this was thought to be a reflection of the increasing size and strength of infants. In very young individuals, the gripping reflex is not well developed, and gorillas are thought to be incapable of supporting their own weight when clinging to the mother's ventrum (Fossey, 1979). Therefore, it is necessary for the mother to support the weight of her infant, even though this increases her travel costs (e.g., Altmann, 1980; Stanford, 1992; Achenbach & Snowdon, 2002). The similar age at which mountain and western gorillas were first able to travel without the support of the mother suggests that *physical* development occurs at a similar pace in these two species (and indeed, although mountain gorillas have faster growth rates than western lowland gorillas overall, differences are not evident at this stage of infancy (Taylor, 1997)).

Table 7.5. Ages (in months) at first and last observation of travelling methods by mountain gorillas (MG), and wild and captive western gorillas (WLG). Data for MGs taken from Fletcher (1994, p.70-71), data for captive WLGs taken from Hoff et al., (1981a, p. 255).

	MGs	***WLGs (present study)***	***WLGs (captive)***
First observation			
Supported ventral	0.5	0.5	1
Unsupported ventral	0.5	1	1
Dorsal	4.5	3	4
Independent	8.5	11	4
Last observation			
Supported ventral	25.5	25	
Unsupported ventral	26.5	21	
Dorsal	55.5	44	

As noted by Fletcher (1994), travel in the unsupported ventral position occurred at later ages when offspring were suckling than those presented in the figure. In this study, a juvenile aged 53 months was observed clinging ventrally while suckling, and in Fletcher's (1994) study, unsupported ventral travel while suckling was last observed at the age of 28.5 months – just over half the age at which it was permitted in western lowland gorillas, so mothers tolerated ventral travel for longer in western lowland gorillas while offspring were suckling.

The results from travelling behaviour did not reflect the continuation of closer proximity to the mother in western lowland gorillas. Mountain gorillas travelled independently earlier than western lowland gorillas, but they continued to travel dorsally for a longer period than western gorillas did. Data for mountain gorillas come from travel-feed and group travel periods: the demands of travel during the latter are likely to be greater than for western lowland gorillas feeding in a bai. Comparable data from western lowland gorillas in the forest are required to draw firm conclusions on differences in the development of travel between mountain and western lowland gorillas, and the implications for the development of independence.

7.3.5. Suckling and Weaning, and Consequences for Reproductive Parameters

Gestation and lactation are the most expensive investments a mother makes for her offspring (Dufour & Sauther, 2002), therefore, mothers are expected to reduce this cost as soon as the development of her offspring allows it. If western lowland gorillas do invest longer in their infants, it is most likely to be manifested in suckling behaviour, and is a direct means by which a mother can increase levels of care in an effort to reduce care-dependent levels of mortality.

The general patterns of suckling in this study were similar to those reported by both Stewart (1988) and Fletcher (2001) with high rates of suckling during the first six months, which then declined throughout the rest of infancy. At Mbeli, the initial rate of suckling was lower than in mountain gorillas (significantly so during infancy: $Z = -2.510$, n = 12, $P = 0.012$), and the rate of 0.5 suckling bouts per hour (associated with the mother's return to oestrus (Stewart, 1988)) was first reached when their infants were younger (**Figure 7.3**, **Table 7.6**). If Stewart's (1988) data are also applicable to western lowland gorillas, then females should return to oestrus when the infants are aged approximately one year. However, it was clear that mothers did not resume oestrus cycles at this stage, and at Mbeli, offspring continued to suckle to an older age than in mountain gorillas (**Table 7.6**). Either Stewart's data are not applicable to western lowland gorillas, and a lower frequency of suckling is sufficient prevent them from returning to oestrus, or suckling rates in the bai are lower than in the forest.

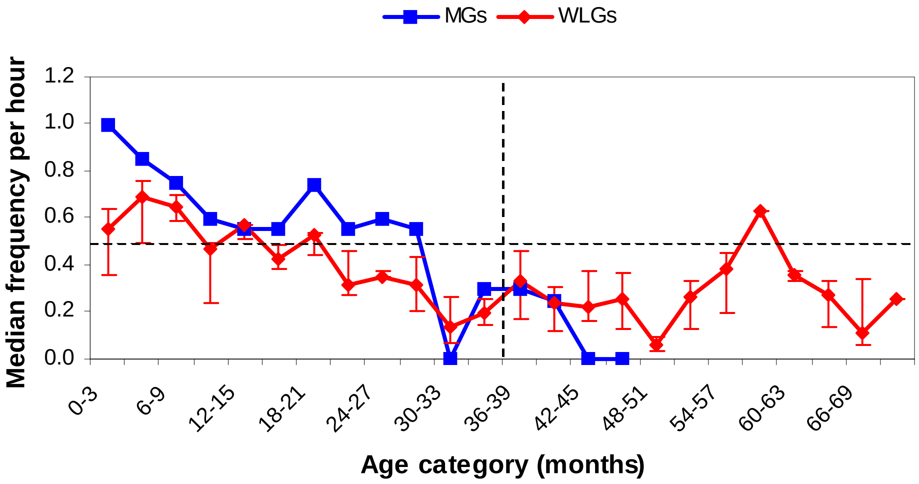

Figure 7.3. Comparison of the median frequency of suckling per hour in mountain (MGs) and western lowland (WLGs) gorillas. Data for mountain gorillas are taken from Fletcher (2001, p. 170). The horizontal dotted line indicates the rate necessary to maintain lactational amenorrhoea in mountain gorillas.

Table 7.6. Comparison of aspects of suckling in mountain (MGs) and western lowland gorillas (WLGs). Mountain gorilla data are from Stewart (1981) and Fletcher (2001).

Feature	***MGs***	***WLGs***
Initial suckling rate	1.5 bouts/hour	0.6 - 0.7 bouts/hour
Age at which suckling rate of 0.5 bouts/hour first observed	18 months	9-12 months
Last age observed to suckle	Median = 43 months (22-62.5 months, n = 5)	Median = 55 months (44-69 months, n = 6)

Interestingly, the data in both this (at 51-54 months of age) and Fletcher's (2001) study (at 34.5 months) showed an increase in the frequency of suckling as offspring approached weaning age. In both studies, suckling frequency increased to high levels within the final year of individuals being observed to suckle for the last time. It was possible that this late increase in suckling frequency represented attempts by offspring to increase suckling frequency as the mother increasingly terminated or refused suckling bouts (*sensu* van Lawick-Goodall, 1971a).

Suckling bout lengths were similar across both mountain gorilla studies and the current study and remained relatively constant during infancy with a median duration of approximately 3 minutes per bout. The duration of bout lengths became more variable as offspring increased in age. Fletcher (2001) noted that individuals who suckled past the age of 40 months often had particularly long bouts, and the same was also true in the current study after infants reached the age of 2.5 years until being weaned (see **Figure 4.8**).

The nature of weaning in both species was similar, with few temper tantrums thrown by offspring, a relatively late age at weaning, and an apparent lack of cough grunts by the mother during the weaning process (Stewart, 1981; Fletcher, 2001), or an increase in whimpering by the infant. (The distance between gorillas and the observer in the current study is likely to have prevented any whimpering from being recorded.) The major difference between mountain and western lowland gorillas in suckling behaviour, and in aspects of the mother-offspring relationship, was the later age at weaning in western lowland gorillas. There was no significant difference (U = 7.0, $N_{WLG, MG}$ = 6, 5, P = 0.144) in the age at which individuals were last observed suckling in the present study compared to Stewart (1981), although western lowland gorillas tended to be older (**Figure 7.4**). This was probably due to the few individuals for whom there were accurate ages at weaning, but it is expected that when more data are available from both mountain and western lowland gorillas, age at weaning will be found to be significantly older in western lowland gorillas.

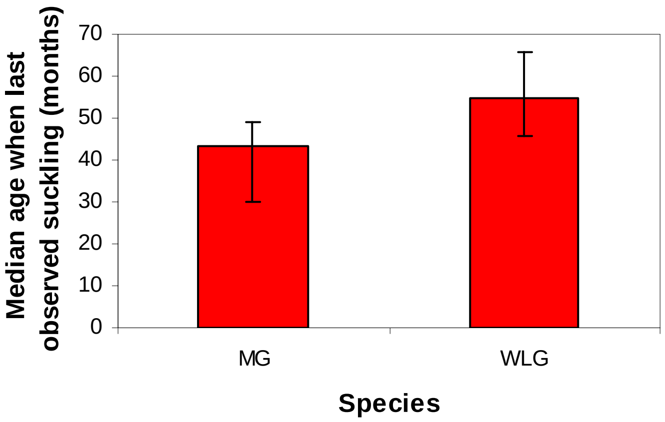

Figure 7.4. Median ages at which mountain (MG) and western lowland (WLG) gorillas were last observed to suckle. Data for mountain gorillas taken from Stewart (1981, p.3.10).

Factors underlying the timing of weaning must relate to how the mother can best direct her resources to gain maximum reproductive fitness, and the ability of offspring to survive on the resources available in the environment, and without the provision of milk (Trivers, 1972; Lee, 1996). The mountain gorilla diet is constant and shows little seasonal variation, with the exception of bamboo shoots (Watts, 1984). In contrast, the diet of western lowland gorillas is ephemeral and varies according to the seasonal availability of fruit (Williamson et al., 1990; Remis, 1997b). Mothers should continue to nurse their offspring so that their survival can be assured, and to remove the need for young individuals to rely on unpredictable fruit sources. The large size of western lowland gorillas enables them to process large quantities of fibrous food that sustains them when fruit is in short supply (Remis, 2000), but smaller individuals may not have a gut of sufficient size or maturity (see Lee, 1996) to allow them to process adequate amounts of fibre in order to fulfil their requirements. Nor is terrestrial herbaceous vegetation (THV) likely to be a suitable weaning food (e.g., Barrett & Henzi, 2000; Barrett et al., in press): in general, THV is not particularly easy to digest, nor is it particularly nutritive (Rogers et al., 2004).

Morphological differences exist between mountain and western lowland gorillas, which indicate that mountain gorillas are better adapted to feeding on fibrous vegetation. These differences include a wider mandibular corpus and symphysis, a larger area for masseter attachment, incisor–molar proportions, and cusp area proportions (Uchida, 1998; Taylor, 2002). Consequently, in cases of fruit shortage, young western lowland gorillas may be less well equipped than mountain gorillas to deal with large quantities of fibrous vegetation, again, providing a reason (i.e., to buffer against potential fruit shortages) why western lowland gorillas should be weaned at a later age.

The transition from suckling to self-sufficiency in food acquisition is one of the riskiest periods of the life span for primates (Janson & van Schaik, 1993; Fragaszy & Bard, 1997), and the age at weaning seems to be an indication of the dietary risk that apes are exposed to. For example, chimpanzees are more persistently frugivorous than western lowland gorillas (Tutin & Fernandez, 1993; Stanford & Nkurunungi, 2003), and in response to fruit shortage, they show flexible grouping patterns in order to continue feeding on fruit rather than change their diet (White & Tutin, 2001; Stanford & Nkurunungi, 2003). Dental features of chimpanzees also point to them having adapted to a largely frugivorous diet (Taylor, 2002). In chimpanzees, age at weaning varies between 5.5 and 8 years (Goodall, 1986; Parker, 1999; Nishida et al., 2003), later than in all gorillas, and suggesting that as a result of the unpredictability of their resources, chimpanzees rely on the mother until independent foraging is more likely to be successful. Similar effects have been found in baboons (Lycett et al., 1998; Barrett et al., in press), seals (Trillmich, 1990) and elephants (Lee & Moss, 1986), where food limitations and drought years have been shown to extend the duration of lactation, presumably as a result of increased risk to the offspring if weaned too early.

A later age at weaning has ramifications for interbirth intervals, since suckling suppresses the return to oestrus in females, and therefore, conception of the next offspring (Stewart, 1988; Sievert et al., 1991). The median interbirth interval in mountain gorillas is 3.92 years, with the period of lactational amenorrhoea accounting for the majority (3.2 years) of this interval (Watts, 1991b). In this study, twelve subjects were aged 4 years or older, and were present in a group with the mother. Eight (75%) were observed suckling during the study period, and only the remaining four had mothers who had given birth again. Thus, in the majority of cases, interbirth intervals at Mbeli were longer than 4 years, consistent with a median weaning age of 55 months (4.6 years). Since the start of the Mbeli Bai Study, few females have produced more than one offspring, and preliminary data put the mean interbirth interval (taking into account only surviving births) at 62.3 months (5.2 years, n = 3) (Robbins et al., 2004). These results are reinforced by similar interbirth intervals in habituated western lowland gorilla studies: Lossi, Republic of Congo, have recorded a median interbirth interval of 5 years (n = 3, range: 4-6 years), and at Bai Hokou, Central African Republic, where a female with a small infant at the start of the study did not have another within the next five years (Robbins et al., 2004).

Interbirth intervals of western lowland gorillas seem intermediate between those of mountain gorillas (and captive western gorillas) at around 4 years, and those of chimpanzees, with a minimum of 5.5 years (Nishida et al., 2003). This is strongly linked with the hypothesis that a higher degree of frugivory and a less flexible diet in response to fruit shortages result in offspring being weaned at later ages, and having a longer developmental period: chimpanzees are not considered mature until 16 years of age for males, and 12 years of age for females (Nishida et al., 2003). In turn, the longer developmental period leads to longer interbirth intervals in species that depend more heavily on fruit (**Table 7.7**). Captive gorilla diets are likely to be of better quality than wild western lowland gorilla diets, and should be comparable to mountain gorilla diets in terms of their constancy and “even distribution”. Therefore, captive western lowland gorillas face considerably reduced feeding challenges than their wild counterparts, and it follows that their interbirth intervals would be more similar to mountain gorillas than to wild western lowland gorillas, if interbirth intervals are determined predominantly by external factors. Interbirth intervals in mountain and captive gorillas may represent the minimum interval for the genus, given their constant access to abundant, stable resources, and in mountain gorillas, the corresponding adaptation of craniodental features, which allow efficient manipulation of this resource (see Uchida, 1998; Taylor, 2002). So, differences between mountain and western lowland gorillas in the length of time taken to reach independence from the mother is consistent with the hypothesis that the availability of resources places constraints on the speed with which western lowland gorillas develop (*sensu* Ross, 1998).

Table 7.7. Levels of frugivory and interbirth intervals in gorillas and chimpanzees. NA = not applicable.

Species	***Habitat***	***Level of frugivory***	***Interbirth interval***
G. b. beringei	Virungas	Low[1]	3.92 years[2]
G. g. gorilla	Captive	NA	4.16 years[3]
G. b. graueri	Highland population	Low[4]	4.6 years[5]
G. b. graueri	Lowland population	Intermediate[4]	> highland population?
Pan paniscus	Wamba	Similar to *G. g. gorilla*[6]	4.8 years[7]
G. g. gorilla	Mbeli, Lossi, Bai Hokou	Seasonally frugivorous[8]	5 years[9]
Pan troglodytes	Mahale, Gombe	High[10]	5.5 – 8 years[11,12]

[1] Watts, 1984
[2] Watts, 1991b
[3] Sievert et al., 1991
[4] Yamagiwa et al., 2003
[5] Yamagiwa & Kahekwa, 2001
[6] Malenky et al., 1994
[7] Furuichi et al., 1998
[8] Remis, 1997b
[9] Robbins et al., 2004
[10] Tutin & Fernandez, 1993
[11] Nishida et al., 2003
[12] Goodall, 1986

In addition to the availability of resources, an alternative factor that may influence age at weaning and therefore, interbirth intervals in gorillas is the level of infanticide in a population (Parker, 1999). Infanticidal males kill the suckling infants of females in an attempt to bring the female back into oestrus so he can mate with her and she can conceive his offspring (Watts, 1989; van Schaik & Kappeler, 1997; Harcourt & Greenberg, 2001). To reduce the likelihood that offspring fall victim to infanticide, mothers may wean their offspring as early as possible, who, as a result, would be required to develop more rapidly. In mountain gorillas, infanticide accounts for 26% of all infant deaths (Robbins & Robbins, 2004), and although it does not occur in every case where it is expected (Sicotte, 2000), this may contribute towards the shorter interbirth intervals. In western lowland gorillas, infanticide is thought to occur, although again, has not occurred in all cases when circumstances predicted it (Parnell, 2002b; Stokes et al., 2003; pers. obs.). Western lowland gorilla mothers may face less pressure to wean offspring early if infanticide occurs less frequently than in mountain gorillas, resulting in the longer interbirth intervals observed in western lowland gorillas. With the apparent absence of infanticide in eastern lowland gorillas (Yamagiwa & Kahekwa, 2001), there may be less need for rapid infant development, and therefore, less pressure on mothers to wean offspring at an early age. If infanticide does not influence age at weaning, the factors that do have an influence may simply rest on the optimal point at which a mother should stop investing in her current offspring and begin investment in the next (Trivers, 1972; Lee, 1996), and the distribution and availability of suitable "weaning foods" in the environment (e.g., Lycett et al., 1998; Barrett et al., in press).

Continued monitoring is required to elucidate the effects of a frugivorous diet and the presence of infanticide on gorilla weaning ages and interbirth intervals. The length of the interbirth interval has important consequences for the demography of populations: long interbirth intervals limit birth rate (the birth rate in western lowland gorillas is lower than in mountain gorillas (Robbins et al., 2004)), and thus population growth. If levels of frugivory do influence weaning age in gorillas, then there may be serious consequences for populations in non-protected areas, where logging of fruiting trees is ongoing. If logging significantly decreases the number and access of apes to fruiting trees, the transition to independence becomes riskier as a result of limited resources. Weaning age would then be predicted to increase, and consequently, population growth will slow. Ape populations that are already declining as a result of increased hunting and disease (White & Tutin, 2001; Bermejo, 2003; Walsh et al., 2003) may find it difficult to recover.

7.4. RELATIONSHIPS WITH SILVERBACK MALES

The most consistent difference in the group compositions of wild mountain and western lowland gorillas groups is the number of silverbacks in each group (Doran & McNeilage, 2001). The most recent survey conducted in the Virunga Volcanoes found 52.9% of mountain gorilla groups contained more than one fully adult male (Kalpers et al., 2003). Four different bai studies have yet to document a multi-male western lowland group (Magliocca et al., 1999; Parnell, 2002a; Latour, 2003; Gatti et al., 2004a), although studies that have tracked gorilla groups have reported their presence (Tutin, 1996; Remis, 1997a). However, it is clear that multi-male groups occur less frequently in western lowland gorillas than in mountain gorillas (Robbins et al., 2004).

In western lowland gorillas, a high percentage of male natal dispersal results in the low percentage of multi-male groups (Parnell, 2002b; Stokes et al., 2003). Consequently, there is little incentive for a female to remain in the natal group if the only available silverback with whom to mate is likely to be her father (see Sicotte, 2001). The conspicuous paucity of multi-male groups suggest that despite potential reproductive benefits (data from mountain gorillas suggest that males who remained in multi-male groups were ultimately more successful than those who left (Robbins, 1995)), other factors, probably related to resource distribution, prevent the formation of multi-male groups as a means to increase male reproductive success (see also (Parnell, 2002a; Stoinski et al., 2004). Alternatively, one-male groups perhaps represent the basic social structure and mating system for the genus, and the high frequency of multi-male groups in the Virungas may have been driven by intense human disturbance (Parnell, 2002a; Stoinski et al., 2004).

The dispersal of both sexes from the natal group in western lowland gorillas (Parnell, 2002b; Stokes et al., 2003) suggests that the need for a close, affiliative relationship with a silverback is unnecessary for either the development of a relationship leading to mating opportunities for females, or for increasing the likelihood that males are tolerated as subordinate followers of the natal group (e.g., Harcourt & Stewart, 1981). Therefore, it is predicted that relationships between immatures and silverbacks are more developed in mountain gorillas than in western lowland gorillas. Captive western lowland silverbacks have been shown to display an active, rather than simply passive interest in immature group members, with attempts made by the silverback to contact, groom and interact with them (Tilford & Nadler, 1978). This seemingly unusual level of involvement by silverbacks may have resulted from the captive situation, whereby immature group members provided a stimulus for the silverback, hence his high rate of interaction with them.

In the current study, there was a conspicuous lack of contact between immatures and silverbacks, and a silverback appeared uncomfortable on the only occasion on which a silverback response was made to contact initiated by an infant. The silverback glanced towards the mother of the infant in much the same way that a juvenile or sub-adult would after an infant made a boisterous, playful approach. In contrast, Enciso (1999) reports that in a captive study, 59-81% of all silverback contact time with group members was spent with infants. In Stewart’s study (2001) on wild mountain gorillas, time in close proximity (within 2m, and recorded during feeding and resting periods) was the most common indication of affiliation between immatures and silverbacks. Immatures were found to spend 8-21% of their time within 2m of the dominant silverback in the group (Stewart, 2001), with close proximity being highest in older infants and lowest in adolescents. In this study, immatures spent a median 3.3% (IQR: 0-6.9%) of time within 2m of the group silverback. There were no clear periods when close proximity to silverbacks increased or decreased in frequency, although the greatest variation occurred during the juvenile period (**Figure 7.5**). Fletcher (1994) found that proximity between immatures and silverbacks tended to be lowest during feeding periods, but even the lowest levels of close proximity observed by Stewart (2001) tended to be higher than those observed in the current study. The bai habitat may not provide a representative view of silverbacks' attitudes towards infants in general. However, both within the bai and forest habitats, a silverback is expected to be preoccupied with feeding given his size, nutritional requirements, and the distribution and availability of resources, so his attitude towards immatures is not expected to change considerably as a result of environment. Without data on silverback-immature relationships in the forest, however, more rigorous comparisons cannot be made.

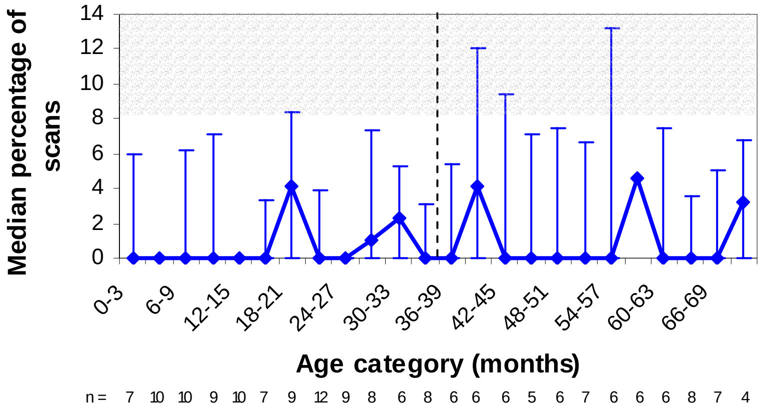

Figure 7.5. The median percentage of scans in which study subjects were within 2m of the group silverback. The shaded section indicates the lower end of the range of values that Stewart (2001) found immatures to spend within 2m of the silverback. $N_{TOTAL} = 42$.

Fletcher (1994) investigated the time spent by immatures within 5m of at least one silverback during feeding periods. Using the same method for calculating comparative mother-offspring contact time from Fletcher’s (2001) data, the median percentage of time that immatures and silverbacks spent within 5m of each other was compared with results from this study (**Figure 7.6**). Although differences between this study and Fletcher’s were not significant over the whole immature period (Z = -1.6, n = 24, P = 0.110), during the juvenile period when individuals were beginning to move out the mother’s proximity more frequently, results did approach significance (Z = -1.726, n = 12, P = 0.084). Data from Fletcher (1994) do not distinguish between the dominant and subordinate silverbacks in the group, but there was a preference for the dominant silverback during feeding periods (Fletcher, 1994). It does appear that immature mountain gorillas tended to be closer to at least one of the silverback in their group than western lowland gorillas, however, it is important to bear in mind that greater association between mountain gorilla immatures and silverbacks may result from mountain gorilla groups being multi-male, and therefore, a greater probability exists of being close to a silverback by chance.

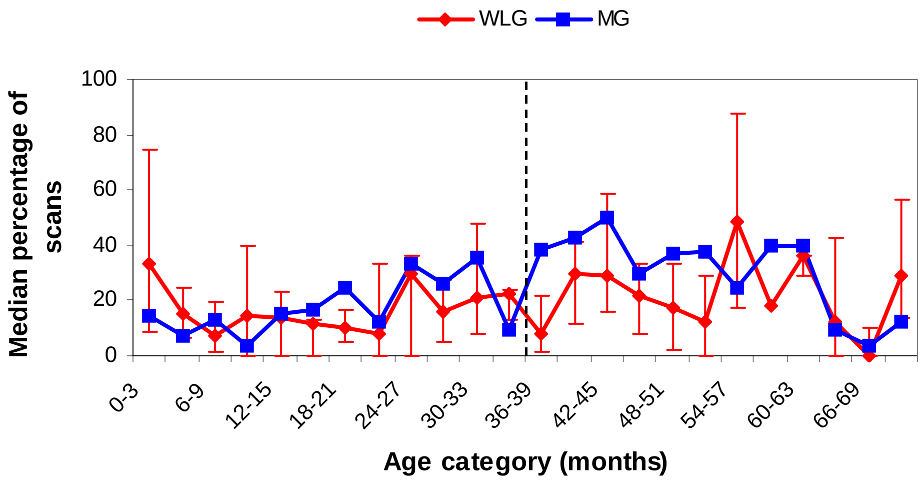

Figure 7.6. Comparison of the time that immatures spent within 5m of a silverback. WLG = western lowland gorillas, results from this study; MG = mountain gorillas, data recorded during feeding periods, and taken from Fletcher (1994), p.111 and p.176.

Proximity between immature-silverback dyads in the current study was less than that recorded during feeding periods in studies of wild mountain gorillas. The general impression was that although western lowland gorilla silverbacks were tolerant of immature group members, they preferred to remain uninvolved with them, and appeared nervous at the direct approach of young infants in particular. This was reflected in the lack of close proximity between immatures and silverbacks, and the occasional ability of infants to “displace” silverbacks. Rest periods are generally periods during which social bonds are maintained and reaffirmed through proximity and grooming (Fossey, 1983; Fletcher, 1994). It is necessary to investigate proximity and levels of interaction between immatures and silverbacks during rest periods in western lowland gorillas, if they form a regular part of their activity budget. The increased daily path lengths of western lowland gorillas, related to higher levels of frugivory than in mountain gorillas (Doran et al., 2004) may result in less time being available for rest periods, although the quantity of fruit, and hence, the time spent feeding, needed to meet requirements also needs to be considered. Additionally, regular rest periods may be less essential in western lowland gorillas because of a reduced quantity of fibrous food consumed that requires prolonged digestion (see Remis, 2000). Large group spreads in foraging western lowland gorillas (Tutin, 1996; Bermejo, 2004) may mean that even if groups do stop and rest between feeding and bouts of travel, immatures may still not be in close proximity to the silverback, and thus able to develop a relationship with him.

In conclusion, close relationships between immature group members and silverbacks occur to a lesser extent in western lowland gorillas than in mountain gorillas, evidenced by a lack of grooming, which was not observed at all during the current study (although lower levels would be expected as observations were conducted during feeding periods), and lower levels of contact and proximity. These results may have been affected by the collection of data in the bai, but the greater daily path lengths of western gorillas (Doran et al., 2004) suggest that limited time may be available to maintain and reinforce social bonds during rest periods. Ultimately, male-female association in gorillas seems to provide protection for infants against infanticidal males (Watts, 1989; van Schaik & Kappeler, 1997; Weingrill, 2000) and to be efficient, it is not necessary to maintain a close relationship with immatures.

7.5. RELATIONSHIPS WITH UNRELATED ADULTS

Close relationships between immature and adult group members are predicted to have limited value to immatures in species where both species are likely to emigrate from the natal group upon reaching puberty, such as in western lowland gorillas. In both mountain and western lowland gorilla groups, with the exception of the mother, immature group members tend to be unrelated to adults (although less so in larger mountain gorilla groups, where rates of natal dispersal are lower), and consequently, relationships with adults are predicted to be weak, with agonism directed towards immatures more commonly than affiliation.

Few studies have conducted detailed observations of the relationships between immature group members and unrelated adult females and blackbacks, probably because very little interaction occurs between them. Those that have addressed these relationships have found that interactions between them were often agonistic, consisting of displacements and aggressive vocalisations (Stewart, 1981; Fletcher, 1994); findings which were replicated in the current study.

Data on the nature of relationships between immatures and blackback males are fewer, with Stewart (1981) stating only that interactions were infrequent, and grooming and play behaviour were seldom observed. Although relatively infrequent, agonism seemed an important part of the relationship between immatures and blackbacks in this study, at least for some blackback males. Play agonism and displacements were hypothesised to serve as a training ground for blackback males, to prepare them in relative safety for life as a solitary male. Although blackbacks do assist with group defence in mountain gorillas (Fossey, 1983), the higher frequency of natal emigration in western lowland gorillas than in mountain gorillas (see **Table 7.1**), suggests that it is perhaps of greater importance to western lowland gorillas that blackbacks gain experience in this type of behaviour. Proximity and interactions between blackback and immature group members were rare in this study, as also reported in others (Stewart, 1981; Fletcher, 1994). Overall, the general similarity of relationships between immature gorillas and unrelated adults in western lowland and mountain gorillas suggests that differences in ecology do not necessarily result in fundamental differences in their relationships, particularly when there is a limited value of investing in these relationships.

7.6. PLAY BEHAVIOUR BETWEEN IMMATURES

Play behaviour in young primates is thought to serve as training for the future (see Chapter Six), and provides a useful insight into the nature of relationships between them. With reference to the types of relationships that are important to adult gorillas (male-male competition, male-female relationships), the social skills that are developed through play behaviour are predicted to be similar in western lowland and mountain gorillas, and therefore, little difference was expected in the nature of play behaviour.

The distribution of play behaviour over the immature period in mountain gorillas (Stewart, 1981; Fletcher, 1994) and western lowland gorillas (Maestripieri & Ross, 2004; current study) was compared (**Figure 7.7**). The data were similar: the amount of time invested in play behaviour increased during infancy, before decreasing during the juvenile period. Play then declined to almost zero towards the end of sub-adulthood. The increase towards the end of infancy seems ubiquitous in gorillas, and coincides with the period when offspring are beginning to move farther from the mother.

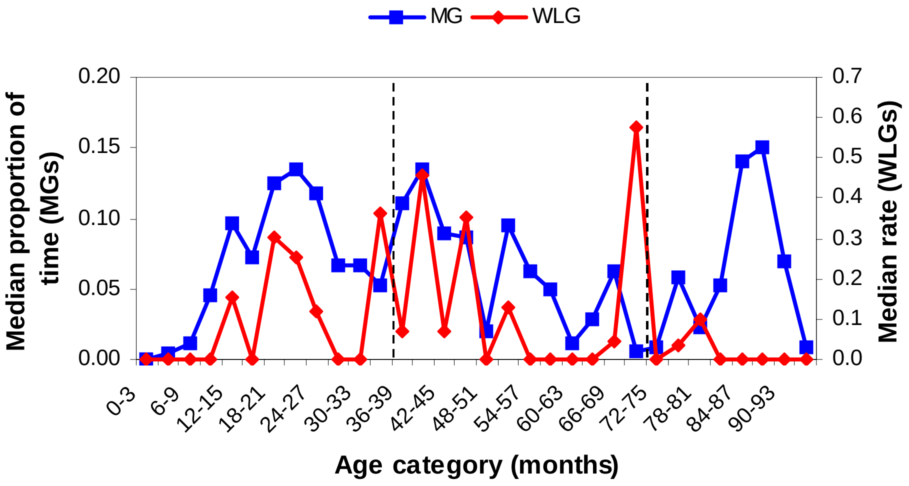

Figure 7.7. Comparison of the distribution of play during the immature period of mountain gorillas (MG) and western lowland gorillas (WLG). Data for MGs are estimated from Fletcher (1994), Figures 4.10a, 5.15a, and 6.7a, and data for WLGs are from the current study.

The motor-training hypothesis suggests that one function of play is to improve motor skills that will be useful later in life (Spinka et al., 2001), and therefore, individuals are predicted to play with peers who are matched for body size and social skills (Maestripieri & Ross, 2004). The distribution of play partner preferences was compared in the current study and Fletcher's study (1994) (**Figure 7.8**). For infants and juveniles of both species, there was a preference for a similarly aged play partner, which was consistent with the hypothesis that most benefit is gained from playing with conspecifics (Maestripieri & Ross, 2004). However, while mountain gorilla sub-adults exhibit a tendency to play with other sub-adults, western lowland gorilla sub-adults preferred juveniles and infants as play partners. The figure below does not take into account the availability of play partners, and although most sub-adults were present in groups with at least one other sub-adult, not all were: more juveniles and infants were present in the population as a whole. Therefore, the apparent reduced preference for like-aged partners in sub-adults may simply have been due to the composition of groups and availability of partners. Similarly, comparisons of the preference for male or female partners was made difficult due to the distribution of males and females in different study groups, however, Fletcher (1994) showed a trend for male and female infants and juveniles to play with males more than was expected. In captive studies on western gorillas, Brown (1988) and Maestripieri (2004) also determined a preference for males as play partners by both males and females.

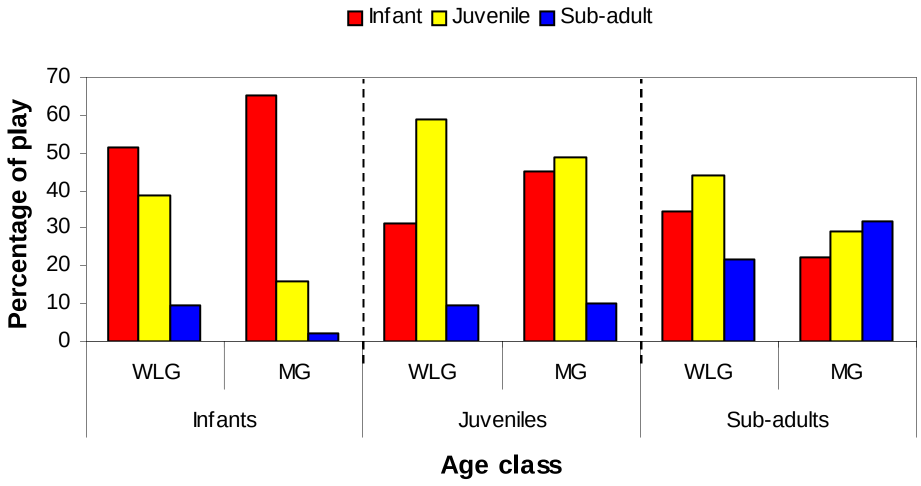

Figure 7.8. Play partner preferences for mountain (MG) and western lowland gorillas (WLGs).

Studies of play behaviour in primates often find that males play more often than females do, and incorporate rougher forms of play more frequently (e.g., Brown, 1988; Fagen, 1993; de Oliveira et al., 2003; Maestripieri & Ross, 2004). This is thought to reflect the fact that competitive interactions between males can influence male reproductive success (Maestripieri & Ross, 2004), therefore, males use play to improve their competitive ability. Consistent differences between the play of males and females have been detected in various studies on gorillas, with males showing higher rates of play, and a greater involvement in rougher forms of play (Stewart, 1981; Fletcher, 1994; Maestripieri & Ross, 2004). These results were mirrored in the present study.

The similarities of the patterning of play across various studies in gorillas are consistent with the hypothesis that in gorillas, play acts as training for the future, in developing both motor and social skills. The higher frequencies of rough play types in immature males act as preparation for male competition in adults, whereas females become familiar with interacting with males by playing more frequently with them, reflecting the strength of the bonds between adult males and females in gorillas (e.g., Harcourt, 1979b; Stokes, 2004). That play behaviour during immaturity appears similar in wild mountain and western lowland gorillas, and in captive western lowland gorillas, suggests that play serves the same purpose: to develop motor and social skills. Regardless of diet and ranging patterns, relationships between males remain competitive (e.g., Sicotte, 1993; Parnell & Nowell, in prep.), and those between males and females are essential for the maintenance of male-female association and protection against infanticide (e.g., Harcourt, 1979b; Stokes, 2004), and therefore, play acts in the same way in mountain and western lowland gorillas.

7.7. CONCLUSIONS

Although in some aspects, the development of relationships within gorilla groups is similar in both mountain and western lowland gorillas (for example, the lack of close relationships between immatures and unrelated adults, and the distribution and nature of play behaviour among immatures), the differing ecology of mountain and western lowland gorillas does affect the development of behaviour. A striking difference between mountain and western lowland gorillas that was not attributable to observations in this study being conducted in the bai environment was the increased age at weaning in western lowland gorillas. This was thought to be a direct result of the frugivorous diet of western lowland gorillas: in order to buffer against potential fruit shortage, mothers allow their offspring to suckle until a later age, resulting in longer inter-birth intervals and lower birth rates in western lowland gorillas than in mountain gorillas.

Differences between mountain and western lowland gorillas in relationships with the silverback were hypothesised to occur as a result of the higher rates of natal dispersal in western lowland gorillas, and consequently, the reduced need to form and maintain relationships with other group members, as they are unlikely to prove beneficial in the future (Fairbanks, 1993). Additionally, western lowland gorillas may have less time available to them for resting and socialising since daily path lengths are increased due to their frugivorous diet (e.g., Doran et al., 2004), or large group spreads may limit the potential for social interaction, resulting in weaker relationships between immatures and individuals other than the mother in western lowland gorillas than seen in mountain gorillas.

Immatures relationships with blackbacks and unrelated adult females tended to consist of agonistic interactions. In the case of blackbacks, these were predicted to prepare blackbacks either for life as a solitary male, or for playing a greater role in protecting the natal group. Relationships with adult females were thought to remain weak as a result of levels of competition that exist between individuals in a social group, the eventual dispersal of many immatures from the natal group, and the lack of frequent coalitions over access to resources.

In conclusion, where the nature of the relationship between adults does not differ between mountain and western lowland gorillas (e.g., female relationships, male-male competition, and the relationship between males and females), relationships formed during immaturity are also similar in both species. However, western lowland gorillas appear to be constrained by the distribution and availability of resources, and it is ecological factors, and their effects (e.g., longer daily ranging, single-male groups and higher rates of dispersal from the natal group) that are most likely to lead to differences in the development of mountain and western lowland gorillas.

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CHAPTER EIGHT

FINAL DISCUSSION

8.1. KEY FINDINGS

The key findings from this thesis are as follows:

- Basic feeding skills are in place by the end of infancy, but immatures are predicted to face difficulties when feeding on fibrous food items (those that are often fallback species in times of fruit scarcity) that are harder to digest or require strength to process. Consistent with this prediction, western lowland gorillas are not weaned until at least one year later after basic feeding skills are developed
- In the period during which western lowland gorillas continue to suckle, immatures maintain close proximity to the mother despite the fact that they are physically independent and can presumably obtain the majority of their diet by themselves. As independence from the mother increases, there was limited investment in relationships with other individuals. Investment instead seemed to be made in developing *skills* through play, alloparenting, and to a lesser extent, agonistic interactions, rather than through developing *relationships* through general affiliative behaviours, such as grooming and time spent in proximity
- Clear differences were found between mountain and western lowland gorillas in the length of investment in offspring by mothers, leading to longer inter-birth intervals and slower population growth in western lowland gorillas. Additionally, relationships between immatures and silverbacks appeared less developed in western lowland gorillas, with lower levels of association and few non-agonistic interactions.

8.2. THE INFLUENCE OF DIET ON BEHAVIOUR

Socioecological differences between mountain and western lowland gorillas, such as ranging patterns (Cipolletta, 2004; Doran et al., 2004), levels of competition between groups (Doran et al., 2002), and therefore, transfer decisions (Stokes et al., 2003), ultimately stem from differences in their habitat, and the response of western lowland gorillas to the distribution and availability of fruit (Doran & McNeilage, 2001; Yamagiwa et al., 2003; Doran et al., 2004). In turn, dietary differences arise as a result of contrasting habitats: the absence of succulent fruit in the diet of mountain gorillas is a consequence of its absence in the habitat (Watts, 1990; Rogers et al., 2004), and when fruit is available, it is incorporated into the diet of gorillas (Yamagiwa et al., 1996; Remis, 1997; Yamagiwa & Kahekwa, 2001; Doran et al., 2002; Rogers et al., 2004). It is reasonable, therefore, to expect that the differences documented in this study between mountain and western lowland gorillas, may also stem from the availability and distribution of items that constitute their diet.

Western lowland gorillas incorporate up to 180 species into their diet (Rogers et al., 2004), and young gorillas learning to feed must learn the identity of these species, their distribution and availability, which parts are edible, and how to eat them. Mountain gorillas incorporate around 60 species into their diet, most of which are abundantly and evenly distributed (Watts, 1996). However, gaining sufficient resources for mountain gorillas is not necessarily a straightforward process: habitat use maximises foraging efficiency, and zones where high quality food is abundant are selected (Watts, 1996), and even avoided to allow regeneration of previously depleted areas (Watts, 1998). Immature mountain gorillas must learn these principles in addition to learning how to feed on items which are defended by hooks, stings and spines (Byrne, 2001). Young mountain and western lowland gorillas, therefore, face different challenges when developing independent feeding behaviour, but (as far as could be determined in this study) develop feeding behaviour similar to that of adults by the end of infancy, in the selection of items and how activity budgets were proportioned. This suggested that despite large differences in their diet, as a consequence of the habitat, immature mountain and western lowland gorillas should possess the feeding skills to allow development of independence from the mother at similar ages.

8.3. THE PERIOD OF IMMATURITY

In great apes, the maturation period is longer than in mammal species of comparable body size (Harvey & Clutton-Brock, 1985; Kappeler et al., 2003), and the length of this period reflects the effort that is required to learn the behaviours that enhance survival in a particular environment (Watts & Pusey, 1993). A striking difference between mountain and western lowland gorillas was found in this study in the length of time required to become independent of the mother. During immaturity gorillas must learn how to survive without the mother. To achieve this, they must become capable of feeding and travelling independently (e.g., Watts, 1985; Doran, 1997), avoiding predation and infanticidal males, and regulating their social relationships with other members of the social group and the population (Walters, 1987), in such a way that promotes female transfer to appropriate groups, or the acquisition of females by males to allow reproduction. The end point of this period of learning is predicted to be the point at which their survival in the environment without the mother is as assured as it can be.

Feeding and locomotor skills developed at comparable rates in mountain and western lowland gorillas, but in this study, western lowland gorillas continued to suckle from the mother when they had developed feeding skills similar to those that allowed mountain gorillas to be weaned. Differences in the habitats of these two species, and their consequences, such as increased costs of foraging and the unpredictability of resources were likely to have resulted in the continuation of suckling into the juvenile period in the western lowland gorillas of this study. First, western lowland gorillas have more food items to learn (Watts, 1996); they also must learn to process them (Parnell, 2001). This takes time, particularly when valuable resources are not annually available (e.g., Williamson et al., 1990; Parnell, 2002b). Bai studies can provide information on the skills at feeding on resources within the bai, and although in this study they were well advanced at an early age, nothing is known of the feeding skills of immatures in the forest. Some items that constitute the adult diet are clearly not easily accessible to immature gorillas, as they lack the strength to obtain or process them (D. Doran, pers. comm.; pers. obs.), but it is questionable whether these limitations are sufficient to increase the period of immaturity in western lowland gorillas relative to mountain gorillas.

Unpredictability in resource availability seems a more likely cause of the variation seen in the period during which mountain and western lowland gorillas depend on the mother. Female gorillas invest considerably in their offspring, both pre- and post-parturition, when the costs of gestation and lactation are considered (Lee, 1996; Recabarren et al., 2000; Dufour & Sauther, 2002). The timing of weaning can be crucial, and mothers who attempt to wean offspring when sufficient quantities of appropriate foods are not available, can waste their investment over the previous years (see Barrett et al., in press). The perennially available diet of mountain gorillas (Watts, 1996) means there is unlikely to be an unsuitable time for weaning: once immature mountain gorillas possess the skills that allow them to feed in a manner similar to adults, there is no reason why they should not be weaned. Feeding skills, developed as much as size and strength allow, may not aid in the survival of young western lowland gorillas if sufficient quantities of suitable foods are not present in the habitat. Judging by the development of feeding skills observed in the bai, western lowland gorillas should be as assured of survival as is possible by the end of infancy. During periods of fruit shortage when immatures may experience a shortage of foods that provide sufficient nutrients and energy, immatures seem to make their needs known to the mother, who responds by suckling her infant. This, therefore, prevents her previous, substantial levels of investment from being wasted, should her offspring fail to meet its needs independently (see Bateson, 1994; Barrett & Henzi, 2000). Rather than Trivers' (1974) theory of parent-offspring conflict describing the development of independence from the mother in western lowland gorillas, Bateson's (1994) dynamic assessment theory where mothers respond to the genuine needs of her offspring may be more appropriate.

In the case of gorillas, and presumably other primates whose resources occur unpredictably in their environment, the period of dependence on the mother seems determined by the availability of resources, fruit, in particular. This period ends when young gorillas are likely to make a successful transition to independence, and to do this, they need not only to have developed the skills to allow them to do so, but the size and strength that allows them to process sufficient quantities of fibrous fallback foods during periods when the availability of fruit is insufficient to meet their needs.

8.4. THE DEVELOPMENT OF USEFUL RELATIONSHIPS

As young primates develop independence from the mother, associations and interactions with other group members become more frequent (e.g., Watts & Pusey, 1993; Fletcher, 1994; Charpentier et al., 2004). Interactions with other individuals allow the development of skills, and the formation of relationships that are predicted to provide current and potentially future benefits (Fairbanks, 1993). Skill development is important to all individuals; for example, play allows behaviours to be practised that might be used in avoiding predation or attracting mates (Spinka et al., 2001); alloparental behaviour allows the practise of maternal skills (Hrdy, 1976).

Engaging in interactions that *develop skills* is always useful, however, investment in *relationships* is most valuable when those relationships are likely to be available in the future.

For gorillas who are likely to emigrate from the natal group (Stokes et al., 2003; Robbins et al., 2004), and therefore, spend little of their reproductive lives with individuals with whom they were immature, the development of skills is predicted to be more important than the development of relationships. In the current study, this was reflected in the levels of association and types of interaction that immatures engaged in with other group members. Contact, close association and grooming in many primate species during immaturity are the basis of coalitions formed as adults (e.g., Seyfarth & Cheney, 1984; Cords, 2002; Silk et al., 2004). In mountain gorillas, coalition formation has been observed, but between female relatives who were immature together (Watts, 1991; Watts, 1994). Conversely, in western lowland gorillas, coalitions have not yet been observed between the usually unrelated adults in social groups (Stokes, 2004), and therefore, limited benefit may exist of investing in relationships with individuals during immaturity.

Active interactions of the type that are predicted to form, maintain and strengthen relationships, as well as close association between immatures and individuals other than the mother, were observed relatively infrequently. Agonism, play and displacements were observed more frequently than affiliation and grooming (although reduced frequencies of these behaviours are expected during feeding periods (e.g., Harcourt, 1978; Fletcher, 1994)), and it is through these more common interactions, in addition to play, that immatures were predicted to learn skills that are important in the future. Any relationships formed between individuals through close association and grooming are unlikely to persist beyond immaturity, and therefore will not be important in the future (see Fairbanks, 1993). However, skills learned through playful interactions with conspecifics, and agonism and displacements received from older individuals are valuable in terms of practise for the relationships that exist between adults. Immatures associate and interact with members of the social group in a way that develops behaviours and skills that will be useful in the future, but avoids investment in relationships that end with transfer from the natal group.

8.5. LIMITATIONS OF THE STUDY AND FUTURE DIRECTIONS

It has proven very difficult to successfully habituate western lowland gorillas (Tutin & Fernandez, 1987), and since initial attempts, few studies have managed to habituate western gorillas to a stage where behavioural data can be collected (Doran & McNeilage, 1998; but see Cipolletta, 1999; Doran et al., 2002; Cipolletta, 2003). Currently, the best opportunity to investigate western gorilla behaviour is provided by bai studies (Magliocca et al., 1999; Parnell, 2002a). Demographic data provided by these studies is second to none, with it being possible to identify an entire population of gorillas, and track movements within, in and out of the population (Magliocca et al., 1999; Parnell, 2002a; Robbins et al., 2004). However, western lowland gorillas spend a fraction of their time in bais (one study estimated that 1% of the day was spent by groups in a bai (Magliocca & Gautier-Hion, 2002)), and the majority of this time is spent feeding (Magliocca et al., 1999; Parnell, 2002a). Group activity is known to affect behavioural patterns in mountain gorillas (Harcourt, 1978), with contact and close proximity tending to be more common during rest periods (Harcourt, 1978; Fletcher, 2001). It is not yet evident how the bai environment effects the manifestation of social behaviour.

As a result of this unknown element, there are limitations to what can be concluded about the development of gorilla behaviour based on results from bai studies. Data were collected during only one type of activity period, but they were also collected from a minority habitat type with abundant (although relatively uniform) resources, which is a stark contrast to the sparsely distributed and ephemeral diet that western lowland gorillas adopt when fruit is available (Remis, 1997; Doran & McNeilage, 1998; Doran et al., 2002). Currently, it is not possible to suggest the extent to which the behaviour recorded in a bai might differ in the forest environment, when gorillas are faced with a greater range of food items and potentially higher rates of competition due to a less even distribution of food (Doran & McNeilage, 1998; Stokes et al., 2003; Doran & McNeilage, 2001).

Many aspects of behavioural development investigated in this study have concurred with predictions made with reference to developmental or ecological theory, and this suggests that accurate accounts of behavioural development can be recorded in bai studies. Basic developmental parameters relating to, for example, suckling can provide unquestionable data, in some senses. If an individual is observed to suckle in the bai, then we can be sure (or as sure as any study can be) that the mother is continuing to produce milk, has not resumed oestrus cycles and is still investing in her current offspring. In this regard, it makes little difference if an individual is observed to suckle in a bai, or in the usual forest environment.

Even with fully habituated groups, it can be difficult to accurately record the social behaviour of gorillas in the forest due to dense vegetation. In addition, the large group spreads recorded in foraging western lowland gorillas (Tutin, 1996; Bermejo, 2004) increase the difficulty of gaining a complete picture of the role of immatures within the social group in the forest. In the absence of accurate data on behavioural development of western lowland gorillas in the forest, the long-term collection of data from bai studies can instead be used to assess the effects of ecology on behavioural development, by using more indirect methods. Predictions regarding dispersal from the natal group can be tested, and providing that immature individuals remain in the study population, relationships between adults can be analysed with respect to the relationships that individuals invested in as immatures. This may be particularly interesting with reference to immature individuals who have immigrated into Mbeli study groups. In mountain gorillas, a strong relationship with the silverback during immaturity increased the likelihood that males remained in the natal group to breed (Harcourt & Stewart, 1981). For individuals who have immigrated into groups as immatures, dispersal as a means to avoid inbreeding is not an issue, therefore, bai studies can evaluate how relationships during immaturity may lead to contrasting reproductive efforts.

Behavioural studies involving immature western gorillas in captivity are in progress (T. Stoinksi; A. Fletcher, pers. comm.). These studies will prove invaluable in analysing behavioural development in the relative absence of ecological pressure, and through doing so, provide a baseline for gorilla development. These studies, together with those from bai studies, may indicate whether patterns of behavioural development in wild western gorillas arise as a result of phylogeny, or as a result of increased ecological pressure as a consequence of their more frugivorous diet and the implications of higher levels of frugivory when compared to mountain gorillas.

Finally, this study has shown that ecological factors, such as resource availability, and its effects on transfer patterns, have inextricable influences on the development of behaviour in western lowland gorillas. In response to ecological pressures and environmental constraints, young western lowland gorillas develop the behaviours and invest in the relationships that best prepare them for a successful transition to adulthood. Feeding skills develop at an early age, and therefore, nutritional independence from the mother can be reached when an immature is physiologically ready, and the availability of resources in the environment allows it. The relationships that are invested in provide current benefits, namely the development of behavioural skills that facilitate the successful transition to adulthood, rather than future benefits.

Where the development of primates is influenced by ecological factors and environmental constraints, and particularly for gorillas, with a long period of maturation, the threat of ecological disturbance has serious implications for population growth rates, and therefore, the survival of populations. The mortality of young individuals is expected to increase in response to ecological disturbance (e.g., Gould et al., 1999; Pavelka et al., 2003; Cheney et al., 2004), and therefore, the continuing pressures of logging, bushmeat and Ebola on gorilla populations have the potential to be catastrophic (Walsh et al., 2003). This highlights the need for studies such as this to determine the effects of ecology on behavioural development, and the successful transition to adulthood. The longevity of gorillas, the long period of dependence on the mother, and consequential long interbirth intervals result in a slow population growth rate, and ecological disturbance is assumed to decrease population growth rates further. It is, therefore, essential that accurate and comprehensive accounts of behavioural development are provided for gorilla populations that have experienced minimal disturbance, such as the Mbeli population. By doing so, the effects of ecological disturbance on behavioural development, and other parameters that are affected can be predicted, and attempts may be then made to identify and address issues that can threaten the survival of gorillas.

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APPENDIX ONE

Appendix 1. Hours of observation for each study subject over the study period. Groups are presented in order of decreasing visit frequency. Rows with a pink background indicate females, those with blue indicate males. Rows without a coloured background indicate individuals of unknown sex.

Name	***Age category (months)***																			***Total***
	0-6	6-12	12-18	18-24	24-30	30-36	36-42	42-48	48-54	54-60	60-66	66-72	72-78	78-84	84-90	90-96	96-102	102-108	108-114	
Noodles' Group																				
Sage	3.7	45.2	31.3	27.8																108.0
Whisky			14.2	37.5	27.0	20.1														98.8
Lyle											17.6	48.0	28.1	18.3						113.0
Jaica															46.3	36.0	25.6	10.6		188.5
Iook															9.7	47.3	36.3	22.9		116.2
Muffin																33.6	37.0	23.9	14.4	108.9
TSB Group																				
Ulysses								17.1	22.9	15.2	13.7									68.9
Moses																27.4	12.8			40.2
Djino																21.0	23.1	18.1	12.4	74.6
Dwayne's Group																				
Piment	24.2																			24.2
Fig		3.8	29.4	18.0	16.0															67.2
Clover				3.5	15.5	24.4	19.1													62.5
Peapod						12.8	21.2	31.6	4.5											70.1
Brie							11.7	17.9	29.8	4.3										63.7
Bob											1.3									1.3
Bean											3.8	29.7	18.0	18.4						69.9
Pepper											2.9	16.0	26.0	21.4						66.3

Name	*Age category (months)*																			*Total*
	0-6	6-12	12-18	18-24	24-30	30-36	36-42	42-48	48-54	54-60	60-66	66-72	72-78	78-84	84-90	90-96	96-102	102-108	108-114	
Zulu Group																				
Howsa	25.6	8.6																		34.2
Jola	9.3	35.3																		44.6
Fang	9.6	8.3	24.1	15.0																57.0
Masai	3.9	6.8	9.7	29.2																49.6
Kung			5.1	7.5	19.3	18.4														50.3
Bofi				8.8	7.5	27.9	5.7													49.9
Khan's Group																				
Toomai	16.2																			16.2
Hathi	12.0	11.9	13.4																	37.3
Mowgli				5.1	18.5	11.2	5.1													39.9
Ikki					5.1	14.1	9.0	6.2												34.4
Mysa						13.4	10.2	11.7												35.3
Kotick							15.3	10.3	12.4											38.0
Louis									13.8	10.1	10.5									34.4
Darzee										20.1	8.0	5.4								33.5
OB1 Group																				
Lando	18.2	3.3																		21.5
Yoda				14.5	10.4															24.9
Sunbeam									16.7	4.3	15.9	3.0								39.9
Kirk										3.4	17.7	3.1								24.2
Elvis													16.0	8.8	15.5	4.4				44.7
Picard															3.8	21.8				25.6
Spalding															15.0	11.8	15.5	5.9		48.2

Name	*Age category (months)*																			*Total*
	0-6	6-12	12-18	18-24	24-30	30-36	36-42	42-48	48-54	54-60	60-66	66-72	72-78	78-84	84-90	90-96	96-102	102-108	108-114	
Hairy Group																				
Kojak	2.3	7.6	2.9																	12.8
Axel		7.8	16.2	2.3	11.6															37.9
Ike											5.8	12.4	0.7	9.8						28.7
George's Group																				
Clyde	2.2	4.1	4.9	4.1																15.3
Custer	2.9	4.3	4.1	3.6																14.9
Nancy		7.7	9.4	8.7	1.1															26.9
Luther			6.9	4.9	4.9															16.7
Betsy								3.1	8.6	9.5										21.2
Mosombo's Group																				
Peter														12.3						12.3
Bear's Group																				
Stanley											9.9									9.9
Livingstone														10.1						10.1
Sulatalu's Group																				
Columbus	7.1	1.0																		8.1
Sangha Group																				
Likouala	0.8	0.2																		1.0
Ndjeke									7.4	0.9	2.7									11.0
Ndoki														7.8		0.6				8.4
UKSB Group																				
DO(Agatha)	2.9																			2.9
Hitchcock		4.7																		4.7
Marple			3.8																	3.8
Sherlock			4.8																	4.8