

**Interunit, environmental and
interspecific influences on
silverback-group dynamics in
western lowland gorillas
(*Gorilla gorilla gorilla*)**

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Declaration

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

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Publications and Presentations

Publications

- Klailova M, Hodgkinson C, Lee PC. 2010. Behavioural responses of one western lowland gorilla (*Gorilla gorilla gorilla*) group at Bai Hokou, Central African Republic, to tourists, researchers and trackers. *American Journal of Primatology* 72:897-906.
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Abstract

While a major benefit of female-male associations in gorillas is protection from infanticidal males, a silverback is also responsible for providing overall group stability and protection from predation and other environmental or interspecific risks and disturbances. A silverback's reproductive success will be a function of his group's survival, his females' reproductive rates and the survival of his progeny. Here, I evaluate the western lowland silverback's role as the protective leader of his group and provide the first detailed behavioural study of silverback-group dynamics for western lowland gorillas from a holistic perspective; in both forested and bai environments, from nest-to-nest. Behavioural data were collected from one single-male habituated western lowland gorilla group, over 12-months starting January 2007 at the Bai Hokou Primate Habituation Camp, Central African Republic. Data collection - instantaneous scans, continuous written records of all auditory signals, nesting data, and *ad libitum* notes on interunit interactions - focused on the silverback and those individuals in his immediate proximity. Analyses were conducted over 258 morning or afternoon sessions, on 3,252 silverback behaviour scans (plus 1,053 additional smell scans), 22,343 auditory signals and 166 nest sites.

Evidence from neighbours to the silverback, group spread, progression, ranging, nesting, human directed aggression and silverback chemosignalling analyses suggest that silverback-group dynamics have developed complex, strategic spatial and social strategies to cope with perceived risk in rainforest environments, which respond to differing habitats, and differing intensities of interunit interactions and interspecific disturbance. I also show that the release of pungent extreme and high level silverback odours may function as both acute and chronic indicators of arousal designed to intimidate extragroup rival males and attract adult females by expressing dominance, strength, and health. Higher level silverback odours may also provide cues for group members to increase vigilance in risky situations, whereas low level smells may function as a baseline identification marker and provide both self and intragroup reassurance. Western lowland silverback-group relationships appear to be centred on providing a strong protective – rather than socially interactive - and stabilizing role to ensure group cohesion and safety, which ultimately increases the likelihood of male reproductive success.



CHAPTER 1

GENERAL INTRODUCTION



CHAPTER 1

GENERAL INTRODUCTION

“In the beginning of his career, in independent life, the gorilla selects a wife with whom he appears to sustain the conjugal relations thereafter, and preserves a certain degree of marital fidelity. From time to time he adopts a new wife, but does not discard the old one; in this manner he gathers around him numerous family, consisting of his wives and their children....The father exercises the function of patriarch in the sense of a ruler....to him the others all show a certain amount of deference....In the matter of government, the gorilla...leads the others on the march, and selects their feeding grounds and places to sleep; he breaks camp, and the others all obey him in these respects. Other animals that travel in groups do the same thing; but in addition to this, the natives aver that the gorillas from time to time hold palavers or rude form of court or council in the jungle. On these occasions, it is said the king presides; that he sits alone in the centre while the others stand or sit in a rough semi circle about him, and talking in an excited manner. Sometimes the whole of them are talking at once, but what it means or alludes to no native undertakes to say, except that it has the nature of a quarrel...As for the succession of the kingship there is no certainty, but the facts point to the belief that on the death of the king, if there be an adult male he assumes the royal prerogative, otherwise the family disbands, and they are absorbed by or attached to other families. Whether this new leader is elected in the manner that other animals appoint a leader, or assumes it by reason of his age, cannot be said; but there is no doubt that in many instances families remain intact for a time after the death of their leader.” [description by Garner RL during his expeditions in the 1800's; in Harcourt & Stewart, 2007a].

1.1 History

The first accounts of gorillas came from fifth century BC by the Carthaginian admiral Hanno, who when exploring the west coast of Africa came across an island full of 'savage hairy people' called 'gorillas' by the interpreters [in Groves, 2003]. Later, Andrew Battell, a European sailor held prisoner in Angola, described human like monsters in what was most likely Cabinda [in Groves, 2003]. In 1902, Captain Robert von Beringe shot two large apes in the Virungas, which Matschie [1903] later classified as *Gorilla beringei*. And so began our fascination with one of human's closest living relatives.

1.2 Taxonomy and Distribution

While several variations of gorilla taxonomy have been proposed [see reviews in Groves, 2003 and; Tuttle, 2003], one of the more accepted classification systems places gorillas into two species and four subspecies: eastern gorillas (*Gorilla beringei*), comprised of the mountain gorilla (*Gorilla beringei beringei*) and the eastern lowland or Grauer's gorilla (*Gorilla beringei graueri*), and; western gorillas (*Gorilla gorilla*), comprised of the western lowland gorilla (*Gorilla gorilla gorilla*) and the Cross River gorilla (*Gorilla gorilla diehli*) [Garner & Ryder, 1996; Groves, 2001; Ruvolo et., 1994; Stumpf et al., 1998].

Two populations of mountain gorillas exist [Robbins et al., 2008] in (a) the Virunga range, which borders Rwanda, Uganda and the Democratic Republic of Congo (DRC), and in (b) the more northern Bwindi Impenetrable National Park, Uganda. There is debate as to whether Bwindi mountain gorillas are a separate subspecies from their Virunga counterparts, although an official distinction has not yet been made [i.e. Sarmiento, 1996; Stanford, 2001]. Mountain gorillas are listed by the IUCN as critically endangered [Robbins et al., 2008] and number approximately 480 individuals in the Virungas, 302 individuals in Bwindi and four orphaned gorillas in a sanctuary in the DRC. [International Gorilla Conservation Program, 2010].

Eastern lowland gorillas range in the Democratic Republic of Congo, most notably Kahuzi-Biega National Park, the Itombwe Mountains and Mt. Tshiaberimu [Robbins et al., 2008]. Eastern lowland gorillas are listed as endangered by the IUCN [Robbins et al., 2008] and though numbers in the 1990's estimated 17,000 individuals [Hall et al., 1998], widespread

poaching in 1999 decimated gorilla populations most likely killing more than half of the gorillas in Kahuzi-Biega National Park alone [Yamagiwa & Kahekwa, 2001].

Western lowland gorillas range in Cameroon, Gabon, the Republic of Congo, Equatorial Guinea, Angola (Cabinda), and the Central African Republic [Walsh et al., 2008]. They are listed as critically endangered by the IUCN [Walsh et al., 2008] and although previous population estimates in the mid 1990s [Harcourt, 1996] totalled over 100,000 gorillas, figures are no longer available as numbers are rapidly decreasing [Walsh et al., 2008]. Cross River gorillas, recently classified as a distinct subspecies, range along the border of Cameroon and Nigeria and exist in approximately 11 fragmented populations [Oates et al., 2007]. They are listed as critically endangered by the IUCN and estimated to number no more than 300 individuals [Oates et al., 2007; Walsh et al., 2008].

1.3 Overall Threats

Remaining gorilla populations face many threats to their survival [Harcourt, 2003; Plumptre et al., 2003; Robbins et al., 2008; Tutin, 2001; Walsh et al., 2008]. Whilst some populations face greater danger than others, almost all are jeopardized by at least one of the following: (a) habitat loss (i.e. logging, mining, human migration and conversion of forest for agriculture), (b) disease (i.e. Ebola, human illnesses), (c) hunting or poaching, and (d) political instability [Plumptre et al., 2003; Tutin, 2001]. The situation is worsened by the fact that most gorillas live outside of protected areas [Harcourt, 1996]. Even many so-called protected regions lack the manpower or political stability to effectively guard species under threat [i.e. Fishlock, 2010; Hodgkinson, 2009]. In addition to the continued risk of human-gorilla disease transmission [i.e. Butynski & Kalina, 1998; Homsy, 1999; McNeilage, 1996], mountain gorillas have been facing a renewed threat from poaching and illegal killings by rebels since 2007 [Robbins et al., 2008]. Eastern lowland populations often live in lawless, war torn regions, rampant with rebels, flooded with refugees and illegal mining camps. They are thus further threatened by the subsequent increased hunting pressure resulting from human migration into or through their habitat [Yamagiwa pers comm. in Parnell, 2002b; Plumptre et al., 2003]. The already fragmented Cross River gorilla habitat is fast disappearing due to fire, encroachment of agriculture, and of course

poaching which is rife within Central Africa and the Congo Basin [Oates et al., 2003; Wilkie & Carpenter, 1999]. The bushmeat trade is just one serious threat to the survival of the western lowland gorilla [Plumptre et al., 2003]. Hunting pressure can be direct or indirect. While in many regions direct hunting pressure is much greater for smaller species (i.e. antelopes, etc), the slow maturation and reproduction rate of gorillas [Steklis & Gerard-Steklis, 2001] makes them extremely vulnerable to even low levels of poaching. In a market survey study in Bayanga, Central African Republic, Hodgkinson [2009] found that although gorillas were rarely seen at the market when compared with other species, the recorded amount was still high enough to threaten the sustainability of gorilla populations within the region (totals did not include unrecorded numbers sold out with of public market stalls – numbers which are probably much higher than those counted in the market due to the illegal nature of gorilla poaching). Additionally snares, although not often set to trap gorillas, can still be a major source of gorilla injury and death [Hall et al., 1998, Noss, 1998, 2000]. Even well protected habitats are not immune; while following the group observed in this study, the gorillas nested within centimetres of unreleased snares on several occasions. One evening they even nested within 30 meters of a large poaching camp most likely occupied with hunters at the time they were nesting [pers. obsv.].

Logging is also a major threat to western gorillas [Minnemeyer et al., 2002; reviewed in Plumptre et al., 2003], not only as a direct loss of habitat but also indirectly through (a) changes in forest structure due to increased fragmentation and the disappearance of seed dispersing species [Tutin & Vedder, 2001; White & Tutin, 2001; Wilkie et al., 2000], and (b) the creation of roads facilitating hunting and human encroachment [Peterson & Ammann, 2003; Tutin & Vedder, 2001]. Disease, particularly Ebola, is also fast becoming an alarming concern for western gorillas. In three outbreaks across Central Africa, gorillas experienced a 95% death rate of all known individuals [Bermejo et al., 2006; Caillaud et al., 2006; Walsh et al., 2008]. Disease, together with logging and hunting are predicted to cause a catastrophic 80% decline in western lowland gorilla numbers within 33 years [Walsh et al., 2003]. In order for a species to be marked as critically endangered, it must show potential for an 80% population decline over

66 years. Walsh et al.'s [2003] predictions of decline are conservative, but still twice as fast as that considered by the IUCN [Walsh et al., 2008].

1.4 Gorilla Socioecology

Like all primates, the social structure of gorillas is influenced by a complex combination of ecological variables and social pressures [Isbell & Young, 2002; Kappeler & van Schaik, 2002; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980]. The manner in which these forces interact shape the socioecology of gorilla subspecies. It is now known that gorilla subspecies differ markedly in several aspects of ecology and behaviour.

The intensively studied mountain gorillas live in high altitude montane forests, feed on an abundant folivorous diet of terrestrial herbaceous vegetation (THV) which varies little seasonally (with the exception of bamboo), and have the narrowest diet of all gorilla subspecies; only six food types are fruit [Fossey & Harcourt, 1977; Watts, 1996; Vedder, 1984]. As a result, day journey length is short; mean path length varies from 500-918m [see review in Doran & McNeilage, 2001], group spread is generally low at no greater than 100m [Doran & McNeilage, 2001], home range size is small at a mean of 4-11 km² [see review in Doran & McNeilage, 2001], and mean group size has increased over time from 9.15 [Watts, 1996] to 11.4 individuals [Gray et al., 2009]. Mountain gorillas form stable, cohesive groups centred around at least one adult silverback. Both females and males undergo natal transfer [Harcourt, 1978a], although only 36% of males [Robbins, 1995] and 72% of females emigrate [Watts, 1996]. Upon adulthood, females who emigrate transfer directly to other groups during intergroup (hereafter also called 'interunit') interactions; when males emigrate, they range solitarily in search of females or in some cases they join all male groups [Fossey, 1983; Harcourt, 1978a; Robbins, 2001; Stewart & Harcourt, 1987; Yamagiwa, 1987a, 1987b]. Kalpers et al. [2003] stated that multimale groups comprised up to 53% of the population, but this number was later revised by Gray et al. [2009] to a much lower 36% of the population. Infanticide accounts for 37% of all mountain gorilla infant mortality [Watts, 1989].

Although western lowland gorilla socioecological organisation is generally similar to that of the mountain gorilla, there are some pronounced differences: (1) even though western lowland

gorillas depend on a uniform distribution of folivorous species throughout the year, they also feed widely on seasonally available fruit; (2) as a result of frugivory, daily path length is longer (mean path length varies between 1000 to > 2000 m), home ranges are larger (10-23 km²), group spread is wider (> 500m) [Bermejo, 2004; Cicolletta, 2004; see review in Doran & McNeilage, 2001; Doran-Sheehy et al., 2004, 2007; Goldsmith, 1999; Remis, 1997a; Tutin, 1996; Tutin & Fernandez, 1991], group sizes are slightly smaller (mean 8-9 individuals) with the exception of Lossi which reported groups with 32 members [see review in Oates et al., 2003 and; Parnell, 2002a] and, gorilla females may avoid intragroup competition by temporarily subgrouping to feed in fruiting trees [Bermejo, 2004; Remis, 1994; Tutin, 1996]; (3) gorillas frequent dry or swampy clearings called 'bais' where they feed on abundant, nutritionally valuable herbs, and in one bai region, on fruit [Doran-Sheehy, et al., 2004]; (4) groups are predominantly single male [Bermejo, 1999; Gatti et al., 2004; Maglicocca et al., 1999; Parnell, 2002a; Remis, 1997b; Tutin, 1996] although multimale nonbreeding groups are known to occur, albeit rarely [Cicolletta, 2004; Gatti et al., 2003, 2004; Levrero, 2005; Levrero et al., 2002]; (5) no individuals have been observed to breed or remain in their natal group [Parnell, 2002b; Stokes et al., 2003], and; (6) infanticide, while strongly suspected at a number of sites, does not universally occur [Stokes et al., 2003].

Reports on eastern gorillas suggest a similar structure to mountain gorillas, although eastern gorillas living in lowland forest feed on a more frugivorous diet [Kuroda et al., 1996; Yamagiwa et al., 1994, 1996; Yamagiwa & Mwanza, 1994; Yamagiwa & Kahekwa, 2001]. Multimale groups are not as prevalent in eastern gorillas as in mountain gorillas [Casimir, 1975; Yamagiwa et al., 1993, 1996; Yamagiwa & Kahekwa, 2001, 2004] and only three recent cases of infanticide have been observed at Kahuzi-Biega National Park since project inception in the late 1960s [Yamagiwa & Kahekwa, 2001, 2004]. The little information known about Cross River gorilla socioecology indicates that they may face greater seasonal changes in frugivory than any other gorilla as a result of a highly seasonal climate with prolonged dry weather in much of their habitat [Oates et al., 2003]. Nesting data suggest that they roam in small groups with eight or fewer nests, although there is evidence of large groups containing up to 38 nests on Afi Mountain [Oates et al., 2003]. It has tentatively been suggested, as in western lowland groups,

that the variation in Cross River nest numbers is due to temporary sub and supragrouping. Since little information is available on the socioecology of the Cross River gorilla, the rest of the thesis will focus on the three other subspecies.

Only a brief overview of gorilla socioecology is provided here. More detail of intra and intergroup interactions and their relation to gorilla socioecology will be provided in the relevant chapters.

1.5 The Western Lowland Silverback, Perceived Risk and Disturbances

Many diurnal primate groups consist of permanent male-female associations [Lee, 1994; van Schaik, 1996]. Early primate models of sociality predicted that most diurnal groups formed as a result of predation risk [Chance, 1955; Crook & Gartlan, 1966; Stewart & Harcourt, 1987]. The socioecological model adds to the framework by predicting that social groupings exhibited by different primate species (or of the same species in different habitats) are based on a complex network of predation, ecological factors, competition, habitat saturation and infanticide avoidance [Isbell & Young, 2002; Sterck et al., 1997; van Schaik, 1989; Wrangham, 1980, 1982].

One key influence in the gorilla socioecological framework is the presence of humans, not only as hunters but also as protectors and observers. Fossey [1974] noted that when one mountain gorilla group crossed a particular open cattle area near the Mt. Visoke slopes, they always undertook this crossing rapidly consuming little food along the way. Additionally, they often maintained a static position on the Mt. Visoke slopes for 3-4 days, surveying the open region before travelling through it. An open, flat cattle area could easily expose the group to poachers which in Fossey's time were common. This gorilla group developed an adaptive strategy in response to the perceived human threat; the relationship between risk and vulnerability can produce complex behaviours [Miller & Treves, 2006].

Another example of human induced influences on gorilla social structure can be seen by examining the last two decades of mountain gorilla demography, which has shown a great increase in mountain gorilla group sizes; one group in particular grew from 20 individuals in

1993 to 65 in 2006 [Vecellio, 2008; Williamson, in press]. While this increase may be due to heterogeneity in habitat quality [McNeilage, 2001; Williamson, in press] and an increase in more attractive (to females) multimale groups - which offer greater infanticidal protection to females with dependent offspring [Kalpers et al., 2003] – the presence of human monitoring teams proffers another likely explanation for the growth in group size. Due to antipoaching teams, quick veterinary intervention, and the constant presence of research groups, tourist groups and armed guards, habituated mountain gorilla groups are afforded a level of protection previously unavailable. Conversely, human presence has also impeded the natural flow of interunit interactions, with unhabituated groups making migration difficult and forcing individuals to remain in their natal groups [Williamson, in press]. Indeed, habituated groups (mean: 16.8 individuals) are significantly larger than unhabituated groups (mean: 5.9 individuals) [Williamson, in press]. Even the increase in multimale units is said to be human influenced; in the 1970's many gorillas were killed for their infants, leading to unstable group relationships. By the 1980's, as group sizes and the number of females within them grew, the number of male infants born into some groups also increased greatly [Williamson, in press]. These infants became fully mature individuals by the mid 1990s and likely contributed to the observed increase in multimale systems [Kalpers et al., 2003; Williamson, in press]. Mountain gorilla groups appear to have developed a complicated adaptive strategy not only in response to the perceived human threat but also to their increased protection by humans.

Since the dominant adult male assumes the control function, providing protection and leadership, he is the crucial element moderating and managing the way groups respond in situations of high perceived risk, such as interunit interactions [Watts, 1996]. While a major benefit of female-male associations is protection from infanticidal males, a silverback's role in providing overall group stability and protection from predation (i.e. humans, leopards) or other environmental risks and disturbances (i.e. elephants) should not be underestimated [Harcourt, 2001].

Mountain gorilla females will cluster around an adult male when danger is detected [Harcourt, 2001], and any human observer who has experienced the wrath of a full silverback charge as a result of unintentionally upsetting a member of his group, will understand the lengths a leader

male will go to in protection of his group. Also western lowland gorilla females nest in trees more often and higher than do silverbacks [Mehlman & Doran, 2002; Tutin et al., 1995]. While the reason for this may be merely structural due to mass differences between males and females (Chapter 3), silverback ground nesting whilst group members remain in trees could also be a strategic position of defence, as seen in baboons and the Budongo chimpanzees [Brownlow et al., 2001; DeVore & Hall, 1965]. Yamagiwa [2001] clearly showed that despite the controversy surrounding protective silverback strategic nesting, leader adult males provide an important protective influence during night nesting periods; eastern lowland groups that did not contain a leader male were more likely to nest in trees than those that did (Chapter 3).

As western lowland gorilla groups are predominantly single male (Section 1.4), western lowland silverback protective functions may be even more vital than for mountain gorilla silverbacks, who can often rely on the support of other adult male members in their group. Additionally aside from the obvious risk of infanticide, much of western lowland habitat is fraught with risks (ie. poaching, elephants, leopards) that have greatly decreased or altogether disappeared in mountain gorilla habitat (Section 1.3; Chapter 3).

While leopards have all but disappeared from montane mountain gorilla habitats [Sholley, 1991], they are still the apex predator (excluding humans) for larger mammals within the rainforests of Central and Western Africa [Henschel, 2008; Jenny & Zuberbuhler, 2005]. Leopards in rainforest environments preferentially hunt medium sized species (7-30 kg) [Hart et al., 1996; Henschel et al., 2005; Ososky, 1998; Ray & Sunquist, 2001] although depletion of preferred prey items through unsustainable bushmeat practices force cats to hunt outside of their favoured weight range [Fay et al., 1995; Henschel, 2008; Nowell & Jackson, 1996]. Evidence from previous studies suggests that forest leopards may adapt their hunting behaviour to follow individual preferences for particular prey species [Jenny & Zuberbuhler, 2005; Zuberbuhler & Jenny, 2002].

Although the actual level of risk faced by western lowland gorillas as a result of leopard predation is uncertain, evidence is mounting to suggest that they along with other apes are targeted as leopard prey. In the early 1960s, Schaller [1963] confirmed the deaths of 2-3 adult

male mountain gorillas due to leopard attack. During a five year period in Taï National Park, Côte d'Ivoire, Boesch [1991] documented nine separate leopard attacks on chimpanzees. Leopard predation was also strongly suspected in the death of a silverback at Mbeli Bai, Republic of Congo, and of a blackback at the Lossi study site, Democratic Republic of Congo [Robbins et al., 2004]. Fay et al., [1995] and Watson [1999] witnessed leopard attacks on adult gorillas at both gorilla habituation study sites (Bai Hokou/Mongambe) in the Dzanga-Sangha Protected Areas Complex, Central African Republic. Furthermore in 1999, the Bai Hokou study group's main silverback was severely injured in an attack which led to his eventual demise. Although the attacking species could not be verified, attempted leopard predation was suspected due to suspicious claw-like markings on the focal adult male's back [Cipolletta, 2003; Cipolletta pers. comm.]. Additional records at Bai Hokou show that leopards were detected near gorilla groups on three occasions and that their presence affected group ranging patterns [Goldsmith, 1999; Klailova pers. obsv.]. Finally, although scavenging cannot be ruled out, gorilla and chimpanzee remains in leopard faeces have been recorded at various rainforest sites [Fay et al., 1995; Hart et al., 1996; Henschel et al., 2005, 2008; Ososky, 1998; Tutin & Benirschke, 1991].

The slow life histories of gorillas coupled with a growing inventory of suspected and verified predation incidents, suggest that the leopard could be an important cause of mortality in some ape populations [Robbins et al., 2004]. However, due to the cryptic nature of the forest leopard and challenges of western lowland gorilla habituation, it has not been possible to systematically assess leopard predation risks to gorilla groups.

More examples of the silverback's protective role and the delicate interplay between infanticide, predation, and disturbance related risks (i.e. elephants) will be detailed in the forthcoming chapters.

Understanding the western lowland silverback's role in relation to his females' reproductive success and therefore his own reproductive success requires an initial assessment of his role, detailing when and how it operates. This appreciation of his role will further enable

understanding of how variations in silverback functions underlie infant survival and female reproductive performance.

1.6 Aims of Thesis

Due to difficulties in habituation and the political instability of western lowland gorilla habitat, this subspecies has remained vastly understudied [Doran-Sheehy & Boesch, 2004]. Most work has focused on ecology [see review in Parnell, 2002b], although the 1990s and early 2000s saw (1) the discovery of swampy clearings where gorilla groups could be monitored, and (2) the successful habituation of several western lowland groups in forest environments [Bermejo, 2004; Cipolletta 2003; Doran-Sheehy & Boesch, 2004; Doran-Sheehy et al., 2004, 2007; review in Nowell, 2005 and Parnell, 2002b]. While a growing body of socioecological information is available, details on behaviour and relationships and their subsequent influences on western lowland gorilla social structure are still paltry in comparison to mountain gorillas.

The only studies to behaviourally assess the role of the western lowland silverback took place in bais [Nowell, 2005; Parnell, 2002b]. These studies were essential and very informative, as they provided the first glimpses of silverback-group dynamics at a time when forest observations were limited; however while bais offer excellent vistas into demography and comparative intergroup interactions and dynamics, using clearings to examine the framework of relationships is highly biased since gorillas spend only 1% of their time in bais, and almost all of that time is spent feeding (not socialising) [Parnell, 2002b]. It also needs noting that Breuer [2008] and Caillaud et al., [2008] quantified the phenotypic traits associated with male reproductive success in western lowland gorillas from bai observations alone; their work will be further discussed in Chapter 7. It is, however, essential to quantify relationship dynamics from a holistic perspective in order to obtain a more complete and realistic picture.

The aim of this thesis is to provide the first detailed account of western lowland silverback-group dynamics, from an intergroup and interspecific perspective. Since females associate with males for protection, how an adult male protects, stabilizes and leads his group is imperative to male reproductive success, which is a function of his group's survival or persistence, his females' reproductive rates, and the survival of his infants. In the complete absence of long-

term data on such outcomes for western lowland gorillas, a description of the nature and expression of one western lowland male's role will be the first such attempt to quantify the potential outcomes and mechanisms by which the study male, Makumba, protected and stabilized his group.

I provide an overview of study methods, daily activities and overall behaviour in Chapter 2 and in subsequent chapters I examine the following:

Chapter 3: the silverback's spatial role in group dynamics in bais and forest environments (as little is known about the silverback's role from a holistic perspective, this chapter provides a basic overview of silverback-group dynamics)

- (a) the silverback's spatial relationship to adult females, immatures and infants
- (b) the silverback's spatial and protective role as a 'babysitter' for young juveniles and infants
- (c) the silverback's spatial relationship to high risk adult females (i.e. pregnant, etc)
- (d) the silverback's spatial location within both his neighbour (5m) group (i.e. periphery, middle) and the entire group (i.e. back, middle, front); does he exert directional control?
- (e) group nest site spatial positioning and its relation to silverback nest placement in a position of defence (i.e. more visible habitat, closer to the largest trail)

Chapter 4: the silverback's role in group dynamics during interunit interactions (hereafter 'interactions')

- (a) the distribution of interactions, their corresponding intensity (i.e. low, medium, high) throughout 2007 and how the focal group's interactions compare to published studies at other gorilla sites
- (b) the peak interaction month of July and its influence on silverback-group dynamics, ranging and nesting patterns
- (c) nesting patterns compared between interaction and non-interaction days, and at different interaction intensities
- (d) the silverback's responses during interactions and according to interaction intensity
- (e) silverback and group auditory signalling rates during interactions and according

to interaction level

(f) group spread on interaction and non-interaction days, and the possibility of strategic interaction timing by the focal silverback or extragroup males

(g) the influence of interactions and interaction intensity on silverback-neighbour dynamics

Chapter 5: the impact of human presence measured by human group type (tourists, trackers, researcher combinations), human group size, and human observer distance on silverback-group dynamics

(a) silverback aggression directed at humans

(b) silverback and group aggression in relation to human group type (i.e. teams with tourists, or research-only teams), size, and human observer-silverback distance (at what distance does silverback aggression to observers markedly decrease?)

(c) the effect of human group type, size and human observer-silverback distance on silverback and group activity budgets

(d) as a result of these analyses, initiate ecotourism guidelines designed to minimize the negative behavioural impact of human presence on habituated western lowland gorilla groups

Chapter 6: the functions and importance of silverback olfactory communication in relation to his social role within the group

(a) the factors which predict varying levels (i.e. low, high, extreme) of silverback odour production

(b) the intricate relationship of varying arousal levels and silverback odour production

(c) the function of silverback odour production in silverback-group dynamics (i.e. activity budgets, interactions, etc)

Through the above explorations, I aim to detail the mechanisms by which the silverback protects his group in situations of perceived risk or disturbance, which is crucial to (1) his safety, (2) his group's safety, and (3) his ultimate tenure as group leader. In doing so, I hope to elucidate novel approaches to examining, investigating, and understanding western lowland silverback-group dynamics.



CHAPTER 2

*STUDY SITE, METHODS,
GROUP DIET & ACTIVITY*



CHAPTER 2

STUDY SITE, METHODS, GROUP DIET & ACTIVITY

2.1 STUDY SITE

2.1.1 Dzanga-Sangha Protected Area Complex

Created in 1990, the Dzanga-Sangha Protected Area Complex (DSPA) of the Central African Republic consists of the Dzanga Sector (495 km²) and the Ndoki Sector (752 km²) of the Dzanga-Ndoki National Park, which is buffered by the Dzanga-Sangha Forest Reserve (3359 km²). The DSPA is part of the Sangha Tri National Complex of protected areas that extends into Nouabale-Ndoki National Park, Republic of Congo and Lobeké National Park, Cameroon. Within the forest reserve, three safari companies have rights to hunting concessions and traditional hunting by local populations in the eight surrounding villages is permitted. The area is home to the largest ethnic group in the region: the BaAka pygmies [Blom et al., 2004]. Although human density in the region is low (1.3 person/km²), population continues to increase as migrants arrive in search of work [C.T.F.T, 1967; Hodgkinson, 2009]. The reserve and park are managed in collaboration with the CAR government, the World Wildlife Fund for Nature (WWF) and until 2009, the German Technical Co-operation (GTZ).

The Dzanga Sector houses the gorilla and elephant tourism/research sites of Bai Hokou, Mongambe and Dzanga Bai. Research was conducted at the Bai Hokou Primate Habituation Camp (2°50'N, 16°28'E; Figure 2.1). The study site is located within the Dzanga Sector of the Dzanga-Ndoki National Park. The Bai Hokou study site was selected in 1997 to develop a long term gorilla habituation project for (1) research, (2) ecotourism, and to (3) monitor the impact of ecotourism on gorilla groups [Carroll, 1997]; although wild gorillas have been studied intermittently at this site since the 1990s [Blom et al., 2001; Carroll, 1997; Goldsmith, 1999; Remis, 1995, 1997a, 1997b, 1999].

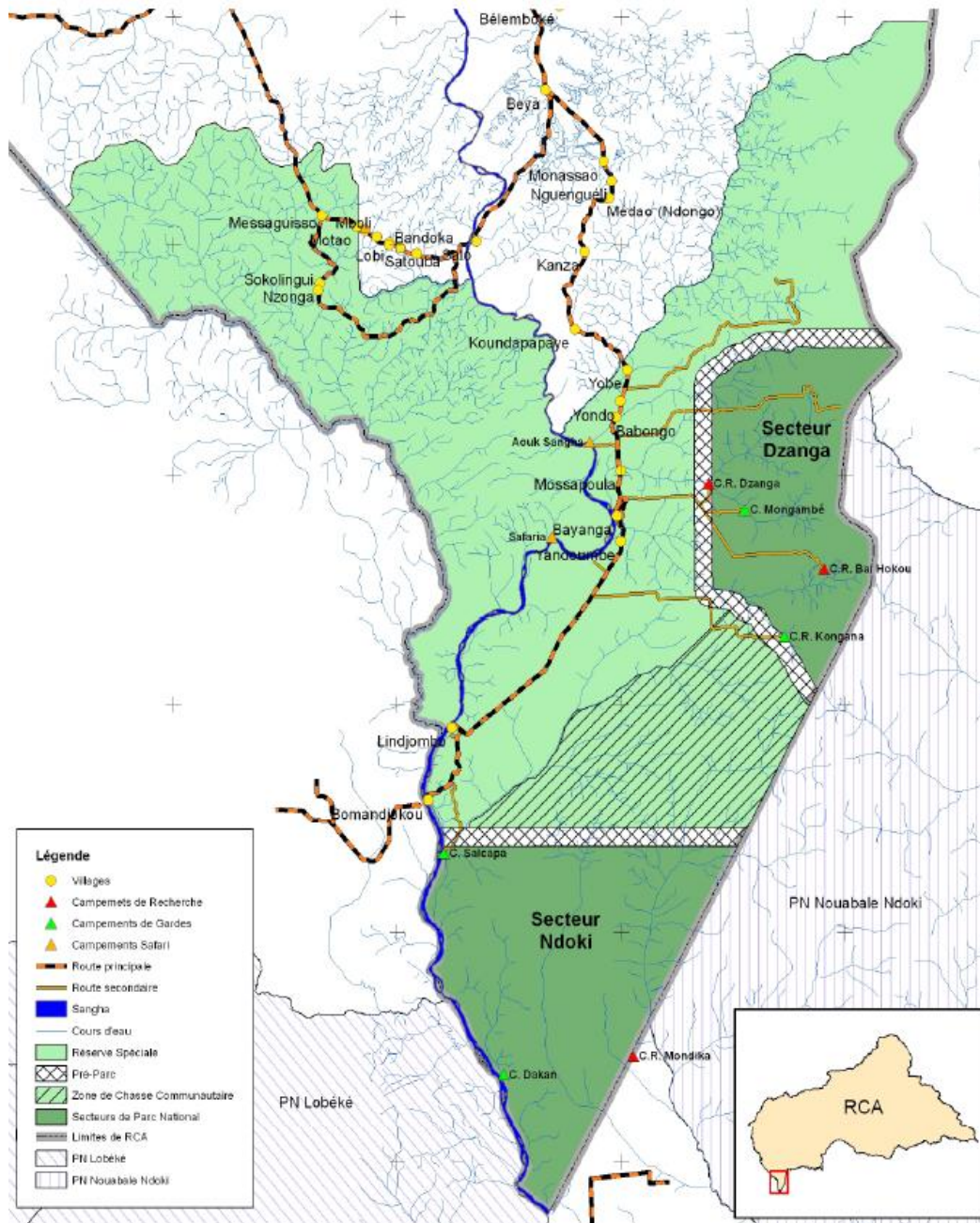
The forest habitat is patchy due to intermittent logging from 1971 to 2004 [Doungoubé, 1990; Hodgkinson, 2009; Noss, 1997]. The region incorporates over twelve major habitat types [Carroll, 1997] predominantly (a) mixed dense semideciduous forest, (b) disturbed forest dominated by *Marantaceae* and *Affromomum* spp., (c) monodominant forest dominated by *Gilbertiodendron dewevrei*, (d) light gaps accompanied by a dense ground layer of herbs, and (e) riverine (*Raphia hookeri*) and marshy clearings known as bais [Blom et al., 2004]. For information on forest density categorisation used in analyses, see Section 2.2.2.

The Dzanga-Sangha region is home to over 105 species of non-volant mammals many of which are endemic to the ecoregion. The area hosts 15 primate species, such as the chimpanzee (*Pan troglodytes*), the black colobus monkey (*Colobus satanas*) and the sun-tailed monkey (*Cercopithecus solatus*) [Blom, 1993; Blom et al., 2001; Noss, 1995]. Ungulates include the bongo (*Tragelaphus euryceros*), the sitatunga (*Tragelaphus speksi*), the forest buffalo (*Syncerus caffer nanus*), two pig species (*Potamochoerus porcus*; *Hylochoerus meinertzhageni*), and seven duiker species (*Cephalophus* spp.) [Fay et al., 1990; Klaus-Hugi et al., 2000; Turkalo & Klaus-Hugi, 1999]. The region is also home to the forest leopard (*Panthera pardus*), the golden cat (*Profelis aurata*), many reptiles and amphibians, high densities (0.6 individuals/km²) of the African forest elephant (*Loxodonta africana cyclotis*) and 379 species of bird from 66 different families [Beresford & Cracraft, 1999; Blake, 2005; Blom, 2001; Green & Carroll, 1991; Henschel & Ray, 2003; Rondeau & Christy, 1999].

The Dzanga-Sangha complex falls into both the subequatorial climate and Congolese equatorial climate zones [C.T.F.T., 1967]; resultantly, the region experiences a dry season between December-February, with peak rainfall in April-May and September-October [Carroll, 1997; Cipolletta, 2003; Hodgkinson, 2009]. Annual rainfall recorded in Bayanga is 1365 mm [Carroll, 1997] and temperature remains relatively constant with an annual average of 26.4°C [Carroll, 1997]. Mean monthly minimum and maximum temperatures range from 20.6°C to 26.4°C and 28.4°C to 35.7°C respectively [Blom et al., 2004; Carroll, 1997; Cipolletta, 2003]. For this study, daily rainfall and daily minimum and maximum temperature were taken from Bai Hokou long term data (Figures 2.2 and 2.3). While year 2007 followed the 'general' pattern of rainfall in previous years (Figure 2.3), it was defined by much larger troughs and generally

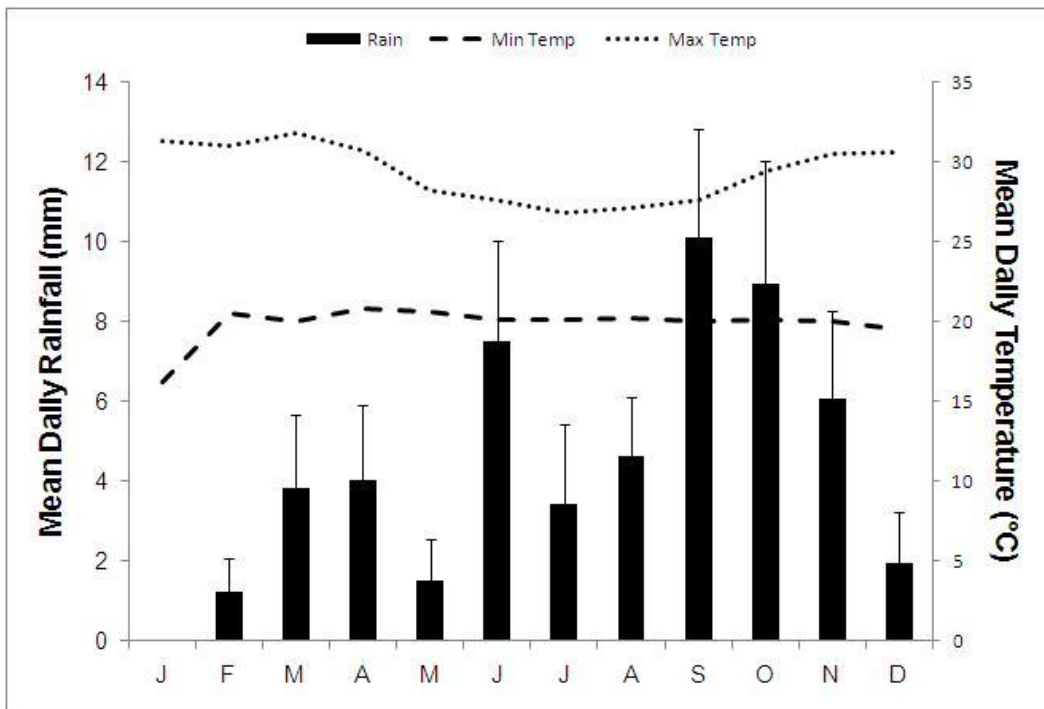
greater peaks in rainfall. The mean daily rainfall in 2007 was 4.4 mm (range 0-78 mm, SD = 10.9 mm, N = 365 days). Temperature remained fairly constant in 2007 (Figure 2.2). The mean daily minimum temperature in 2007 was 19.9°C (range 12.2°C - 33.3°C, SD = 2.02°C, N = 336 days) and the mean daily maximum temperature in 2007 was 29.4°C (range 19.4°C - 35.6 °C, SD = 2.95°C, N = 336 days).

Figure 2.1 Study Site Location in the Central African Republic



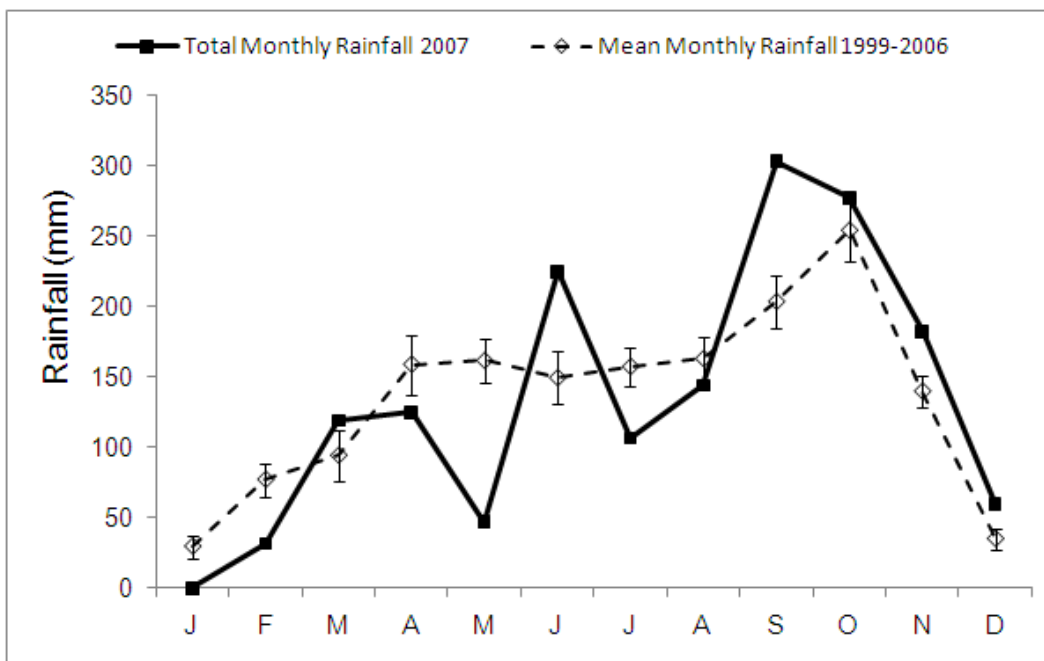
Source: GTZ in Hodgkinson [2009]

Figure 2.2 Mean Daily Rainfall and Temperature for 2007



Source: Bai Hokou Long Term Data

Figure 2.3 Mean Monthly Rainfall 2007 compared to 1999-2006



Source: Bai Hokou Long Term Data

2.1.2 The Study Group - Makumba

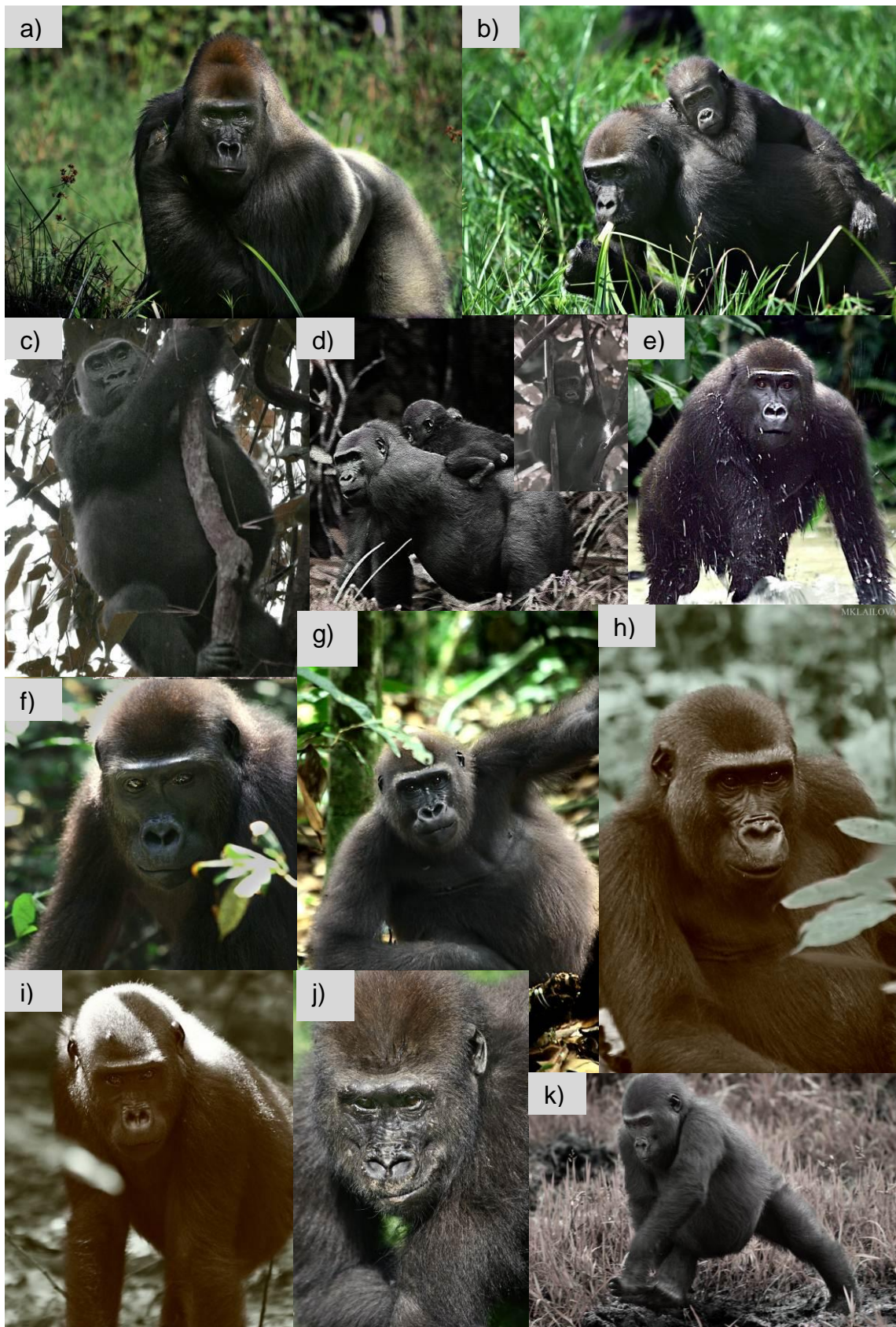
Habituation began in 2000 and the group was opened to tourists in September 2004. The group consisted of one silverback and four adult females with their offspring in 2000, but one female emigrated in early 2006 after the death of her infant. The remaining three adult females were residents from the onset of habituation (Table 2.1 and Figure 2.4).

Table 2.1 The Makumba Group Birthdates, Ages and Family Trees

| Figure 2.4 Codes | Individual | Sex | Birth & Age at Start of Study Period | Offspring/Mother |
|------------------|---------------|-----|--------------------------------------|--------------------------------|
| (a) | Makumba | ♂ | Adult Silverback | - |
| (b) | Mopambe | ♀ | Adult | Bokata, Mai, Etefi |
| (c) | Malui | ♀ | Adult | Tembo, Mossoko Abuli, Mio |
| (d) | Bombe | ♀ | Adult | Mobangui, Essekerende, Silo |
| (e) | Kunga | ♂ | 1998-1999; 8-9 years | Mopatapata ^a |
| (f) | Etefi | ♀ | 1999-2000; 7-8 years | Mopambe |
| (g) | Silo | ♂ | 1999-2000; 7-8 years | Bombe |
| (h) | Mio | ♀ | 2000-2001; 6-7 years | Malui |
| (i) | Mai | ♀ | Jan 2003; 48 months | Mopambe |
| (j) | Essekerende | ♂ | Mar 2003; 46 months | Bombe |
| (k) | Mossoko Abuli | ♂ | Feb 2004; 35 months | Malui |
| (b) | Bokata | ♀? | Jan 10 2006; 12 months | Mopambe |
| (d) | Mobangui | ♂? | Jul 23-27 2006; 5 months | Bombe |
| na | Tembo | ♂? | Dec 4 2007 | Malui |

^aMopatapata emigrated in early 2006 after the death of her infant due to unknown circumstances. She left her son Kunga behind upon emigration.

Figure 2.4 Makumba Group Family



Precise ages are known only for Bokata, Mobangui, Mossoko Abuli, Essekerende, and Mai. Ages of the other individuals in the group were estimated when habituation began based on the Harcourt et al., [1980] age divisions described in Watts [1990a]. Age-sex class categories for this study were based on Parnell's [2002a] classification system (Table 2.2) which also used Harcourt et al., [1980] / Watts [1980a] age descriptions as its foundation. This system was chosen because its broad age classes appeared to match the developmental phases of individuals in the Makumba group. Breuer et al., [2009] recently suggested that western lowland gorilla development was slower than in mountain gorillas due to increased frugivory. They suggested that western lowland gorillas remained infants until they were four years old (instead of three). This would place Mossoko Abuli, a three year old, into the infant category. However, the former age classification system was considered more appropriate here since (1) Mossoko spent a great deal of his time out of his mother's presence (Chapter 3), (2) the age gap between him and the other two infants was great, and (3) he generally behaved as a young playful juvenile seeking the attention of other juveniles and the silverback, although he was still seen suckling from time to time.

Taking Breuer's et al., [2009] classification system into consideration, age-sex classes were categorised as: (1) adult females - defined as all females above the age of eight at the start of the study period. This includes Malui, Bombe and Mopambe. Although Etefi may have been ~8 years when data collection commenced, she was not included as an adult female because her age bordered between adolescence and adulthood [Breuer et al., 2009], and unlike the other adult females, she was a presumed natal daughter of the silverback and thus may have had different proximity goals in relation to Makumba than did the three non-natal adult females; (2) immatures and infants - defined as all non-adult individuals within the group at the start of the study period. This includes, Kunga, Etefi, Silo, Mio, Mai, Essekerende, Mossoko Abuli, Bokata, Mobangui and Tembo; (3) old immatures - defined as all individuals above the age of six years old at the start of the study period. This includes Kunga, Etefi, Silo and Mio; (4) young immatures - defined as all individuals between the ages of 3-6 years old at the start of the study period. This includes Mossoko Abuli, Essekerende, and Mai. Mossoko Abuli was only one month shy of the three year criteria at the start of the study period, and was thus included in this category; (5) infants - defined as all individuals between the ages of 0-3 years old. This

includes Bokata, Mobangui, and Tembo. Since Tembo was born at the end of the study period, his data were not included in analyses unless noted otherwise.

Table 2.2 Age-Sex Class System Employed in This Study

| Age-Sex Class | Corresponding Age Range (Years) |
|----------------------|--|
| ^a | |
| Infant | Birth to 3 |
| Juvenile | 3 to 6 |
| Subadult | 6 to 8 |
| Blackback male | 8 to 12 |
| Adults | |
| Adult female | 8+ |
| Young silverback | 12 to 15 |
| Silverback | 15+ |
| ^b | |
| Adult Females | >8 |
| Immatures & Infants | All non-adult individuals |
| Young Immatures | 3-6 |
| Old Immatures | >6 |

^aBased on Parnell's [2002a] classification system which is a variant of Harcourt et al., [1980] and Watts [1990a] age divisions. ^bRepresents broader categories used in analyses which also takes into consideration a variant of Breuer et al., [2009] classification system.

2.2 DATA COLLECTION

2.2.1 Basic Data Summary

The Makumba group was followed from nest to nest by a team of trackers (range 2–4) and researchers (range 1–3). Researchers accompanied gorilla trackers during morning (7 am–12 pm) and/or afternoon (12–6 pm) sessions. Research team size was not allowed to exceed seven people, and every effort was made to keep researcher and tracker numbers well below this limit. Tourists (391 in 2007) would join the main team for either the morning or the afternoon session, and stay with the gorillas until a maximum 60 minutes of visibility had been achieved (not necessarily consecutively) or earlier, if they expressed a wish to return to camp. Only one

tourist visit (with a maximum of three tourists per visit) was allowed per session. Total observer group size (trackers, researchers, and tourists) was also not allowed to exceed seven people.

2.2.2 Scan Sampling

Data collection focused on the silverback, Makumba, and those individuals in his immediate proximity. Instantaneous scans [Altmann, 1974] were taken on the silverback every 10 minutes. If visibility of the silverback was lost for more than 10 minutes, scanning restarted at the point of re-contact. For data collected during each scan complete with definitions where necessary, see Table 2.3.

Table 2.3 Scan Data Collection Categories

| Scan Data Collection Categories | Definition |
|--|---|
| Silverback position | sit, stand, lying down |
| Silverback behaviour | feed, move, rest (including social) |
| Silverback visual monitoring of observers ^a | ignore, low, medium, high |
| Distance of recorder to the silverback | nearest meter |
| Silverback height | tree, ground |
| Silverback smell ^b | none, very low, low, high, extreme |
| Number of 'neighbours within 5m' of the silverback (hereafter 'neighbour') | |
| Identification of neighbours to the silverback | |
| Distance of neighbours to the silverback ^c | nearest meter |
| Neighbour position, behaviour and height | same as for silverback above |
| Individuals within 6-10m of the silverback | presence, absence |
| Group activity | feed, move (including stand; stand most often represented a transitional phase), rest (including social), mixed - defined as the majority activity observed where at least two individuals other than the silverback must have been present |
| Forest density ^d | dense, moderate, open |
| Forest zone ^d | <i>Marantaceae</i> and <i>Affromomum</i> |

| | |
|--|--|
| | spp., riverine (<i>Raphia hookeri</i>), clearing/bai, mixed, primary (<i>Gilbertiodendron Dewevrei</i>), transition |
| Silverback location in his group of neighbours | periphery, middle |
| Silverback location within the entire group | front, middle, back |
| Group spread ^e | close, midrange, dispersed |
| Wind ^f | presence, absence |
| Number of tourists | |
| Number of researchers and trackers | |
| Location on map of group's range ^g | ~ location marked within every one 500m x 500m quadrat. Each quadrat was further subdivided into nine 166m x 166m plots and ~ location was marked within one of these plots. |

^aDefined as (1) ignore: silverback was unaware of human presence or was not paying observers any attention (i.e. feeding with back turned), (2) low: silverback made occasional glances towards observers but continued with his activity (i.e. observer team approached him and he looked our way initially but then continued with the activity he was performing prior to our advance), (3) moderate: silverback still continued with the activity he was performing prior to our advance, whilst keeping a keen eye on the observers (i.e. regular glances and soft barks which represent mild aggression or warning signals – see Chapter 4 and 5 for detail on soft barks), (4) high: silverback was constantly monitoring observers whilst paying little attention to his former activity (i.e. barked or charged observers and was visibly very uncomfortable with human presence – see Chapter 4 and 5 for detail on barks).

^bDefined as: (0) no odour was detected, (1) slight odour detected but not stronger than the smell of surrounding vegetation, (2) odour detected at the same level as the smell of surrounding vegetation, (3) odour detected was stronger than the smell of surrounding vegetation, (4) odour detected was overpowering and was the first or only element smelled in the surrounding air (similar to the smell of burned coffee); for more detail see Chapter 6.

^cExact distances from the silverback to an individual in a tree were recorded (i.e. base of tree was not used as a distance category from the neighbour).

^dDefined as (1) dense: a minimum of 75% of the body of a gorilla could only be seen no further than 0-5m away, (2) moderate: a minimum of 75% of the body of a gorilla could only be seen no further than 6-10m away, (3) open: a minimum of 75% of the body of another gorilla could be seen further than 11m away.

Note that open forest density environments include bays and monodominant forests, such as *Gilbertiodendron dewevrei* forests. Moderate forest density environments include semideciduous forests which house a wide diversity of species varying in undergrowth density. Dense forest environments include thick riverine (*Raphia hookeri*) habitats and secondary growth forests dominated by young trees, saplings and herbs such as *Marantaceae* and *Affromomum* spp. [Blom et al., 2004].

^eDefining group spread has always been a topic of debate and is not easy to calculate for western lowland gorillas due to their large potential group spread (> 500m), which necessitates several research groups to follow different parts of the group and the possible subgroups that can occur during feeding [Chapter 1]. Since most western lowland gorilla groups contain only one adult silverback, it is likely that as the 'protector' of the group, most major changes in group dynamics will be mirrored in the behaviour of the adult male. Defining group spread based on the number of individuals within close range of the silverback should accurately reflect changes in group cohesiveness. Therefore, group spread was categorised as (1) close: seven or more individuals within 20 meters of the focal silverback, (2) midrange: 4-6 individuals within 20 meters of the focal silverback on the ground or within 50 meters of the silverback when in a tree, (3) dispersed: less than or equal to three individuals within 20 meters of the focal silverback.

The fifty meter category was used in the midrange definition only because there were times where individuals were high in the canopy but still within hearing and visual presence of both Makumba and the researcher. When the group was dispersed, no more than three other group members were heard or seen.

^fDefined as the presence of a breeze or a strong wind; included in Chapter 6 smell analyses only.

^gSee Section 2.2.4.

2.2.3 Auditory Sampling

In addition to scans, continuous records of all auditory signals were made for Makumba and gorillas in his presence (within human earshot). Auditory signals were categorised by age–sex class of the performer (Section 2.1.2), and defined as any sound made by a gorilla, either vocally or via other signals (i.e. ground slapping, tree breaking, chest beating, and hand clapping). If an individual exhibited a repeat of an auditory signal less than five seconds after the earlier one, this was counted as one bout [as per mountain gorilla data collection protocol; Hodgkinson pers. comm.]. As western lowland gorilla auditory communication (vocal or via other auditory signals) has not yet been classified, definitions were taken from published work on mountain gorilla vocalisation categorisations [Fossey, 1972; Harcourt & Stewart, 2001]. Since a different set of auditory categories and signals were used in the analyses of each chapter, definitions and groupings will be outlined separately in the methods section for each data chapter. Note that while auditory signalling rates were also analysed for adult females and immatures, their results may be under-represented. Since Makumba was followed 100% of the time, only auditory signals heard when in Makumba's presence will have been recorded.

2.2.4 Ranging and Nesting Data Collection¹

Group movements were measured on a 1:20 000 map, upon which we plotted nest site location (Figures 2.5 and 2.6). Nesting location and movement was determined through a reference system of trails marked every 100 meters, distance pacing, compass bearing and identification of known landmarks. Efforts to use GPS units were made, although the extensive forest cover made it very difficult to locate satellite signal in a timely fashion, which influenced our ability to stay in contact with the group.

Ranging data using the reference trails and compass bearings were taken continuously. Nesting data were recorded the morning of each observation session. Maps were divided into 500 meter x 500 meter quadrats (corresponds to squares grids in Figures 2.5 and 2.6), and further subdivided into nine 166 meter x 166 meter plots. Approximate nest and ranging location was marked within one of these 9 plots. The silverback's nest was always identified by its size and the size of faeces deposited in the nest as well as the presence of silver hairs. Due to time limitations it was not possible to accurately identify individuals who belonged to other nests. Whilst age-sex classes of nests were categorised based on nest and faeces size, these categories were not used in analyses due to the difficulty in ensuring accurate identifications. A nest was defined as a marked sleeping spot either on bare ground or on leaves. A nest site was defined as a collection of nests built on the same night all within a radius of 50 meters [Kuehl et al., 2007; Maisels pers. comm.; Williamson, 1988]. For data collected at each nest site complete with definitions where necessary, see Table 2.4.

¹Unfortunately clearer or fully digitized maps were unavailable at the Bai Hokou Primate Habituation Camp. Maps presented here are scanned versions of those used to plot the Makumba group's ranging and nesting patterns.

Table 2.4 Nest Site Data Collection

| Scan Data Collection Categories | Definition |
|--|--|
| Silverback nest type | bareground, minimal leaves, herbaceous |
| Silverback height | see Table 2.3 |
| Silverback nest site forest density | see Table 2.3 |
| Silverback nest site forest zone | see Table 2.3 |
| Distances of all other nests to the silverback and to their closest neighbour ^a | nearest meter |
| All other group member nest heights | see above |
| All other group member nest types | bareground, minimal leaves, herbaceous |
| Nest site spatial patterning ^b | fan, circle, irregular |
| Silverback location of nest in relation to entire nest site ^c | periphery, middle |
| Individual closest to the largest trail and distance to that trail ^d | nearest meter |

^aExact distances from the silverback to an individual in a tree were recorded (i.e. base of tree was not used as a distance category from the neighbour). Likewise exact distances from one individual to another in a tree were recorded.

^{b,c,d}See Chapter 3 for definitions.

Figure 2.5 Nest Sites from January - July 2007

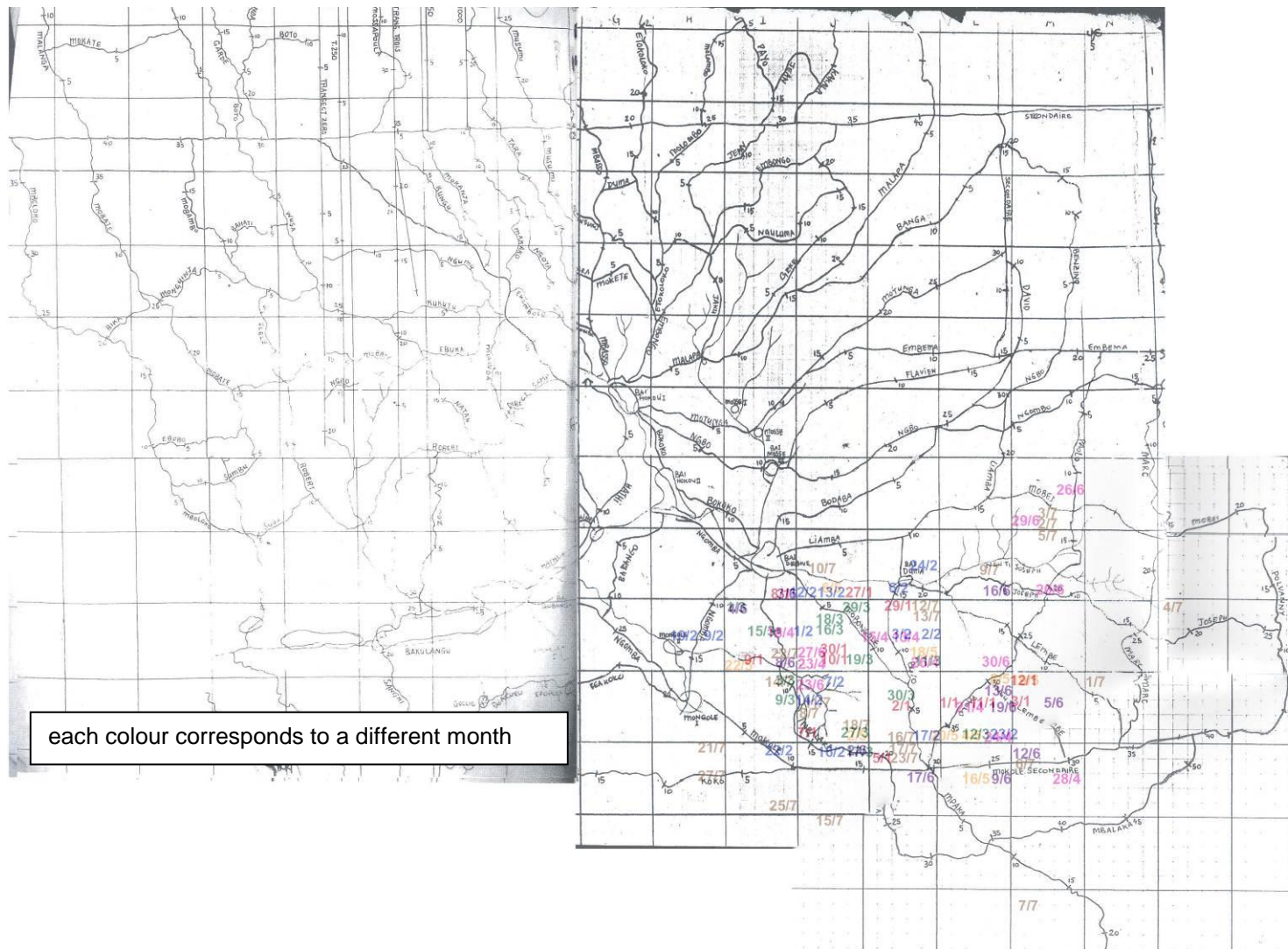
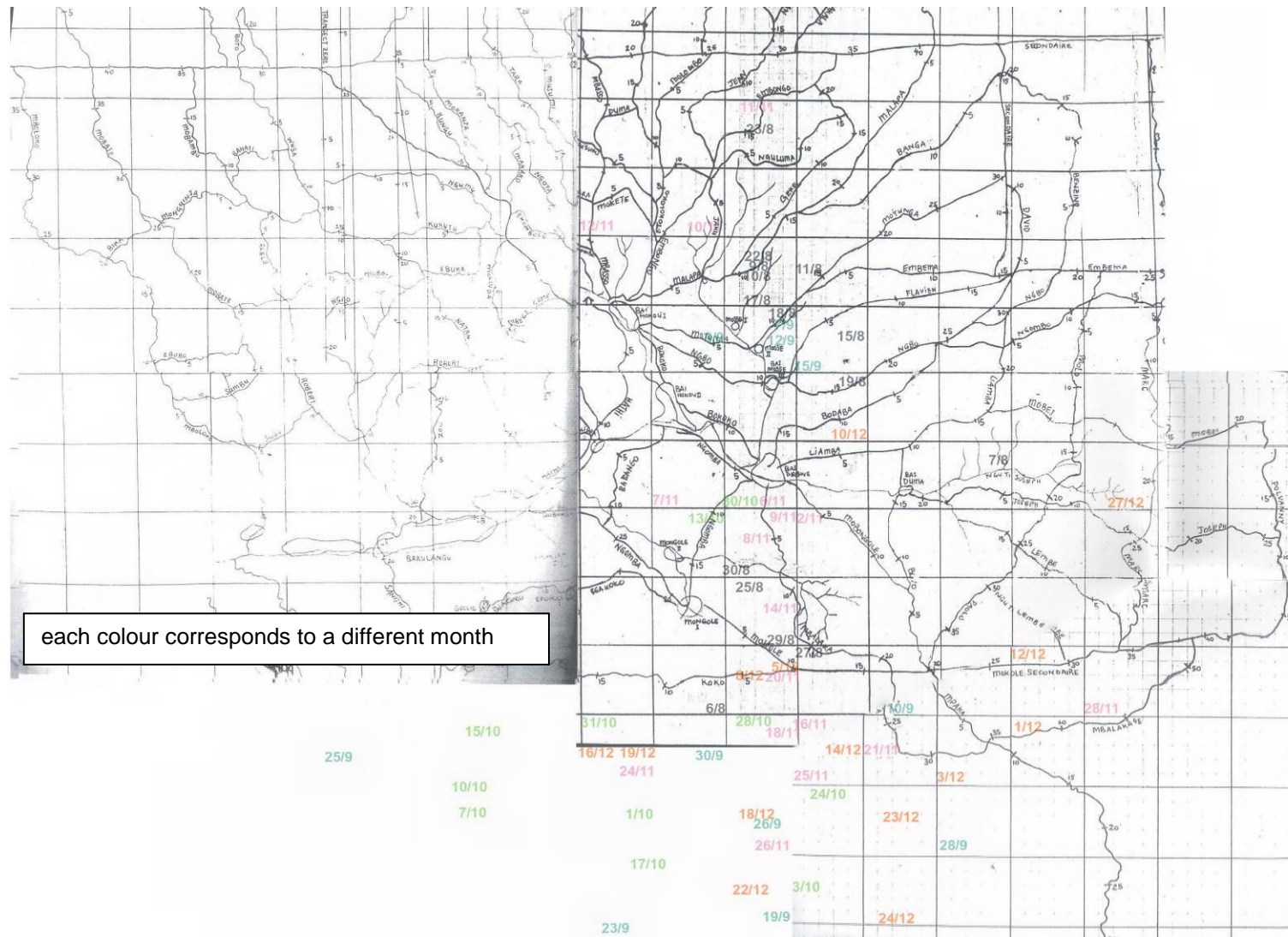


Figure 2.6 Nest Sites from August - December 2007



2.2.5 Interunit Interaction

Ad libitum data were recorded on all interunit interactions (hereafter ‘interactions’) that occurred during the study year. An interaction was defined as occurring when the Makumba group, in particular the focal silverback, communicated with another extragroup male. Communication may have been one sided – where an attempt to communicate was made by an extragroup male but ignored by Makumba and vice versa - or two sided - where both units responded and reacted. Interunit interactions between the Makumba group (with focus on the silverback) and extragroup males (either solitary or other group males) were divided into the following categories according to the potential threat level: (1) **low**, where (a) traces (i.e. disturbed soil, presence of blood, etc), ranging and nests indicated a potential interaction but the focal group and the focal group silverback behaved normally when observer contact was made, or (b) the focal silverback behaved in a manner suggesting the presence of another unit, although the unit was not heard or seen by the observer (i.e. Makumba was chest-beating, patrolling or displaying to an unknown cue); (2) **medium**, where auditory exchange between the focal group silverback and another unit occurred, and; (3) **high**, where auditory and visual exchange between the focal group silverback and an extragroup unit occurred with or without physical contact².

2.2.6 Individual Session and Hourly Roll Call

If an individual was seen at least once in any given session, irrespective of Makumba’s presence, then he or she was noted as present. These session-wide attendance records were collected to capture large-scale changes within the group (i.e. transfers, etc). An hourly identity record (also called roll call) of all individuals was collected during each recording session and defined as any individual seen (at any distance) within each hour of recording time, *when in the presence of Makumba only*. If Makumba was present for less than 45 minutes of any hour of

²Some (N = 5) high level interactions were defined from traces only. These are exceptions, where a high level interaction occurred during a previous session and it was clear by traces (i.e. disturbed soil, presence of blood, etc), nesting, and ranging that the interaction continued or that another high level interaction occurred in the observer’s absence.

recording time, the associated hourly roll call was excluded from final analyses. Individual roll calls take into account situations where group members may be close to or in the vicinity of the silverback, although not within five meters of him. The first two months of scans were dropped from analyses when hourly roll call was included, since roll call collection only began in March. Despite this reduction in sample size, roll call was still used in many analyses as this form of recording was the most accurate way to assess the presence of individuals within Makumba's vicinity. Individual hourly roll call captured hourly movements of each gorilla, whereas session presence noted only if each individual was spotted once during the entire session (not limited to Makumba's presence) and silverback-neighbour data was restricted to only those individuals within five meters of the silverback.

2.2.7 Intraobserver and Interobserver Reliability

Intraobserver reliability was checked by regularly testing accuracy when in the presence of an experienced researcher. Distances, forest density and visibility, all measured by eye, were tested regularly. Data were recorded by two researchers: researcher one (myself), N = 201 sessions; researcher two, N = 57 sessions. Prior to beginning official data collection I spent three months following the Makumba group and four months following captive groups, piloting protocols. The second researcher spent six months in the field following the Makumba group prior to assisting this study. Additionally, the second researcher underwent a two month training period involving data collection procedures for this study. Interobserver reliability tests were conducted several times a month to ensure accuracy. During these tests both researchers recorded data over the same session and researcher responses were the same > 90% of the time. Any differences noted were minimized by further training and spending more time data collecting in unison. Smell data collection followed the same interobserver protocol as above; more detail regarding smell sensitisation is provided in Chapter 6. Following additional training, a total of N = 10 nests were recorded by two other researchers at the field site.

2.2.8 Camp Data

Camp data - collected daily by the researcher or assistant following the Makumba group - involved keeping a continuous record of ranging, intergroup interactions, initial behavioural reactions upon contact each morning, and of foods eaten daily by the Makumba group (Section 2.4). Camp data is stored in Bai Hokou long term records, and was used in this thesis only where further elucidation of analyses were necessary and where permission was given.

2.3 DATA ANALYSIS

2.3.1 Data Grouping

Data were analysed using the raw or grouped (by session) data sets. Data set type will be specified in each chapter. For both the raw and grouped data, observer-silverback distances were categorised to control for the potential effects of visual binning as (1) 1–5m, (2) 6–10m, (3) 11–15m, (4) 16–20m, and (5) 21+m. Distances of nests to nearest neighbours and to the silverback were not binned as accurate measurements were achieved by pacing.

Data were categorised in the following manner when grouped by session:

(1) median observer-silverback distance scores were calculated to control for the times when the silverback was in a tall tree and thus unlikely to be affected by human presence or direct aggression towards observers.

(2) mean research team, tourist and total observer numbers were calculated and corrected for the number of minutes that different human group sizes were present; means were used due to the absence of outliers (Chapter 5).

(3) as the following are purely categorical, modal scores were calculated for silverback position, behaviour and height, group activity, neighbour positions and behaviour, and forest zones.

(4) if wind was recorded in any scan for a session, that session was coded as 'windy' (N = 133 sessions) and where no wind was noted, the session was coded as still (N = 125); sessions were either quite windy or very still thus this grouping represented the conditions most accurately.

(5) a mean hourly rate relative to the number of minutes of observation in each session was calculated for all auditory signals; auditory signals were only analysed by session to minimize the effects of dependence.

(6) a mean hourly forest density, silverback visual monitoring of observers, and number of neighbours (within 5m) to the silverback score was calculated to (a) correct for varying observation minutes, and (b) allow for a standardised and comparable measure across categories.

(7) proportion of each odour type (i.e. low, high, etc) was calculated out of total smell recordings for each session (Chapter 6); proportions were used to ensure that the higher smell ratings were not artificially suppressed by a large number of zeros as may have been the case had rates been calculated.

(8) proportion of each group spread type (i.e. close, dispersed, etc) was calculated out of total group spread recordings for each session; proportions were used to ensure that certain group spread ratings were not artificially suppressed as may have been the case had rates been calculated.

(9) proportional presence in Makumba's vicinity for each session for each individual and age-sex class were calculated from hourly roll calls; justification is the same as in points (7) and (8).

(10) if the recorder collected data during both an afternoon and morning session of the same day, the same rain and temperature rating was associated to each session since temperature and rainfall were recorded on a daily basis only.

(11) nesting data were analysed ungrouped for the most part; where grouping was necessary, justification is provided in the relevant chapters.

(12) silverback location in his neighbour group and in the entire group, and the presence of individuals within 6-10 meters of the silverback were not analysed by session; thus grouping was not necessary.

(13) in some analyses, data were also grouped into time blocks to analyse differences throughout the day. Time blocks were equally divided into three hour intervals based on the time of day when scans started and finished into (a) early morning 0600–0900, (b) late morning 0901–1200, (c) early afternoon 1201 – 1500, and (d) late afternoon 1501–1800.

2.3.2 Analytical Tests

All statistical analyses were conducted using the SPSS statistical package, version 16 and PASW 18. Probabilities were two-tailed and considered significant when $p < 0.05$. The main tests used throughout the thesis were:

Logistic Regressions

As many variables were categorical or nominal, this test proved extremely effective as I was still able to model data and control for the potential influences of biasing factors. Forward stepwise logistic regressions were used throughout, as there was no *a priori* knowledge to describe which factors may predict or affect the outcome variable. As this test does not require normalized data, all analysis was conducted on non-transformed data. Correlation matrices of all potential variables were calculated and any highly correlated ($r > 0.800$) predictors were excluded from the analysis. Additionally multicollinearity tests were carried out by running linear regressions, and outliers found in the residual tests were biologically significant and thus were not excluded from the analysis [Field, 2005]. Nagelkerke R^2 is reported for all logistic regressions as they are corrected versions of the Cox & Snell R^2 measures [Nagelkerke, 1991].

Simple Linear and Linear Multiple Regressions

For any quantitative, continuous and unbounded variables, this test proved very useful since as above, I was able to model data and control for the potential influences of biasing factors. Outcome variables were normalised using square root or log transformations where necessary. Forward stepwise regressions were used for the same reasons as above.. Again only forward stepwise linear multiple regressions are reported in the thesis. Correlation matrices of all potential variables were calculated and any highly correlated ($r > 0.800$) predictors were excluded from the analysis. Additionally multicollinearity tests were carried out, and although data were noted as being statistically independent (Section 2.3.5), Durbin-Watson tests confirmed lack of autocorrelation. Any outliers found in the residual tests were biologically significant and thus were not excluded from the analysis. Heteroscedasticity and linearity assumptions were checked by plotting standardised residuals. Adjusted R^2 values are reported [Field, 2005].

Bivariate (Pearson's and Spearman's) and Partial Correlations

Spearman's correlations were used on non-normally distributed, untransformed data. Pearson's correlations were used on normally distributed data. If additional control variables were necessary, partial correlations were used and data were normalised (if necessary) using square root or log transformations [Field, 2005].

Hierarchical ANOVAS and ANCOVAS

For continuous or nominal/interval variables with categorical factors (often more than two categories), this test proved useful for the same reasons listed in points (1) and (2). Variables were normalised using square root or log transformations where necessary. Where variances were unequal, Games-Howell post hoc tests were reported; where variances were equal, Hochberg's post hoc tests were reported [Field, 2005].

Chi Square Tests

Where modelling was not necessary or where categorical data could not fit into logistic regression models, chi square tests were used. When categories were not assumed to be equal, expected values were calculated and the calculation procedure was justified in each relevant analyses. Pearson chi square results are reported. In all but a few cases, expected frequencies greater than five occurred in less than 20% of cells, where no expected frequencies below one occurred [Field, 2005]. Some analyses in Chapter 3 suffered from small sample sizes, thus expected frequencies less than five did occur in more than 20% of cells. Results for these analyses are noted in the appropriate sections and should be interpreted with caution.

2.3.3 Power of Design

In behavioural studies, power is often highly variable and can be a misleading way to test the accuracy of data analyses. This is because one rare event may have long-term outcomes which are therefore statistically impossible to assess, while constant sampling for common events may provide the illusion of high power as well as high precision. Like many behavioural studies, the power of tests in this study ranged from 75% to 95%, since in some cases, there could be a maximum of 43 predictor variables to explain outcomes for a sample size of less than 200. While the power of the test will likely be lower for logistical regressions, a low power design simply indicates a high probability of encountering a type II error during analyses; not finding a significant result when there really is one. Thus, where results are significant, power analyses were redundant. However, the possibility (although a generally low possibility) of encountering a type II error remains in some analyses.

2.3.4 Graphing

Error bars of +/- 1 standard error of the mean are represented on graphs (apart from percentage graphs and graphs based on frequencies or counts). Even when nonparametric statistics were used, I often plotted means so as to reduce the visual confound of many zeros. Where clearer visual representation was necessary, error bars of +/- 2 standard error of the mean were used.

2.3.5 Sampling Independence

In order to minimize autocorrelation between successive samples of behaviour, certain data categories were analysed using a cumulative rate of change plot, as described in in Martin & Bateson [1986] and Slater [1973]. As it is not feasible to assess dependence in each and every data category, only certain more 'important' and highly used categories were examined here. Since the silverback was the focus of the study and his behaviour was likely to affect group behaviour and vice versa, Makumba's activity budget was analysed to ensure there were no 'overall' autocorrelation issues. The other categories were analysed because they were often used as outcome or dependent variables in analyses. Smell data independence sampling is

specific to Chapter 6 only. March-April were chosen as the baseline subset tested in the following analyses as these appeared to represent relatively 'baseline' months, which were generally low in interunit encounters. Running independence tests on the entire year's data would not be useful since this would mask important shifts in behaviour that need to be examined. The first major break in slope of the cumulative rate of change plots was designated as the point at which behaviours became statistically independent [i.e. Martin & Bateson, 1986; Slater, 1973]. While in some cases, secondary or tertiary breaks may have been larger than the first break in slope, I chose to use the first break because choosing secondary or tertiary breaks would have meant the deletion of a large amount of data, which would result in an inability to analyse results. The loss of significant numbers of interesting or important observations in order to achieve a spurious level of statistical "independence" seemed counterproductive. Furthermore, I was interested in the temporal sequence of behavioural events which would have been lost by the elimination of all autocorrelation. The goal of this exercise was not to achieve complete and perfect independence, which in the study of behaviour is never possible, but to ensure that data samples were robust enough for statistical analyses. The first break in slope of the cumulative plots below (Figure 2.7 - 2.11) illustrates that scans recorded a minimum of ten minutes apart from each other can be considered independent and can all be used in analyses. Smell data collection was essentially a continuous data set of no fewer than five minutes between each smell recording (see Chapter 6 for details). The smell cumulative rate of change plot indicates that smells recorded a minimum of five minutes apart from each other can be considered independent and were therefore all used in analyses (Figure 2.12).

Additionally, it should be noted that the mean interscan interval was 16 minutes, which is greater than the minimum 10 minute separation between behavioural scans. The mean intersmell interval was 12 minutes, which again is greater than the minimum five minute separation between smell scans.

Figure 2.7 Cumulative Rate of Change Plot in Silverback Activity Budget

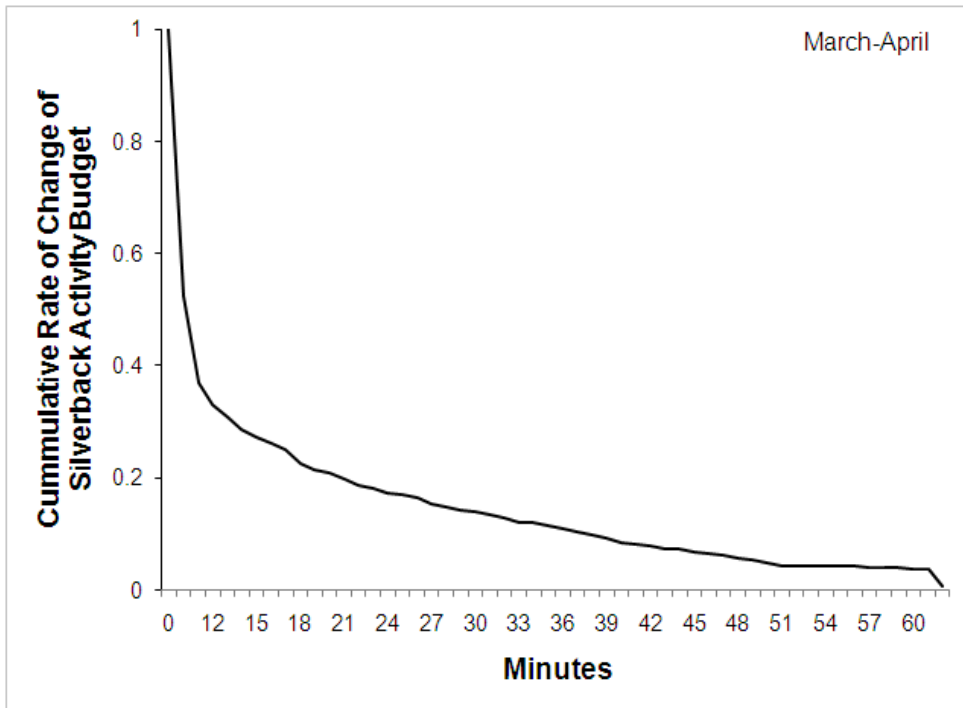


Figure 2.8 Cumulative Rate of Change Plot in Silverback Location in His Group of Neighbours (within 5m)

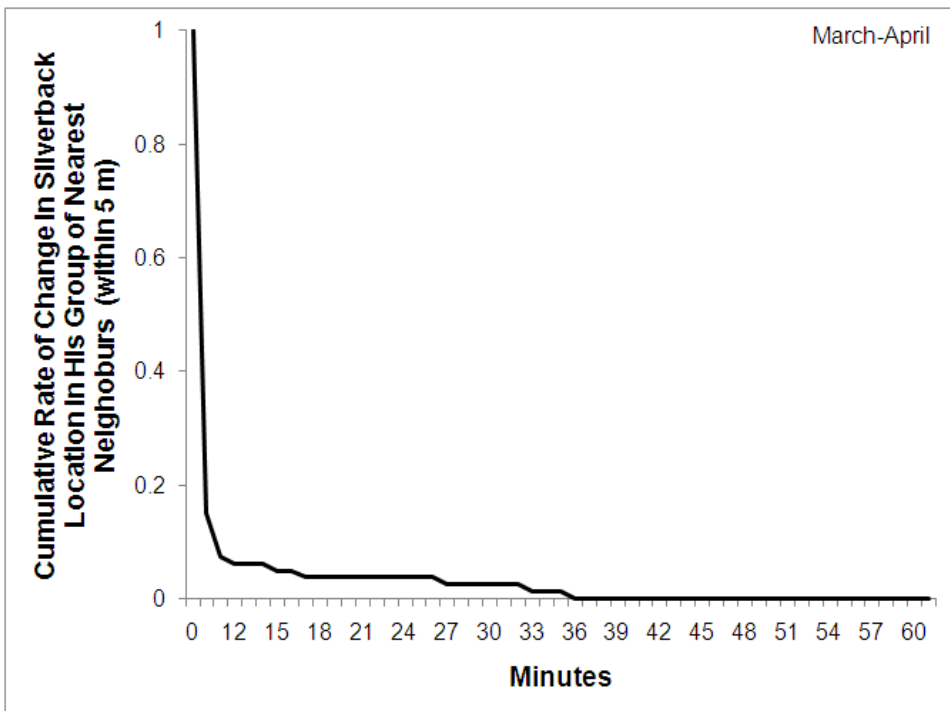


Figure 2.9 Cumulative Rate of Change Plot in Silverback Location within the Entire Group

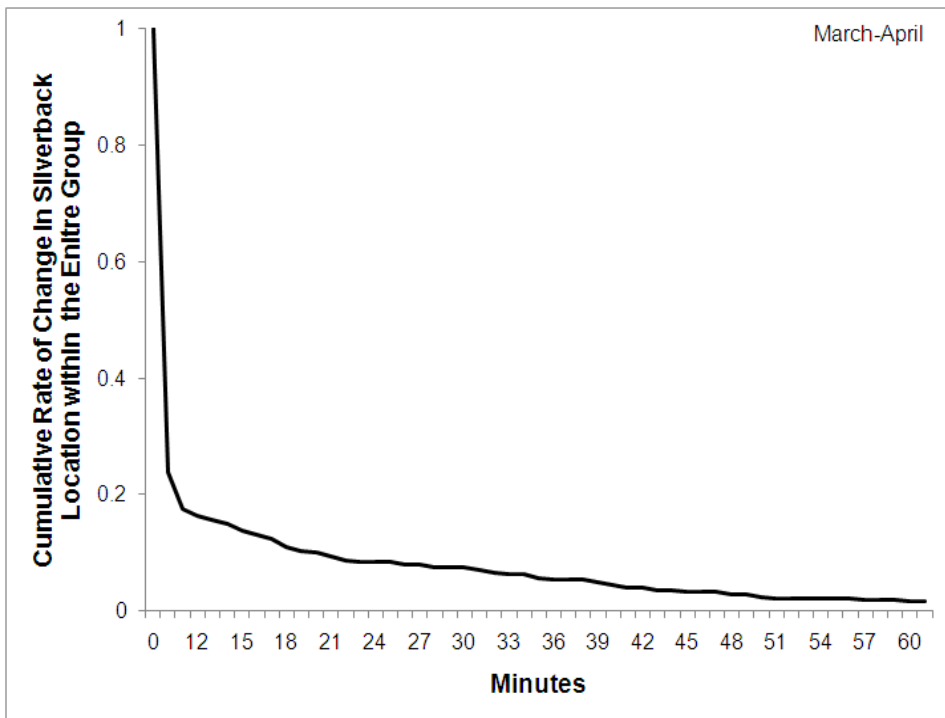


Figure 2.10 Cumulative Rate of Change Plot in Group Spread

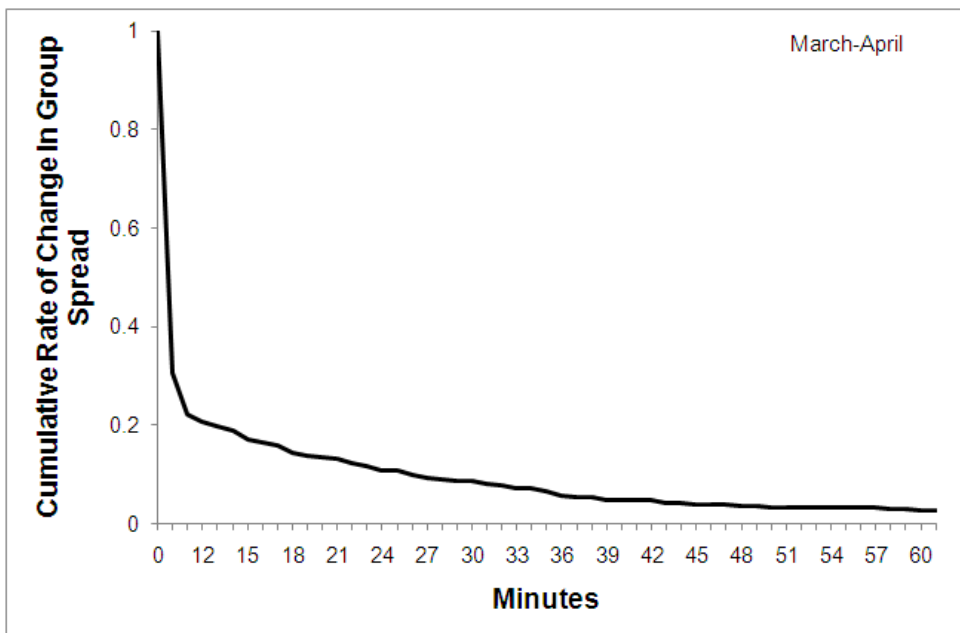


Figure 2.11 Cumulative Rate of Change Plot in Numbers of Neighbours to the Silverback (within 5m)

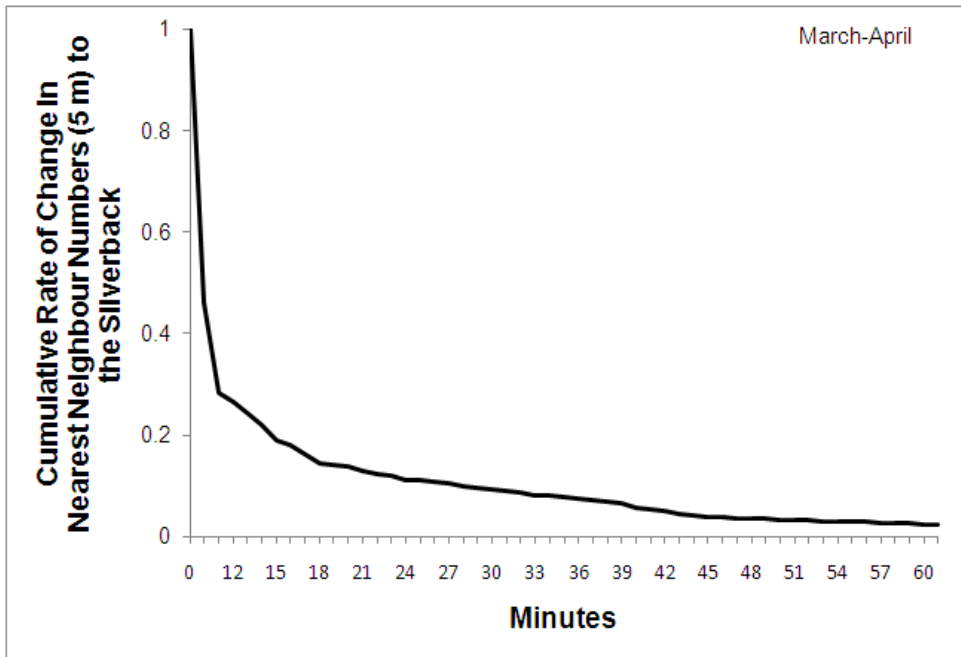
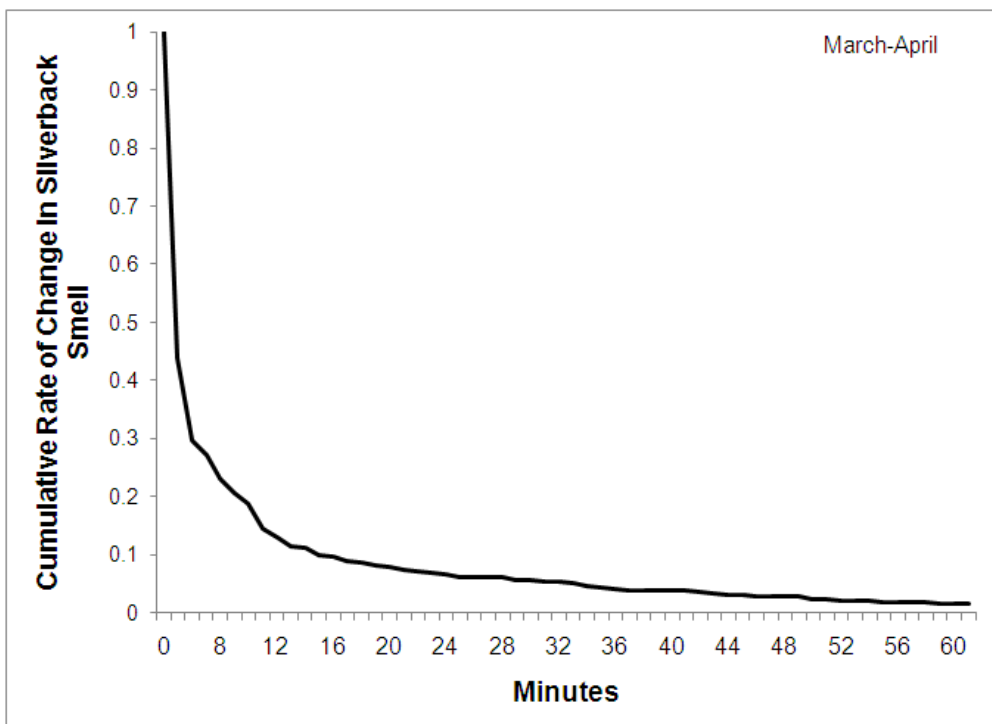


Figure 2.12 Cumulative Rate of Change in Smell^a



^aNote that this is based on a minimum of five minutes between each smell recording

2.4 DATA COLLECTION TOTALS, MAKUMBA GROUP DIET & ACTIVITY

2.4.1 Monthly Data Collection Totals

Table 2.5 summarises the total number of observation sessions per month.

Table 2.5 Morning and Afternoon Observation Sessions per Month

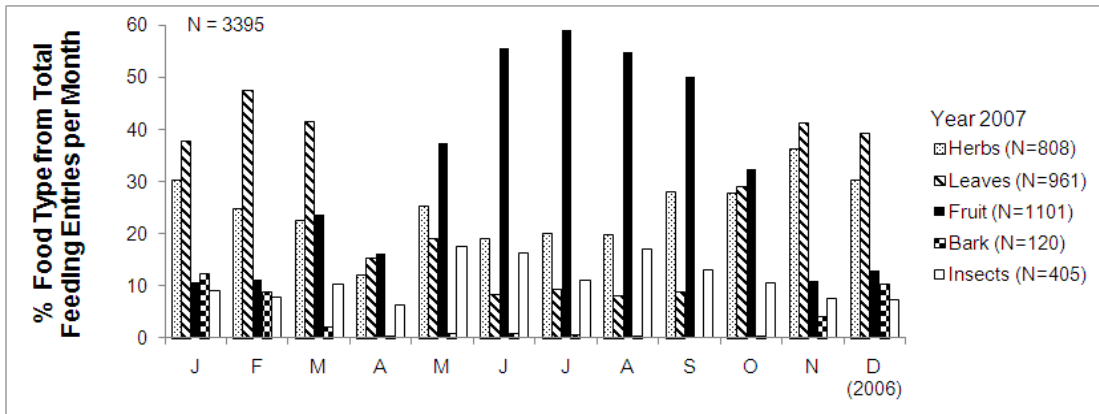
| Month | # of Morning Sessions | # of Afternoon Sessions | Total # of Sessions |
|-------|-----------------------|-------------------------|---------------------|
| Jan | 15 | 10 | 25 |
| Feb | 15 | 15 | 30 |
| Mar | 12 | 8 | 20 |
| Apr | 9 | 6 | 15 |
| Ma | 13 | 6 | 19 |
| Jun | 16 | 12 | 28 |
| Jul | 17 | 18 | 35 |
| Aug | 11 | 11 | 22 |
| Sep | 10 | 14 | 24 |
| Oct | 13 | 10 | 23 |
| Nov | 15 | 13 | 28 |
| Dec | 14 | 10 | 24 |

2.4.2 Makumba Group Diet: Temporal Changes

This section is provided as a general overview and not intended to be a detailed analysis of diet. Feeding patterns were important to describe, even generally, as they potentially related to inter and intragroup dynamics that occurred in 2007. Monthly dietary changes were calculated as the proportion of food types out of all food types seen to be eaten in each month. Food types were classified as fruit, leaves, herbs, bark or insects (Figures 2.13-2.19). Fruit feeding was further described by noting the top five most fed on fruits per month, calculated as the proportion of fruit species seen eaten the most number of days in each month out of all fruit species seen eaten in each month (Figure 2.20). Data were analysed from Bai Hokou long term camp data, collected continuously while following the group. Plants were identified with the expertise of the BaAka and with the help of guides produced from previous botanical work done

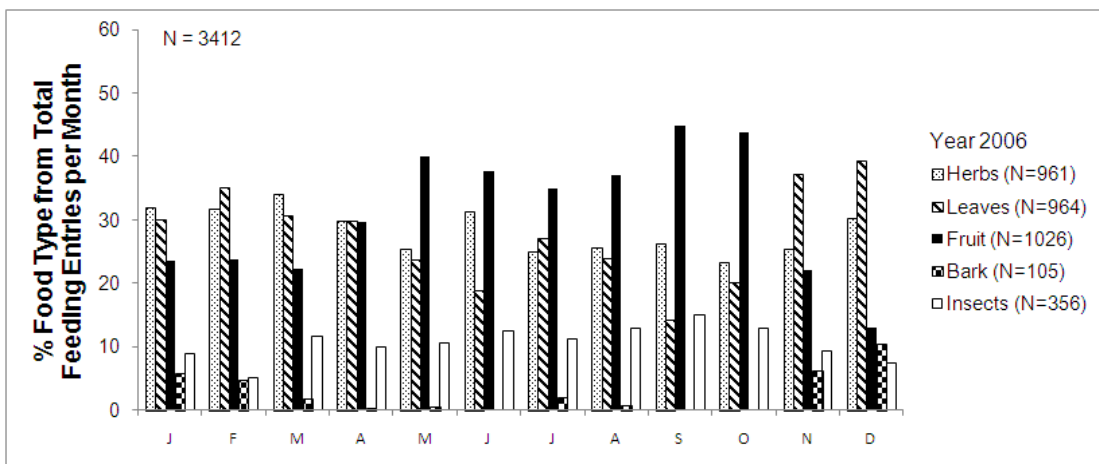
in the region. A food was marked as eaten if a minimum of one individual was observed feeding on it or if fresh feeding traces were seen. Since this does not take into account the 'amount' of fruit eaten on a given day, such analysis is only meant to be a broad indicator of feeding patterns. For more detailed analysis of the Makumba group foraging strategies, refer to Masi [2007].

Figure 2.13 Makumba Group Monthly Diet Changes by Food Category in 2007



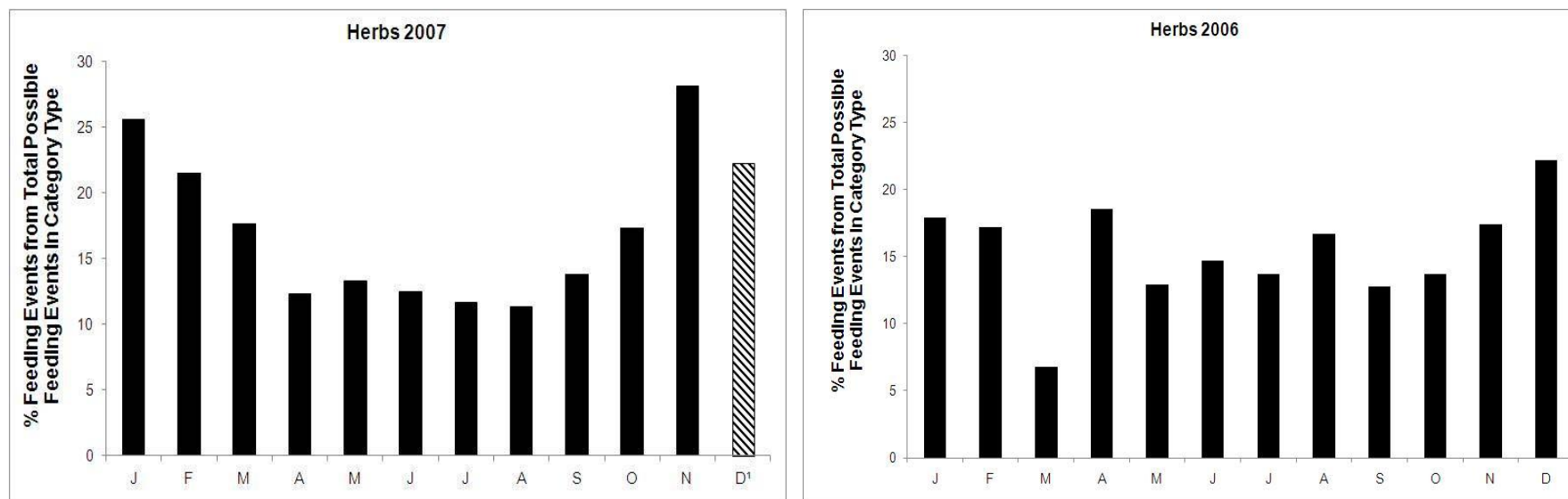
N refers to the total number of feeding events recorded in 2007(Section 2.4.2) where N in each food category type refers to the total number of feeding events recorded across each category in 2007. December 2007 data are unavailable; December 2006 is substituted here for reference only (December 2006 not included in total N for year 2007)

Figure 2.14 Makumba Group Monthly Diet Changes by Food Category in 2006



N refers to the total number of feeding events recorded in 2007(Section 2.4.2) where N in each food category type refers to the total number of feeding events recorded across each category in 2006.

Figure 2.15 Makumba Group Herb Feeding Patterns 2006-2007



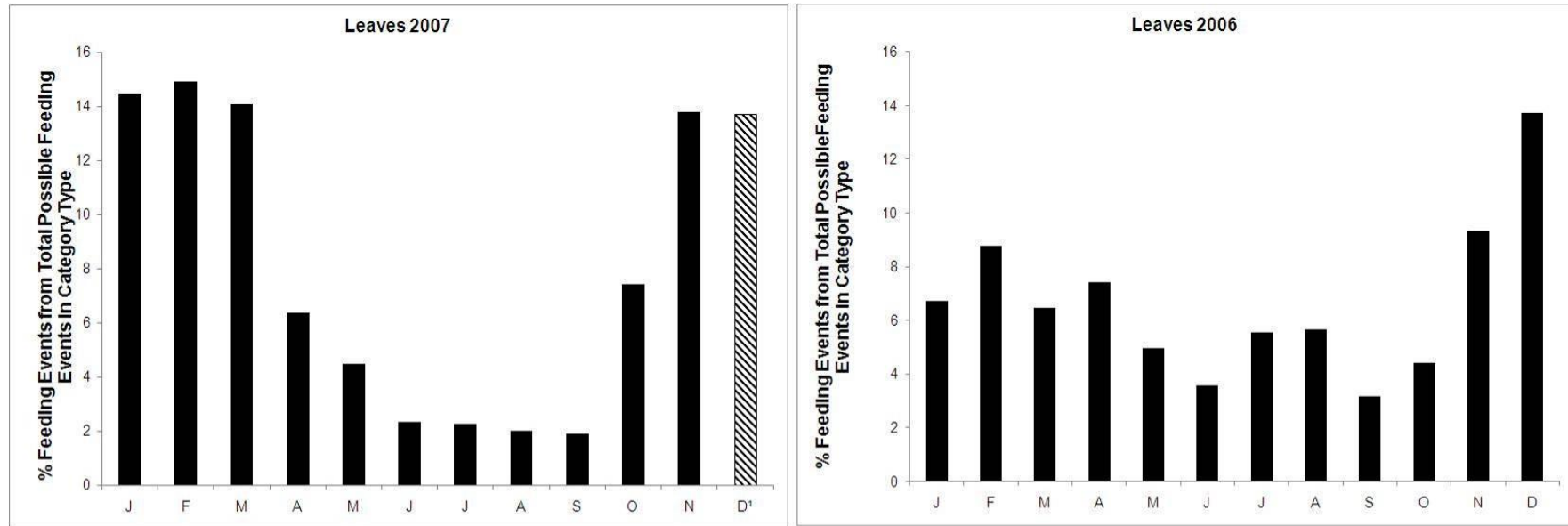
¹Represents December 2006 for reference only; December 2007 feeding data are unavailable

Total recorded feeding events (RE) and total possible feeding events (TPE) in 2007 is: Jan N =143/558; Feb N = 79/368; Mar N = 93/527; Apr N = 57/464; May N = 70/527; Jun N = 60/480; Jul N = 56/480; Aug N= 49/432; Sep N = 66/480; Oct N = 86/496; Nov N = 135/480.

RE/TPE in 2006 is: Jan N =83/464; Feb N = 82/476; Mar N = 82/1209; Apr N = 89/480; May N = 60/464; Jun N = 73/496; Jul N = 68/496 Aug N= 83/496; Sep N = 61/476; Oct N = 81/496; Nov N = 81/464, Dec N = 131/589.

Total possible feeding events is defined as the total number of times a gorilla had the opportunity to feed on each herb species recorded in the feeding log in each month

Figure 2.16 Makumba Group Leaf Feeding Patterns in 2006-2007



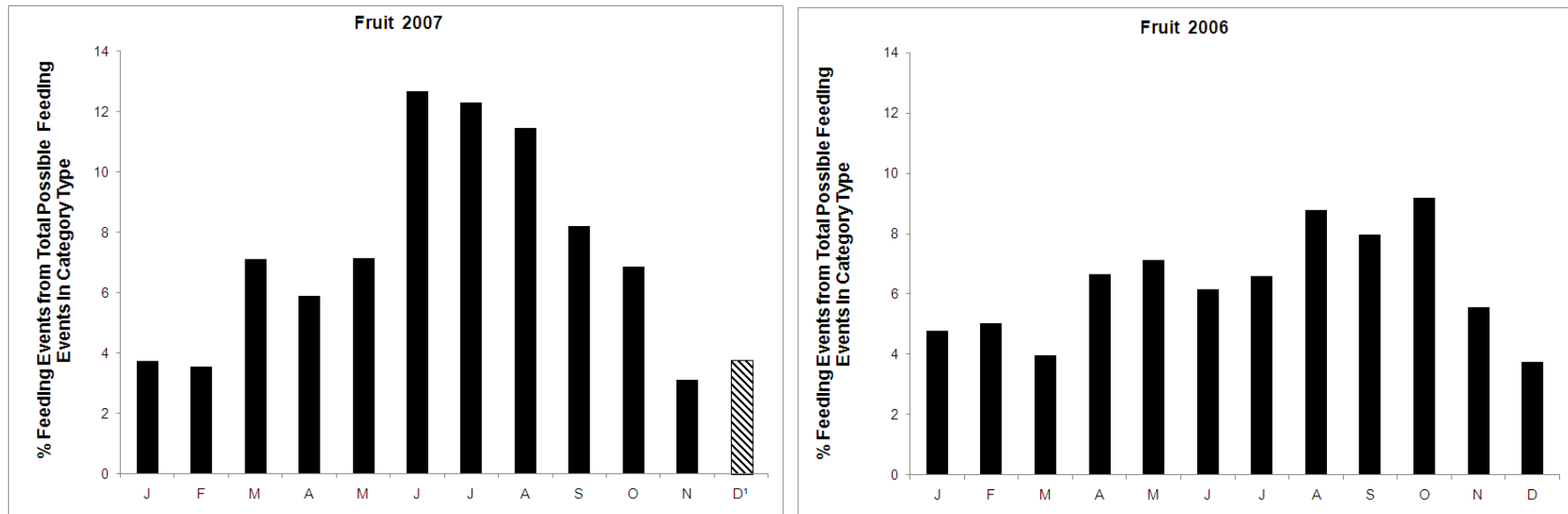
¹Represents December 2006 for reference only; December 2007 feeding data are unavailable

Total recorded feeding events (RE) and total possible feeding events (TPE) in 2007 is: Jan N = 179/1240; Feb N = 151/1012; Mar N = 170/1209; Apr N = 72/1131; May N = 53/1178; Jun N = 26/1110; Jul N = 26/1140; Aug N = 20/999; Sep N = 21/1110; Oct N = 90/1209; Nov N = 153/1110.

RE/TPE in 2006 is: Jan N = 78/1160; Feb N = 91/1036; Mar N = 74/1147; Apr N = 89/1200; May N = 56/1131; Jun N = 44/1230; Jul N = 74/1333 Aug N = 77/1364; Sep N = 33/1036; Oct N = 59/1333; Nov N = 119/1276, Dec N = 170/1230.

Total possible feeding events is defined as the total number of times a gorilla had the opportunity to feed on each leaf species recorded in the feeding log in each month

Figure 2.17 Makumba Group Fruit Feeding Patterns in 2006-2007

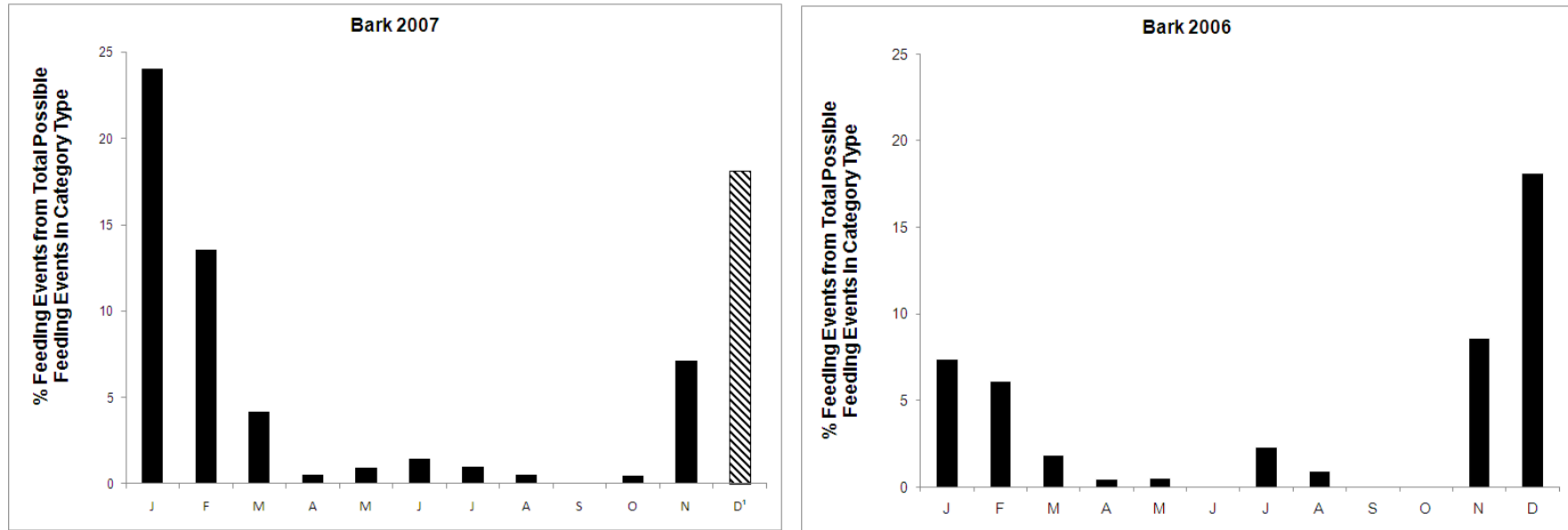


¹Represents December 2006 for reference only; December 2007 feeding data are missing

Total recorded feeding events (RE) and total possible feeding events (TPE) in 2007 is: Jan N = 51/1364; Feb N = 36/1012; Mar N = 97/1364; Apr N = 77/1305; May N = 104/1457; Jun N = 175/1380; Jul N = 166/1350; Aug N = 136/1188; Sep N = 118/1440; Oct N = 100/1457; Nov N = 41/1320. RE/TPE in 2006 is: Jan N = 61/1276; Feb N = 62/1232; Mar N = 54/1364; Apr N = 90/1350; May N = 95/1334; Jun N = 88/1426; Jul N = 96/1457 Aug N = 120/1364; Sep N = 105/1316; Oct N = 128/1395; Nov N = 71/1276, Dec N = 56/1488.

Total possible feeding events is defined as the total number of times a gorilla had the opportunity to feed on each fruit species recorded in the feeding log in each month

Figure 2.18 Makumba Bark Feeding Patterns in 2006-2007

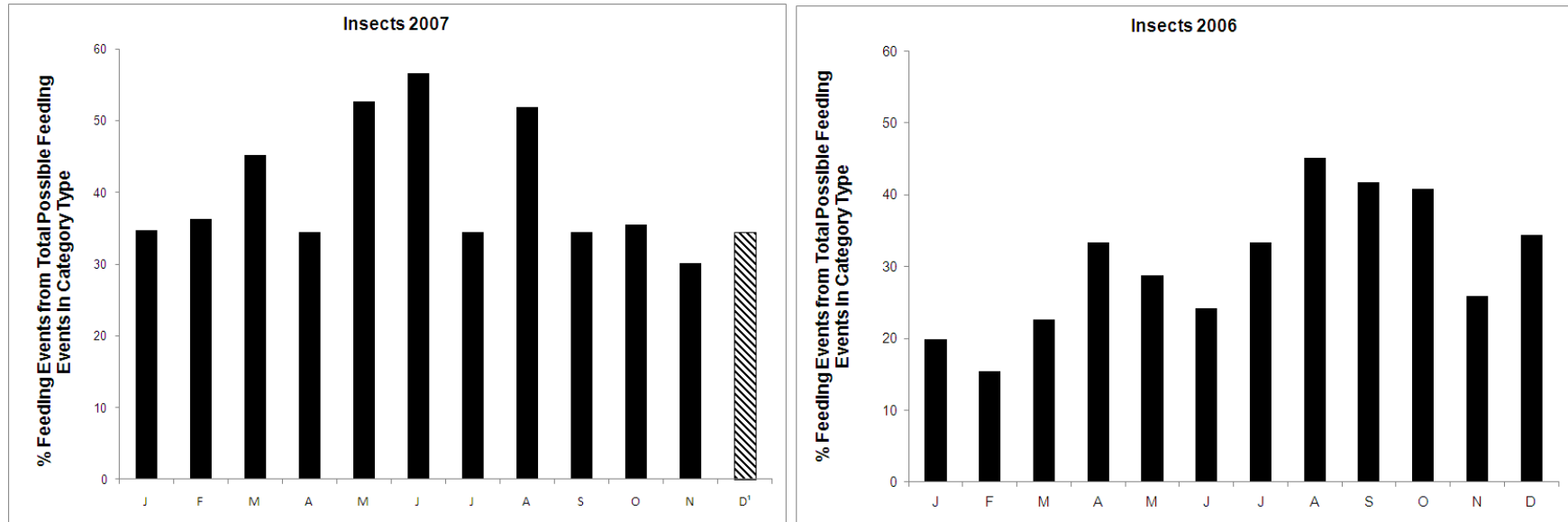


¹Represents December 2006 for reference only; December 2007 feeding data are missing

Total recorded feeding events (RE) and total possible feeding events (TPE) in 2007 is: Jan N = 58/241; Feb N = 28/207; Mar N = 9/217; Apr N = 1/203; May N = 2/217; Jun N = 2/210; Jul N = 2/210; Aug N = 1/189; Sep N = 0/210; Oct N = 1/217; Nov N = 15/210. RE/TPE in 2006 is: Jan N = 15/203; Feb N = 12/196; Mar N = 4/217; Apr N = 1/210; May N = 1/203; Jun N = 0/210; Jul N = 5/217; Aug N = 2/217; Sep N = 0/196; Oct N = 0/217; Nov N = 20/232, Dec N = 45/248.

Total possible feeding events is defined as the total number of times a gorilla had the opportunity to feed on each bark species recorded in the feeding log in each month

Figure 2.19 Makumba Insect Feeding Patterns in 2006-2007



¹Represents December 2006 for reference only; December 2007 feeding data are missing

Total recorded feeding events (RE) and total possible feeding events (TPE) in 2007 is: Jan N =43/124; Feb N = 25/69; Mar N = 42/93; Apr N = 30/87; May N = 49/93; Jun N = 51/90; Jul N = 31/90; Aug N= 42/81; Sep N = 31/90; Oct N = 33/93; Nov N = 28/90. RE/TPE in 2006 is: Jan N =23/116; Feb N = 13/84; Mar N = 28/124; Apr N = 30/90; May N = 25/87; Jun N = 29/120; Jul N = 31/93 Aug N= 42/93; Sep N = 35/84; Oct N = 38/93; Nov N = 30/116, Dec N = 32/93.

Total possible feeding events is defined as the total number of times a gorilla had the opportunity to feed on each insect species recorded in the feeding log in each month

Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 (UK = unknown)

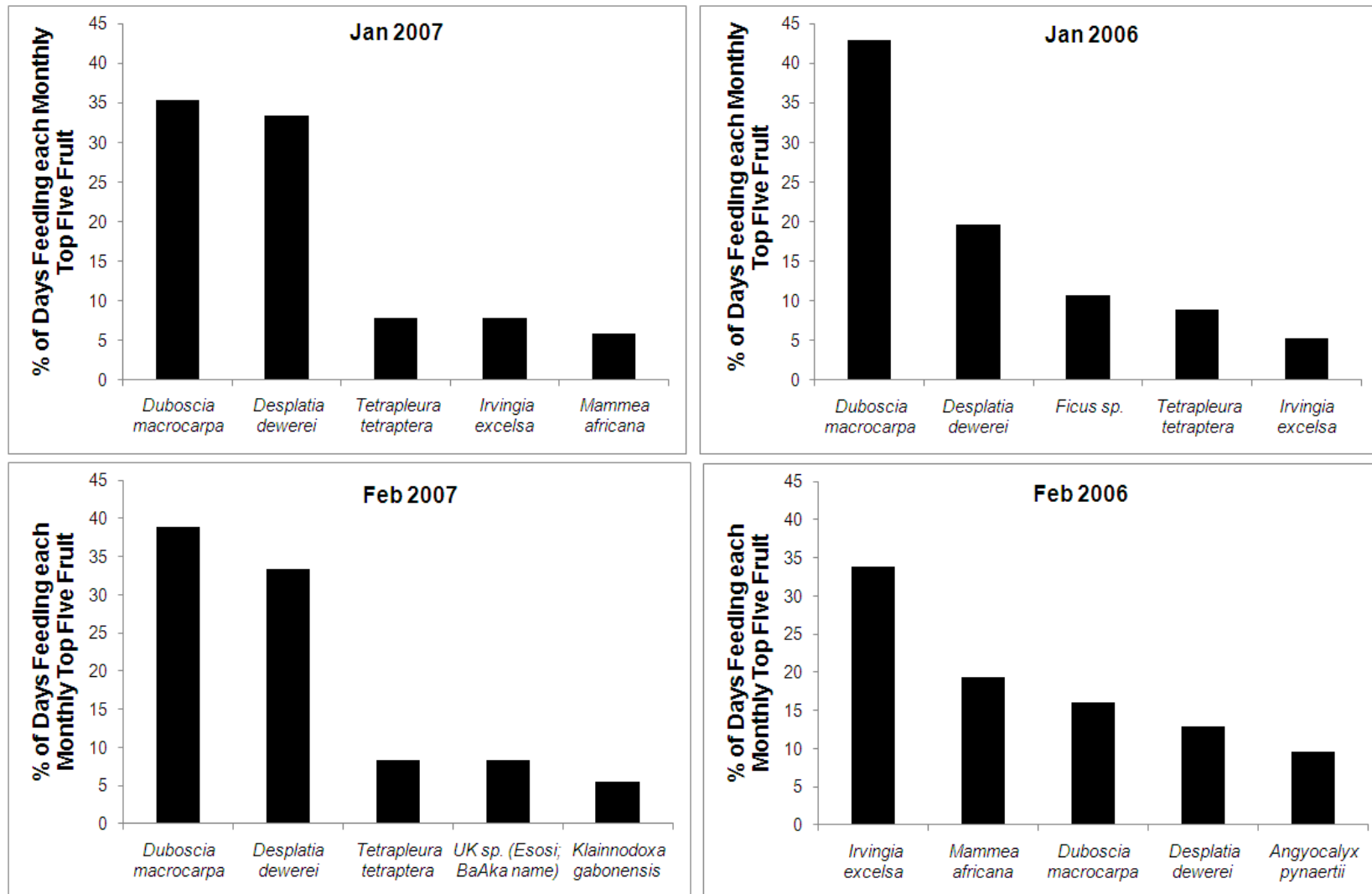


Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 Continued (UK = unknown)

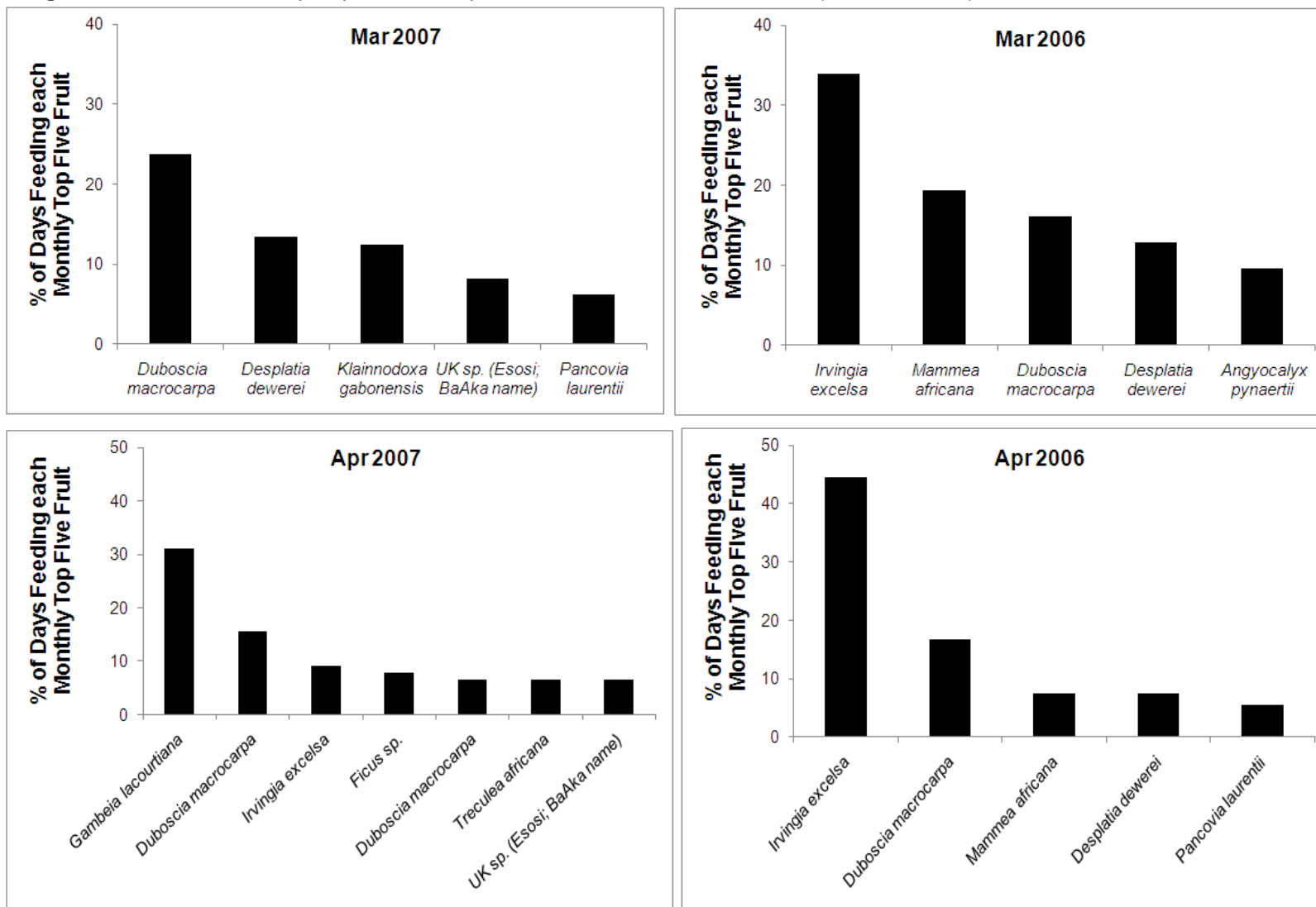


Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 Continued (UK = unknown)

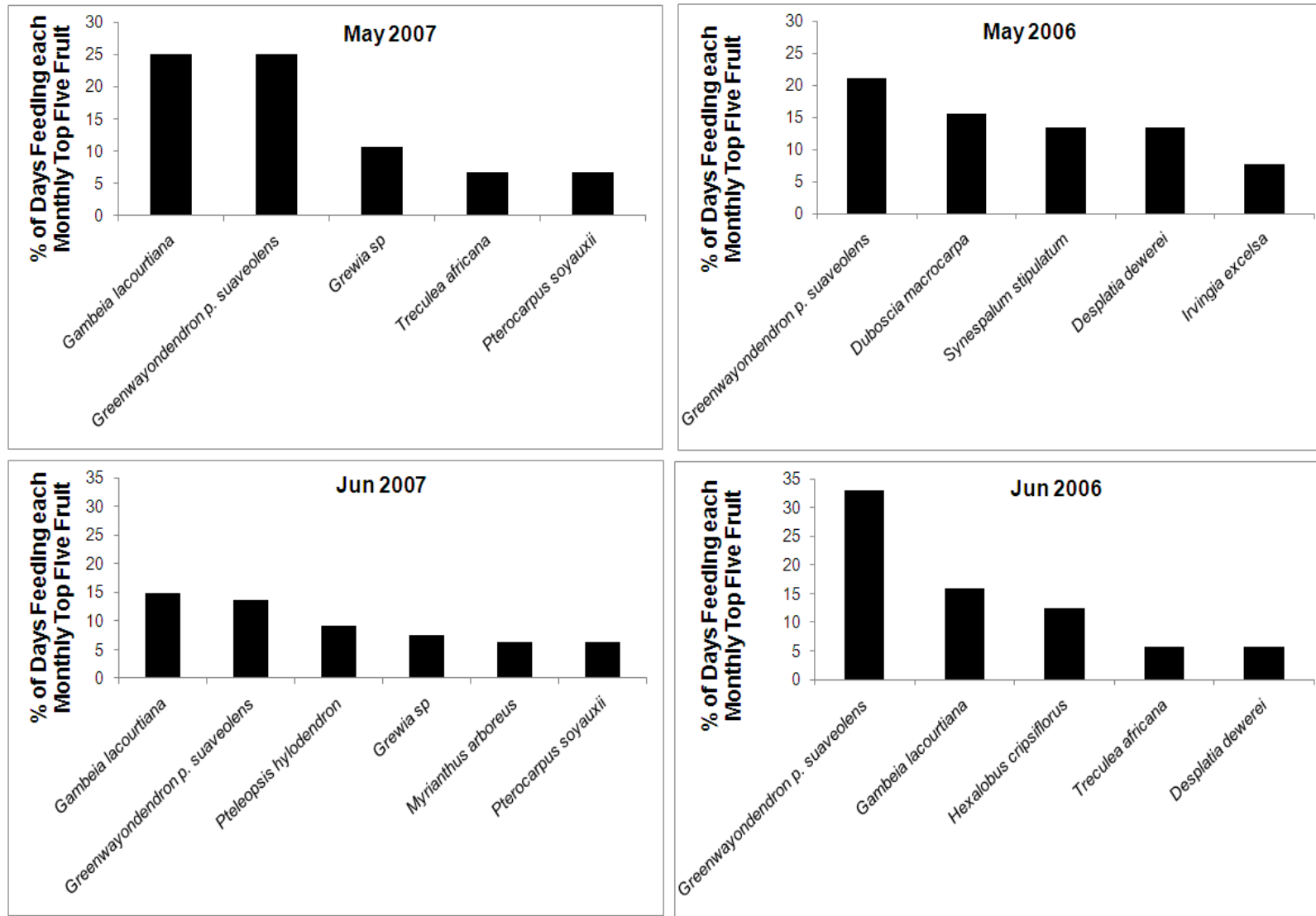


Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 Continued (UK = unknown)

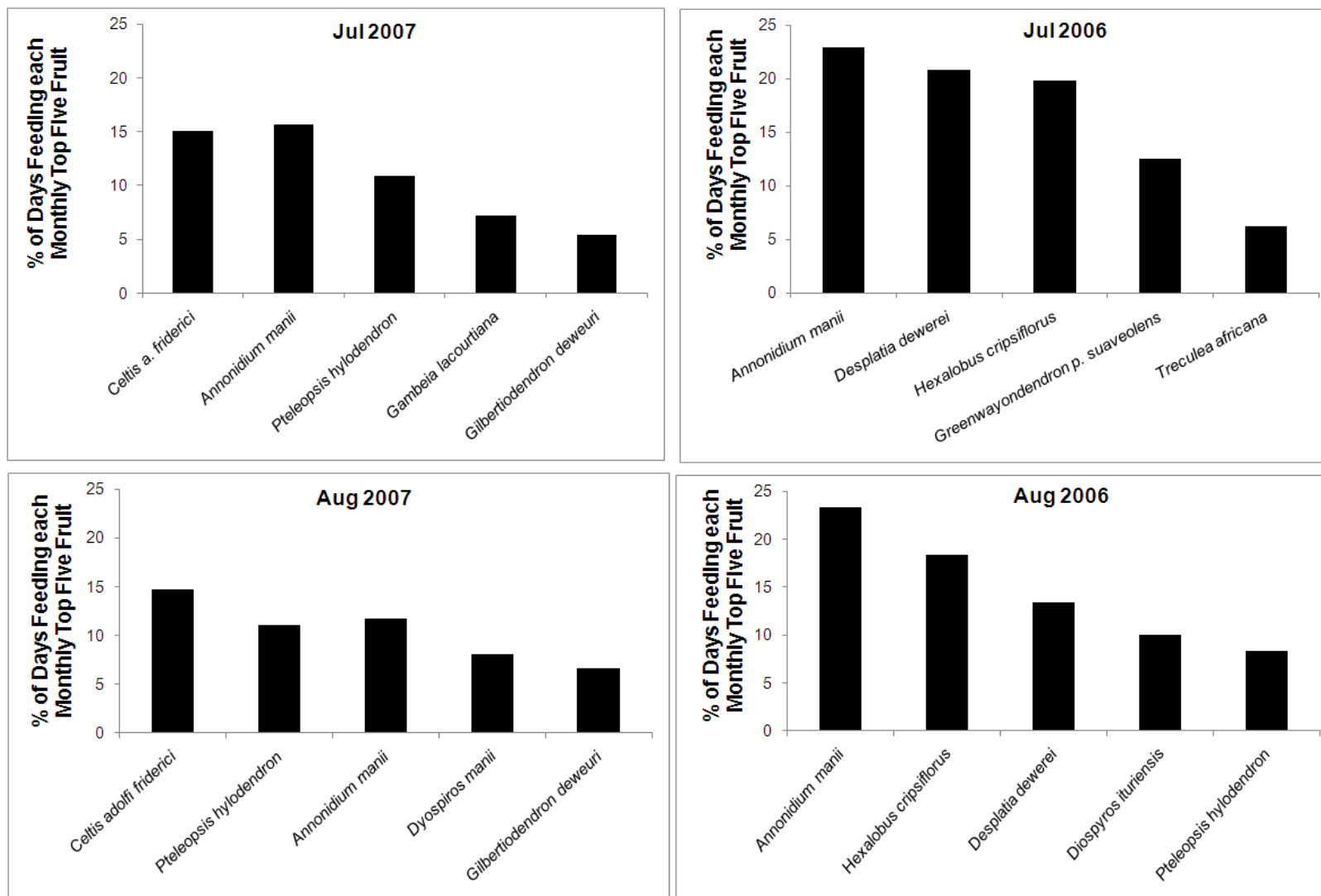


Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 Continued (UK = unknown)

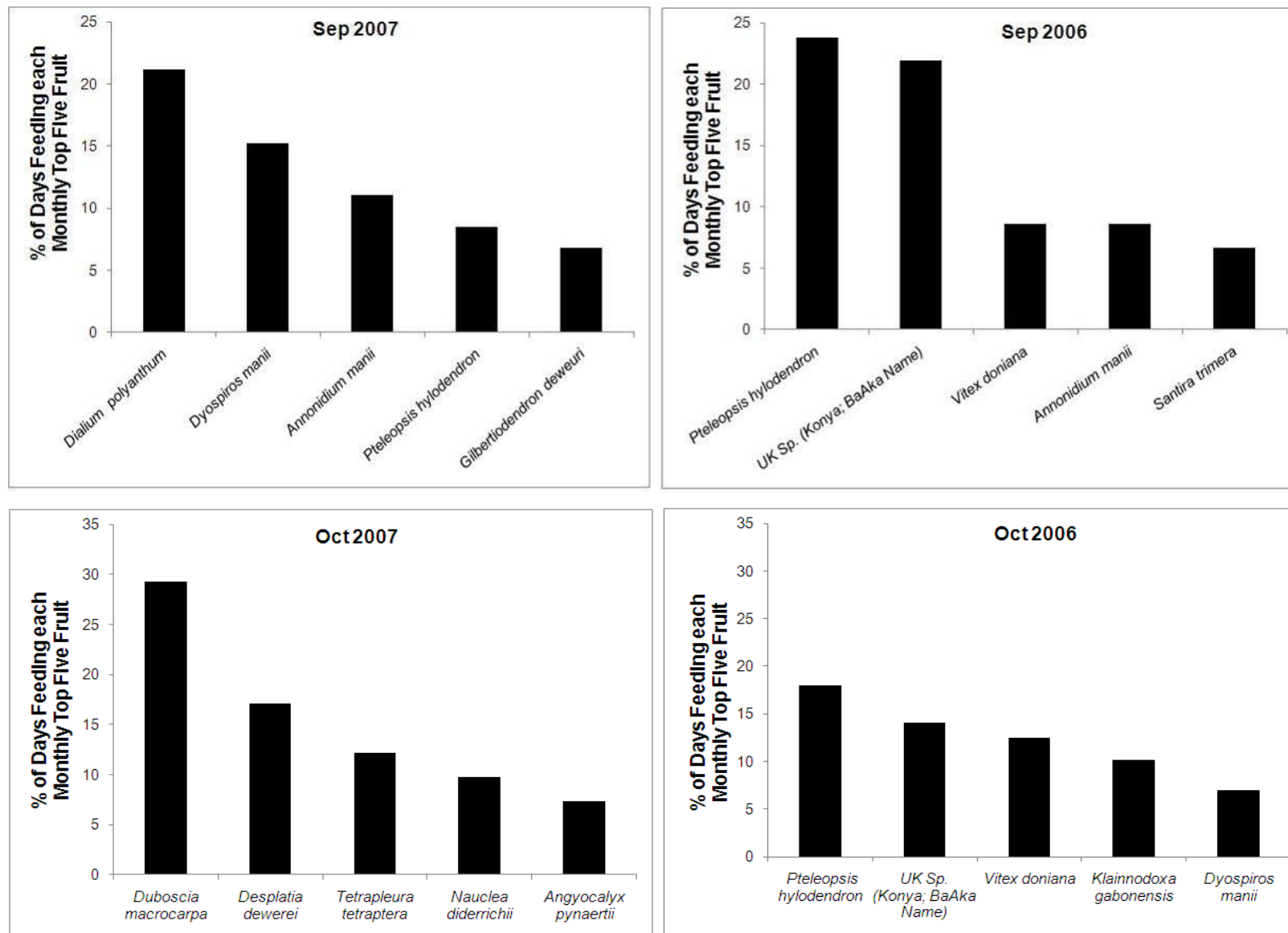
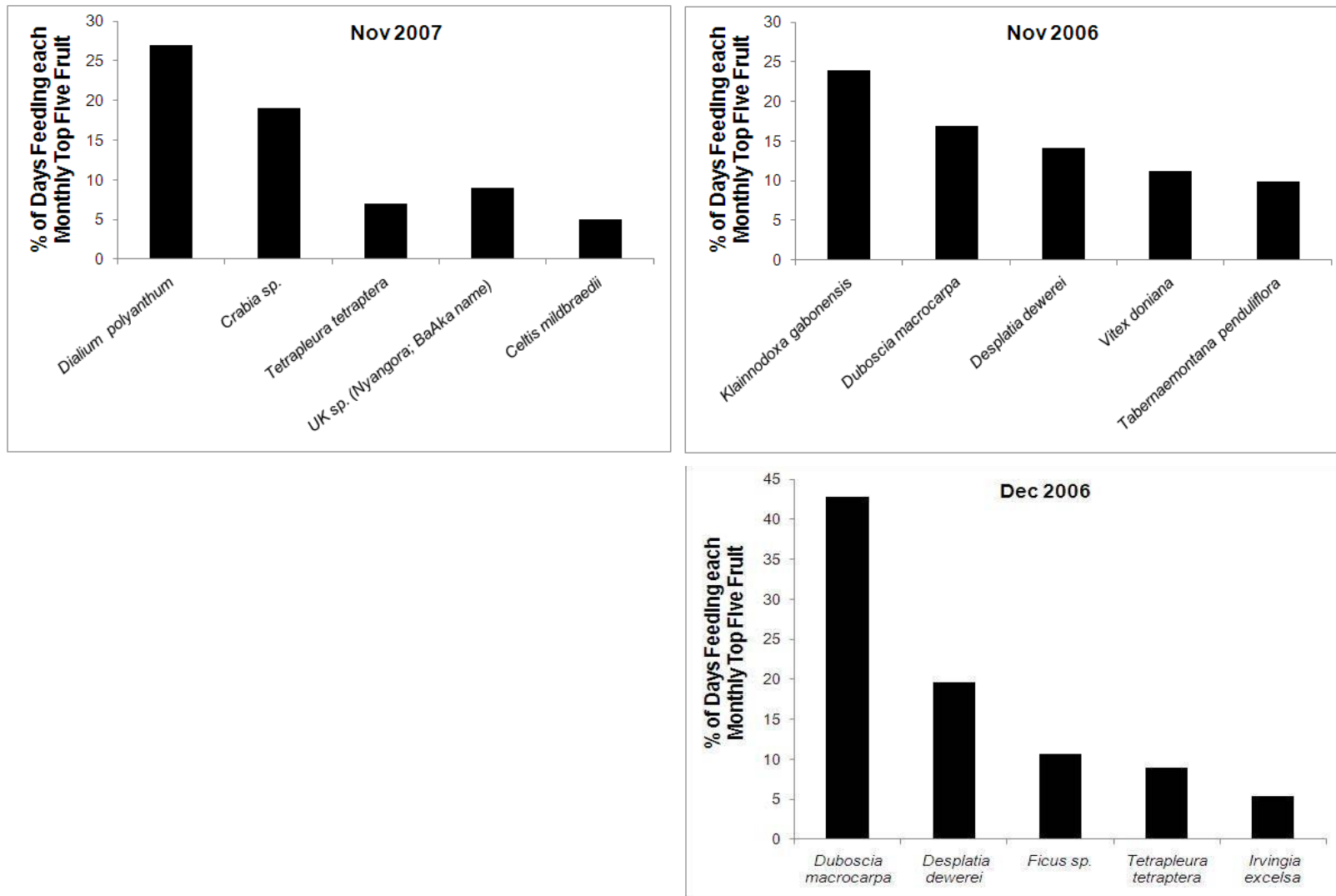


Figure 2.20 Makumba Group Top Five Fruits per Month in 2006-2007 Continued (UK = unknown)



2.4.3 Makumba Group Activity Budget

Note that this section, like feeding patterns, is provided as a general overview and not intended to be a detailed analysis. As with diet, activity budgets were also important to briefly describe, as they may have related to some inter and intragroup dynamics that occurred in 2007. Group activity was defined as the majority activity observed; at least two individuals other than the silverback must have been present to define the group's activity. Activities were categorised as feeding, moving (including standing; standing often represented a transitional phase) , and resting (including social), and a mixed category was added for group activities (Table 2.3). For a detailed analysis of the Makumba group activity budgets earlier in the habituation period, refer to Masi [2007]. The group spent the highest percentage of their time feeding both when the full data set was considered (Figure 2.21) and within each time block (Figure 2.23). When considering activity changes across time blocks, the group spent considerably more time feeding in the early morning, whereas the late morning and early afternoon were characterized by a high variety of activities (Figure 2.24); individuals were not acting in unison but instead they appeared to be varying their behaviour, perhaps as a result of differing foraging strategies and age class stratification. The late afternoon also suggests a preponderance of mixed activities, although time spent resting was considerably lower than in the previous time blocks (Figure 2.24). The silverback spent relatively equal time overall feeding and resting (Figure 2.22). He appeared to maintain similar patterns to those of his group in reference to activity changes across time blocks (Figures 2.25 and 2.26).

Figure 2.21 Group Activity Budget as Percentage of Scans

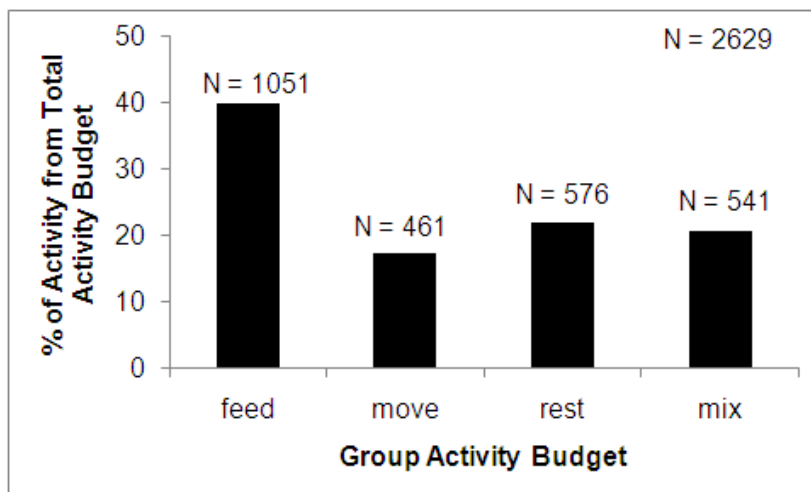


Figure 2.22 Silverback Activity Budget as Percentage of Scans

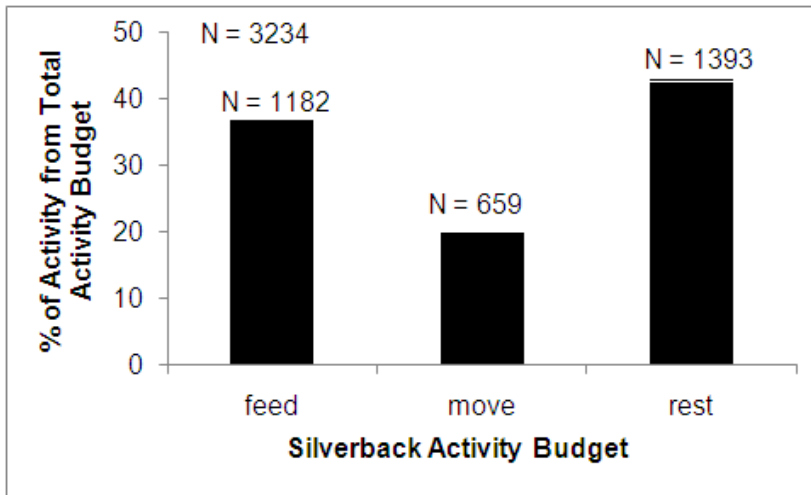


Figure 2.23 Group Activity Budget within Time Blocks

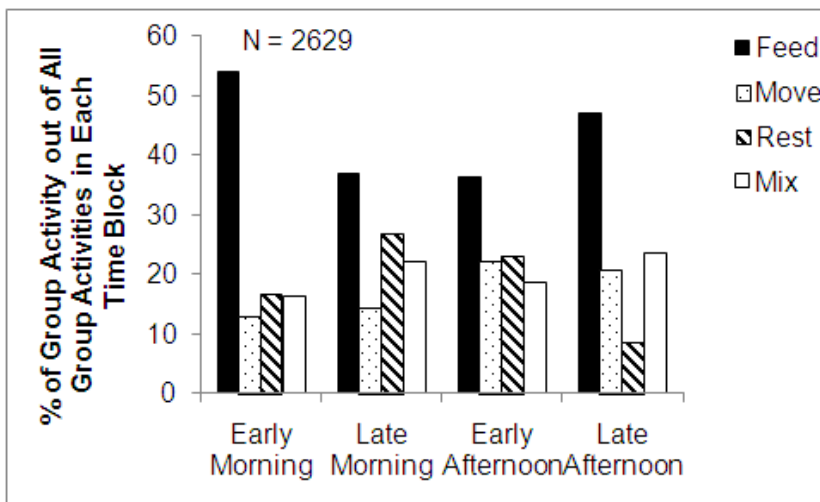
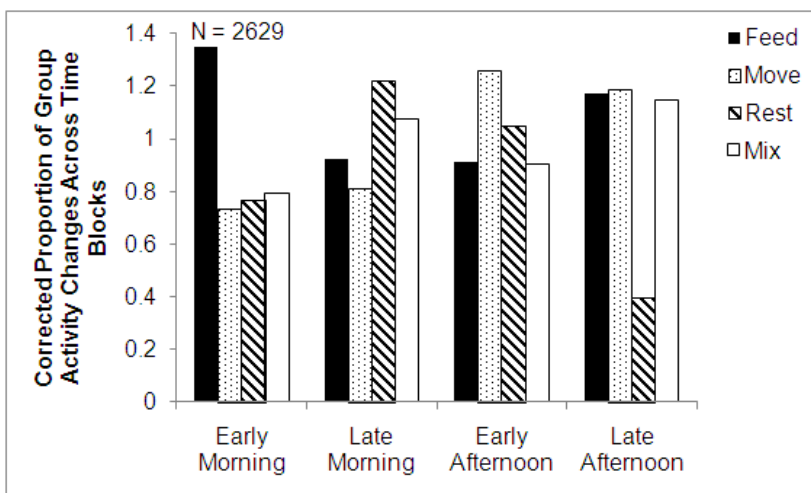


Figure 2.24 Group Activity Budget Across Time Blocks^a



^aCorrected for the percentage of scans in each activity type in relation to the distribution of scans throughout the day

Figure 2.25 Silverback Activity Budget within Time Blocks

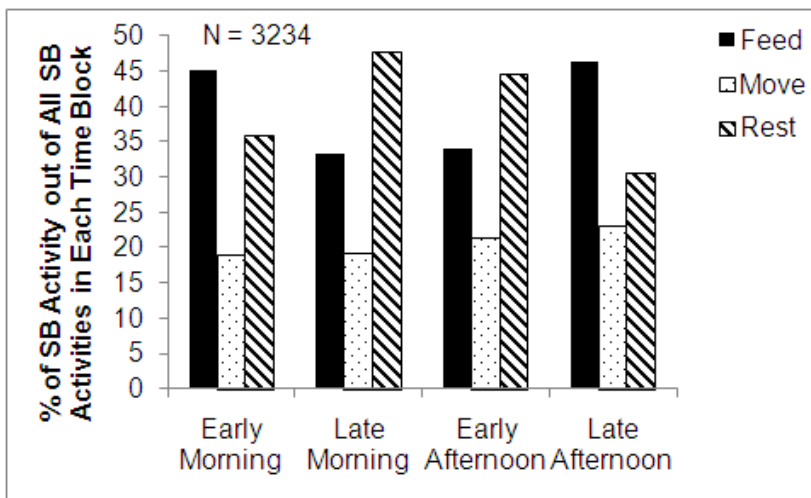
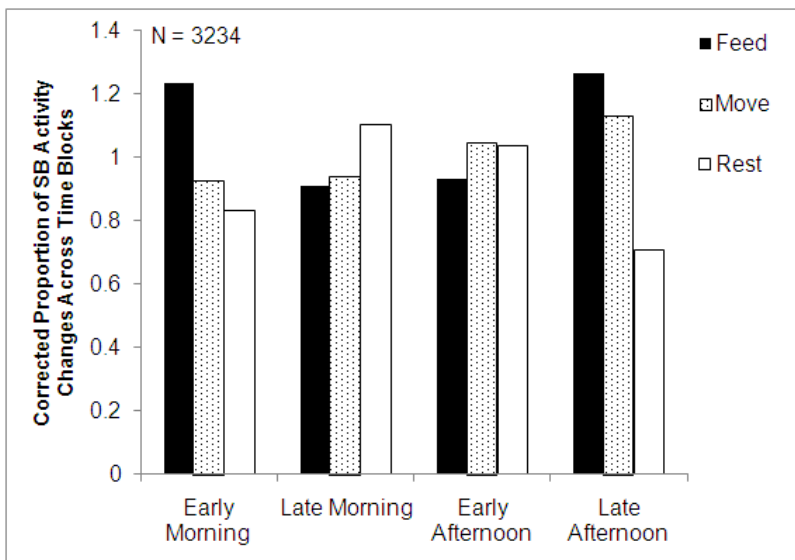


Figure 2.26 Silverback Activity Budget Across Time Blocks^a



^aCorrected for the percentage of scans in each activity type in relation to the distribution of scans throughout the day



CHAPTER 3

THE SILVERBACK & HIS GROUP



CHAPTER 3

THE SILVERBACK & HIS GROUP

3.1 ABSTRACT

Many diurnal primate groups are composed of permanent male-female associations. In mountain gorillas, the adult male assumes the control function, providing protection, leadership and mediating conflict within his group. While it seems highly likely that the risk of infanticide is a benefit of female-male associations, a silverback's role in providing overall group stability and protection from predators (i.e. humans, leopards) and other risks or disturbances (i.e. elephants) should not be underestimated. Little is known about western lowland gorilla silverback-group social and protective dynamics, particularly in forest environments. Here I provide the first detailed account of western lowland adult male-group social dynamics from a spatial and protective perspective. Makumba was found to play an active protective role within his group similar to those seen in mountain gorillas, however, Makumba still spent nearly half of his overall time alone with no neighbours within 5m. The opposite occurred in riskier bai environments, where he was more likely to have a neighbour than to be alone. Young immatures were most likely to be a neighbour to the silverback, and like mountain gorilla dominant males, he appeared to act as a "babysitter" for small groups of young juveniles and infants. This role may be particularly important for western lowland gorilla females who often forage hundreds of meters away from their leader male. Each female spent approximately the same proportion of time as a neighbour within 5m to Makumba in 2007. Females were found as neighbours to the silverback as a function of their degree of risk. Makumba spent more time in the middle of his neighbour group as interaction level increased and as the number of females and older immatures increased. As the entire group dispersed, Makumba was more likely to remain in the rear of the group, which may reflect a more protective position. During potentially risky periods and as the number of neighbours to the silverback increased, Makumba was more

likely to be nearer the front of the group, which may reflect a leading position. Makumba's nest site location suggested that he intentionally placed himself in areas where he could monitor the group's nest site and alert group members to danger or disturbance. Results suggest that Makumba has developed complex spatial strategies to cope with perceived risk in the rainforest environment.

3.2 INTRODUCTION

3.2.1 Risk, Resources and Grouping

Early models of primate sociality predicted that most diurnal groups form as a result of predation risk [Chance, 1955; Crook & Gartlan, 1966; Stewart & Harcourt, 1987] and that the distribution of resources within a habitat largely determined the social relationships between females; the 'ecological' model [Wrangham, 1980]. While these models help to explain the mechanisms behind female-bonded systems, the socioecological model adds to the framework by predicting that the social groupings exhibited by different primate species (or of the same species in different habitats) are based on a complex network of predation, ecological factors, competition, habitat saturation and infanticide avoidance [Sterck et al., 1997; van Schaik, 1989; Wrangham, 1982].

Many diurnal primate groups consist of permanent male-female associations [Lee, 1994; van Schaik, 1996]. Females are greatly affected by ecological variables due to the high cost in parental investment of offspring and slower reproductive rates (in comparison to males); as a result, their distribution is often limited by the distribution of food within their habitat. Males, whose parental investment costs are generally low, are more highly influenced by the distribution of females within their habitat than by food [Clutton-Brock, 1989; Davies, 1991; Trivers, 1972].

Within group female-female relationships are proposed to differ based on the quality and distribution of food [Sterck et al., 1997; Wrangham, 1980]. Where food is patchily available both in its quantity and quality, females develop strict dominance hierarchies where fitness gains are

made mainly through cooperation by relatives, but also by non-relatives. The cost of female dispersal in these groupings is very high, resulting in female philopatry [Chapais, 1992; Sterck et al., 1997]. Where food is abundant, the cost of forming strict female-female alliances and maintaining long standing female-female relationships often outweighs the benefits, resulting in 'non-female-bonded' or 'dispersal-egalitarian' groups with weak or absent female linear hierarchies [Sterck et al., 1997; Wrangham, 1980]. The cost of emigrating in non-female-bonded groups is low, since kin support and non-kin reciprocal support relationships are not imperative to the fitness of the dispersing individual [Sterck et al., 1997; Wrangham, 1980].

Why would females want to disperse if food is abundant where they are and competition in their current group is low? In order to maximize reproductive output or receive better protection from predation or infanticidal males, females may choose to emigrate into groups with multiple males or better male leaders [Palombit, 1999; Sterck et al., 1997; Watts, 1996, 2000; Wrangham, 1979]. This implies that male-female relations within groups, while not as comprehensively studied, are also important [Doran & McNeilage, 2001; van Schaik, 1996], particularly for non-female-bonded groups whose dispersal costs are low and thus ability to exercise greater male choice by emigrating may in many situations be high. Paternal investment in offspring can also influence male-immature relations, which could be limited only to predation and infanticide protection or could also include an active social interest in their childrens' development [Nowell, 2005; Stewart, 2001].

Certain species show great intraspecific variation (i.e. Hanuman langur; *Semnopithecus entellus*) in group social structure due to differences in habitat and food distribution [Koenig et al., 1998]. In gorilla society, groups are non-female-bonded and both males and females emigrate from their natal group (Chapter 1). Western and eastern gorillas live in different ecosystems, where food type and distribution varies significantly (Chapter 1). As a result, western and eastern group social structure and the type and quality of within group relationships may vary according to gorilla species or subspecies.

3.2.2 Mountain Gorilla Relationships

The abundant availability of food and lack of seasonality in mountain gorilla habitat (Chapter 1) has reduced the need for adult female-adult female competition, and resulted in the expression of a weak dominance hierarchy [Harcourt, 1979a, 1979b; Watts, 1985, 1994a, 1994b, 1996]. Additionally, female dispersal means that many will reside in groups with few or no close relatives [Harcourt, 1979a; Watts, 1985, 1994a, 1994b, 1997; Harcourt & Stewart, 1987, 1989; Stewart & Harcourt, 1987; although see Watts, 1994a and Yamagiwa & Kahekwa, 2001]. Nevertheless, female mountain gorillas still do compete over food enough for a dominance hierarchy to form regardless of its strength: over 90% of supplants in two Virunga groups were due to food; they spend time near and support kin more often and more intensely than non-kin; they have been shown to harass new immigrants when group size is large, and they ally to protect relatives from harm and to provide access to resources. But the distinguishing feature by comparison to many species with strong dominance hierarchies, is that mountain gorilla females do not use alliances to manipulate the status of their kin nor is there a need to compete or cooperate intensively since food is generally widespread [Harcourt, 1979a; Harcourt & Stewart, 2007a; Harcourt, 2001; Harcourt & Stewart, 1989; Stewart and Harcourt, 1987, Watts, 1985, 1988, 1994a, 1992, 1996, 1997].

Worth mentioning is Robbins et al., [2005] analysis of 30 years of mountain gorilla data, which suggests that females have a stronger dominance hierarchy than previously thought. Adult female dominance hierarchies tend to correlate with tenure within the group, and for immatures, with age [Harcourt & Stewart, 1987; Watts, 1985], although the most dominant within any gorilla group will always be the adult male [Harcourt, 1979b]. Adult females may also compete for time with their leader males [Harcourt, 1979a, 1979b]

The adult male assumes the control function, providing protection, leadership and mediating conflict within his group [Watts, 1996; Chapter 1]. He often intervenes in adult female contests, negating female-female competition to ensure that new immigrants are protected and long standing residents are appeased [de Waal, 1982; Harcourt, 1979b; Harcourt & Stewart, 2007b, Watts, 1991b, 1996]. A silverback's objective for reproductive success is to acquire and then

'retain' as many adult females as possible [Fossey, 1974, 1983; Schaller, 1963; Yamagiwa, 1986, 1987b]. By allowing competition to escalate, he risks discord amongst his group and the prospect of female emigration [Harcourt & Stewart, 1987; Watts, 1994a, 1997].

Since the adult male is responsible for providing protection and control within a group of 'generally' non-bonded females, silverback-adult female relations, unlike female-female associations, are very strong [Harcourt, 1979a, 1979b; Stewart & Harcourt, 1987; Watts, 1996]. Females are very attracted to the dominant male preferring to spend more time near him than to other females; a relationship that is amplified when females have young offspring or are sexually receptive, where females are responsible for negotiating proximity¹ [Harcourt 1979a, 1979b]. In fact, Harcourt [1979a] showed that much of female time spent together was due to a simultaneous attraction to the dominant male.

Birth can dramatically affect adult female time spent near the silverback [Harcourt, 1979b; Section 3.2.4.2]. Harcourt [1979b] noted that when compared to the 11 months pre-parturition, one female increased time near the dominant male threefold over the 10 days post-parturition. An interesting exception to Harcourt's [1979b] finding is described by Elliot [1976] who observed that a newly immigrated female was more likely to be near the dominant silverback of one group, than the only other resident female who had a 1-2 month old infant. Prior to the acquisition of the immigrant, the resident female who had just given birth spent most of her time within 5m of the leader male. While both females were equally vulnerable for different reasons, females, especially those in single male groups, may be forced to alternate close access to the silverback.

Female time spent in proximity to the dominant silverback was negatively correlated with infant age whereas infant time spent next to the dominant silverback was positively correlated with age [Harcourt, 1979a, 1979b]. Although Watts [1992, 1994a] also found strong female partiality for the leader male, he did not find a similar correlation regarding maternal proximity and infant

¹Proximity has been shown to be an accurate indicator of social relationships in gorillas [Brown, 2001].

age. It should be noted that the Watt's study group was exceptionally large for that time period, potentially making access to the silverback by other gorillas more difficult.

The risk of infanticide (afflicting 37% of infants in the Virunga population) is theorized to be the basis of the attraction between females with dependent offspring and adult males [Stewart, 2001; Watts, 1989; Chapter 4]. Harcourt [1979a, 1979b] also found that as infants matured and the mother's time near the dominant silverback decreased, infant time close to the silverback increased. Many mountain gorilla studies have shown a strong attraction to silverbacks on the part of young immatures [i.e. Elliot, 1976; Fletcher, 1994; Fossey, 1979; Schaller, 1963; Stewart, 1981]. Adult males can provide a spatial focus for immature interactions, whilst being under the protective guise of a paternal figure [Stewart, 2001]. Additionally when in proximity of leader males, immatures may: (1) gain added access to otherwise unobtainable resources by being shielded from intragroup competition; (2) develop strong bonds with the adult male or become a close ally – immature males who developed close bonds with silverbacks were more likely to stay in their natal group than disperse, and; (3) use the dominant male as a focal point, to moderate mother-offspring conflict when maternal attention is being withdrawn [Harcourt et al., 1976; Harcourt & Stewart, 1981; see review in Stewart, 2001].

In addition to receiving protection, females with infants may seek proximity to adult males so their offspring can become familiarized with the male leader. Cheney Seyfarth [1976; in Harcourt, 1979b] found that infant baboons who spent little time in close proximity to a leader male became easily distressed in his presence. Likewise, Nowell [2005] observed a western lowland silverback who never affiliated with a particular infant become visibly uncomfortable when contact was initiated by that same infant². Even though increasing the time that mother-offspring dyads spend near a silverback may cost an adult female vital feeding time during a period of high energy requirements (lactation), it allows both the male and the infant to become comfortable in each other's presence. Once her infant is partially weaned, the female can then afford to forage further afield whilst her offspring remain in the presence of a protective individual. During group travel-feed times, infants can spend more time with the dominant

² While this section pertains only to mountain gorillas, I included this particular observation of western lowland gorillas as it is highly relevant.

silverback than their mother who may be feeding up to 100m from the dominant male³ [Doran & McNeilage, 2000; Harcourt, 1978b]. This form of babysitting benefits not only the mother and the infant, but also the adult male whose protective function increases the survival chances of his offspring and the likelihood that the satisfied mother will remain a resident in his group [Harcourt 1979b; Stewart, 2001]. Immature sex and age may also influence the type of relationship a silverback has with each young individual; adolescent females are more likely to associate with silverbacks than adolescent males, although once adulthood is reached this difference is no longer significant [Fairbanks, 1993; Stewart & Harcourt, 1987; Watts & Pusey, 1993]. While adolescent males are potential competitors, unrelated adolescent females are potential mates and related females can still learn from adult male interactions, indirectly maximizing silverback reproductive success.

Although the risk of infanticide is a major benefit of female-male associations, a silverback's role in providing overall group stability and protection from predation (i.e. by humans or leopards) and other risks or disturbances (i.e. elephants) should not be underestimated [Harcourt, 2001; Chapter 1]. As detailed in Chapter 1, Section 1.5, gorillas appear to have developed adaptive strategies in response to perceived threats; the relationship between risk and vulnerability can produce complex behaviours [Miller & Treves, 2006].

3.2.3 Eastern Lowland Gorilla Relationships

As a result of increased fruit availability, eastern lowland gorillas exhibit greater frugivorous tendencies than do mountain gorillas (Chapter 1). Although increased seasonality in food availability and distribution with fruit eating should predict greater within group competition (Section 3.2.1 and 3.2.2), social structure and proximity relationships are similar to those of the mountain gorilla [Yamagiwa, 1983; Yamagiwa & Kahekwa, 2001; Chapter 1]. This similarity suggests that the ecological differences between the subspecies are not distinct enough to produce marked social differences [Yamagiwa & Kahekwa, 2001]. While females with dependent offspring and immatures (except blackbacks) stay in close proximity to the

³ Unlike Harcourt [1978b], a subsequent study by Fletcher [1994] found that proximity between immature and silverbacks was lowest during feeding.

silverback for over 50% of feeding and resting time, they favour the leader male's presence during the resting period over the travel-feeding period; dependent immatures however often remain in close proximity to the silverback during foraging periods [Yamagiwa, 1983].

One notable difference from mountain gorillas, is that eastern lowland gorillas rarely suffer from infanticide. Females, even those with infants, can disperse together after the death of their leader male and have been observed to roam in the absence of a protector silverback for several years without being targeted by infanticidal males [Yamagiwa & Kahekwa, 2001; Chapters 1 and 4]. If males are not required to protect offspring from infanticide, then why do females maintain male-female associations at all and why is this non-female-bonded species often seen dispersing in groups? Yamagiwa & Kahekwa [2001] suggest that while infanticidal risks may be low (although see Chapter 4; the observation of infanticidal events appears to be increasing), predation risks may be high. They provided evidence for this theory by illustrating that groups that did not contain a leader male were more likely to nest in trees than those that did (Chapter 1).

3.2.4 Western Lowland Gorilla Relationships

3.2.4.1 Wild

While eastern lowland gorilla frugivory does not appear to cause marked social structure differences in comparison to mountain gorillas, the opposite is said for the even more frugivorous western lowland gorilla, whose seasonal habitat and highly frugivorous nature have been proposed as the causes of the distinct differences in social grouping between western lowland and mountain gorillas (Section 3.2.1; Chapter 1). Doran & McNeilage [1998, 2001] predicted that a high level of frugivory would increase within group competition, but only for favoured fruits from medium to large trees; creating the potential for stronger female dominance hierarchies. This hypothesis has remained untested due to the difficulty of following western lowland gorillas in forest environments. Even though western lowland gorilla females all appear to undergo natal or secondary transfer (Chapter 1), Bradley et al., [2007] have shown that over 40% of adult females had an adult female relative in their group. They suggest that dominance hierarchies and female-female relationships may be more developed in western lowland gorillas

due to female emigration into groups with relatives. However while infanticide has not yet been confirmed, many putative cases suggest that lowland females, especially those with dependent offspring, will still be highly attracted to adult males [Stokes et al., 2003; Chapter 4].

Several studies have attempted to shed light onto the social dynamics of western lowland gorillas by studying groups that frequent bais. Parnell [2002b] showed that despite having the highest potential rate of interaction, females associated the least in comparison to any other age-sex class. Adult female-silverback interaction indices were also low in bais compared to mountain gorillas. Stokes [2004] found weak evidence of a female hierarchy, which she suggested was highly variable and individualistic. Additionally, like Parnell [2002b], she showed that adult females were not significantly likely to be in close proximity to silverbacks. Finally, Nowell [2005] found: (1) immature proximity to the silverback remained at low levels; (2) immature age and sex did not affect the amount of time spent nearby silverbacks, and; (3) as in mountain and eastern lowland gorillas, immatures were attracted to the silverback but the adult male was responsible for preventing close proximity or more frequent affiliative interactions when foraging in bais.

Various theories have been proposed to explain this apparent difference in western lowland gorilla relationships from mountain and eastern lowland gorillas: (1) the high level of visibility afforded in bais may have relaxed the need for keeping such a close rein on immatures [Nowell, 2005]; (2) western lowland gorilla silverback-immature relationships are more socially passive, because a silverback must invest more time remaining vigilant to predators and infanticidal males [Nowell, 2005], and; (3) while bais offer excellent vistas into demographical and comparative intergroup studies, using clearings to examine the framework of relationships is highly biased since gorillas spend only 1% of their time in bais, and almost all of that time is spent feeding [Parnell, 2002b].

3.2.4.2 Captive

Many studies have investigated captive western lowland group social relations. Here I provide a short summary of the findings for the bulk of studies which hold significance to intragroup relations and the role of the silverback male:

(1) Tilford & Nadler [1978] found that the silverback of a single-male group was strongly attracted to infants, but initially developed relationships with them based on his previous relations with their mothers. As infants aged, male behaviour towards an infant became less dependent on his relationship with his mother. Affiliative relations with adult females may help promote paternal certainty, which may therefore lead to differential paternal investment in offspring versus non-offspring.

(2) Hoff et al., [1998] found that the loss of a silverback male in a single-male group resulted in an increase in group aggressive behaviour and general social disorder. A previous study by Hoff et al., [1982] found similar effects when the dominant silverback was removed from his group. Upon return to the group, the silverback exhibited an increase of agonistic behaviour while adult female agonism declined immediately. Less et al., [2010] found that the death of a dominant silverback in a multimale group resulted in a decrease in overall feeding time and an increase in self-directed behaviours. Margulis et al., [2003] noted that the introduction of a silverback into a gorilla group resulted in an increase of group affiliative behaviours. These studies attest to the stabilizing, mediating and controlling role of silverbacks within their units.

(3) Nakamichi & Kato [2001] found that: (1) females with dependent offspring did not remain closer to the group silverback than females without dependent offspring; (2) certain females spent more time in proximity to the silverback than others; (3) male immature age (beginning with older immatures) was negatively correlated with proximity to the silverback, and; (4) silverback-adolescent male relationships shared closer bonds if the silverback had spent more time with the immature when he was younger. Nakamichi & Kato [2001] suggest that the lack of infanticide in captive populations in comparison to wild populations, may have resulted in the adult female relationship differences noted above. Maestriperi et al., [2002] found that like mountain gorillas (Section 3.2.2), infant proximity to their mothers decreased with age, although infant-silverback relationships were not specified.

(4) Stoinski et al., [2003] found that juveniles and other mothers were the primary neighbours to new mothers in the first month post-parturition. Proximity to the silverback was not sought out prior to or post-parturition. Bingham & Hahn [1974] observed a gorilla prior and post-parturition, and found that she spent much of her time isolating herself from social encounters in both the pre- and post-birth phase. Fischer [1983] also found that pregnant females typically withdrew

from all individuals pre-parturition, whilst they avoided adult males and associated with other mothers post-parturition. McCann & Rothman [1999] found that the introduction of five hand-reared infants into a single-male group resulted in marked silverback-infant associations. Over 60% of silverback time was spent close to an infant, and over 10% was spent within an infant cluster. Infants associated with each other and most often with the silverback. But Meder [1990] found that silverbacks struggled to adjust to hand-reared infants, responding most often with sexual or aggressive advances. Unrelated infants may commonly promote aggressive reactions in infanticidal species [Fossey, 1984; Watts, 1990a], however, there are also many cases where silverbacks accept potentially unrelated infants into their group with a surprising amount of tolerance (Chapter 4).

(5) Scott & Lockard [2006] found that when females were exposed to defendable clumped food resources, they exhibited weak within group competition and did not form strictly egalitarian relationships. As in mountain gorillas, dominance hierarchies were based on tenure within the group [Scott & Lockard, 1999].

3.2.5 Progressions and Silverback Protective Placement

Consistent spatial arrangements of animal groups are a well known phenomenon within the animal kingdom [Browns & Orians, 1970]. The progression of individuals, particularly protective positions of adult males in risky situations has received much attention in other primates where positioning is expected to alter according to the level of perceived danger [Altmann, 1979; Bicca-Marques & Calegario-Marques, 1997; Hockings, 2007; Norton, 1986; Itani & Suzuki, 1967; Priston, 2005; Rhine, 1975; Rhine & Westlund, 1981; Rhine & Tilson, 1987; Rhine et al., 1985; Waser, 1985]. As the larger, more dominant and protective sex, adult males should be more likely to move into the riskiest positions within a progression – either the front or the rear, depending on the perceived risk and the context. For example: chimpanzee alpha males often occupy a protective rearward position when crossing larger roads [Hockings, 2007], whilst chacma baboon adult males position themselves in the front of their troop when approaching potential danger (i.e. waterholes) and at the back when moving away from risky situations [Rhine & Westlund, 1981].

Gorilla progressions are much understudied. Yamagiwa [1983] showed that eastern lowland gorilla dominant silverbacks occupied the rear or front of a progression in seven out of eight observations. Females with dependent offspring clustered in the middle of the progression – the safest and most protected location. Schaller [1963] observed that when mountain gorilla groups move rapidly, the silverback was more likely to occupy the lead position, but when the groups moved more slowly, the leading male was more likely to travel in the middle or rear of his group. Additionally, it has always been taken for granted that silverbacks are responsible for exerting complete directional control over a group [Yamagiwa 1987b]. Such complete control is questionable in western lowland species, where females often forage far from their leader males.

3.2.6 Nesting

Nest site choice in primates (including gorillas) is influenced by many variables, such as rainfall, temperature, season, habitat type, availability of nesting material, distance to human settlements, resources and water [see review in Anderson 1998, 2000; Groves & Sabater Pi, 1985; see review in Lukas et al., 2003 and Weiche & Anderson, 2007].

Additionally, and arguably most importantly, primates must also consider predation and disturbance risks when picking a nest site [Anderson, 2000]. Goodall [1962] found that chimpanzees in Gombe nested in forest edges and in trees located over gullies or streams; such locations provided effective lookouts and made nest access by predators difficult. When compared to their Equatorial Guinea counterparts who faced comparatively less predation due to the closed nature of the forest canopy, Senegalese chimpanzees of woodland-savannah and predator rich habitats nested in more open trees, higher and often in larger groups [Baldwin et al 1981; Tutin et al., 1983]. A similar pattern was found for the chimpanzees of Fongoli, who faced little threat of predation and therefore nested at lower heights than their Senegalese counterparts [Pruetz et al., 2008].

The location of individuals within a nest site (spatial arrangement) is thought to be influenced by predation and other disturbances [Groves & Sabater Pi, 1985]. Brownlow et al., [2001] noted that adult male chimpanzees in Budongo nested lower than females in trees at night [DeVore &

Hall, 1965]. Adult male chimpanzees at Budongo, like baboons [DeVore & Hall, 1965], may have chosen to nest in a strategically more protective position such that predators (i.e. leopards) will confront the adult male before they can reach any other more vulnerable troop members [DeVore & Hall, 1965].

In gorillas, spatial protection of individuals by the dominant silverback is a contentious issue. Much of the early literature claimed that silverbacks adopt a position of defence during nest formation by nesting at the base of a tree or a location of optimal viewing [Allen, 1931, Ascheimeier, 1922, Derochette, 1941, Valker, 1931]. Pitman [1935] also suggested that individual nesting positions were selected to maximize visual contact of members and Dyce Sharp [1927] noted that group member nests were all visible to the adult male. Yet Groves & Sabater Pi [1985] and Williamson [1988] noted that nests were often hidden from others in thick vegetation and not always selected to maximize visual contact of members. Groves & Sabater Pi [1985] showed that in medium sized groups (5-8 individuals) the silverback was more likely to take up a 'special' position within the group, although the exact type of position was not specified. Kawai & Mizuhara [1959] noted that mountain gorilla silverbacks were more likely to nest at the periphery of their group while females with dependent offspring were more likely to nest in the centre in close proximity of the silverback. However, Hess [1992] found that while adult females nested near the silverback, he took a more central nesting position within the group. Casimir [1979] found no individual patterns to nest sites, and Schaller [1963], Goodall [1974], and Williamson [1988] found no evidence of male strategic positioning, although Schaller [1963] noted that the silverback was responsible for determining nesting location and timing. But, Elliott [1976] showed that blackback males were more likely to nest peripherally the night before an intergroup interaction, in the direction of the extraunit. Additionally, western lowland gorilla females nest in trees more often and higher than silverbacks [Mehlman & Doran, 2002; Tutin et al., 1995]. While the reason for this may be merely due to differences in body mass and the vegetation's capacity for structural support [Remis, 1994], silverback ground nesting whilst group members nest in trees could also be seen as an adult male position of defence [DeVore & Hall, 1965]. Gorilla groups respond to predation pressure and disturbance from elephants by nesting above ground during periods of perceived risk. For example: Remis

[1993] found that smaller and therefore more vulnerable groups of western lowland gorillas were more likely to nest arboreally than larger groups. Yamagiwa & Kahekwa [2001] clearly showed that despite the controversy surrounding silverback strategic nesting, leader adult males provide an important protective influence during night nesting periods [Section 3.2.3; see also Tutin et al., 1995, and Williamson, 1998].

3.2.7 Chapter Aims

The nature of wild western lowland silverback protective roles within his group remains significantly understudied. How do silverback-neighbour relationships differ between bai and forest habitats? Do silverback-female neighbour relationships vary over time? Does the silverback take a frontward or rearward position within the group? Does the silverback strategically position his nest in defence of his group and how does this relate to large trail location, especially in regions of high elephant traffic? Previous studies - due to habituation constraints – have been forced to focus on social dynamics within limited bai settings. Here I provide the first detailed account of western lowland adult male–group social dynamics from a protective perspective, throughout their entire environment.

3.3 METHODS & ANALYSIS

3.3.1 Definitions and Sampling Independence

Age-sex categories of neighbours, forest density categories, hourly roll call or hourly presence close to the silverback, group spread, and all other definitions and specifications used in this chapter are presented in Chapter 2. Independence of overall scans, of neighbour scans, of silverback location in his neighbour group scans, and of silverback positioning in his entire group scans were also discussed in Chapter 2.

3.3.2 Analysis Overview

Final analyses were conducted on 3, 252 silverback scans and 166 nest sites. For this chapter, data were generally analysed on the raw (ungrouped) data set. Session groupings (based on

258 sessions) were used to analyse age-sex classes of neighbours to the silverback and age-sex class proportions of hourly presence close to the silverback (for hourly roll call definitions see Chapter 2). Chi square analysis, forward stepwise logistic regressions, and forward LR multiple regressions were the primary analytical tools used in this chapter. For more detail, see Chapter 2.

3.3.3 Silverback-Neighbour Spatial Relationships

(1) What are the silverback-neighbour dynamics to all age-sex classes in both bays and forest environments and in relation to all age-sex classes? (2) Does he play a 'babysitting' role for young immatures and infants?

Data on the frequency of neighbour scans were analysed using chi square analyses. When silverback-neighbour age-sex class spatial dynamics in forests and bays were investigated (Section 3.4.2 and 3.4.3), results were based on *all* silverback first nearest neighbour (NN1) to fourth nearest neighbour (NN4) observations. For example: NN1 results are based on all occasions when Makumba had a NN1, regardless of the actual number of neighbours present within 5m in each scan. Also note that NN1 represents the closest neighbour to the silverback within 5m, NN2 represents the second closest neighbour to the silverback within 5m, and NN10 represents the furthest neighbour to the silverback within 5m. This means that sample sizes differed from the babysitting analysis (Section 3.4.4; also see Section 3.4.1) where scans that had only one neighbour to the silverback (or only two neighbours, or only three neighbours) were considered. Data were only analysed up to NN4, because NN5 - NN10 represented a very small percentage of the data set (Table 3.5) resulting in age class subdivision sample sizes too small for analysis. Infants were not analysed as a category due to small sample sizes. Data were analysed according to forest-bay divisions based on knowledge learned from preliminary analyses (Section 3.4.1), which showed that proximity (within 5m) to the silverback presence differs in bay and forested environments. Expected values were calculated using the following equation:

(number of individuals in age-sex category/total number of individuals) * (total number of scans for that particular NN category; i.e. total number of NN1 scans)

Analyses exploring silverback-neighbour spatial relationships on an individual level (within each age-sex class) also used chi square tests. Note that for these analyses, expected values were assumed to be equal and infants were included since data here were analysed within rather than across categories. Bonferroni corrections (N-1 design for repeat tests of different hypotheses on the same data set) were applied where necessary and noted in the relevant analyses. In some cases, expected frequencies were less than five due to small sample sizes. In these cases, noted in the relevant analyses, probabilities/results should be viewed with caution (Chapter 2).

For analyses of babysitting events, chi square tests were also used. To minimize the possibility that a young individual's mother may be present outside the 5m neighbour demarcation, only occasions where the group was most dispersed (where a maximum of three individuals were heard or seen within 20m of the silverback; see Chapter 2 for definitions) were included here. Although using the dispersed-only scans diminished biases, there was still a possibility that an immature or infant's mother may be present from 6-20m of the silverback. If a gorilla was present within 6-20m of the silverback, this individual remained unknown since the dense forest did not allow for detailed data collection. However, during data collection I did note presence or absence of any individuals within 6-10m of the silverback (individual identification was not possible for the same reasons noted above). To further reduce the bias of potential mother presence 6-20m from the silverback, I then further divided analysis into occasions where individuals were present or absent within 6-10m in relation to silverback-immature or infant neighbour scans.

Seasonal changes in adult female neighbours to the silverback were explored using simple linear regressions in the grouped session format (N = 258), with mean proportional presence of each individual female per session as a neighbour (within 5m) to the silverback as the outcome variable, and month (linear) as the predictor variable. To explore changes in female presence outside of the 5m neighbour demarcation, mean hourly proportional presence per session of each individual female close to the silverback (see Chapter 2 for hourly roll call definition) was used as the outcome variable, and month (linear) as the predictor variable. Since hourly roll call data collection began in March, two months of scans were not included in the linear regressions

(N = 66 sessions). Even though a sizeable number of sessions was excluded for these analyses, it was necessary (and perhaps more biologically significant for western lowland gorillas who often forage far from their leader males) to explore changes in an adult female's relative closeness to the silverback (i.e. not just within 5m), particularly during higher risk months. Even though 66 sessions are eliminated when hourly roll call data are used in analyses, results show 'roll call' to be a more accurate measure of changes in individual presence near the silverback (Chapter 6 and Chapter 2).

3.3.4 Silverback Spatial Location in His Group

- (1) What is the silverback spatial positioning in his group of neighbours and in his entire group?
- (2) What factors predict silverback spatial location in his 5m neighbour group and in his entire group?

Data on silverback spatial positioning were examined using chi square tests and logistic regression analyses, and were based on the frequencies of scans where the silverback was in the middle or periphery of his neighbour group (of 2+ neighbours), and where the silverback was in the rear or middle/front of his entire group. As there is no *a priori* knowledge for which factors predict silverback location in his group of neighbours, the logistic regression models contained 19 predictors (Table 3.1) all of which could have potentially predicted or affected silverback –neighbour group spatial location. Final analyses for silverback spatial location within his neighbour group were based on a sample size of 644. This sample size falls well within that necessary for analysis of 19 predictors (if measured conservatively at four to five data points for every loss in degree of freedom, the model would require a minimum sample size of 95) [i.e. Hatcher, 1994; K. Howie pers. comm.].

Table 3.1 Predictors Included in Forward Stepwise Logistic Regressions for Silverback Location within His 5m Neighbour Group

| Predictors |
|--|
| Month |
| SB Behavioural State (three categories) |
| Group Spread |
| Group Behavioural State (four categories) |
| Forest Density |
| Number of Neighbours to SB (5m) |
| Bai or Other Forest Type (two categories) |
| Grouped Observer-SB Distance |
| Total Observers |
| Season (two categories) |
| Interaction Presence or Absence (two categories) |

Analyses of how intergroup interaction level affected the silverback's location within his cluster of neighbours were based on a sample size of 98 scans and 14 predictors (Table 3.2). This sample size again falls within that necessary for analysis of 14 predictors. Interaction level was determined as low, medium or high based on the vocal and behavioural responses of the silverback to the known or suspected presence of an extragroup male or another group. These are fully defined in Chapter 2.

Table 3.2 Predictors Included as Controls for the Interaction Level Forward Stepwise Logistic Regressions for Silverback Location within His 5m Neighbour Group^a

| Predictors |
|---|
| Month |
| SB Behavioural State (three categories) |
| Group Spread |
| Forest Density |
| Number of Neighbours to SB (5m) |
| Bai or Other Forest Type (two categories) |
| Grouped Observer-SB Distance |
| Total Observers |
| Season (two categories) |
| Interaction Level |

^aGroup activity was not entered into the final equation as the sample size for some of the activity categories were very small.

The effect of presence or absence of adult females or immatures on silverback location in his neighbour group were analysed using forward LR linear regressions in grouped format (N = 258 sessions), with proportional silverback location per session in the middle of his neighbour group as the outcome variable and adult female or old immature neighbour presence as the predictor variable. Results were additionally controlled for month from start of the study to take into effect habituation, season, daily rainfall (mm), maximum temperature (°C), mean total observers, and grouped observer-silverback distance. Since young immatures were almost always present as a neighbour to the silverback at least once within a session, this analysis used the mean proportion of young immatures and infants per session seen as a neighbour to the silverback and silverback presence or absence per session in the middle of his neighbour group. As a result, Figure 3.7 was presented oppositely to Figures 3.5 and 3.6. Only infants who were seen alone (without the presence of their mother as a neighbour to the silverback) were included here. As there again was no *a priori* way of describing which factors may predict silverback location in his entire group, logistic regression models contained 25 predictors (Table 3.3) all of which could have potentially affected silverback spatial location in his entire group. Final analyses were based on a sample size of 2361, which is within that necessary for analysis of 25 predictors.

Table 3.3 Predictors Included in Forward Stepwise Logistic Regressions for Silverback Location in His Entire Group^a

| Predictors |
|--|
| Month |
| SB Behavioural State (three categories) |
| Group Spread |
| Group Behavioural State (four categories) |
| Forest Density |
| Number of Neighbours to SB (5m) |
| Bai or Other Forest Type (two categories) |
| Grouped Observer-SB Distance |
| Total Observers |
| Season (two categories) |
| Interaction Presence of Absence (two categories) |
| Time Block (four categories) ¹ |
| Bai vs Other Forest type (two categories) |

^aTime block was added as a predictor due to the potential effect time, and therefore silverback or group activity (Chapter 2) may have had on the spatial location of the silverback within the entire group.

Analyses of the effect of intergroup interactions on silverback location within his entire group were based on a sample size of 436 and 25 predictors. For a list of predictors used see Table 3.3 but note that interaction presence or absence was replaced with interaction level (low, medium or high; see above and Chapter 2).

The effect of presence or absence of adult females or immatures on silverback location in his entire group were explored using forward LR linear regressions in grouped format (N = 258 sessions), with proportional silverback location per session in the back of the entire group as the outcome variable and mean hourly presence per session of adult females and immatures close to the silverback as the predictor variable. Results were additionally controlled for month to take into effect habituation, season, daily rainfall (mm), maximum temperature (°C), mean total observers, and grouped observer-silverback distance.

3.3.5 Silverback Nesting and Nest Site Spatial Arrangement

(1) What is the silverbacks' nesting position preference in relation to the largest trail at the nest site? (2) Does spatial nest site pattern reflect a silverback-group strategic system of defence?

Data on silverback nesting position close to the trail relative to other group members were first examined using chi square analysis. The largest trail within a 20m radius of the nest site was recorded and analysed here. When the silverback was closest to the largest trail, his nest was located a median of 5m away. When another individual was located closest to the largest trail, their nest site was also located a median of 5m away.

Next, the factors which may predict silverback nest site position were examined. As there was no *a priori* knowledge about which factors may predict silverback nest site placement relative to the largest trail, the logistic regression models contained 10 predictors (Table 3.4) all of which could potentially affect silverback nest site placement. Final analyses were based on a sample size of 151 nests, which is well within that necessary for analysis of 10 predictors. Exact distances from the silverback to an individual in a tree were recorded (i.e. base of tree was not used as a distance category from the neighbour). A median distance of all other group

members (as a unit instead of individually) was calculated. Median values were used to control for outliers where individuals nested in trees.

Table 3.4 Predictors included in the Forward Stepwise Logistic Regression for Silverback Nest Site Placement Closest to the Largest Trail^a

| |
|--|
| Predictors |
| Daily Rainfall (mm) |
| Season (two categories) |
| Maximum Temperature (°C) |
| Presence or Absence of Tree Nests (two categories) |
| Interaction Presence or Absence (two categories) or Interaction Level ¹ |
| Median Distance of All Group Members to the SB (m) |
| Forest Density |

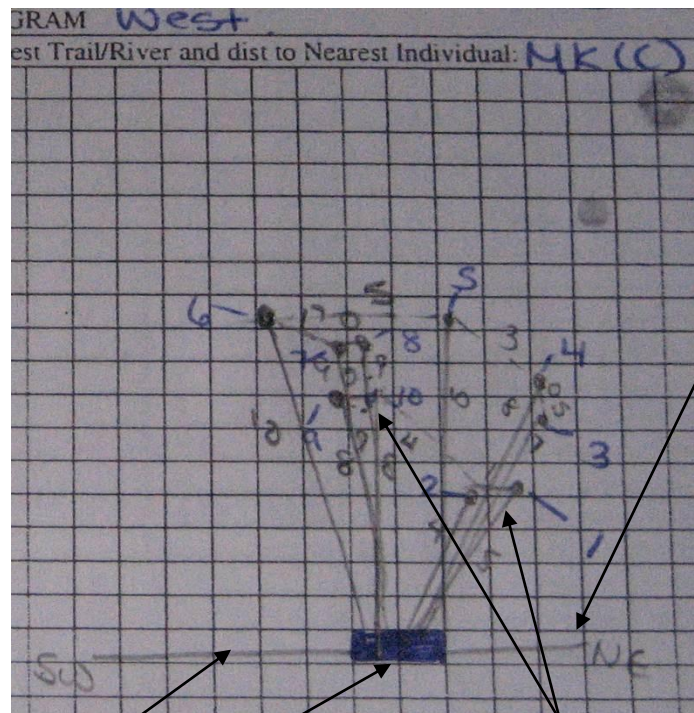
^aInteraction presence or absence and interaction level were entered separately in two models.

Three predominant patterns of nest site spatial arrangement emerged throughout the course of the year:

- (1) 'fan' design, which consisted of a silverback nest located at the periphery of the group while all other individual nests were splayed out away from the silverback in a fan like shape (Figure 3.1a-3.1b). In order for nest site spatial arrangement to be defined as a 'fan', group members cannot nest beyond the periphery of the silverback nest. Therefore nest site arrangement forms a half moon (180°) shape (Figure 3.1a).
- (2) 'circle' design, which consisted of the silverback nest located in the middle of the group where all other individuals nested around the silverback nest in a circular fashion.
- (3) 'irregular' design, which consisted of no obvious nesting site spatial pattern. Nest sites which were not quite a fan and not quite a circle were placed in this category (Figure 3.1c -3.1d).

Due to the potential for confusing circle and irregular nest spatial arrangements and due to small sample sizes of circle or irregular nests recorded in the field, both circle and irregular nests were grouped into one category for analysis. Data were analysed using chi square tests.

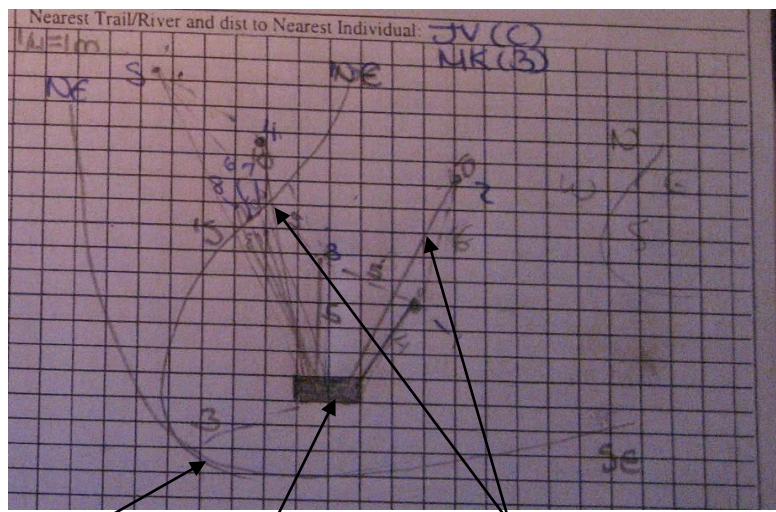
Figure 3.1a Fan Design Example One



If an individual nests below this line, the spatial arrangement can no longer be considered a pure 'fan' or half moon (180°) and the nest site spatial design becomes irregular

Largest Trail **SB** **Group Members**

Figure 3.1b Fan Design Example Two



Largest Trail **SB** **Group Members**

Figure 3.1c Circle Design

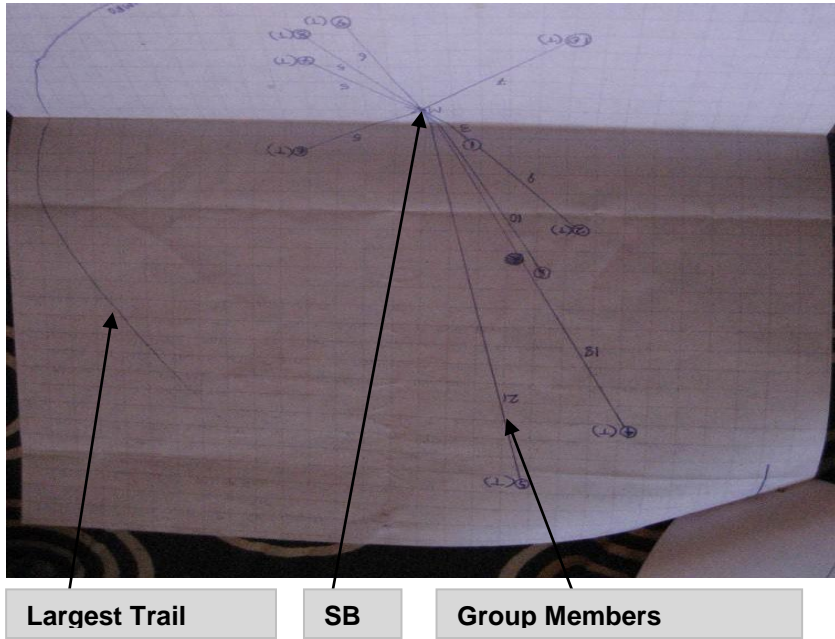
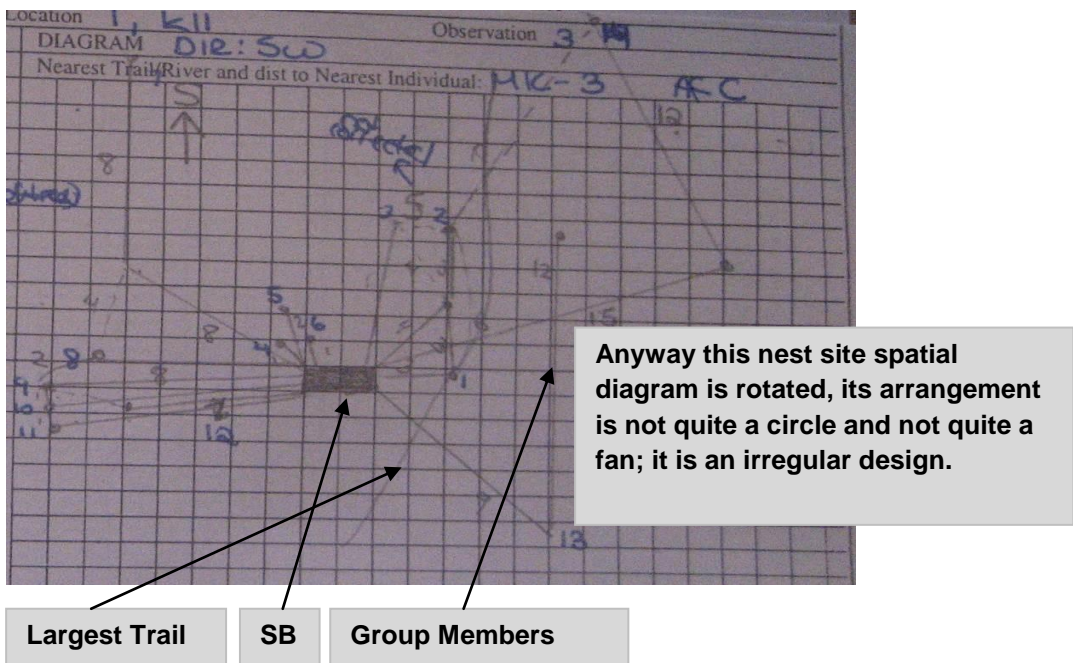


Figure 3.1d Irregular Design



The influence of forest density was examined through a modal group forest density and silverback score in relation to the 'fan' and 'circle or irregular' nest site spatial arrangement. Silverback and group nest site placement in relation to forest density were directly compared using chi squared analysis.

3.4 RESULTS

3.4.1 Overview

Results are based on 3216 scans of neighbours within 5m of the silverback (hereforth simply 'neighbours'). Table 3.5 reports the number of scans belonging to each nearest neighbour (NN) category (i.e. nearest neighbour 1 or NN1, nearest neighbour 2 or NN2). The silverback spent just over half of his time alone (51%) with no neighbours, and just under half of his time in the presence of at least one neighbour (49%). The silverback was no more likely to be alone than to have a neighbour overall ($X^2 = 0.55$, $df = 1$, $p = 0.459$, $N = 3216$).

Table 3.5 Neighbours within 5m of the Silverback^a

| Number of Neighbours | Total | % of Total |
|----------------------|-------|------------|
| None | 1629 | 50.6 |
| 1 | 697 | 21.7 |
| 2 | 448 | 13.9 |
| 3 | 280 | 8.7 |
| 4 | 102 | 3.2 |
| 5 | 25 | <1 |
| 6 | 25 | <1 |
| 7 | 7 | <1 |
| 8 | 2 | <1 |
| 9 | 0 | 0 |
| 10 | 1 | <1 |

^aTotals are based on numbers of neighbours specific to each distinct nearest neighbour category (i.e. how many scans had only one neighbour? How many scans had only two neighbours? How many scans had only three neighbours?)

3.4.1.1 Silverback-Neighbour Comparisons in Bais

Results are based on 157 scans of neighbours when in bais (Table 3.6) The silverback spent only 26% of his time alone, whereas 74% his time in bais was spent in the presence of at least one neighbour. The silverback was significantly more likely to have a neighbour than no neighbours in bais ($X^2 = 35.83$, $df = 1$, $p < 0.001$, $N = 157$).

Table 3.6 Silverback-Neighbour Scans in Bais

| Number of Neighbours | Total | % of Total |
|----------------------|-------|------------|
| None | 41 | 26.1 |
| 1 | 40 | 25.4 |
| 2 | 38 | 24.2 |
| 3 | 21 | 13.4 |
| 4 | 11 | 7 |
| 5 | 4 | 2.5 |
| 6 | 1 | <1 |
| 7 | 0 | 0 |
| 8 | 1 | <1 |

3.4.1.2 Silverback-Neighbour Comparisons in Open Forested Environments

Results are based on 215 scans of neighbours in open forested environments (Table 3.7). Unlike bai environments, the silverback spent 45% of his time alone, whereas 55% of his time in open forested environments was spent in the presence of at least one neighbour. Makumba was no more likely to be alone, than to have a neighbour in open forested environments ($X^2 = 2.05$, $df = 1$, $p = 0.152$, $N = 215$).

Table 3.7 Silverback-Neighbour Scans in Open Forested Environments

| NN | Total | % of Total |
|----|-------|------------|
| 0 | 97 | 45.1 |
| 1 | 63 | 29.3 |
| 2 | 31 | 14.4 |
| 3 | 15 | 7 |
| 4 | 6 | <1 |
| 5 | 3 | <1 |

3.4.2 Age-Sex Classes of Neighbours to the Silverback

Statistical results of comparisons between age-sex classes as neighbours to the silverback are presented in Table 3.8.

3.4.2.1 Nearest Neighbour One (NN1) Forests and Bais

Forests Only

Results are based on 1,287 NN1 scans. Age-sex class totals were: adult females (af) - 373 scans; immatures (i) - 848 scans; where old immatures (oi) – 169 scans and young immature (yi) – 679 scans; infants (inf) - 66 scans, and; immatures & infants (ii) – 914 scans. Of the 321 mother-infant dyad possibilities, infants were seen as a NN1 without their mother's presence within 5m of the silverback in only 33 scans. However, young immatures were significantly more likely to be a NN1 to the silverback than were adult females, whereas adult females were significantly more likely to be a NN1 to the silverback than were old immatures. Young immatures were also significantly more likely to be a NN1 to the silverback than were old immatures.

Bais Only

Results are based on 112 NN1 scans. Age-sex class totals were: adult females (af) - 13 scans; immatures (i) - 98 scans; where old immatures (oi) – 28 scans and young immature (yi) – 70 scans; infants (inf) – one scan, and; immatures & infants (ii) – 99 scans. Of the 11 mother-infant dyad possibilities, infants were seen as a NN1 without their mother present within 5m of the silverback in only one scan. Young immatures were significantly more likely to be a NN1 to the silverback than were adult females, however old immatures were no more likely to be a NN1 to the silverback than were adult females. Young immatures were significantly more likely to be a NN1 to the silverback than were old immatures.

3.4.2.2 Nearest Neighbour Two (NN2) Forests and Bais

Forests Only

Results are based on 692 NN2 scans. Age-sex class totals were: adult females (af) - 140 scans; immatures (i) - 323 scans; where old immatures (oi) – 102 scans and young immature

(yi) – 221 scans; infants (inf) - 229 scans, and; immatures & infants (ii) – 552 scans. Of the 324 mother-infant dyad possibilities, infants were seen as NN2 without their mother present within 5m to the silverback in only 21 scans. Young immatures were significantly more likely to be a NN2 to the silverback than were adult females, whereas adult females were no more likely to be a NN2 to the silverback than were old immatures. Young immatures were also significantly more likely to be a NN2 to the silverback than were old immatures.

Bais Only

Results are based on 76 NN2 scans. Age-sex class totals were: adult females (af) - nine scans; immatures (i) - 57 scans; where old immatures (oi) – 27 scans and young immature (yi) – 30 scans; infants (inf) – 10 scans, and; immatures & infants (ii) – 67 scans. Of the 16 mother-infant dyad possibilities, infants were never observed as a NN2 without their mother present within 5m of the silverback. Young and old immatures were significantly more likely to be a NN2 to the silverback than were adult females. Young immatures were no more likely to be a NN2 to the silverback than were old immatures.

3.4.2.3 Nearest Neighbour Three (NN3) Forests and Bais

Forests Only

Results are based on 340 NN3 scans. Age-sex class totals were: adult females (af) - 50 scans; immatures (i) - 216 scans; where old immatures (oi) – 76 scans and young immature (yi) – 140 scans; infants (inf) - 74 scans, and; immatures & infants (ii) - 290.scans. Of the 124 mother-infant dyad possibilities, infants were seen as a NN3 without their mother's presence within 5m of the silverback in only six scans. Young immatures are significantly more likely to be a NN3 to the silverback than adult females, whereas adult females are no more likely to be a NN3 to the silverback than old immatures. Young immatures are also significantly more likely to be a NN3 to the silverback than old immatures.

Bais Only

Results are based on 36 NN3 scans. Age-sex class totals were: adult females (af) – six scans; immature (i) - 24 scans; where old immatures (oi) – 10 scans and young immature (yi) – 14

scans; infants (inf) – six scans, and; immatures & infants (ii) – 30 scans. Of the eight mother-infant dyad possibilities, infants were never observed as a NN3 without their mother present within 5m of the silverback. Additionally, neither young nor old immatures were more likely to be a NN3 to the silverback than were adult females. Young immatures were no more likely to be a NN3 to the silverback than were old immatures.

3.4.2.4 Nearest Neighbour Four (NN4) Forests and Bais

Forests Only

Results are based on 112 NN4 scans. Age-sex class totals were: adult females (af) - 23 scans; immatures (i) - 64 scans; where old immatures (oi) – 23 scans and young immature (yi) – 41 scans; infants (inf) – 25 scans, and; immatures & infants (ii) – 89 scans. Of the 36 mother-infant dyad possibilities, infants were observed as a NN4 without their mother present within 5m of the silverback in only four scans. Young immatures were significantly more likely to be a NN4 to the silverback than were adult females, whereas old immature were no more likely to be a NN4 to the silverback than were adult females. Young immatures were significantly more likely to be a NN4 to the silverback than were old immatures.

Bais Only

Results are based on 17 NN4 scans and should be viewed with some caution. Age-sex class totals were: adult females (af) - seven scans; immatures (i) - 10 scans; where old immatures (oi) – four scans and young immatures (yi) – six scans; infants (inf) – 0 scans, and; immatures & infants (ii) – 30 scans. Of the four mother-infant dyad possibilities, infants were never observed as a NN4 without their mother present within 5m of the silverback. Young and old immatures were no more likely to be a NN4 to the silverback than were adult females. Young immatures were no more likely to be a NN4 to the silverback than were old immatures.

Table 3.8 Age-Sex Class of NN1 to NN4 in Forests and Bais

| N | Habitat | Type | X ² | df | Sig | N | Obs ^a | Exp ^a | Obs ^a | Exp ^a |
|---|---------|--------------------|----------------|----|--------|------|------------------|------------------|------------------|------------------|
| | | | | | | | N | N | N | N |
| 1 | Forest | oi-yi ^a | 480.97 | 1 | <0.001 | 848 | 169 | 485 | 679 | 363 |
| 1 | Forest | af-yi | 89.01 | 1 | <0.001 | 1052 | 373 | 526 | 679 | 526 |
| 1 | Forest | af-oi | 29.91 | 1 | <0.001 | 542 | 373 | 310 | 169 | 232 |
| 1 | Bai | oi-yi | 32.67 | 1 | <0.001 | 98 | 28 | 56 | 70 | 42 |
| 1 | Bai | af-yi | 39.15 | 1 | <0.001 | 83 | 13 | 41.5 | 70 | 41.5 |
| 1 | Bai | af-oi | 1.95 | 1 | 0.162 | 41 | 13 | 17.4 | 28 | 23.6 |
| 2 | Forest | oi-yi | 87.16 | 1 | <0.001 | 323 | 102 | 185 | 221 | 138 |
| 2 | Forest | af-yi | 18.18 | 1 | <0.001 | 361 | 140 | 180.5 | 221 | 180.5 |
| 2 | Forest | af-oi | 0.07 | 1 | 0.795 | 242 | 140 | 138 | 102 | 104 |
| 2 | Bai | oi-yi | 2.59 | 1 | 0.107 | 57 | 27 | 33 | 30 | 24 |
| 2 | Bai | af-yi | 11.31 | 1 | 0.001 | 39 | 9 | 19.5 | 30 | 19.5 |
| 2 | Bai | af-oi | 4.11 | 1 | 0.043 | 36 | 9 | 15 | 27 | 21 |
| 3 | Forest | oi-yi | 41.17 | 1 | <0.001 | 216 | 76 | 123 | 140 | 93 |
| 3 | Forest | af-yi | 42.64 | 1 | <0.001 | 190 | 50 | 95 | 140 | 95 |
| 3 | Forest | af-oi | 0.52 | 1 | 0.471 | 126 | 50 | 54 | 76 | 72 |
| 3 | Bai | oi-yi | 2.74 | 1 | 0.098 | 24 | 10 | 14 | 14 | 10 |
| 3 | Bai | af-yi | 1.82 | 1 | 0.718 | 20 | 6 | 9 | 14 | 11 |
| 3 | Bai | af-oi | 1.00 | 1 | 0.317 | 16 | 6 | 8 | 10 | 6 |
| 4 | Forest | oi-yi | 12.56 | 1 | <0.001 | 64 | 23 | 37 | 41 | 27 |
| 4 | Forest | af-yi | 5.06 | 1 | 0.024 | 64 | 23 | 32 | 41 | 32 |
| 4 | Forest | af-oi | na | 1 | na | 66 | 23 | 23 | 23 | 23 |
| 4 | Bai | oi-yi | 1.67 | 1 | 0.197 | 10 | 4 | 6 | 6 | 4 |
| 4 | Bai | af-yi | 0.08 | 1 | 0.782 | 13 | 7 | 6.5 | 6 | 6.5 |
| 4 | Bai | af-oi | 0.30 | 1 | 0.545 | 11 | 7 | 6 | 4 | 6 |

^aObserved and expected results are listed respective of the age-sex class order in the 'Type' Category.

3.4.3 Individual Neighbours to the Silverback

3.4.3.1 Nearest Neighbour One (NN1) in Forests and Bais

Forests Only

No particular adult female or old immature was significantly more likely to be a NN1 to the silverback (Table 3.8a and 3.8b). However, Mossoko Abuli (Mb), the youngest immature was significantly more likely to be a NN1 to the silverback than were either of the other young immatures. The second youngest immature, Essekerende (Es), was significantly more likely to be a NN1 than was the third youngest immature, Mai (Ma) (Table 3.8c). The second youngest infant, Bokata (Bok), was significantly more likely to be NN1 than was the youngest infant, Mobangui (Mob) (Table 3.8).

Table 3.8a NN1 Adult Females in Forests Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-------|-----|-------------------|--------------------|--------------------|-------|
| Af | 1.95 | 2 | 0.377 | 373 | 117 | 119 | 137 | 124.3 |

¹Bombe ²Mopambe ³Malui

Table 3.8b NN1 Old Immatures in Forests Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|-----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 0.68 | 3 | 0.878 | 169 | 45 | 38 | 44 | 42 | 42.3 |

¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.8c NN1 Young Immatures in Forests Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|-------|----------------|----|--------|-----|-------------------|-------------------|-------------------|-------|
| Yi | 212.80 | 2 | <0.001 | 679 | 86 | 200 | 393 | 226.3 |
| Es-Ma | 45.44 | 1 | <0.001 | 286 | 86 | 200 | | 143 |
| Ma-Mb | 196.76 | 1 | <0.001 | 479 | 86 | | 393 | 239.5 |
| Es-Mb | 62.90 | 1 | <0.001 | 593 | | 200 | 393 | 296.5 |

Bonferroni correction p < 0.025 ¹Mai ²Essekerende ³Mossoko Abuli

Table 3.8d NN1 Infants in Forests Only

| Type | X ² | df | Sig | N | Bok ¹ N | Mob ² N | Exp N |
|---------|----------------|----|--------|----|--------------------|--------------------|-------|
| inf | 10.94 | 1 | <0.001 | 33 | 26 | 7 | 16.5 |
| mob-bok | | | | | | | |

¹Bokata ²Mobangui

Bais Only

No particular adult female, old immature or young immature was differentially likely to be a NN1 to the silverback (Table 3.8e-g); although adult female sample sizes are very small, making statistics problematic. The eldest infant, Bokata (Bok), was seen only once as a NN1 without his mother within 5m of the silverback, thus infant analysis could not be performed.

Table 3.8e NN1 Adult Females in Bais Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|--------------------|--------------------|-------|
| af | 2.46 | 2 | 0.292 | 13 | 3 | 7 | 3 | 4.3 |

¹Bombe ²Mopambe ³Malui

Table 3.8f NN1 Old Immatures in Bais Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| oi | 4.86 | 3 | 0.183 | 28 | 3 | 8 | 11 | 6 | 7 |

¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.8g NN1 Young Immatures in Bais Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------|
| yi | 0.80 | 2 | 0.670 | 70 | 20 | 24 | 26 | 23.3 |

¹Mai ²Essekerende ³Mossoko Abuli

3.4.3.2 Nearest Neighbour Two (NN2) in Forests and Bais

Forests Only

No particular adult female was significantly more likely to be a NN2 to the silverback (Table 3.9a). Etefi (Et), the second eldest immature was significantly more likely to be a NN2 to the silverback than were Kunga (Ku), the eldest immature, or Silo (Si) (Table 3.9b). Mossoko Abuli (Mb), the youngest immature was significantly more likely to be a NN2 to the silverback than Mai, the third youngest immature, and more likely to be a NN2 to the silverback than Essekerende (Es), the second youngest immature. The second youngest immature, Essekerende (Es), was not significantly more likely to be a NN2 than the third youngest immature, Mai (Ma), although there was a trend to suggest that Essekerende (Es) was more likely to be a NN2 than Mai (Ma) (Table 3.9c). The second youngest infant, Bokata (Bok), was

significantly more likely to be a NN2 than was the youngest infant, Mobangui (Mob) (Table 3.9d).

Table 3.9a NN2 Adult Females in Forests Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|------|-----|-------------------|--------------------|--------------------|-------|
| Af | 0.74 | 2 | 0.59 | 140 | 50 | 42 | 48 | 46.7 |

¹Bombe ²Mopambe ³Malui

Table 3.9b NN2 Old Immatures in Forests Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|-------|----------------|----|-------|-----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 13.69 | 3 | 0.003 | 102 | 16 | 38 | 31 | 17 | 25.5 |
| Ku-Et | 8.96 | 1 | 0.003 | 53 | 16 | 38 | | | 27 |
| Ku-Mi | 4.79 | 1 | 0.029 | 47 | 16 | | 31 | | 23.5 |
| Ku-Si | 0.03 | 1 | 0.862 | 33 | 16 | | | 17 | 16.5 |
| Et-Mi | 0.71 | 1 | 0.399 | 69 | | 38 | 31 | | 34.5 |
| Et-Si | 8.02 | 1 | 0.005 | 55 | | 38 | | 17 | 27.5 |
| Mi-Si | 0.04 | 1 | 0.043 | 48 | | | 31 | 17 | 24 |

Bonferroni Correction p < 0.01 ¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.9c NN2 Young Immatures in Forests Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|-------|----------------|----|--------|-----|-------------------|-------------------|-------------------|-------|
| Yi | 38.94 | 2 | <0.001 | 221 | 43 | 62 | 116 | 73.7 |
| Ma-Es | 3.44 | 1 | 0.064 | 105 | 43 | 62 | | 52.5 |
| Ma-Mb | 33.52 | 1 | <0.001 | 159 | 43 | | 116 | 79.5 |
| Es-Mb | 16.38 | 1 | <0.001 | 178 | | 62 | 116 | 296.5 |

Bonferroni correction p < 0.025 ¹Mai ²Essekerende ³Mossoko Abuli

Table 3.9d NN2 Infants in Forests Only

| Type | X ² | df | Sig | N | Bok ¹ N | Mob ² N | Exp N |
|---------|----------------|----|------|----|--------------------|--------------------|-------|
| inf | 3.86 | 1 | 0.05 | 21 | 15 | 6 | 10.5 |
| mob-bok | | | | | | | |

¹Bokata ²Mobangui

Bais Only

No particular adult female or old immature was significantly more likely than any other adult female or old immature to be a NN2 to the silverback (Table 3.9e-f); although adult female sample sizes are very small, making statistics problematic. Mossoko Abuli (Mb), the youngest

immature, was not significantly more likely to be a NN2 to the silverback than Essekerende (Es), the second youngest immature, but was significantly more likely to be a NN2 to the silverback than Mai (Ma), the third youngest immature (Table 3.9g). Essekerende (Es), the second youngest immature, was significantly more likely to be a NN2 than Mai (Ma), the third youngest immature (Table 3.9g). No infants were observed as a NN2 without their mother present within 5m of the silverback.

Table 3.9e NN2 Adult Females in Bais Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-------|---|-------------------|--------------------|--------------------|-------|
| af | 2.67 | 2 | 0.264 | 9 | 1 | 5 | 3 | 3 |

¹Bombe ²Mopambe ³Malui

Table 3.9f NN2 Old Immatures in Bais Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 2.19 | 3 | 0.535 | 27 | 6 | 8 | 9 | 4 | 6.8 |

¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.9g NN2 Young Immatures in Bais Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|-------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------|
| yi | 7.40 | 2 | 0.025 | 30 | 3 | 14 | 13 | 10 |
| Ma-Es | 7.19 | 1 | 0.008 | 17 | 3 | 14 | | 8.5 |
| Ma-Mb | 6.25 | 1 | 0.012 | 16 | 3 | | 13 | 8 |
| Es-Mb | 0.85 | 1 | 0.847 | 27 | | 14 | 13 | 13.5 |

Bonferroni Correction $p < 0.025$ ¹Mai ²Essekerende ³Mossoko Abuli

3.4.3.3 Nearest Neighbour Three (NN3) in Forests and Bais

Forests Only

No particular adult female or old immature was significantly more likely to be a NN3 to the silverback (Table 3.10a and 3.10b); although adult female sample sizes are very small, making statistics problematic. However, Mossoko Abuli (Mb), the youngest immature was significantly more likely to be a NN3 to the silverback than Mai (Ma), the third youngest immature but was not significantly more likely to be a NN3 to the silverback than Essekerende (Es), the second youngest immature. The second youngest immature, Essekerende (Es), was significantly more likely to be a NN3 than the third youngest immature, Mai (Ma) (Table 3.10c). The second

youngest infant, Bokata, (Bok) was no more likely to be a NN3 than was the youngest infant, Mobangui (Mob); although the sample size was very small making statistics problematic (Table 3.10d).

Table 3.10a NN3 Adult Females in Forests Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mai ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|--------------------|--------------------|-------|
| Af | 1.12 | 2 | 0.571 | 50 | 20 | 14 | 16 | 16.7 |

¹Bombe ²Mopambe ³Malui

Table 3.10b NN3 Old Immatures in Forests Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 5.16 | 3 | 0.076 | 76 | 18 | 24 | 17 | 17 | 25.3 |

¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.10c NN3 Young Immatures in Forests Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|-------|----------------|----|--------|-----|-------------------|-------------------|-------------------|-------|
| Yi | 20.63 | 2 | <0.001 | 140 | 22 | 64 | 54 | 46.7 |
| Ma-Es | 20.5 | 1 | <0.001 | 86 | 22 | 64 | | 43 |
| Ma-Mb | 13.45 | 1 | <0.001 | 76 | 22 | | 54 | 38 |
| Es-Mb | 0.85 | 1 | 0.357 | 118 | | 64 | 54 | 59 |

Bonferroni correction p < 0.025 ¹Mai ²Essekerende ³Mossoko Abuli

Table 3.10d NN3 Infants in Forests Only

| Type | X ² | df | Sig | N | Bok ¹ N | Mob ² N | Exp N |
|------|----------------|----|-------|---|--------------------|--------------------|-------|
| Inf | 0.67 | 1 | 0.414 | 6 | 4 | 2 | 3 |

mob-bok

¹Bokata ²Mobangui

Bais Only

No particular young or old immature was significantly more likely to be a NN3 to the silverback (Table 3.10f and 3.10g). Note that in both cases sample sizes were very small, making statistics problematic. No infants were observed as a NN3 without their mother present within 5m of the silverback, so analysis was not carried out. Analysis on adult female NN3 was not possible due to the presence of a '0' in one of the categories, although both Bombe and Mopambe were observed as a NN3 the same number of times (Table 3.10e).

Table 3.10e NN3 Adult Females in Bais Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-----|---|-------------------|--------------------|--------------------|-------|
| Af | na | na | na | 6 | 3 | 3 | 0 | na |

¹Bombe ²Mopambe ³Malui**Table 3.10f** NN3 Old Immatures in Bais Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 3.71 | 3 | 0.294 | 14 | 3 | 4 | 6 | 1 | 3.5 |

¹Kunga ²Etefi ³Mio ⁴Silo**Table 3.10g** NN3 Young Immatures in Bais Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------|
| Yi | 1.40 | 2 | 0.497 | 10 | 2 | 5 | 3 | 3.3 |

¹Mai ²Essekerende ³Mossoko Abuli

3.4.3.4 Nearest Neighbour Four (NN4) in Forests and Bais

Forests Only

No particular adult female, old or young immature was significantly more likely to be a NN4 to the silverback than was any other (Table 3.11a-3.11c). Additionally, the second youngest infant, Bokata, (Bok) was no more likely to be a NN4 than was the youngest infant, Mobangui (Mob); although the sample size was very small, making statistics problematic (Table 3.11d).

Table 3.11a NN4 Adult Females in Forests Only

| Type | X ² | df | Sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|--------------------|--------------------|-------|
| Af | 0.61 | 2 | 0.738 | 23 | 8 | 9 | 6 | 7.7 |

¹Bombe ²Mopambe ³Malui**Table 3.11b** NN4 Old Immatures in Forests Only

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 4.30 | 3 | 0.230 | 23 | 5 | 4 | 10 | 4 | 5.8 |

¹Kunga ²Etefi ³Mio ⁴Silo**Table 3.11c** NN4 Young Immatures in Forests Only

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------|
| Yi | 0.923 | 2 | 0.629 | 41 | 14 | 11 | 16 | 13.7 |

¹Mai ²Essekerende ³Mossoko Abuli

Table 3.11d NN4 Infants in Forests Only

| Type | X ² | df | Sig | N | Bok ¹ N | Mob ² N | Exp N |
|---------|----------------|----|-------|---|--------------------|--------------------|-------|
| inf | 1.00 | 1 | 0.317 | 4 | 3 | 1 | 2 |
| mob-bok | | | | | | | |

¹Bokata ²Mobangui

Bais Only

No particular young immature was significantly more likely to be a NN4 to the silverback than any other (Table 3.11g); although sample sizes again were very small, making statistics problematic. No infants were observed as a NN4 without their mother present within 5m of the silverback. Adult female and old immature chi square analyses were not possible due to the presence of a '0' in one of the categories, although Bombe and Malui were observed as a NN4 at similar frequencies (Table 3.11e and Table 3.11f).

Table 3.11e NN4 Adult Females in Bais Only

| Type | X ² | df | sig | N | Bo ¹ N | Mop ² N | Mal ³ N | Exp N |
|------|----------------|----|-----|---|-------------------|--------------------|--------------------|-------|
| af | na | na | na | 7 | 4 | 0 | 3 | na |

¹Bombe ²Mopambe ³Malui

Table 3.11f NN4 Old Immatures in Bais Only

| Type | X ² | df | sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-----|---|-------------------|-------------------|-------------------|-------------------|-------|
| oi | na | na | na | 4 | 3 | 0 | 1 | 4 | na |

¹Kunga ²Eteti ³Mio ⁴Silo

Table 3.11g NN4 Young Immatures in Bais Only

| Type | X ² | df | sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|------|----------------|----|-------|---|-------------------|-------------------|-------------------|-------|
| yi | 1.00 | 2 | 0.607 | 6 | 2 | 1 | 3 | 2 |

¹Mai ²Essekerende ³Mossoko Abuli

3.4.4 The Silverback and His Role in 'Babysitting'

While the results thus far indicate that younger immatures tended to be preferred neighbours of the silverback, inferring that the silverback was in fact 'babysitting' is probably not entirely accurate, since an immature's mother may still be close by though not within the 5m cut-off

used in the above analysis. An additional way to further investigate the possibility that the silverback may act as a 'babysitter' was to focus on occasions when the group was most dispersed; by only analyzing those observations where a maximum of three individuals were heard or seen within 20m of the silverback (Chapter 2).

3.4.4.1 Individual and Age-Sex Class Patterns when Only One Neighbour to the Silverback is Present and Group Spread is Dispersed

Results are based on 237 scans. Age-sex class totals were: adult females (af) - 20 scans; immature (i) - 187 scans; where old immatures (oi) – 23 scans and young immature (yi) – 164 scans; infants (inf) – eight scans, and; immatures & infants (ii) – 195 scans. Immatures and infants were significantly more likely to be the only neighbour to the silverback than were adult females (Table 3.12a). Old immatures were no more likely to be the only neighbour to the silverback than were adult females (Table 3.12a). No particular old immature was significantly more likely to be the only neighbour to the silverback (Table 3.12b). Young immatures were significantly more likely to be the only neighbour to the silverback than were adult females and old immatures (Table 3.12a). However, the youngest immature, Mossoko Abuli (Mb) was significantly more likely to be the only neighbour to the silverback than were either Essekerende (Es), the second youngest immature, or Mai (Ma), the third youngest immature. Essekerende (Es) was significantly more likely to be the only neighbour to the silverback than was Mai (Ma) (Table 3.12c). Bokata (Bok), the oldest infant was observed as the only neighbour to the silverback 100% of the time when compared with Mobangui, the youngest infant.

Additionally, when a young immature was the only neighbour to the silverback other (unknown) individual(s) within 6-10m of the silverback were significantly more likely to be absent than present ($X^2 = 5.97$, $df = 1$, $p = 0.015$, $N = 141$). When an old immature was the only neighbour to the silverback, other (unknown) individual(s) within 6-10m of the silverback were no more likely to be absent than present ($N = 12$; 6 absent, 6 present), although 12 scans were unidentified. For infants, even though other (unknown) individual(s) within 6-10m of the silverback were more likely to be present than absent, this difference was not significant ($X^2 =$

0.16, df = 1, p = 1.0, N = 8; 2 absent, 6 present); although sample sizes were very small making statistics problematic.

Table 3.12a Age-Sex Classes as the Only Neighbour to the Silverback

| Type | X ² | df | Sig | N | Obs ^a N | Exp ^a N | Obs ^a N | Exp ^a N |
|--------------------|----------------|----|--------|-----|--------------------|--------------------|--------------------|--------------------|
| Af-ii ^a | 28.59 | 1 | <0.001 | 215 | 20 | 54 | 195 | 161 |
| Oi-yi | 154.14 | 1 | <0.001 | 187 | 23 | 107 | 164 | 80 |
| Af-yi | 112.70 | 1 | <0.001 | 184 | 20 | 92 | 164 | 92 |
| Af-oi | 0.18 | 1 | 0.674 | 43 | 20 | 19 | 23 | 24 |

^aObserved and expected results are listed respective of the age-sex class order in the 'Type' Category

Table 3.12b Old Immatures as the Only Neighbour to the Silverback

| Type | X ² | df | Sig | N | Ku ¹ N | Et ² N | Mi ³ N | Si ⁴ N | Exp N |
|------|----------------|----|-------|----|-------------------|-------------------|-------------------|-------------------|-------|
| Oi | 2.91 | 3 | 0.405 | 23 | 9 | 4 | 4 | 6 | 5.8 |

¹Kunga ²Etefi ³Mio ⁴Silo

Table 3.12c Young Immatures as the Only Neighbour to the Silverback

| Type | X ² | df | Sig | N | Ma ¹ N | Es ² N | Mb ³ N | Exp N |
|-------|----------------|----|--------|-----|-------------------|-------------------|-------------------|-------|
| Yi | 95.87 | 2 | <0.001 | 164 | 9 | 45 | 110 | 54.7 |
| Ma-Es | 24.00 | 1 | <0.001 | 54 | 9 | 45 | | 27 |
| Ma-Mb | 85.72 | 1 | <0.001 | 119 | 9 | | 110 | 59.5 |
| Es-Mb | 27.26 | 1 | <0.001 | 155 | | 45 | 110 | 77.5 |

Bonferroni correction p < 0.025 ¹Mai ²Essekerende ³Mossoko Abuli

Table 3.12d Infants as the Only Neighbour to the Silverback

| Type | X ² | df | Sig | N | Bok ¹ N | Mob ² N | Exp N |
|------|----------------|----|-----|---|--------------------|--------------------|-------|
| Inf | na | na | Na | 8 | 8 | 0 | na |

¹Bokata ²Mobangui

3.4.4.2 Maternal Presence and Silverback-Immature Neighbours During Dispersed Group Spreads

Results are based on 106 scans. The mother was significantly more likely to be absent rather than present, when her son or daughter was one of a maximum of two neighbours to the silverback when the group was most dispersed (Table 3.13). The presence of an adult female as a neighbour to the silverback in addition to an immature or infant neighbour to the silverback who was not her offspring occurred in only one scan. The mother was significantly more likely

to be absent when old and young immatures were one of the two neighbours to the silverback during dispersed groups (Table 3.13). The mother was significantly more likely to be present when her infant was one of the two neighbours to the silverback during dispersed groups (Table 3.13).

When the two neighbours to the silverback were both young immatures or young immature/infant combinations, other (unknown) individual(s) within 6-10m of the silverback were no more likely to be absent than present ($X^2 = 0.73$, $df = 1$, $p = 0.394$, $N = 22$); although five scans were unknown. When any combination of immature/infant were the only two neighbours to the silverback, other (unknown) individual(s) within 6-10m of the silverback were no more likely to be absent than present ($X^2 = 1.98$, $df = 1$, $p = 0.160$, $N = 41$).

Table 3.13 Maternal Presence as a Neighbour to the Silverback, when the Group is Most Dispersed and when there is a Only a Maximum of Two Neighbours to the Silverback

| Type | X^2 | df | Sig | N | Abs ^a N | Pres ^b N | Exp N |
|----------|-------|----|--------|-----|--------------------|---------------------|-------|
| ii & inf | 27.51 | 1 | <0.001 | 106 | 80 | 26 | 53 |
| oi | 4.456 | 1 | 0.035 | 11 | 9 | 2 | 5.5 |
| yi | 49.61 | 1 | <0.001 | 75 | 68 | 7 | 37.5 |
| inf | 9.80 | 1 | 0.002 | 20 | 3 | 17 | 10 |

^aAbsent ^bPresent

A mother was no more likely to be absent rather than present, when her son or daughter was a neighbour to the silverback in those cases where only three neighbours were seen and the group was most dispersed (Table 3.14). Results are based on 39 scans. The presence of an adult female as a neighbour to the silverback in addition to an immature or infant neighbour to the silverback who was not her offspring, occurred in only five scans. The mother was no more likely to be absent rather than present when an old or young immature was one of three neighbours to the silverback in these dispersed groups (Table 3.14); note old immature sample sizes were very small, making statistics problematic. The mother was significantly more likely to be present when an infant was one of the three neighbours to the silverback (Table 3.14).

Table 3.14 Maternal Presence as a Neighbour to the Silverback when the Group is Most Dispersed and when there is a Maximum of Three Neighbours to the Silverback

| Type | X ² | df | Sig | N | Abs ^a N | Pres ^b N | Exp N |
|----------|----------------|----|-------|----|--------------------|---------------------|-------|
| ii & inf | 0.64 | 1 | 0.423 | 39 | 17 | 22 | 19.5 |
| oi | 1.00 | 1 | 0.317 | 4 | 3 | 1 | 2 |
| yi | 0.18 | 1 | 0.670 | 22 | 12 | 10 | 11 |
| inf | 6.23 | 1 | 0.013 | 13 | 2 | 11 | 6.5 |

^aAbsent ^bPresent

3.4.5 Changes in Proximity between Females and the Silverback over Time

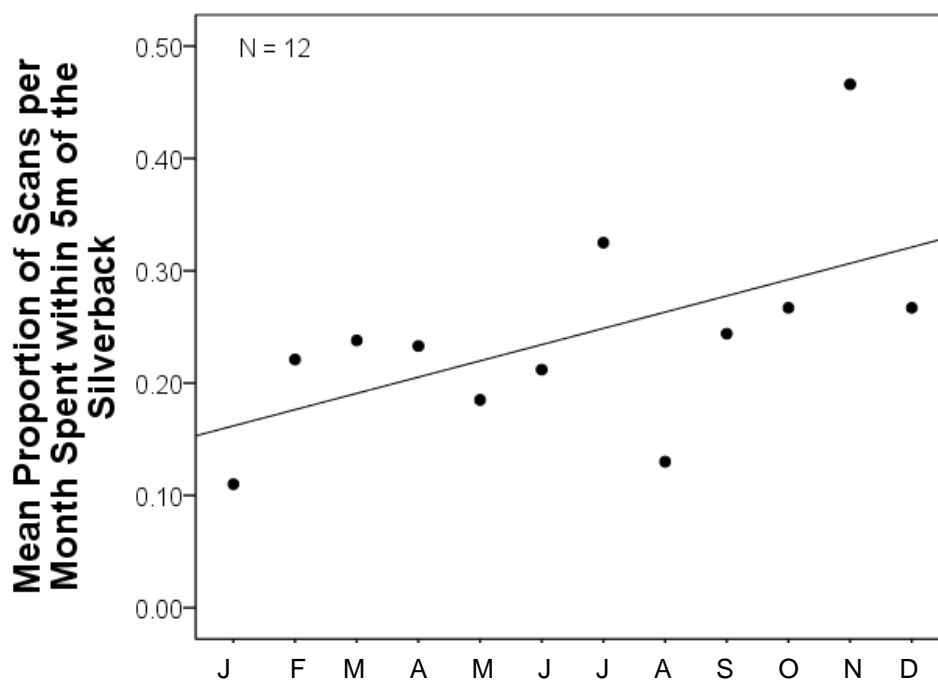
Adult females were observed as neighbours to the silverback 740 times. Mopambe was seen as a neighbour 208 times (33%), Bombe was seen 204 times (32%) and Malui was seen 224 times (35%). Each female spent approximately the same proportion of time as a neighbour to Makumba in 2007. Additionally, only one adult female was a neighbour to Makumba in 315 scans and two adult females were neighbours to Makumba at the same time in only 48 scans. Since three adult females were neighbours to Makumba at the same time in only two scans, this category was omitted from analysis. Makumba was significantly more likely to have only one adult female as a neighbour at any given time by comparison to two adult females ($X^2 = 196.39$, $df = 1$, $p < 0.001$, $N = 363$).

However, Malui was the only female whose presence as a neighbour to Makumba increased significantly and temporally throughout the study period (Malui: $B = 0.016$, $SE = 0.006$, Standardised Beta = 0.154, $df = 1,251$, $p = 0.014$, $R^2 = 0.020$, $N = 252$, Figure 3.2; Mopambe; $B = -0.006$, $SE = 0.006$, Standardised Beta = -0.065, $df = 1, 250$, $p = 0.306$, $N = 251$; Bombe; $B = -0.010$, $SE = 0.006$, Standardised Beta = -0.108, $df = 1, 250$, $p = 0.089$, $N = 251$).

Was Malui's linear increase over the year as a neighbour to Makumba an artefact of poor habituation? If so, one would expect Malui to have aggressed humans the most, and for this aggression to decrease as habituation and thus the year progressed. However, Bombe by far aggressed human observers the most (Chapter 5) while there was no significant change in aggression by Malui towards humans as the year progressed ($B = 0.006$, $SE = 0.004$, Standardised Beta = 0.100, $df = 1,254$, $p = 0.113$, $N = 255$). Intragroup dynamics appeared to

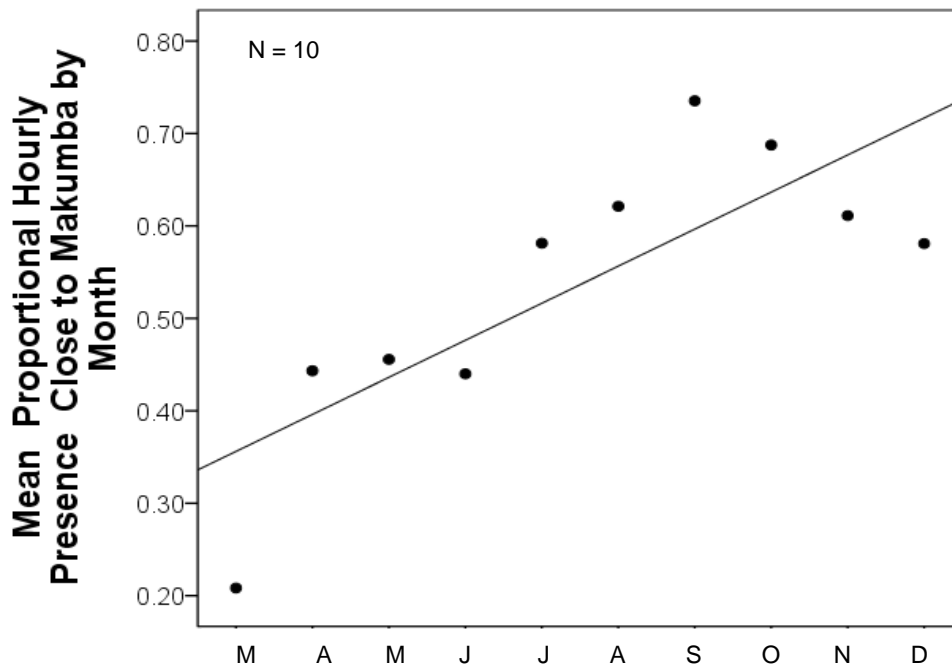
be influencing Malui's increasing presence as a neighbour to Makumba; she was pregnant and gave birth Dec 4th. Figure 3.2 shows a clear outlier in November. When November is excluded from analysis, Malui's increasing temporal presence as a neighbour to the silverback disappears ($B = 0.009$, $SE = 0.007$, Standardised Beta = 0.086, $df = 1,227$, $p = 0.193$, $N = 228$). This month is biologically significant as it was the month before Malui gave birth, and should therefore remain in the analysis; November may have represented a risky period for Malui just prior to birth.

Figure 3.2 Mean Proportion of Malui's Monthly Scans Spent within 5m of the Silverback



Mopambe was the only female whose hourly presence close (or hourly roll call) to Makumba increased throughout the study period (Malui: $B = 0.006$, $SE = 0.010$, Standardised Beta = 0.047, $df = 1,188$, $p = 0.523$, $N = 189$; Mopambe: $B = 0.033$, $SE = 0.009$, Standardised Beta = 0.250, $df = 1,188$, $p = 0.001$ $R^2 = 0.058$, $N = 189$, see Figure 3.3; Bombe: $B = -0.008$, $SE = 0.010$, Standardised Beta = -0.064, $df = 1,188$, $p = 0.386$, $N = 189$).

Figure 3.3 Mopambe's Mean Hourly Presence Close to the Silverback per Month^a

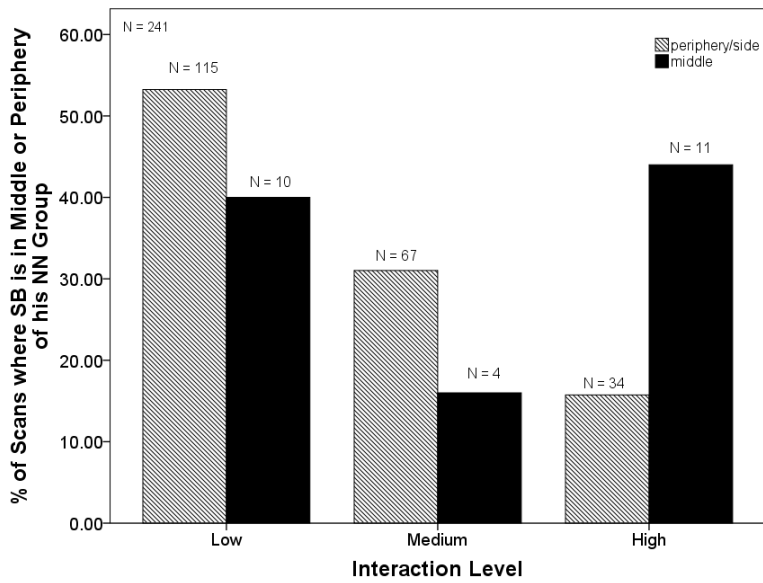


^aJanuary to Mid-March is excluded from analysis, since hourly data collection only began in Mid-March (Section 3.3.3). When March is excluded from analysis, results are still significant ($B = 0.026$, $SE = 0.010$, Standardised Beta = 0.190, $p = 0.010$, $df = 1, 179$, $R^2 = 0.031$, $N = 180$ sessions and 9 months)

3.4.6 Silverback Location in His 5m Neighbour Group

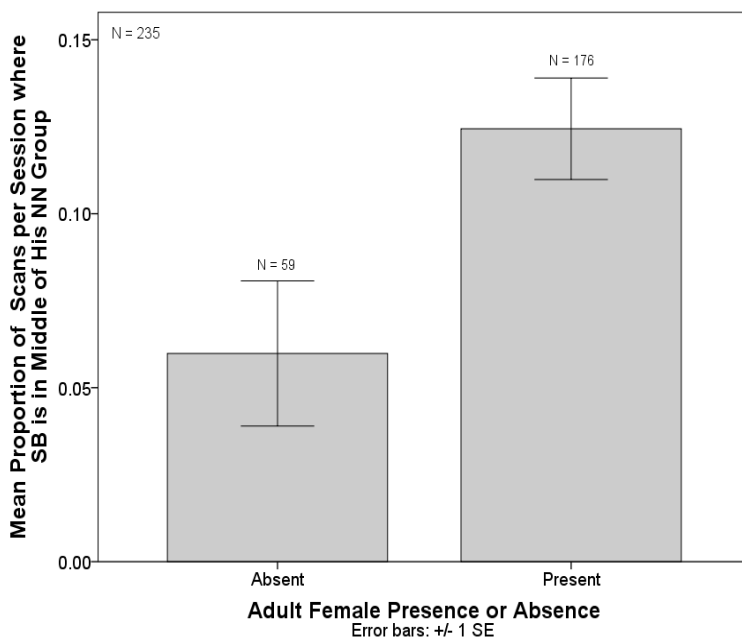
Results are based on 1481 scans. Makumba was seen in the (1) middle of his neighbour group in 174 scans, and (2) at the periphery of his neighbour group in 1307 scans. Makumba was significantly more likely to be located at the periphery of his neighbour group than the middle ($X^2 = 866.77$, $df = 1$, $p < 0.001$, $N = 1481$). His location was unrelated to seasonal, temporal or environmental variables (see predictors, Table 3.1). However, as interaction level with extragroup members increased, the silverback was significantly more likely to be located in the middle of his neighbour group ($B = 0.587$, $SE = 0.347$, $Wald = 6.111$, $df = 1, 3$, $Exp(B) = 2.356$, $p = 0.013$, $R^2 = 0.134$, $N = 98$; Figure 3.4; for predictors see Table 3.2).

Figure 3.4 Interaction Level in Relation to Silverback Location in His 5m Neighbour Group



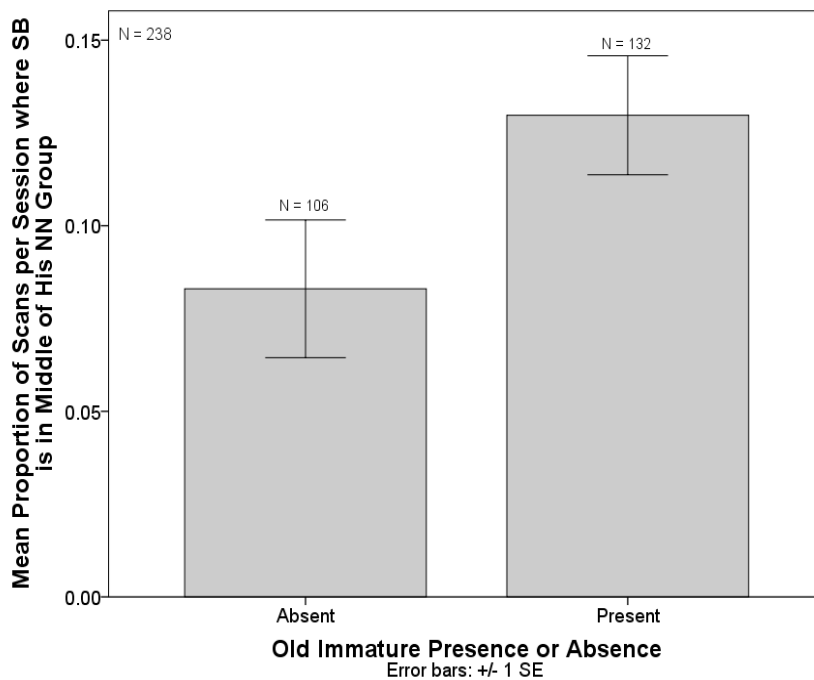
The silverback was significantly more likely to be in the middle of his neighbour group when adult females were present within that group ($B = 0.125$, $SE = 0.039$, Standardised Beta = 0.207 , $df = 1, 234$, $p = 0.001$, $R^2 = 0.039$, $N = 235$, Figure 3.5; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and grouped observer-silverback distance).

Figure 3.5 Silverback Location in the Middle of His 5m Neighbour Group in Relation to the Adult Female Presence within His Group



In addition, the silverback was significantly more likely to be in the middle of his group of neighbours when old immatures were present ($B = 0.088$, $SE = 0.034$, Standardised Beta = 0.166 , $df = 1$, 237 , $p = 0.010$, $R^2 = 0.023$, $N = 238$, Figure 3.6; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and grouped observer-silverback distance).

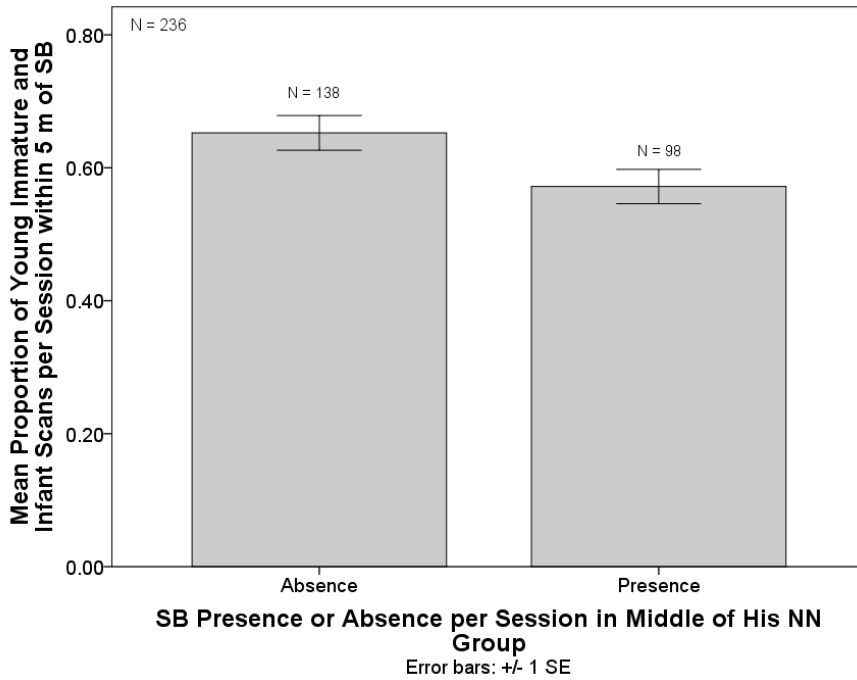
Figure 3.6 Silverback Location in the Middle of His 5m Neighbour Group in Relation to the Old Immature Presence within His Group



By contrast, the silverback was significantly more likely to be at the periphery of his group of neighbours, as the proportion of young immature and infants increased within that group ($B = -0.151$, $SE = 0.056$, Standardised Beta = -0.170 , $df = 1$, 235 , $p = 0.008$, $R^2 = 0.025$, $N = 236$, Figure 3.7; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and grouped observer-silverback distance). Additionally, in relation to young immatures, as mean total observers increased, the silverback was more likely to be at the periphery of his group of neighbours, although this relationship just failed to reach significance ($B = -0.121$, $t = -1.453$, $p = 0.056$, $N = 236$). The remaining control variables, apart from month ($B = -0.016$, $SE = 0.005$, Standardised Beta = -0.215 , $p = 0.007$, $R^2 = 0.039$, $df = 1$,

236, N = 236) were not significant (season $p = 0.228$; maximum temperature $p = 0.610$; daily rainfall $p = 0.902$, grouped observer-silverback distance $p = 0.902$).

Figure 3.7 Silverback Presence or Absence in the Middle of His 5m Neighbour Group in Relation to the Mean Proportion of Young Immatures and Infant Scans per Session^a



^aThis graph is structured oppositely to Figures 3.5 and 3.6 (see Section 3.3.4 for rationale)

A similar trend regarding mean total observers and silverback periphery location was found for older immatures (mean total observers $B = -0.122$, $t = -1.923$, $p = 0.056$; month $B = -0.012$, $SE = 0.005$, Standardised Beta = -0.167 , $df = 1$, 237 $p = 0.010$; $R^2 = 0.039$, $N = 238$; season $p = 0.228$, maximum temperature $p = 0.665$, daily rainfall $p = 0.138$, grouped observer-silverback distance $p = 0.167$), and adult females (mean total observers $B = -0.122$, $t = -1.965$, $p = 0.051$; month $B = -0.015$, $SE = 0.005$, Standardised Beta = -0.203 , $df = 1$, 234 $p = 0.001$, $R^2 = 0.037$, $N = 235$; season $p = 0.228$, maximum temperature $p = 0.416$, daily rainfall $p = 0.250$, grouped observer-silverback distance $p = 0.161$).

3.4.7 Silverback Location within the Entire Group

Results are based on 3008 scans. Makumba was seen at the (1) front of the group in 229 scans, (2) back of the group in 1998 scans, and (3) middle of the group in 781 scans. Makumba was significantly more likely to be in the back rather than the front ($X^2 = 1405.19$, $df = 1$, $p < 0.001$, $N = 2227$) or middle of the group ($X^2 = 532.96$, $df = 1$, $p < 0.001$, $N = 2779$). Makumba was significantly more likely to be in the middle of the group than the front of the group ($X^2 = 301.69$, $df = 1$, $p < 0.001$, $N = 1010$).

As the group dispersed, the silverback was more likely to be in the back of the group ($R^2 = 0.094$; Figure 3.8a and Table 3.15). In order to control for habituation biases, month was entered as a linear variable in the model; and as the year progressed, Makumba was significantly more likely to be in the back of the group ($R^2 = 0.028$; Figure 3.8b and Table 3.15). As grouped observer-silverback distance increased, Makumba was less likely to be at the back of the group ($R^2 = 0.019$; Figure 3.8c and Table 3.15).

The silverback was significantly more likely to be in the back of the group in the late morning and early afternoon when compared to early morning (early morning was used as the baseline reference category since it should be the most stable part of the day; the group should normally be cohesive and preparing to leave their nests), but no more likely to be in the back of the group in the late afternoon when compared to early morning (overall variable $R^2 = 0.007$; Figure 3.8d and Table 3.15). As total numbers of observers increased, Makumba was significantly more likely to be in the back of the group ($R^2 = 0.003$; Figure 3.8e and Table 3.15), and as the number of neighbours within 5m to Makumba increased, he was significantly less likely to be in the back of the group ($R^2 = 0.002$; Figure 3.8f and Table 3.15). For predictors, see Table 3.3.

Table 3.15 Logistic Regression of Factors Predicting Silverback Location in the Back of the Entire Group: Overall Model $X^2 = 282.88$, $df = 8$, $p < 0.001$, $R^2 = 0.153$, $N = 2361$

| Predictors | B | S.E. | Wald | df | Model R ² at each step | Exp(B) | Sig |
|---|---------|-------|---------|----|---|--------|--------|
| Constant | - 1.640 | 0.293 | 31.237 | 1 | - | 0.194 | <0.001 |
| Group Spread | 0.765 | 0.071 | 116.164 | 1 | 0.094 | 2.150 | <0.001 |
| Month | 0.091 | 0.013 | 49.929 | 1 | 0.122 | 1.095 | 0.004 |
| Grouped Observer-SB Distance | -0.282 | 0.048 | 34.968 | 1 | 0.141 | 0.754 | <0.001 |
| Time Block (cat ^a – ref. ^b early morning) | | | 13.437 | 3 | 0.148 | - | 0.004 |
| Time Block (early morning – late morning) | 0.431 | 0.154 | 7.814 | 1 | - | 1.539 | 0.005 |
| Time Block (early morning -early afternoon) | 0.433 | 0.159 | 7.398 | 1 | - | 1.542 | 0.007 |
| Time Block (early morning - late afternoon) | 0.089 | 0.185 | 0.232 | 1 | - | 1.093 | 0.630 |
| Total Observers | 0.103 | 0.045 | 5.277 | 1 | 0.151 | 1.108 | 0.022 |
| Neighbours to SB (5m) | -0.071 | 0.035 | 4.119 | 1 | 0.153 | 0.932 | 0.042 |

^acategory ^b reference category

Figure 3.8a Silverback Location within the Entire Group as a function of Group Spread

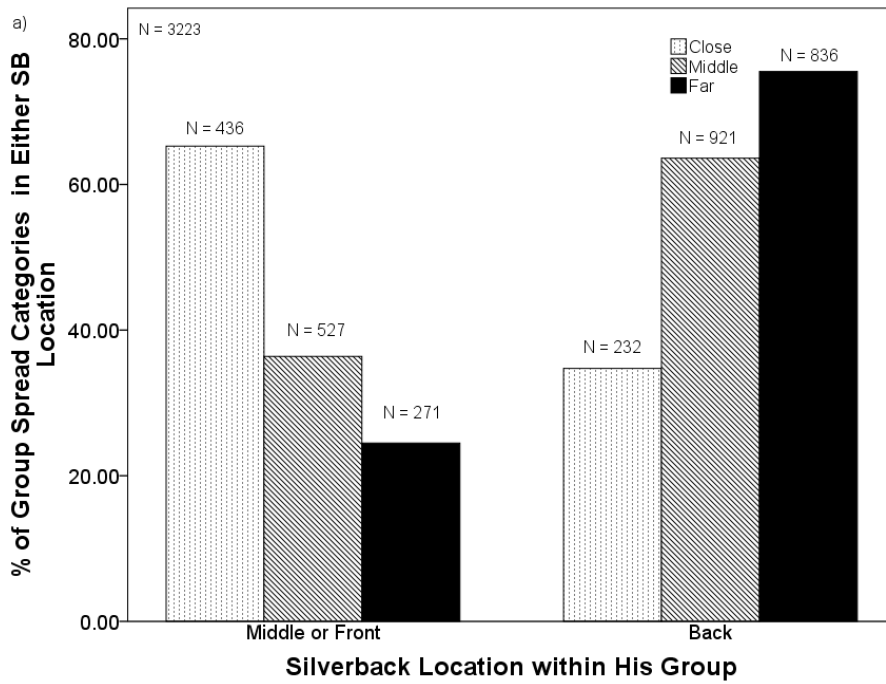
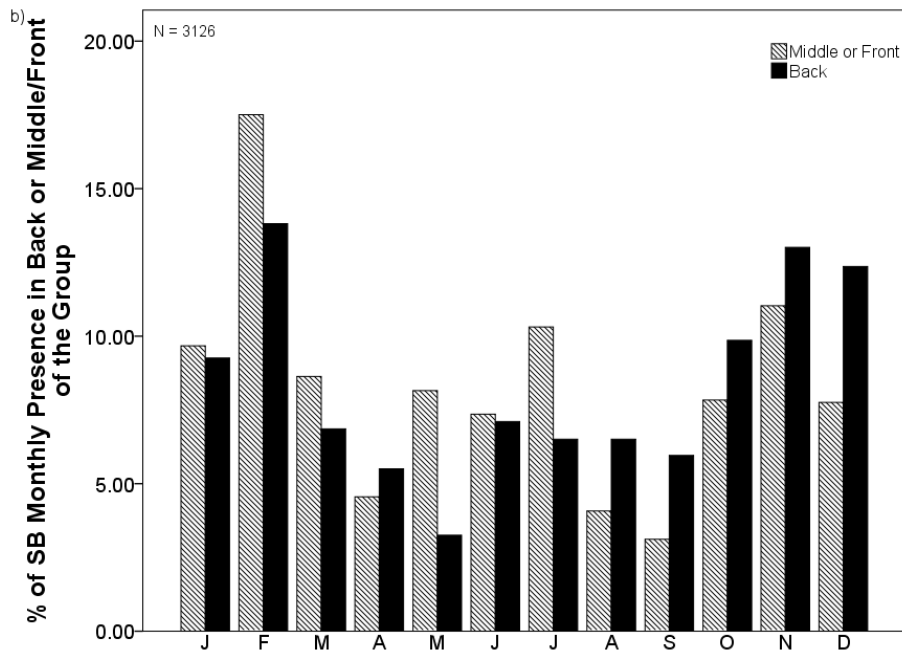


Figure 3.8b Silverback Location within the Entire Group by Month



Jan Middle/Front N (mf) 121, Back (b) 185; Feb mf 219, b 276; Mar mf 108, b 137; Apr mf 57, b 110; May mf 102, b 65; Jun mf 92, b 142; Jul mf 129, b 130; Aug mf 50, b 130; Sep mf 39, b 119; Oct mf 98, b 197; Nov mf 138, b 260; Dec mf 97, b 24

Figure 3.8c Silverback Location within the Entire Group as a function of Observer-Silverback Distance

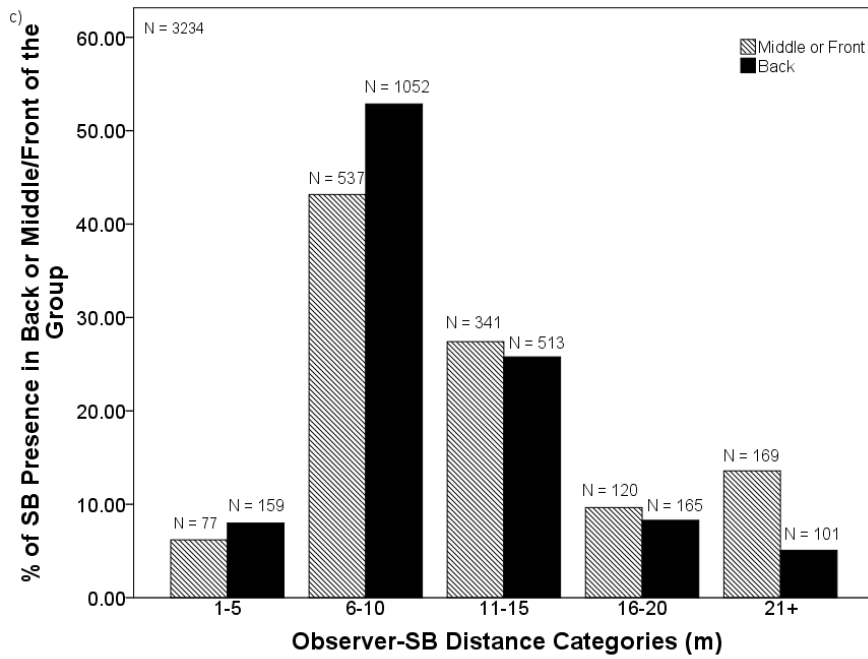


Figure 3.8d Silverback Location within the Entire Group by Time Block

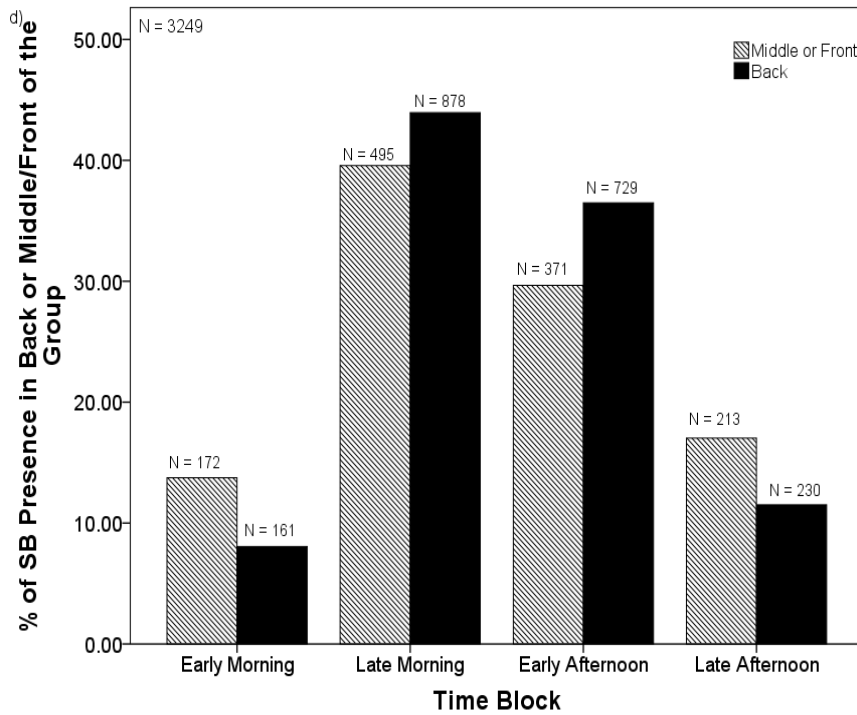


Figure 3.8e Mean Total Number of Observers in Relation to Silverback Location within the Entire Group

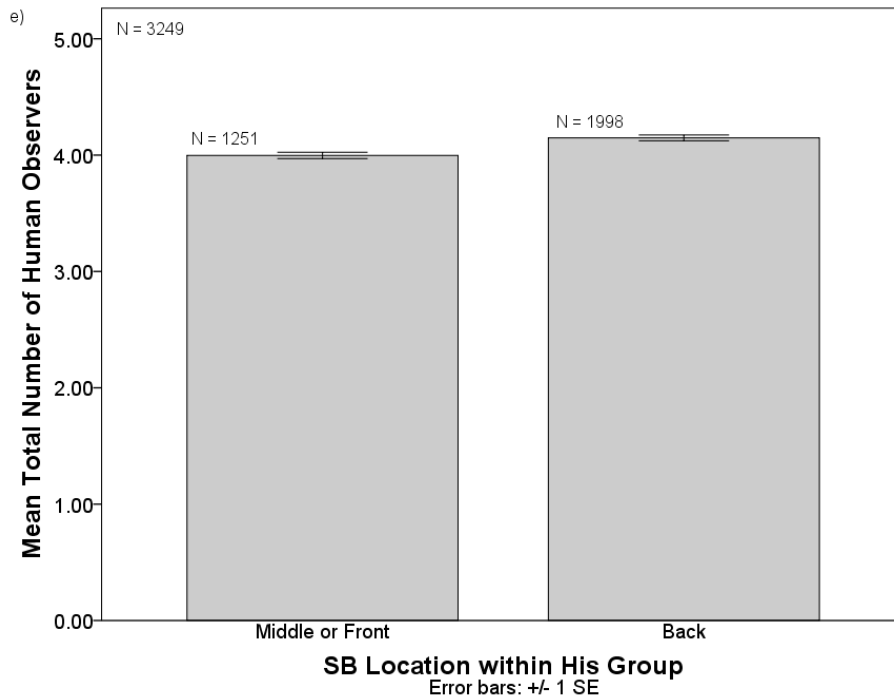
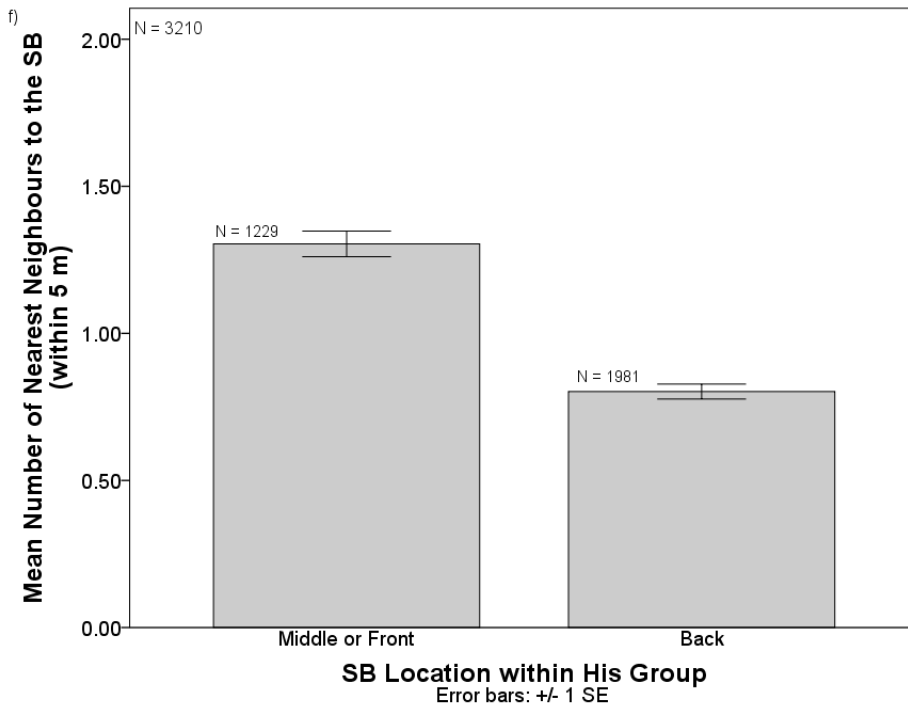
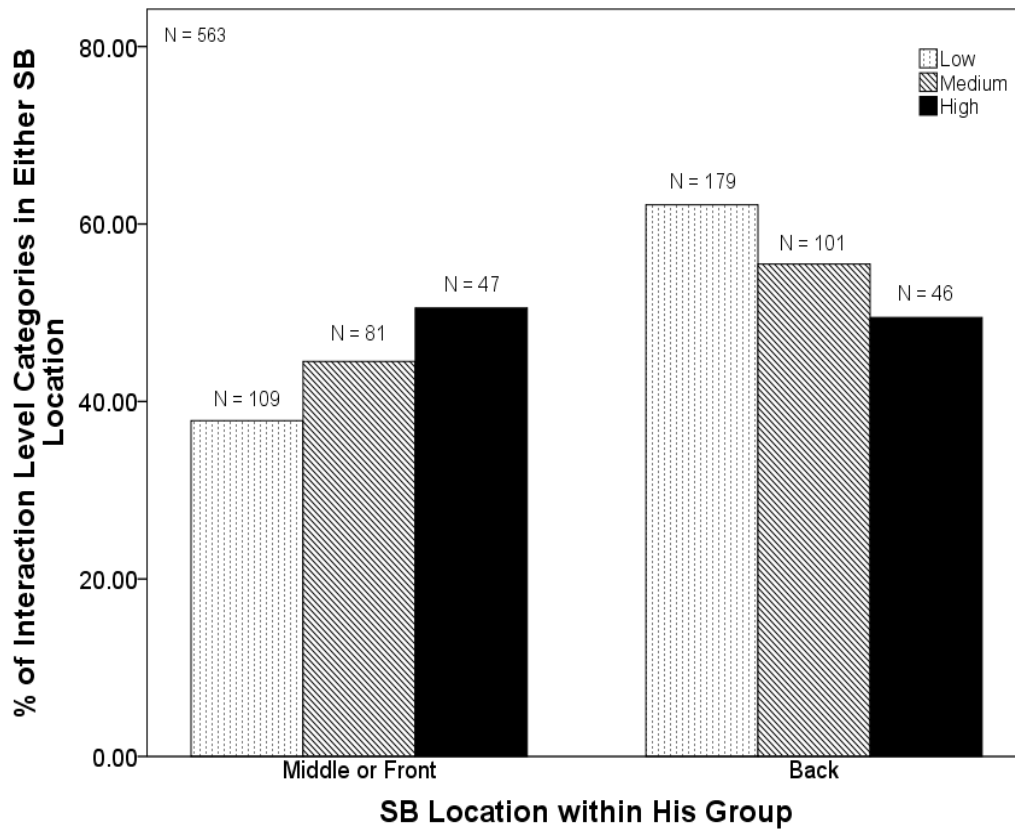


Figure 3.8f Mean Number of Neighbours (5m) to the Silverback in Relation to Silverback Location within the Entire Group



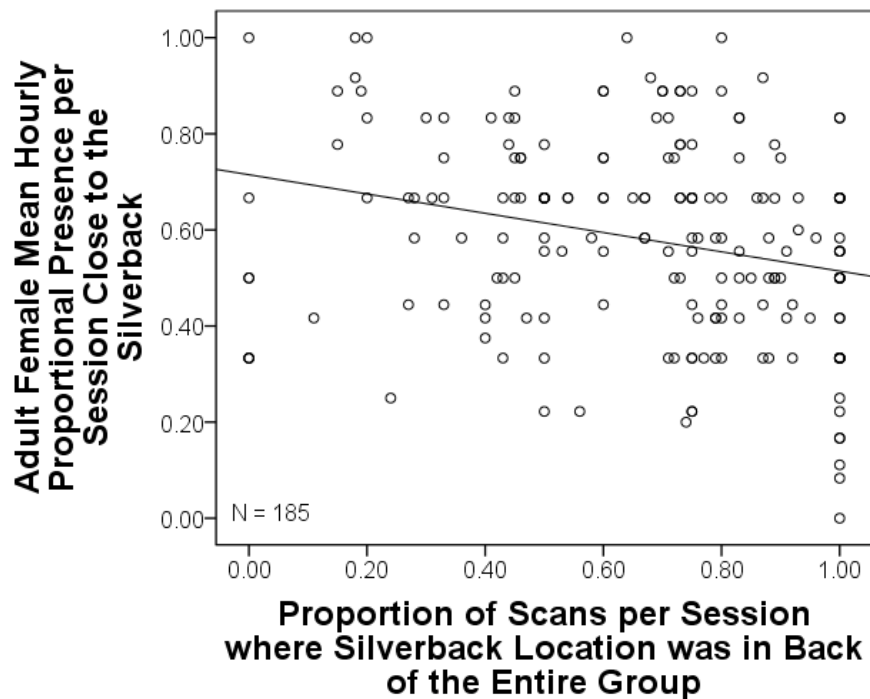
Additionally, as interaction level increased, the silverback was less likely to be in the back of the group ($B = -0.405$, $SE = 0.145$, $Wald = 7.845$, $df = 1, 9$, $Exp(B) = 0.667$, $p = 0.005$, $R^2 = 0.014$, $N = 436$; Figure 3.9). For predictors, see Table 3.2.

Figure 3.9 Interaction Level in Relation to Silverback Location within the Entire Group



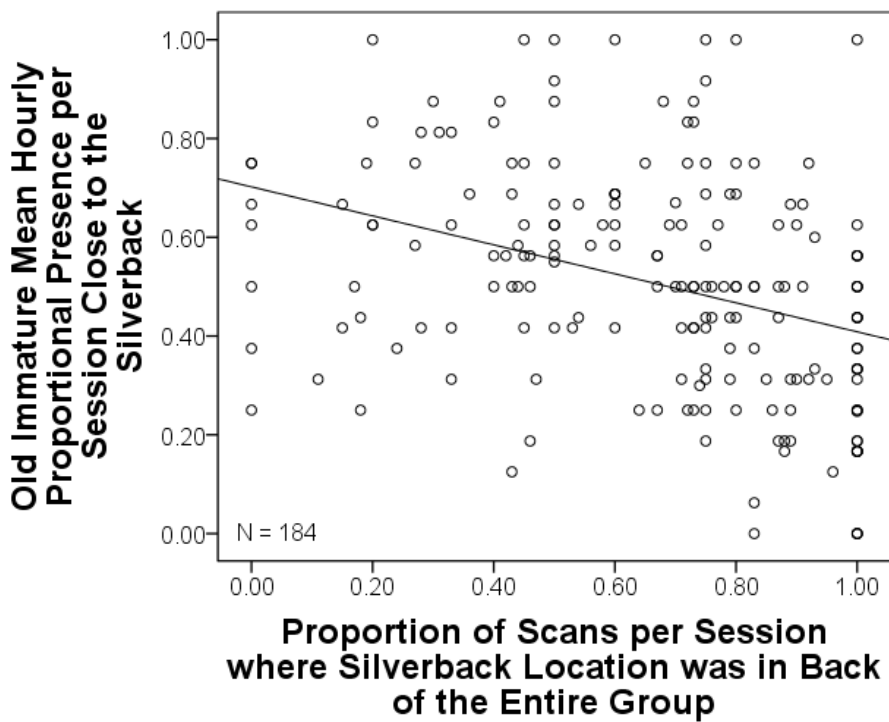
The silverback was significantly less likely to be in the back of his group, as adult female proportional hourly presence close to the silverback increased ($B = -0.343$, $SE = 0.087$, Standardised Beta = -0.262 , $df = 1, 184$, $p < 0.001$, $R^2 = 0.057$, $N = 185$, Figure 3.10; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and median grouped observer-silverback distance).

Figure 3.10 Mean Hourly Presence of Adult Females Close to the Silverback per Session in Relation to the Proportion of Scans per Session where the Silverback was Located at the Back of his Entire Group



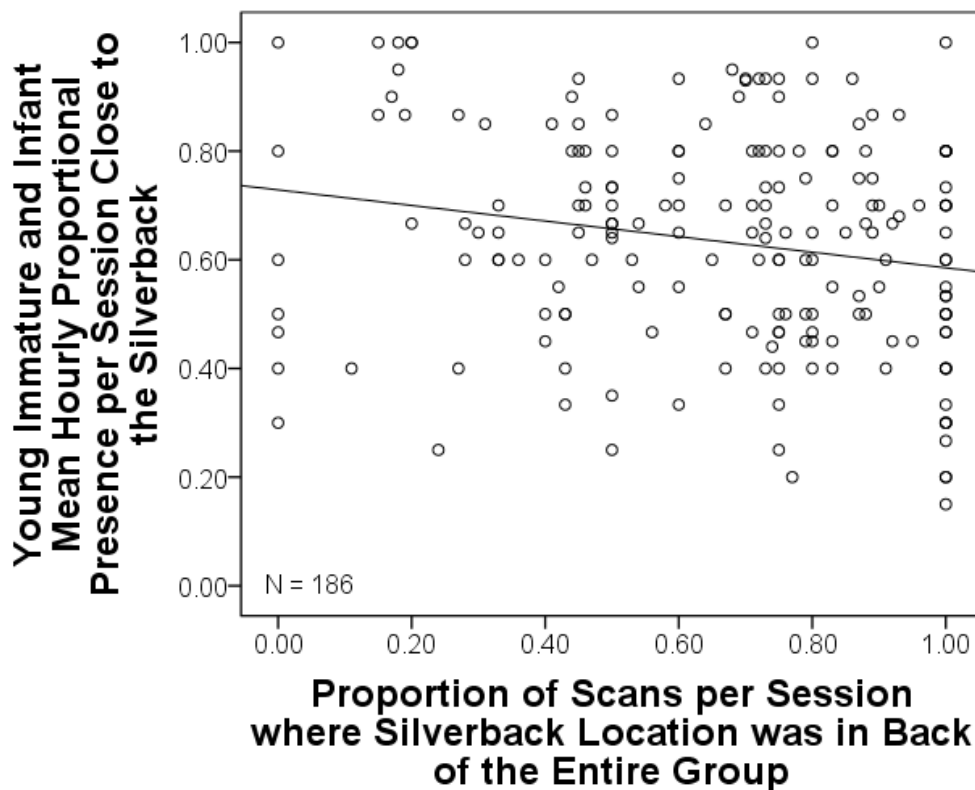
As with female presence, the silverback was significantly less likely to be in the back of his group, as old immature proportional hourly presence close to the silverback increased ($B = -0.408$, $SE = 0.081$, Standardised Beta = -0.338 , $df = 1, 183$, $p < 0.001$, $R^2 = 0.12$, $N = 185$, Figure 3.11; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and median grouped observer-silverback distance).

Figure 3.11 Mean Hourly Presence of Old Immatures Close to the Silverback per Session in Relation to the Proportion of Scans per Session where the Silverback was Located at the Back of his Entire Group



Again, the silverback was significantly less likely to be in the back of his group, as young immature and infant proportional hourly presence close to the silverback increased ($B = -0.297$, $SE = 0.093$, Standardised Beta = -0.215 , $df = 1, 185$, $p = 0.002$, $N = 186$, $R^2 = 0.042$, Figure 3.12; controlled for month to take into effect habituation, season, daily rainfall, maximum temperature, mean total observers and median grouped observer-silverback distance).

Figure 3.12 Proportion of Scans per Session where the Silverback was Located at the Back of his Entire Group in Relation to the Mean Hourly Proportional Presence per Session of Young Immatures and Infants Close to the Silverback



In all the age-sex classes noted above, rainfall was also a predictor of silverback location. As daily rainfall increased (mm) the silverback was significantly less likely to be located at the back of the group (adult female hourly presence model: $B = -0.007$, $SE = 0.002$, Standardised Beta = -0.250 , $df = 1, 184$, $p < 0.001$, $N = 185$, $R^2 = 0.058$; old immature hourly presence model: $B = -0.007$, $SE = 0.002$, Standardised Beta = -0.262 , $df = 1, 183$, $p < 0.001$, $N = 184$, $R^2 = 0.076$;

young immature and infant hourly presence model; $B = -0.007$, $SE = 0.002$, Standardised Beta = -0.251 , $df = 1$, 185 , $p < 0.001$, $N = 186$, $R^2 = 0.045$).

3.4.8 Silverback Nesting

A total of 166 nest sites were recorded in 2007. Of the 155 nest sites where the location of the largest trail was known, the silverback was the sole individual closest to the largest trail on 107 nights, whereas another individual was the sole individual closest to the largest trail on 48 nights. Makumba was significantly more likely to nest closest to the largest trail than were other group members ($X^2 = 22.458$, $df = 1$, $p < 0.001$, $N = 155$).

As individuals nested further away from the silverback (expressed as one total median group distance per nest site), Makumba was significantly more likely to nest closest to the largest trail ($R^2 = 0.095$; Figure 3.13 and Table 3.16). As forest surrounding the silverback's nest site became less dense, he was significantly more likely to nest closest to the largest trail ($R^2 = 0.04$; Figure 3.14 and Table 3.16). No other factors entered into the models, including interaction level significantly predicted silverback nest site location in relation to the largest trail. For predictors, see Table 3.4.

Table 3.16 Logistic Regression of Factors Predicting Silverback Nest Location Closest to the Largest Trail: Overall Model $X^2 = 15.29$, $df = 2$, $R^2 = 0.135$, $p < 0.001$, $N = 151$

| Predictors | B | S.E. | Wald | df | Model R^2 at each step | Exp(B) | Sig |
|---|---------|-------|-------|----|--------------------------------|--------|-------|
| Constant | - 1.735 | 0.744 | 4.555 | 1 | - | 0.176 | 0.020 |
| Median Distance of All Group Members to the SB (m) | 0.144 | 0.053 | 7.363 | 1 | 0.095 | 1.155 | 0.007 |
| SB Nest Site Forest Density | 0.585 | 0.274 | 4.555 | 1 | 0.135 | 1.794 | 0.04 |

Figure 3.13 Median Distance of All Group Members to the Silverback in Relation to Silverback Nest Site Location Closest to the Largest Trail

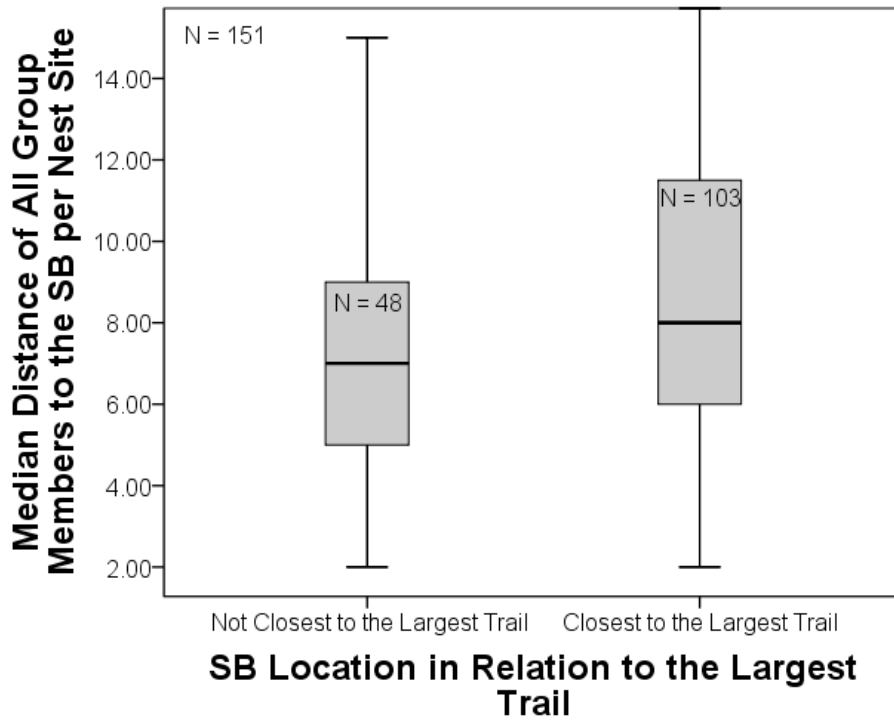
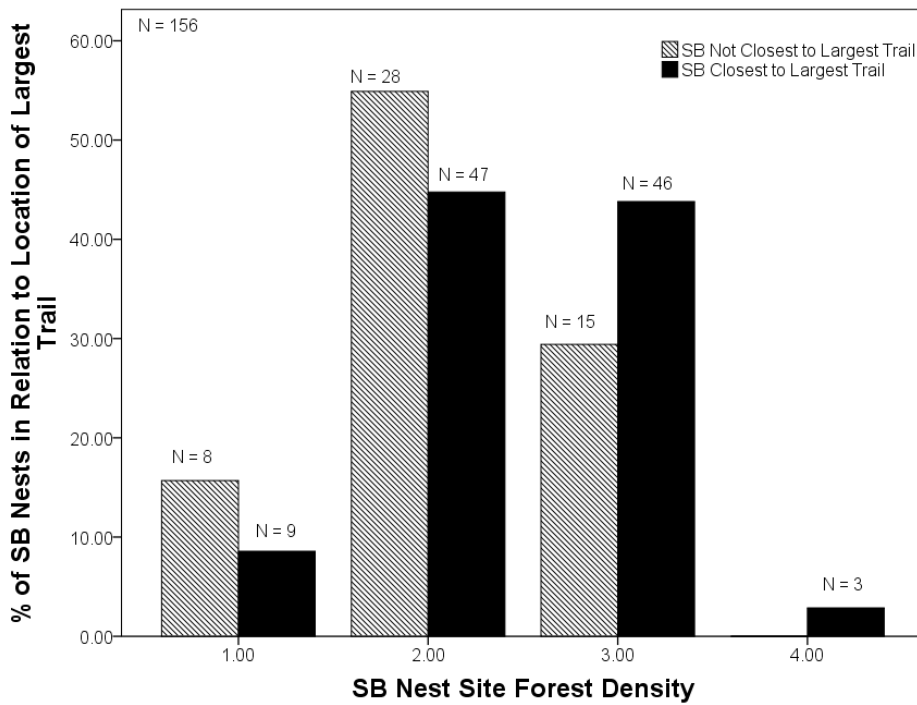


Figure 3.14 Silverback Nest Site Forest Density in Relation to Silverback Nest Site Location Closest to the Largest Trail



3.4.9 Nest Site Spatial Arrangement

Of the 160 nest sites where the spatial nest site arrangement was known, the ‘fan’ arrangement was observed on 141 nights, whereas the circle or irregular design was observed on 19 nights. The ‘fan’ design was significantly more likely to occur than the circle or irregular design ($X^2 = 93.03$, $df = 1$, $p < 0.001$, $N = 160$). This arrangement also suggested that the silverback was more likely to nest peripherally than not. See Section 3.3.5 for examples of either design.

When nest site arrangement was a fan design, the silverback’s nest was significantly more likely to be located in moderate forest types than were those of the remainder of the group ($X^2 = 9.89$, $df = 1$, $p = 0.002$, $N = 85$; Table 3.16) and significantly less likely to be located in dense forest than those of the remainder of the group ($X^2 = 3.898$, $df = 1$, $p = 0.048$, $N = 187$; Table 3.16). The silverback was no more likely to be seen in dense or moderate forest than the remainder of the group when nest site arrangement was a circle or irregular design (dense forest: $X^2 = 1.29$, $df = 1$, $p = 0.257$, $N = 7$; moderate forest: $X^2 = 0.14$, $df = 1$, $p = 0.705$, $N = 28$; Table 3.16). Analysis was performed on moderate and dense forest types only, since the silverback and modal group nest site forest density scores in the open category were the same, and only occurred on 3 exceptional circumstances (Chapter 4).

Table 3.16 Forest Density Scores for Silverback Nests and Group Nests in Relation to Nest Site Spatial Arrangement

| Fan Shape | SB | Total Group Mode | Other Shape | SB | Total Group Mode |
|-----------|-----|------------------|-------------|----|------------------|
| Open | 3 | 3 | Open | 0 | 0 |
| Moderate | 57 | 28 | Moderate | 5 | 2 |
| Dense | 80 | 107 | Dense | 13 | 15 |
| Total | 140 | 138 | Total | 18 | 17 |

3.5 DISCUSSION

This study clearly indicates that Makumba played an active protective role within his group and while data suggested that silverback-group relationships share the basic social foundations seen in mountain and eastern gorillas, there were also some obvious differences. Makumba spent only half of his time within 5m of at least one neighbour; however when bai environments were considered separately, the silverback was significantly more likely to have a neighbour than no neighbour. If the greater likelihood of neighbours in bais was simply an artefact of better observer visibility in open environments, then the silverback-neighbour results observed in bai environments would also be expected in the most open of forested environments. However in open forest habitats, Makumba again spent nearly half of his time alone. Even though Nowell [2005] suggests that the openness of bais relaxes the need for close proximity (particularly for immatures) near the silverback (her categories ranged from 2-10m), results here indicated the opposite. At least for the Dzanga region, bais could be perceived as risky environments.

While bais afford greater visibility, the sense of security that hidden dense environments may provide is lacking in clearings. In forest clearings animals congregate to feed or socialize, notably elephants, buffalo and gorillas [Fishlock, 2010; Nowell 2005; Parnell, 2002b]. Elephants can be very aggressive, particularly when males are in musth or when they feel threatened. Buffalo on the other hand are simply unpredictable. While these animals can and often do coexist peacefully in bai environments, there are occasions when this is not the case [pers. obsv.; Turkalo pers. comm.]. The sheer openness means that escape routes from charging elephants or buffalos via trees are not as easily accessible as in the forest [Parnell, 2002b]. Additionally, the swampy and muddy nature of bais can make quick escapes difficult [Fishlock, 2010; Parnell, 2002b; pers. obsv.]. This vulnerability may explain why the Makumba group almost always stayed relatively close to the forest edge when feeding in large clearings [pers. obsv.].

At Mbeli Bai, Parnell [2002b] noted that gorillas (especially silverbacks and blackbacks) almost always monitored the location of elephants when in bais, although the level of surveillance

varied. Levrero [2005] found that adult males were most responsible for monitoring behaviours when in Lokoué Bai, Republic of Congo, and 5.5% of group activity time was spent on surveillance. Although not specifically measured in this study, Makumba appeared to monitor his group and the bai intensely (more intensely than in forests), by constantly changing direction to survey while bai feeding. It can be suggested that the Makumba group was familiar with individual elephants in the area, for they often reacted with caution to some and nonchalance to others.

Gorillas spend most of their time in bays feeding, not socializing [i.e. Levrero, 2005; Parnell, 2002b]. Thus clustering near the silverback in bays most likely holds a strong protective function. Parnell [2002b] observed upon detection of a crocodile, that individuals quickly sought proximity close to their dominant male who then led them away from the area. A silverback will aggress animals much larger than itself in protection of his group [Parnell, 2002b; pers. obsv.].

Silverback-neighbour analysis revealed interesting similarities to mountain and eastern lowland gorillas and again stressed the protective nature of the silverback-group relationship. In forest environments, young immatures were significantly more likely to be NN1-NN4 than were both adult females and old immatures. Adult females were only significantly more likely than old immatures to be the closest neighbour (NN1), but NN2-NN4 showed no significant difference among these age-sex classes. In bay environments, young immatures were significantly more likely than adult females to be NN1-NN2, and when compared to old immatures, were only significantly more likely to be a NN1 to the silverback, whereas adult females were generally no more likely to be NN1-NN4 than were old immatures.

In forests, young immatures were the most likely age class to be seen as any neighbour (NN1-NN4) to the silverback. In mountain gorillas, older immature males decrease time spent in close proximity to the silverback (Section 3.2.2), thus it is not surprising that adult females were more likely to be a NN1 to Makumba than were the older immatures, two of which were male and two of which were adult or nearly adult females. While young immatures were again the age class most likely to be seen as a neighbour to the silverback in bays, this difference disappeared at distance further from the silverback. Two possibilities could explain this difference: (1) in bays,

young immatures may take less interest in being a 'further' (i.e. still a neighbour but not the closest one) neighbour to Makumba because they may prefer to stay closer to their mothers when they are not able to remain very close to the silverback, or; (2) while young immatures still maintain the closest positions to Makumba, the potentially riskier bai may cause an increase in competition for the 'further' (i.e. NN4) neighbour positions, causing a tug of war situation resulting in an equalization across age-sex classes. One anomaly needs noting: old immatures were more likely to be a NN2 to Makumba than were adult females in bais. This apparently contradicts earlier evidence that older immatures in this study decreased their proximity to the silverback, except that (1) earlier results referred to NN1, most likely a more sought out position, and (2) in riskier bai environments, older immatures particularly females may have sat closer to the silverback to offer greater protection to their younger siblings whilst their mothers spent necessary time feeding. In fact, the two older immature females were seen as a neighbour to the silverback in a greater proportion of bai scans than were the old immature males.

Due to the limited visibility and effects of habituation, detection of all individuals within 5m was not always possible or accurate. Therefore responsibility for proximity remains unknown as does the possibility that certain individuals may have sat closer to the silverback because they were seeking proximity with another individual rather than to Makumba.

Age-sex class neighbour preferences in both forest and bai environments followed the same predictable pattern as discussed in by Stewart [2001], Harcourt [1979a, 1979b], and Watts & Pusey [1993], among others (Section 3.2.2): (1) the older the infant was, the more likely he/she was to be a neighbour to the silverback; (2) the more juvenile the young immature (i.e. the 'younger' young immature) was, the more likely he/she was to be a neighbour to the silverback, and; (3) adolescent females were more likely to be a neighbour to the silverback than were adolescent males. Also worth mentioning is the fact that infants were seen alone as neighbours of the silverback in forest environments only in all but one scan; perhaps they were more likely to be near or in contact with their mother in riskier bai environments.

But do western lowland silverbacks babysit as seen in mountain gorillas (Section 3.2.2)? Results from this study indicate that they do, but in small groups. For analysis, only scans where the group was most dispersed (i.e. where a maximum of three individuals were present within 20m of the silverback) were included into this analysis to reduce the possibility that another gorilla (potentially a mother) could be present but not visible out of the 5m silverback-neighbour delineation. In situations where the group was most dispersed and where only one neighbour to Makumba was present, young immatures were the most likely neighbour. In these dispersed situations preferences were again as expected regarding silverback protective functions (see above and Section 3.2.2); the 'youngest' young immature was most commonly seen as the neighbour to the silverback and the oldest infant was the only infant to be seen as a neighbour to the silverback. Additionally during these dispersed contexts, individuals were more likely to be absent at distances of 6-10m from the silverback. Of course there was still a chance that up to two individuals may have been present within 11-20m of Makumba, however (1) forests can be very dense, and even if a mother is potentially present at these distances, it is likely that she will not be within visible and caretaking range of her infant, and; (2) due to the thick forest it was often difficult to confirm with 100% certainty that individual's were absent within 20m of the silverback. However, in most situations when the group was most dispersed, it appeared that individuals remained within close proximity to the silverback when present and therefore in the visual field of the recorder.

When the group was most dispersed and only two neighbours to Makumba were present, and where at least one individual was a young immature, the mother was significantly more likely to be absent as the other neighbour to the silverback. When at least one individual was an infant, the mother was significantly more likely to be present as the other neighbour to the silverback. Another gorilla was no more likely to be present rather than absent within 6-10m of the silverback, for both age-sex classes.

When the group was most dispersed and three neighbours to Makumba were present where at least one individual was a young immature, the mother was no more likely to be present than absent. However when one neighbour was an infant, the mother was significantly more likely to be present as a neighbour to the silverback. These results indicate that Makumba did act as a

babysitter, but generally only with one or two individuals at a time. An interesting future analysis would be to examine silverback babysitting relationships in terms of group activity budgets as has been done in earlier mountain gorilla studies (Section 3.2.2).

When analysing the year in total, all adult females spent an equal amount of time as a neighbour to the silverback in both bais and forest environments. This result implies that Makumba shared his time equally amongst the adult females or that the adult females shared their time equally with Makumba. This sharing of access is further revealed by the fact that Makumba was more likely to have only one adult female neighbour at any given time. As mentioned in Section 3.2.2, a silverback's objective in order to maximise his reproductive success is to acquire and then 'retain' as many adult females as possible; by allowing competition for access to escalate, he risks discord amongst females in his group, and the prospect of their emigration. Although speculative in the absence of proximity matrices and measures of responsibility for proximity, the fact that adult females shared 'sole' access to Makumba suggest that like Harcourt's [1979b] and Yamagiwa's [1983] studies on mountain and eastern lowland gorillas respectively, adult females were more attracted to the silverback than each other.

When analysing data in a temporal sequence over the course of the study year, Malui's presence as a neighbour increased throughout the study period and this increase was not an artefact of habituation. Malui was pregnant, and she gave birth at the beginning of December. As her pregnancy progressed she spent more and more time as a neighbour to the silverback. Malui's presence as a neighbour to Makumba increased dramatically the month before she gave birth, and then decreased substantially in December. Harcourt [1979b] found that one female increased time spent near the dominant male threefold over the 10 days post-parturition when compared to the 11 months pre-parturition (Section 3.2.2). Although he did not look specifically at the month prior to birth, the female preferred to stay in close proximity to the adult male directly after birth. Malui's patterns contradict those noted by Harcourt [1979b] but direct comparison is difficult because he included all 11 months prior to birth in his analysis, and I included the entire month after birth instead of just the 10 days post-parturition. Infants are highly attractive and in captivity, western lowland females tend to cluster with other mothers and

immatures after birth (Section 3.2.4.2). Malui's post-birth decrease in proximity to the silverback (when compared to November) may have been a result of other group members' competition for access to the newborn, although without complete relationship matrices this theory can only remain speculative. Additionally whilst not within the 5m neighbour delineation, Malui may have still remained within visual and auditory proximity to the silverback.

In November, Malui was visibly pregnant and close to parturition; this time may also have been tense since an intergroup interaction or a violent intragroup fight could have potentially harmed the offspring or the mother. Interestingly, Makumba's rate of herding Malui and copulations increased dramatically by comparison to the other adult females in the group. Herding began around two months post-conception: did Makumba know she was pregnant? At this point she was certainly not outwardly appearing pregnant. Infanticide risks (Section 3.2.2 and Chapter 4) suggest that Malui would be less willing to emigrate at this point, so why would Makumba herd her more? Perhaps in anticipation of a new infant, Makumba was either intimidating her or displaying his protective abilities to ensure she would stay within the group [Parnell, 2002b]. It is also possible that Makumba was unaware of Malui's pregnancy, since increases in herding appear to have coincided (within a month) with the start of the high intergroup interaction period (Chapter 4). As she was the only female with an almost fully weaned infant, he might have been more aggressive towards her in order to block any attempts to emigrate. Post-conception mating is proposed to be a tactic used by pregnant females to compete with other females for sperm and to ensure paternity [Doran et al., 2009]. Paternity assurance may explain the higher rate of Malui-Makumba post conception sex.

Mopambe increased her time spent close to Makumba over the study period. Why? Figure 3.3 clearly shows that this increase began in July, which coincided with the start of the high level interunit interaction period. This period began with a two week intensive interunit interaction leading to Etefi's emigration out of and then ultimately back into her natal group (Chapter 4). Mopambe is the mother of Etefi, and as such she may have been more affected by these and subsequent interactions in the latter half of the year than were the other adult females. This may explain why she remained in closer vicinity to the silverback from July onwards. September saw a peak in her close proximity. By September, the group had completely range shifted and

began to occupy foreign areas. Mopambe's peak in closeness to Makumba may have reflected a build up of nervousness (due to past and present interactions involving her daughter, the only female of emigration age), which magnified when entering completely unfamiliar regions.

Few studies on silverback spatial configuration (excluding nesting; see below) have been published. Yamagiwa's [1983] and Schaller's [1963] short descriptions of gorilla progression, found that the dominant silverback took potentially protective or leadership positions either in the front or the rear of the group (Section 3.2.5). Both neighbour-silverback and group-silverback spatial patterning were analysed in this study. Makumba was more likely to remain on the periphery of his 5m neighbour group. During 'normal' daily routines, Makumba may prefer locating himself at the periphery of his neighbour group; he was by definition still within 5m of all neighbours. Additionally, it may simply be more peaceful to be on the periphery of a boisterous group of young immatures (his most likely neighbours) than in the middle of them. As adult female and older immature presence as neighbours to the silverback increased (who are less likely to attempt potentially annoying interactions with the silverback), Makumba was more likely to be located in the middle of his neighbour group. Additionally, as interunit interaction intensity increased (Chapter 2), Makumba was more likely to move into the middle of his neighbour unit; therefore the middle may reflect a protective spatial response in situations of higher perceived risk or perhaps also at times where individuals are competing for access to the silverback. Whilst not significant, I found a strong trend towards an increase in silverback peripheral location as the number of human observers increased. It is possible that the silverback acted as a protective barricade when there were many human observers. Habituation stages (i.e. the fact that observers were more likely to access the silverback when he was at the periphery of his neighbour group) was controlled for in the analysis; while results did show that Makumba was more likely to be in the middle of the group as the year progressed, whether this was due to habituation or internal group dynamics which also changed dramatically over the course of the year (Chapter 4), remains unknown.

The assertion that the silverback is responsible for exerting complete daily directional control over his group, particularly in western lowland gorillas where females can forage far from their leader males, is questionable (Section 3.2.5). Makumba was more likely to be located in the

back of his entire group over the front or middle. However, his position changed according to group dynamics. As the group became more dispersed, Makumba was more likely to be at the back of the entire group. As the number of neighbours to the silverback increased, Makumba was more likely to be in the middle/front of the entire group. The group was most spread out in the late morning and early afternoon (Chapter 4) when they were more likely to be exhibiting mixed behaviours (and therefore difficult to keep track of; Chapter 3); and Makumba was more likely to be in the back of the group in these periods. He was also more likely to be in the back of the group as observer-silverback distances decreased. That month entered the model as a linear variable with an increasing trend towards silverback location at the back of his group suggests that social-group dynamics influenced this relationship, not habituation levels. Additionally, as interunit interaction level and presence of all age-sex categories 'close' to Makumba increased, the silverback was more likely to move into the middle/front of the entire group. Finally, as rainfall increased the silverback was significantly more likely to be located in the middle/front of his entire group.

During peak feeding times when the group was most dispersed, Makumba was most likely to remain in the protective rear, ensuring that all individuals passed by safely (Section 3.2.5). In addition, as the number of neighbours and presence of all age-sex classes within Makumba's vicinity increased (i.e. as the group became more cohesive), the silverback was more likely to be near the leading front of the group. Finally during potentially risky periods, such as intense interunit interactions or high periods of rainfall, the silverback was again more likely to be nearer the leading front of the group keeping its members away from the source of danger. Rainfall deserves special mention since it might not be thought of as a risk. In rainforest environments, rain can be all encompassing and loud; movement during these times can be very risky since approaching danger (i.e. elephants) cannot be heard or seen. In these situations, it would make sense for the silverback to move into a position where individuals could see him and where he could lead them to safer ground if necessary.

On the basis of the evidence here, I suggest that western lowland silverbacks in single male groups may be responsible for, or at least play a strong role in determining the initial feeding direction of their groups. While adult females forage, the silverback waits in the protective rear

until they return to him, or until he moves to them. Once the group has reconvened, he may then determine the group's next direction of movement. During periods of higher perceived risk, he may be more likely to take a more forward position and move his group out of danger.

Nesting site patterning could be regarded as an extension of the silverback protective spatial arrangement theory. While data regarding the silverback's nesting defence role are varied and somewhat contentious (Section 3.2.6), Makumba placed his nest in areas that maximized his protective role. Previous research has discussed optimal visibility as a silverback strategy during nesting, but no published study has examined the nature of nest placement in relation to animal trail location. In rainforest environments, trails, especially large ones are known as elephant highways and are also the main pathways of movement for predatory leopards [Henschel & Ray, 2003]. Makumba was over twice as likely to be located next to the largest trail as was another group member within a 20m radius of the nest site. As other group members nested further away from him, he was more likely to nest closest to the largest trail, and as the forest density in his nesting area became more open (Bai Hokou consists of very patchily distributed habitat; Chapter 2), he was also more likely to nest closer to the largest trail. Makumba appeared to perceive the larger trails as a risk to the safety of his group, and as the protective leader, he appeared to nest in a location where he could monitor trail usage and alert group members to danger or disturbance if necessary.

My results are similar to Kawai & Mizuhara's [1959] study, which noted that the silverback was more likely to nest on the periphery of his group (Section 3.2.6); Makumba was over 7 times more likely to nest on the periphery of his group than in another location. In addition his group formed a consistent 'fan' nest site spatial pattern, where Makumba nested on the periphery and all other individuals nested in a fanlike shape around him (Section 3.3.5). For many primates concealment in vegetation can be an effective antipredator strategy [Anderson, 2000; Section 3.2.6]. Note that Gorillas seem to seek more open areas (areas with open canopy cover) for nest building [Casimir, 1979; Williamson, 1988] although the dense western lowland gorilla forest may constrain these choices. Tutin et al. [1995] found that Marantaceae forest, light gaps, and secondary forest with streambeds and open understory were important factors in nest site selection. At Bai Hokou, Remis [1993] found that nests were equally spread across

most habitat types within the region, most likely as a result of the patchy habitat. However, she also noted that gorillas did avoid primary open *Gilbertiodendron dewevrei* stands. While the Makumba group almost completely avoided *Gilbertiodendron dewevrei* forest (apart from three exceptional circumstances where visibility was of primary importance due to extremely aggressive interunit interactions; Chapter 4), the ‘fan’ design observed appeared to be related to forest density and visibility. Makumba positioned himself in more open patches while other group members preferred denser patches; this relationship was only apparent when nest sites were arranged in a ‘fan’ design. In these cases, Pitman [1935] and Dyce Sharp’s [1927] theories seem to hold true (Section 3.2.5): Makumba may have been selecting areas with better visibility so he was able to watch over his group, whilst other group members preferred the safety and comfort of denser patches. Based on results from a western lowland gorilla captive study, Weiche & Anderson, [2007] also suggested that apes may choose to sleep in areas that maximize visibility. Indeed, several other gorilla studies found that wild gorilla groups tend to nest at the edge of forest gaps [review in Weiche & Anderson, 2007]. It is possible that Makumba not only maximized visibility by choosing sites in more open areas than other individuals, but the group as a whole may have maximized visibility by often choosing to nest at forest edges. Although data were not collected on nest site placement in relation to forest edges, it would be an interesting avenue for future study.

Overall, my results demonstrate Makumba’s crucial protective and stabilizing role within his group. As western lowland gorilla groups are predominantly single male (Chapter 1), the western lowland silverback’s protective functions may be even more vital for this species than for mountain gorilla silverbacks, who can often rely on the support of other adult male members in their group. Aside from the obvious risk of infanticide, much of western lowland habitat is wrought with risks (i.e. poachers, elephants, leopards) that have been nearly extirpated in mountain gorilla habitat. The Dzanga-Sangha region contains dense numbers of potentially high risk elephants. Dzanga bai, located about 15 km from Makumba’s home range is home to more elephants than seen at any other bai in Central Africa [Fishlock, 2010]. Additionally the region suffers hugely from poaching, and may be one of the last forest leopard (the gorilla’s only natural predator besides humans) sanctuaries within Central Africa [Henschel, 2008].

While a silverback's individual character may also play a role in his overall protectiveness, there is no doubt that western lowland groups have developed complex spatial and social strategies to cope with perceived risk in rainforest environments.



CHAPTER 4

*SILVERBACK – GROUP
DYNAMICS DURING
INTERUNIT INTERACTIONS*



CHAPTER 4

SILVERBACK-GROUP DYNAMICS DURING INTERUNIT INTERACTIONS

4.1 ABSTRACT

Until recently the application of socioecological models to western lowland gorillas has been impeded by the lack of habituated groups. Since a female can disperse several times in her life, encounters with 'strangers' offer her the chance to assess her satisfaction with her current group. Extragroup males are expected to seek out encounters that may attract females to their unit, whereas males with fertile females may seek to avoid or drive away extragroup units, thereby decreasing the risk of female emigration. Little is known about silverback social and protective roles and group sociality during interunit interactions in western lowland gorillas. The Makumba group took part in 79 interactions in 2007 compared to 15 in 2006. They experienced more interactions in 2007 than any other published study based on one focal unit. A total of 21 (27%) high level, 27 (34%) medium level and 31 (39%) low level interactions occurred during the study. High level interactions started in July and led to the transfer of a recently matured natal female (Etefi) out of, and then eight days later, back into the Makumba group. During this period Makumba patrolled the group's core area, continuously reused the same resource patches, and nested at the same sites sequentially. When Etefi returned to Makumba, the group dramatically shifted core and home range area for the remainder of the study. Makumba showed differential response types according to interaction intensity; silent responses were only witnessed during high level interactions and aggressive auditory signalling without movement or patrolling was favoured during low level interactions and absent during high level interactions. Immature play signals also dramatically dropped during high level extraunit encounters, and as high level interaction rates increased, neighbour numbers within 5m of the silverback increased, and the group became more cohesive. Makumba only nested in open habitats during high level

interactions, but preferred to nest in dense habitats during low level interactions and on non-interaction days. Extragroup units appeared to target the Makumba group during the early afternoon when the group was most spread out, or alternatively at dawn or during the night when the group was most cohesive. Results suggest that western lowland group gorillas respond according to the perceived threat of an extragroup unit. In addition western lowland gorilla interunit interactions involve an extremely complex, highly strategic framework of approaches and responses. Infanticide may be a vital risk factor affecting the strategies of western lowland adult males during encounters when a group contains females with dependent infants.

4.2 INTRODUCTION

4.2.1. The Socioecological Model – Dispersal and Intergroup Competition

As discussed previously, most primate species live in groups, and compete with other groups for resources or mates (Chapters 1 and 3). The importance of interunit interactions (hereafter referred to as 'interactions') vary within a species and are dependent on several, often non-mutually exclusive factors such as; spatiotemporal distribution of resources, group social structure, type of dispersal (i.e. female or male philopatric), and territoriality [Wilson, 2007; Robbins & Sawyer, 2007]. In many group living primates, males transfer between female kin bonded breeding units; i.e. baboons (except for the hamadryas baboon, *Papio hamadryas*), Hanuman langurs (*Semnopithecus entellus*), and macaques [review in Harcourt, 1978a]. Humans and a number of other primates exhibit systems where female transfer is just as common or more common than male transfer; i.e. red colobus [Marsh, 1979], chimpanzees [Nishida & Kawanaka, 1972], hamadryas baboons [Moore, 1984], Thomas langurs (*Presbytis thomasi*) [Steenbeek, 1999, Steenbeek et al., 1999; Sterck 1997], atelins [Strier, 1999], gibbons [Sommer & Reichard, 2000] and gorillas.

Gorillas are typically viewed as non-territorial since their home range is generally too large to be economically defended [Brown, 1964]. Consequently, a unit's (a unit can be composed of one solitary male, an all-male or a mixed group) home range often overlaps with other groups and solitary males [Fossey & Harcourt, 1977; Remis, 1994; Tutin, 1996; Watts, 1987; Yamagiwa,

1987a, 1987b]. While both sexes disperse, 40-50% of mountain gorilla males remain in their natal unit [Kalpers et al., 2003; Schaller, 1963; Stoinski et al., 2009; Robbins, 1995; Weber & Vedder, 1983].

It is likely that gorillas evolved a one-male per group structure since they do not exhibit traits characteristic of multimale systems (i.e. large testes size, large sexual swellings in females, etc). Regardless, changes in ecological variables over time have made multimale groups advantageous [Robbins & Robbins, 2005]. The lifetime reproductive success of mountain gorilla males who have become dominant in their natal group is double that of those who have emigrated [Robbins & Robbins, 2005]. Dominant group males also have slightly better fitness as a result of keeping one subordinate in their unit and only slightly worse fitness by keeping additional subordinates [Robbins & Robbins, 2005].

Mountain gorilla females display minimal intragroup feeding competition due to the relatively uniform distribution of folivorous plants, which comprise the bulk of their diet (Chapter 3). According to Wrangham's [1980] ecological model, female bonding and dominance hierarchies only exist where feeding competition occurs; thus it is no surprise that mountain gorillas exhibit fragile hierarchies and weak female-female bonds (Chapter 3) greatly reducing the costs associated with transfer in female-bonded species. The high range overlap in gorilla units means that females can easily transfer directly into other groups without being forced to range over long distances without male protection. Low female-female bonding and a general lack of hierarchical and kin based resource contests suggest that immigrants are not likely to be harassed or to suffer increased feeding competition in new groups (Chapter 3).

In female dispersing species, male mate defence (as opposed to resource defence) is thought to be the underlying "pull" in most interunit encounters [Steenbeek, 1999]. Males are able to maximize reproductive output by ensuring that females spend their time feeding instead of remaining vigilant to intruders or predators. A good protector male is not only providing direct protection (against predation and infanticide) but also indirect protection (via resource defence), which may in turn make him more attractive to more females [Robbins & Sawyer, 2007]. A male who consistently disrupts his group's feeding routines and ranging so as to avoid other

units instead of actively driving other units away, may not be an attractive mate as it suggests that he is not a capable protector [Watts, 1994c].

While inbreeding avoidance explains why females transfer out of their natal groups [Stokes et al., 2003], it does not explain secondary dispersal [Stokes et al., 2003; Watts, 1996]. Mountain gorilla females transfer to groups with fewer females and more males [Watts, 2000]. They show higher reproductive output with significantly shorter interbirth intervals in multimale groups as opposed to single male groups [Gerard-Steklis & Steklis, 2001; Stokes et al., 2003]. Multimale groups offer better protection from predators and infanticide. A female may choose to disperse several times in her lifetime if she is not satisfied with the level of protection afforded by the current males in her group [Gerard-Steklis & Steklis, 2001; Robbins, 1995; Stokes et al., 2003; Watts, 2000]. This theory is even more compelling since females tend to leave their current group for another after they have suffered the loss of an infant [Stokes et al., 2003]. All infants are at mortality risk during social encounters, even when accompanied by male protector(s), however, mountain gorilla infants in single-male groups are more likely to die than those in multimale groups [Robbins, 1995; Watts 1989]. While infanticide accounts for 37% of all mountain gorilla infant mortality, 75% of infanticide occurs to infants whose mothers were not accompanied by an adult male [Watts, 1989].

If a male gorilla leaves his natal group, he becomes solitary or joins an all-male non-breeding group, although the latter is less likely to occur [Robbins, 1995, 2001; Schaller, 1963; Yamagiwa, 1987a, 1987b]. All-male mountain gorilla groups and the mechanisms through which they form, disperse, and range, are discussed in Fossey, [1983]; Harcourt, [1978a]; Robbins, [2001]; Stewart & Harcourt, [1987] and; Yamagiwa [1987a, 1987b]. As they represent somewhat of an anomaly in gorilla group composition and do not appear to actively seek females [Yamagiwa, 1987a], I focus on the solitary male. A solitary male will gradually move his home range away from that of his family group in search of potential emigrant females. Males will actively participate in interunit encounters to either acquire females or to defend breeding access to females already belonging in their group [Parnell, 2002b]. A solitary male will be extremely motivated to gain females and become a reproductively producing unit. His ranging is highly influenced by the presence of other mixed groups and intergroup encounters, and he

can spend many days silently tracking groups to potentially learn more about the females within them [Fossey 1974; Fossey, 1983; Schaller 1963; Yamagiwa, 1986, 1987b].

Gorilla females can assess males as protectors during interunit interactions [Watts, 1994c]. Since an encounter offers females the chance to re-assess their satisfaction in her current group, extragroup males should seek out encounters that provide an opportunity to attract females to their unit. Likewise, males with mature females should avoid those same encounters, circumventing the risk of female emigration [Sicotte, 1993]. Female-male bonding in gorillas suggests that a solitary male's best strategy for acquiring females is not through force, but instead through luring and coercing females away from their groups by gaining their trust [Harcourt, 1978a; Robbins, 1995; Yamagiwa 1986, 1987b]. Even though the infanticide hypothesis predicts that females will not leave their current silverback if they are either pregnant or nursing an infant [Sicotte, 2001; Sterck, 1997; Stokes et al., 2003; van Schaik, 1996], if an extragroup male kills the infant, the female is more likely to leave her current group and mate with the attacker male [Watts, 1989; Hrdy, 1979]. As a result, solitary males are rarely tolerated by group males and are viewed as the most dangerous neighbours to silverbacks with fertile females [Harcourt, 1978a].

Groups travel farther on days after interactions and may abruptly range shift as a result of extremely aggressive interactions [Caro, 1976; Cipolletta, 2004; Watts, 1994c, 1998, 2000; Yamagiwa, 1986]. While food distribution has a large effect on ranging, interunit interactions can override feeding-based decisions and dramatically change movement and home range use [Fossey, 1974; Goodall, 1977; Vedder, 1984].

4.2.2 Mountain Gorilla Interactions

Schaller [1963] reported that silverbacks were most frequently involved in initiating interunit encounters, and responses varied from agonism to peaceful mingling. Serious fights were never observed. Harcourt [1978a] found that 80% of 19 encounters were agonistic where 50% of 16 interactions led to physical contact. Interactions were more agonistic between newly formed groups (one silverback with one female and her offspring, or lone silverbacks) than in established groups (groups defined as consisting of one silverback with two adult females

where at least one offspring was a minimum of two years old). Sicotte [1993] noted that encounters led to slightly less agonism (74% of 58 encounters) and only 17% of these interactions led to contact aggression. Unlike Harcourt [1978a] she found that interunit responses were based on the number of potential female emigrants in a group; agonism increased as the number of potential female emigrants – parous cycling females without infants – increased.

4.2.3 Eastern Gorilla Interactions

Multimale groups exist in eastern gorillas but are not as prevalent as in mountain gorillas (Chapter 1) and only three cases of infanticide have been recently observed at Kahuzi-Biega National Park [Yamagiwa & Kahekwa, 2001, 2004]. Of 14 other social situations where infanticide could have occurred, none resulted in the death of an infant [Yamagiwa & Kahekwa, 2001]. Moreover upon the death of a group silverback, the abandoned females with offspring ranged alone for 29 months without being targeted by infanticidal males [Yamagiwa and Kahekwa, 2001]. Yamagiwa and Kahekwa [2004] theorize that this lack of infanticide may be due to high genetic relatedness of males in the region, and that the new observations of infanticide may be due to a shift in population structure as a result of the civil war which killed many individuals, and thus most likely reduced the relatedness of close neighbours.

4.2.4 Western Lowland Gorilla Interactions

Western lowland groups are predominantly single-male, although multimale non-breeding groups are known to occur, albeit rarely (Chapter 1). Many of these all-male groups were formed due to the disintegration of a mixed group rather than the active immigration of males, and most became breeding units at different points during their study [Parnell, 2002b]. The clumped distribution of fruit in western lowland gorilla habitats may change the nature of some interunit interactions; resource defence may play a larger role in western lowland gorilla encounters than in mountain gorillas. Even though patchily distributed fruit will increase home ranges making territory defence even more difficult [Brown, 1964; Parnell, 2002b], it is possible that territorial behaviour may vary depending on local ecological variables [Parnell, 2002b; Tutin, 1996]. Smaller areas with highly sought after resources may be defensible and defence economically worthwhile [Parnell, 2002b; Tutin, 1996].

4.2.5 Western Lowland Gorilla Interactions in the Forest

At Lopé, interactions were often related to access to fruit trees [Tutin, 1996], although high level aggression leading to physical contact was not directly associated with resource defence. Nonetheless it appeared that groups in the core of their home range had some level of dominance over those in the periphery, since core groups never communicated their approach to a contested fruit tree but others did [Tutin, 1996]. Of the 40 encounters that occurred over 11 years, 22 involved two groups, and 16 involved a group and solitary male (two were unknown), where nine of the 16 involved lone males silently tracking groups. A further seven group-solitary male interactions occurred close to large fruiting trees and involved auditory exchanges only. Tutin [1996] suggests that opportunities for female transfer may occur as units are drawn into closer proximity due to fruiting events. Intergroup interactions mainly occurred close to ripe fruit, and generally involved agonistic auditory exchanges, although tolerance was observed between two groups who nested in close proximity to each other on a few occasions. While several temporary range shifts (up to three months) took groups into areas of exceptionally high fruit concentrations, a more permanent shift in one group was related to the movements of another group [Tutin, 1996]. At Mondika, while intergroup encounters for one focal western lowland gorilla group occurred four times more frequently than in mountain gorillas, they were more likely to be calm rather than aggressive. Additionally, interunit encounters had no consistent effect on the focal group's daily path length and monthly range [Doran-Sheehy et al., 2004]. At Bai Hokou, interunit encounters were more likely to be aggressive rather than tolerant [Cipolletta, 2004], and both monthly range and mean daily path length were greater during busy interaction periods. Additionally, Cipolletta [2004] observed a temporary female acquisition-related range shift. For one focal group at Lossi, interactions with other groups generally arose at the periphery of their range, appeared to involve access to fruiting trees, and most commonly resulted in tolerant responses although avoidance and contact aggression were also noted. However, interactions with lone males occurred throughout the focal group's home range, did not involve access to fruit, and most commonly resulted in aggressive or avoidance behaviours [Bermejo, 2004]. As at other sites, groups occasionally nested within close proximity to other groups. Subgrouping during nesting has also been reported by Goldsmith [1996] and Remis

[1997a], although results were based on nest counts of unhabituated gorillas and may therefore be subject to bias [Kuehl et al., 2007; Remis, 1993; Todd et al., 2008; Tutin et al., 1995].

4.2.6 Western Lowland Gorilla Interactions at Bais

Bais offer another unique variation to western lowland gorilla interunit interactions, unseen in mountain gorillas (Chapter 1). In Maya Nord Bai, the most common response to encounters was to 'ignore' (62%) the presence or advances of another unit. Agonism – mainly initiated by adult males - occurred in only 29% of the interactions [Magliocca, 2000; Magliocca & Querouil, 1997; Magliocca & Gautier-Hion, 2004]. At Lokoué Bai, interaction intensity was not correlated with how well established a group was or how many potential emigrants a group had [Section 4.2.2; Harcourt, 1978a; Levrero et al., 2002; Sicotte, 1993]. However, the frequency of aggressive behaviour increased when females were present [Caillaud et al., 2008; Levrero et al., 2002]. When multiple units were present at Mbeli Bai, 58% of interaction possibilities resulted in an 'ignore' reaction. Of the 144 encounters that gave rise to interactions, the most common response was aggression, followed by affiliation; although responses were not always mutually exclusive [Levrero, 2005; Olejniczak 1994; Parnell, 2002a, 2002b]. All interactions involving only adult males were agonistic and appeared unrelated to resource defence [Parnell, 2002b]. Females at Mbeli Bai preferred to leave larger groups and immigrate into smaller groups, consistent with greater intragroup feeding competition predicted for frugivores [Doran & McNeilage, 2001; Stokes et al., 2003]. However, female group choice did not affect reproductive success [Stokes et al., 2003], although this appears to be based on only one generation. At Lokoué Bai, 41% of 894 encounters did not lead to an interaction. Of those that did, the most common response was aggression [Levrero, 2005]. When interactions between solitary and group males occurred, the most common reaction by the group male was agonism. Silverbacks and blackbacks were involved in the majority of aggressive interactions [Levrero, 2005].

4.2.7 Male Protection During Western Lowland Gorilla Interactions

As stated above, western lowland gorilla groups are predominantly single-male. This implies that male dispersal is the rule. Gatti et al., [2004] found that lone males at Mbeli, Maya Nord and Lokoué Bai accounted for over 46% of the population seen at these bais. Mountain gorillas

and eastern gorilla solitary males represent a much smaller proportion of those populations; 1.9% and 3.5%, respectively [Gatti et al., 2004; Sholley, 1991; Yamagiwa et al., 1993]. Due to the low success rate of emigrating mountain gorilla males and the biased adult sex ratio in mixed gorilla groups, male-male competition should be severe in western gorillas [Robbins et al., 2004]. Yet an elevated degree of tolerance is observed at different western gorilla sites (see above), and even though infanticide is highly suspected to occur, its occurrence is not universal [Stokes et al., 2003]. While high genetic relatedness of neighbouring males at some sites may help explain these results [Bradley et al., 2004; Bradley et al., 2005], varying levels of aggression towards extragroup males should be a function of the perceived threat and relatedness of that male, as well as group composition [Robbins et al., 2004]. In western lowland gorillas the frequency of agonistic interactions varies considerably across the different populations, and solitary males represent a strong threat since they will be more willing to incur heavy costs in the pursuit of female acquisition [Watts, 1994c].

The costs incurred during violent interactions can be severe in western gorillas, as there are no other adult males in the group to help with protection or to take over if the leader male dies. At Mbeli Bai, group disintegration occurs three times more often than in mountain gorilla groups [Kalpers et al., 2003; Parnell, 2002a ; Robbins, 1995; Stokes et al. 2003]. Therefore, male protection and quality may be even more vital to the western lowland female's reproductive success.

4.2.8 Chapter Aims

While the ecological mechanisms underlying gorilla interunit interactions and the range of responses to encounters by groups or solitary individuals have received attention, no published study has detailed the effects of interunit interactions on intragroup dynamics. For example: How does group spread change before and after an interaction? How are the silverback and group auditory signals influenced by interactions of varying levels of threat? How does proximity to the silverback change before and after interactions occur? Here, I provide the first detailed study which assesses how silverback-group social dynamics change in response to interunit encounters of varying threat levels, using a large sample (relative to other studies) of 79 interactions.

4.3 METHODS & ANALYSIS

4.3.1 Makumba Group Range Overlap with Other Groups and Extragroup Males

The Makumba group home range overlaps with a minimum of three other gorilla groups. Information on other gorillas in the region has been acquired over 10 years of following traces, bumping into, and attempting habituation on other groups. Traces of solitary males were followed (not routinely) throughout the study year, and information from these traces as well as chance repeated meetings suggest that at least four solitary males shared home range with Makumba. Still, data on other groups and solitary males in the area may be underrepresented since no study at Bai Hokou has focused solely on determining the exact number of gorillas in the region. Also, groups may shift their range due to interunit encounters and resource availability (see introduction).

4.3.2 Definitions and Sampling Independence

For age-sex categories of neighbours to the silverback, forest density categories, hourly roll call or hourly presence close to the silverback, group spread categories, and all other definitions and specifications used in this chapter, see Chapter 2. Also see Chapter 2 for sampling independence of overall scans, of neighbour scans, and of group spread scans.

4.3.3 Interactions and Interaction Level Scoring

For definitions, see Chapter 2. Interactions were separated by a minimum of one session; 65 interactions occurred on different days and 14 interactions occurred on the same day, in either the morning or afternoon observation session. A total of 79 interactions occurred in 2007, and 46 of these interactions occurred during recording sessions, where 44 occurred on different days (Section 4.4.1).

Each session with an interaction was listed as a separate interaction, regardless of whether the same individual or group may have been responsible for several interactions occurring over several continuous sessions. Previous work on the independence of interactions generally involved bai studies (where all units could be seen) [Parnell, 2002b] or well known multiple

mountain gorilla groups [Robbins & Sawyer, 2007; Sicotte, 1993]. Interactions were assessed as independent when one group moved out of an area, when group composition had changed (i.e. female transfer) or in Parnell's [2002b] case, when 30 min passed without an encounter between two units or when the context of their behaviour altered. Robbins & Sawyer [2007] followed Sicotte's [1993] methodology and categorised multiple day interactions from the same units as one interaction. Such assessment for western lowland gorillas in rainforest habitat was simply not possible, as efforts to habituate and follow just one group can take decades of effort and teams of manpower alone. Nonetheless, as mentioned in Section 4.3.1, effort was directed into following the traces of extragroup males involved in high level interactions with the Makumba group during the study period, although routine follows were not feasible. Secondly, many interactions in forest environments may not involve the physical transfer of individuals (only two out of 79 recorded interactions in this study involved female transfer) [see also Sicotte, 1993]. The main goal of this chapter was to assess silverback and group responses, and to evaluate how silverback-group dynamics change as a result of interaction presence and interaction intensity, irrespective of whether the same individual or group was responsible for several altercations over successive sessions. Each interaction, while it may have been temporally related to a previous one, had the potential to change in intensity, and therefore had the potential to influence the Makumba group behaviour patterns in different ways. It is for these reasons that I scored interactions as independent if they occurred in separate sessions on the same day.

4.3.4 Auditory Definitions

Continuous records of all auditory signals were made for Makumba and those gorillas in his presence (i.e. within human and therefore silverback earshot) as described in Chapter 2. Auditory signals were categorised by age-sex class – adult male (one silverback), adult females (three individuals), and all immatures (seven individuals plus two infants) – and defined as any sound made by a gorilla, either vocally or via other signals (ground slapping, tree breaking, chest beating, displaying, and hand clapping) (Chapter 2). For analyses in this chapter, auditory categories were grouped and defined according to Table 4.1. As western lowland gorilla auditory communication (vocal or via other auditory signals) has not yet been classified, I

adapted definitions from published work on mountain gorilla vocalisation [Fossey, 1972; Harcourt & Stewart, 2001].

A total of 22,343 auditory signals were recorded throughout the study period. Of these signals, 2,195 were loud auditory signals emitted by the silverback, 8,373 were soft auditory signals emitted by the silverback, 4,110 were auditory signals emitted by other group members (not including play signals), and 4,366 were play signals of which 99% were given by immatures, <1% (N = 24) by the silverback, and <1% (N = 3) by adult females.

Table 4.1 Auditory Categories

| Auditory Category | Auditory Signals | Age-Sex Class Groupings |
|----------------------------------|--|---|
| Loud ¹ | Bark, Soft Bark, Charge, Display ^a , Scream, Hoot, Chest-Beat, Angry Whinny ^b | Silverback |
| Soft ² | Belching In All Forms (i.e. Short Belch ^c Talking Belch ^d , Singing Belch ^e , Long Belch ^f , Whinny ^g , Sex Whinny ^h) | Silverback |
| Play ³ | Chest-Beat, Play Grunt, Body Slap | Not Grouped by Age-Sex Class (Although 99% was Made by Immatures – See Below) |
| Grouped Loud & Soft ⁴ | All of the Above Not Including Play | Adult Females & Immatures |

¹These are used to communicate with and repel extragroup units, to express agonism (i.e. barking; Chapter 5), and to 'search' for group members who are not in visual range of the silverback. ^{1a} Displays include tree breaking, ground slapping, and tree slapping. ^{1b} Angry whinnies were only heard from the silverback, and appeared to be used as an urgent impatient call for group members to come together.

²These are 'conversational' vocalizations used to communicate with group members who are in close auditory range of the silverback. ^{2c} Short belches are the most common form of communication with other individuals in the group and sounds like a grunt. ^{2d} Talking belches are a long succession of belches, usually in communication with other individuals who join in. ^{2e} Singing belches appears to be associated to food and are similar to 'humming'. ^{2f} The long belch is similar to a single short belch except that the long belch is extended and can last several seconds (this is different from the talking belch which is a

succession of separate belches), and appears to be used in connection with whinnies and hooting when the silverback or group members are trying to locate another group member. It is possible that the long belch is also used in extragroup communication since it is often seen in combination with hooting. However, since its volume is quiet and most likely detectable only by individuals in close vicinity, it is more likely used in intragroup communication and as such was placed in the soft auditory signal category. ^{2g}Whinnies are used most commonly by the silverback to call group members together. ^{2h}Sex whinnies are calls which solicit sex.

³While in some instances, chest-beating and hand clapping may be a form of long-calling, they were mainly used in play by the juveniles. Play auditory signals were grouped into a separate category as they represent a different form of communication in comparison to both soft and loud auditory signals.

⁴Even though loud and soft auditory signals are very different, they were grouped together for adult females and immature individuals. This is partially due to a limited sample size for adult females and immatures, but also because the main communicator with extragroup males is the silverback. Thus, loud auditory signals for other group members should not be as strongly influenced by extragroup males as for Makumba. Since Makumba was the primary communicator for the group, I aimed to test whether the group becomes quiet (by decreasing both loud and soft signals) in order to listen to Makumba. For these reasons, both loud and soft adult female and immature auditory signals were grouped together.

4.3.5 Analysis Overview

Final analyses were conducted on 3,252 silverback scans and 166 nesting sites (Chapter 2). For this chapter, data were generally analysed on the raw (ungrouped) data set, with control factors included in relevant analyses. Where session groupings were used to analyse auditory data, hourly auditory rates for each age-sex class division and category type were calculated relative to the number of minutes of observation in each session (Chapter 2). Type 1 ANOVA, forward stepwise logistic regressions, forward LR multiple regressions, and Chi Square analyses were the primary analytical tools used in this chapter. For more detail, see Chapter 2.

4.3.6 Makumba Group Interactions and Other Published Studies

(1) How were interactions and their levels distributed throughout the data collection period? (2) How did the Makumba group interactions that occurred in 2007 compare to published studies at other gorilla sites?

Multisite comparator responses were grouped into 'aggressive and avoid' or tolerant behaviours based on descriptions in Table 4.2. Comparing interunit responses during interactions across

sites and gorilla species must be done with caution, as the definitions used by different sites or researchers are not standardised, such that directly comparing results can lead to inaccurate conclusions. Typically, aggressive and avoidance responses are separated, although this technique can cause errors when comparing across sites. For example, in Karisoke distant communication involving chest-beats and hoots was defined as avoidance [Sicotte, 1993] whereas in Lossi, avoidance was defined as 'moving quietly away from a group or solitary male' [Bermejo, 2004]. Additionally, agonistic and avoidance responses are not always mutually exclusive [i.e. Parnell, 2002b]. In this study, Makumba exhibited both aggressive and avoidance behaviours during the same interaction 11 times. Aggressive and avoidance categories were therefore pooled together for the multisite comparison. A similar problem occurs with the tolerant category, with researchers at several sites defining tolerance as completely ignoring another gorilla unit's attempt to communicate [Bermejo, 2004; Cipolletta 2006; Doran-Sheehy et al., 2004; Magliocca & Gautier-Hion, 2004; Robbins & Sawyer, 2007] and others such as Lopé [Tutin, 1996], defining tolerance as displaying without movement out of the interaction area. Parnell [2002b] further subdivided tolerance into 'ignore', where no reaction was recorded, and 'tolerate', where individuals spent time in close proximity (within 30m) without displays and with or without affiliation. Some sites do not provide a detailed definition [Sicotte, 1993; Doran-Sheehy, 2004] simply stating behaviour as 'mingling' or 'tolerating' or 'ignoring' without additional description. Standardisation issues are further compounded as observation hours, study sites (bai versus forest environments), habituation levels, number of study groups (many versus one focal group) and interaction independence ratings differ (Parnell, 2002b; Sicotte, 1993; Section 4.3.2).

The Makumba group data for the multisite comparison was based on the 44 interactions recorded during observation sessions in 2007. Ten of these interactions started in the early morning as evidenced by disrupted nesting patterns, ranging and as evidenced by Makumba's behaviour upon observer contact suggestive of an ongoing interaction. As it is possible that a critical response may have occurred before the researcher began recording on these days (i.e. patrol or movement out of the area due to interaction), categories for this cross-site comparison were based on the 34 interactions where exact response patterns were known.

Table 4.2 Definitions Used for the Makumba Group Interactions

| Response | Description |
|--------------------|---|
| Aggressive & Avoid | (a) Chest-Beating with/without Patrol, Contact, or Movement, or Silence with/without Patrol or Movement (b) Chest-Beating with Patrol, Contact or Movement, or Silence with Patrol or Movement |
| Tolerant | (a) Attempt to Communicate by Extragroup Males Completely Ignored by Makumba (b) Chest-Beating without Movement or Patrol or Contact |

4.3.7 Peak Interaction Month July and Silverback-Group Dynamics

How did peak interaction month July influence silverback-group dynamics?

This is a multi-tiered question that involved: (a) providing detailed insight into events surrounding the start of high level interactions which led to Etefi's (recently matured natal female) transfer out of, and then eight days later, back to the Makumba group; (b) determining the relative influence of fruit availability to the peak interaction period July; (c) determining the effects of peak interaction month July on the Makumba group's core and home range; (d) determining patterns of movement and resource use during the events surrounding Etefi's transfer period, and; (e) determining overlapping nesting patterns in relation to peak interaction period July, and during interaction events surrounding Etefi's transfer period.

These questions have been explored by providing a full narrative describing the progression of events directly from my field notes, and by showing nest patterning and daily group movement patterns from July 1st-July 17th (the period leading to the build up, transfer and eventual return of Etefi). Fruit abundance scores are detailed in Chapter 2. For information on nest site data collection see Chapter 2. In order to allow for comparative measurements of home range size, a 250m x 250m grid was superimposed on the map [Cipolletta, 2003]. Ranging data were split into two periods: January-July before and during peak interaction period; and August-December after peak interaction period, although high level interactions continued at decreased rates throughout the remaining five months of the study period. Core and home range areas were

calculated according to Cipolletta's [2003] methods, modified from Watts [1998]. Home range was calculated as the sum of all 250m x 250m quadrants entered by the group, and core area was calculated as the sum of quadrants that, in descending order of entry number, cumulatively accounted for 75% of the group's total quadrant entries. Ranging data were available for 365 days in 2007. The Makumba group never slept at the same nest site twice during 2007. Nests were considered to be overlapping when they occurred within the same 166m x 166m quadrant. As this also occurred infrequently, sample sizes were too small to run any statistical tests, although observations are discussed.

Autocorrelation of ranging data, a major statistical problem in attempting to relate range use to resources or the presence of other groups [De Knecht et al., 2010], was explored using nest site placement (N = 166). Since only one nest was constructed per day, the distance between successive nests indicates the potential for spatial constraints in ranging – measured on a continuous basis. Nest site placement within the mapped areas (Chapter 2, Figures 2.5 and 2.6) was compared with ranging data (Section 4.4.6, Figure 4.5). Although nest site placement followed an overall similar pattern to daily ranging, the gorillas never nested in the same place twice, and rarely nested in overlapping quadrants (Section 4.4.7). These results suggest that while ranging and nesting were obviously constrained by the possible distance that could be travelled between successive nests, they were not strictly dependent on each other in successive events. As such, I analysed continuous ranging on a daily basis in relation to interactions.

4.3.8 Forest Density and Nesting in Relation to Interactions

Does the forest density surrounding Makumba's nest site vary between interaction and non-interaction days or as a result of different interaction levels?

For forest density definitions, see Chapter 2. Forest density scores were based on silverback position only, since he was the main protector and extragroup male communicator during interunit interactions. Forest density scores were normally distributed. A Type 1 hierarchical ANOVA was used to control for potential influencing environmental factors on interaction and non-interaction days (rainfall, maximum temperature). Additionally, a forward stepwise logistic

regression was used with forest density type as the outcome variable, and interaction level, rainfall and maximum temperature as the predictor variables. Where no predictor was included in the final model, all variables were entered in order of contribution so appropriate statistics could be reported.

4.3.9 Auditory Signalling Rates and Interactions

Are Makumba and group auditory signalling rates affected by interaction levels?

For auditory category definitions and age-sex class divisions analysed, see Section 4.3.4 and Chapter 2. The number of auditory signals one hour before an interaction to one hour after an interaction were calculated, but several pre or post-interaction hours had missing minutes, thus, a mean bi-hourly auditory signalling rate was calculated taking missing observation minutes into effect. Data were analysed using a type 1 hierarchical ANOVA, and relevant factors for each analysis were controlled for (Section 4.4.9). Auditory signalling rates were normalised using square root transformations where necessary. Note that while auditory signalling rates were also analysed for adult females and immatures, their results may be under-represented. Since Makumba was followed 100% of the time, only auditory signals heard when in Makumba's presence will have been recorded.

Only loud auditory silverback signalling rates (Table 4.1) were used when grouping responses during high level interactions. Total auditory signalling rates were not used because loud auditory signals were the main means of intergroup communication (Section 4.3.4). Responses were grouped into either (a) 'silent/quiet', or; (b) 'loud' reactions¹. Responses were grouped according to a histogram of Makumba's loud auditory signalling hourly rates per session, which followed a normal distribution. An hourly rate which fell in the first quartile of this distribution was categorised as a 'quiet' response (<2.99, range 0- 2.67). An hourly rate which fell in the remaining quartiles were categorised as 'loud' responses (>3.00, range 3.69-11.51). In addition, responses were corroborated with *ad libitum* notes written during each high level interaction (Table 4.3).

¹To avoid confusion, note that loud auditory signalling rates, and 'loud' responses during high level interactions use the same word (i.e. loud) but are defined differently and are not the same. Loud auditory signalling rates are defined in Section 4.3.4, and 'loud' responses are defined in Section 4.3.9

Table 4.3 Field Note Descriptions of Quiet and Loud Silverback Responses During High Level Interactions

| Date | Interaction Type | Description |
|--------|------------------|--|
| July 6 | Loud | The group was sleeping, Makumba walked off, and then screaming from the adult females began. Makumba raced back and we ran off after him. Makumba ran towards the solitary male and started chest-beating, tree breaking, and strutting. The group had already moved off at this point, but Makumba kept returning to the solitary male, chest-beating, displaying and then running off, only to return again (Section 4.4.3). |
| July 7 | Quiet | We bumped into the group while they were eating. They were dead silent. They all moved very cohesively and quietly. There was no play, no vocalisations, and when Makumba belched they were quiet belches (Section 4.4.3; see also Section 4.4.10 for my definition of a quiet belch). |
| July 8 | Quiet | We kept walking in circles trying to find them, knowing that the group was close by but they were not making a sound. We found them when Makumba ‘silent’ charged us by jumping out of the bushes, staring us down. Until mid-afternoon it was silent apart from several quiet belches (Section 4.4.10); at one point we even bumped into Malui ² and she just sort of jumped, looked at us and quickly walked off (Section 4.4.3). |
| July 9 | Loud | We started hearing chest-beating and screaming and we saw diarrhoea and smelled a strong gorilla odour, although I think it was coming from the solitary male as it was an unfamiliar smell. We heard a lot of screaming. Then Makumba showed up, looked at us and then angrily ate Djele ³ (displayed using food) and looked directly at the |

² Malui is normally quite aggressive to humans (Chapter 5)

³ *Haumonia danckelmaniana*

| | | |
|---------|-------|--|
| | | solitary silverback who was about 10 meters away. We lost Makumba while trying to catch up to him, but found him after, hooting and chest-beating, and several individuals were in trees (definitely Mopambe, Mai, Malui and Mossoko Abuli). It was very silent again at the end of the afternoon. We kept running into elephants everywhere probably because the group was being so quiet and not alerting the elephants to their presence (Section 4.4.3). |
| July 10 | Loud | We ran into the group quite quickly. The group didn't seem more spread out today but yet Makumba was whinnying (see Section 4.3.4 for definition) a lot! Makumba appeared to be returning to the first interaction site area, at which point he started chest beating and whinnying more, even when his group was close. The juveniles were hooting as well (Section 4.4.3). |
| July 13 | Loud | Once the solitary male started chest-beating, Makumba started chest beating and left the group to patrol. He would return to the group and then leave again, and the group remained very silent throughout. Makumba water displayed by chest-beating in the water (Section 4.4.3). |
| July 15 | Quiet | When we heard the solitary male scream very near to us, our group hid in the bushes and went dead silent apart from one quiet belch from an unknown individual, and hid in the bushes. Kunga patrolled silently (Section 4.4.3; see Section 4.4.10 for my definition of a quiet belch). |
| Aug 23 | Loud | Once the interaction started, Makumba chest-beat, displayed and moved his group out of the area quickly. Once the group had moved out of the area, whenever he heard the solitary male, he would display, strut, chest-beat, tree break and violently strip leaves from saplings, while the group moved off again. |
| Sep 10 | Loud | When the solitary male started screaming, Makumba ran towards the male and started hooting and chest-beating, while the group hid in a |

| | | |
|--------|-------|--|
| | | Marantaceae patch and remained quiet. Then Makumba hooted and chest-beat, and all of the group walked out of the Marantaceae patch, passed us by and re-joined Makumba. |
| Sep 12 | Loud | Everything was going pretty normally until we heard a scream from a juvenile and Makumba bolted in the direction of the scream. Bombe and another juvenile who were with Makumba then bolted in his direction. The whole group then moved very quickly. We heard and saw a confused group, making panicky bark noises and then the group moved quickly east while Makumba stayed behind, chest-beating, strutting and tree breaking. He then ran off quickly to catch up with the group. When we caught up to Makumba and his group, they were moving single file out of the area. |
| Oct 16 | Quiet | The interaction began when we heard one extragroup male chest-beating in one direction, then another from another direction. Makumba got up and immediately got the group together who remained very quiet and moved off. We continued hearing chest-beats from the extragroup males but nothing from Makumba, while he moved off with the group and guarded any individuals trying to veer in the direction from where the extragroup chest-beats were heard. |

4.3.10 Makumba's Responses to Varying Interaction Levels

This analysis involved a more holistic approach, by considering not only Makumba's auditory response to interactions but all the different types of responses witnessed (i.e. fleeing, patrolling, etc). Even though 44 interactions occurred during recording sessions, only 33 interactions were appropriate for use in this calculation. Seven low level interactions were excluded since interaction start was uncertain and I may have thus missed some responses before recording started. Four medium level interactions were excluded due to missing observation minutes or in one case, because the interaction happened at the end of the day and continued after we had to return to camp. Due to small sample sizes further divided into

categories, it was not possible to statistically test relationships. Additionally, any unique, previously undescribed anecdotal observations of silverback or group responses to high level interactions were noted. Again, although these responses deserved special mention, statistical analysis was not possible as they occurred very rarely.

4.3.11 Silverback-Group Dynamics and Interactions in Relation to Group Spread, Neighbours to the Silverback, and Time of Day.

(1) Do interactions and interaction levels influence group spread or neighbours (within 5m) to the silverback? (2) Do interactions occur at different times of the day? (3) Does group spread change at different times of the day on interaction and non-interaction days?

For definitions and scan independence, see Chapter 2. Data were analysed using hierarchical ANOVA and forward multiple regressions, and controlled for the relevant factors. A Bonferroni correction (N-1 design for repeat tests of different hypotheses on the same data set) has been applied to all final model multiple regression results, which after correction, were considered significant when $p < 0.025$.

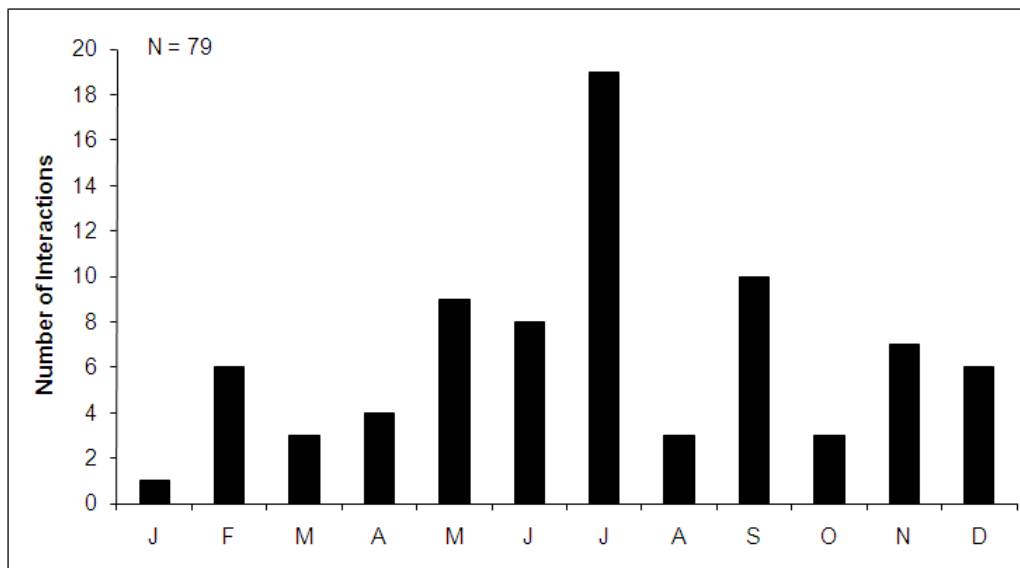
For time of day effects, data were analysed using chi squares tests. Time of day was split into five groups: (a) Night; anytime from after we left camp to 5:59, (b) early morning; 6:00-8:59, (c) late morning; 9:00-11:59, (d) early afternoon; 12:00-14:59, (e) late afternoon; 15:00-18:00 (Chapter 2). Group spread changes according to time of day was compared between interaction and non-interaction days, using a hierarchical ANOVA with time of day and interaction presence or absence as factors. No other control variables were used in this analysis because of the minimal effect other factors had on all previous analyses.

4.4 RESULTS

4.4.1 Overview

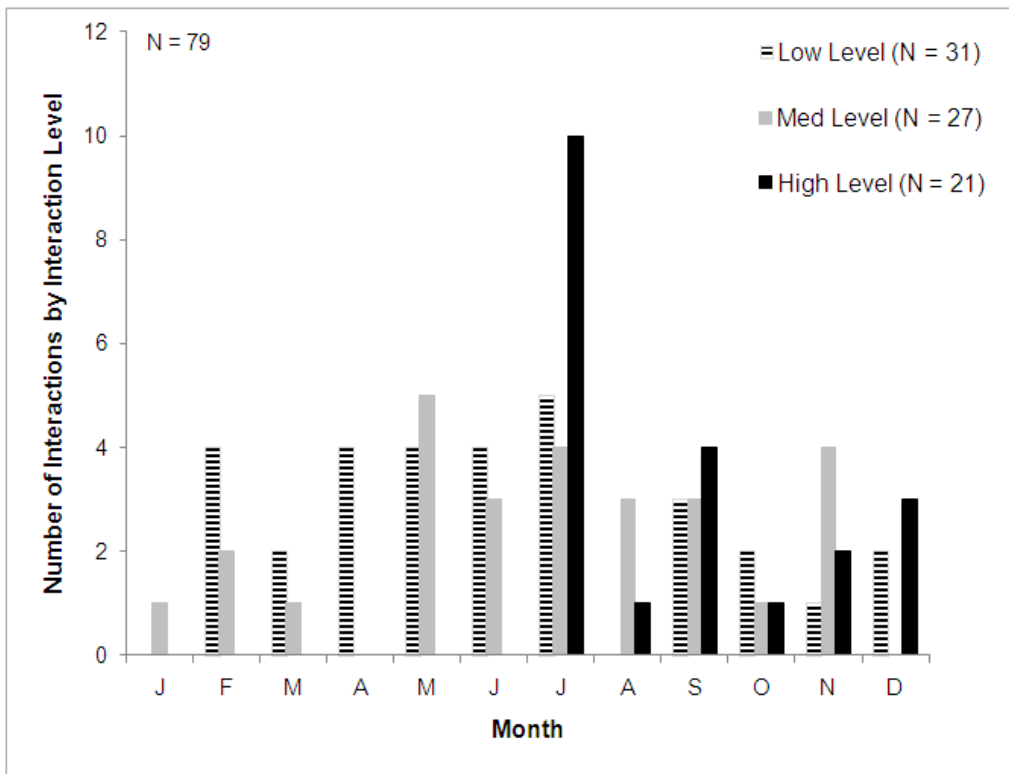
A total of 79 interunit interactions occurred during the study period (Figure 4.1) over 79 observation sessions and 65 days. Of these 79 interactions, 46 occurred during 46 recording sessions over 44 days. Two of these 46 interactions involved following traces only, and thus direct scan and vocalisation data were available for 44 interactions. Interaction numbers differ significantly between months ($X^2 = 36.291$, $df = 11$, $p < 0.001$, $N = 79$: Figure 4.1).

Figure 4.1 Total Interactions per Month During 2007



A total of 21 high (27%), 27 medium (34%) and 31 (39%) low level interactions occurred during 2007. High level interactions were absent in the first half of the study year, started in July, and then continued at decreased rates until the end of the study period (Figure 4.2). Of these totals, 11 high (25%), 11 medium (25%), and 22 low level (50%) interactions occurred during data recording sessions.

Figure 4.2 Total Number of Interactions per Month by Interaction Level



4.4.2 Comparisons across Sites

Table 4.4 presents a basic multisite comparison of published data on gorilla interunit interactions, with clarifications of definitions noted where necessary. The Makumba group experienced more interactions in one year, than has been reported for any other published study based on one focal group. Additionally, tolerance levels are more similar to those seen in mountain gorillas, as the group did not exhibit tolerance at any point during the study year.

Table 4.4 A Multisite Wild Gorilla Comparison of Responses to Interunit Interactions

| Species ^a | Study Site | Study Duration | Recorded Interactions | Frequency of Interaction | % Aggressive or Avoid | % Tolerant |
|----------------------|---|---|---|--------------------------|--|---|
| WLG | Bai Hokou Primate Habituation Camp; Dzanga-Ndoki National Park, Central African Republic; This Study | 2007-2008; 12 months; continuous sampling | 79; one focal group 34; where researcher was present at start of interaction | 6.6/month | <i>na</i> (a) 100 or (b) 79 | <i>na</i> 0; ignore 21; displays only without patrols or movement out of interaction area |
| WLG | Mondika Research Center; Dzanga-Ndoki National Park, Republic of Congo ¹ | Nov 2001- Oct 2002; > 100 hours contact time/ month | 48; one focal group | 4/month | 58 | 42 |
| WLG | Lossi Study Area, Odzala National Park, Republic of Congo ² | 1995-2000; uneven sampling; 4-30 days/month | 22; one focal group | 1.4% observation time | ^b with groups 35 with solitary males 100 | ^b with groups 65 with solitary males 0 |

¹Doran-Sheehy et al. [2004]

²Bermejo [2004]

| | | | | | | |
|-----|---|-------------------------------------|-------------------------------------|-----------|--|--|
| WLG | Bai Hokou Primate Habituation Camp; Dzanga-Ndoki National Park, Central African Republic ³ | 2003-2004; 564 days | 38; one focal group | 2/month | 71 | 29; defined as ignore |
| WLG | Lopé National Park, Gabon ⁴ | Oct 1983- May 1994; uneven sampling | 40; mainly based on one focal group | <1/month | mainly aggressive | some tolerance |
| WLG | Maya Clearing, Odzala National Park, Republic of Congo ⁵ | 1996-1998; 132 days | 238; multiple groups | <i>na</i> | 29 | 71; 62 defined as neutral, 9 pacific |
| WLG | Lokoué Bai, Odzala National Park, Republic of Congo ^{6a} | 67 Days (preliminary study) | 125; multiple groups | <i>na</i> | 40 | 60 defined as pacific occasionally leading to mingling |
| | Lokoué Bai, Odzala National Park, Republic of Congo ^{6b} | 2001 – 2003 418 days | 894; multiple groups | <i>na</i> | 56 mixed aggressive and affiliative; 36 aggressive only; | 41; ignore |

³Cipolletta [2006]

⁴Tutin [1996]

⁵Magliocca & Gautier-Hion [2004]

^{6a}Levrero et al., [2002] and ^{6b}Levrero [2005]

| | | | | | | |
|-----|--|------------------------------------|---|-----------|--|---|
| WLG | Mbeli Clearing, Nouabele-Ndoki National Park, Republic of Congo ⁷ | Jan 1997 – Oct 1999 737 days | 345; multiple groups | <i>na</i> | 54 aggressive only; plus 18 non mutually exclusive responses | 40 defined as ignore, or remaining within 30m of each other or exhibiting overt affiliation; plus 18 non mutually exclusive responses |
| MG | Karisoke Research Centre, Rwanda Volcanoes National Park, Rwanda ⁸ | 1981-1989 8 years | 58; multiple focal groups | <1/month | 93 | 7; defined only as mingling |
| MG | Bwindi Research Center, Bwindi Impenetrable National Park, Uganda ⁹ | Sep 1999- Aug 2006 2375 days | 61; one focal group (only 40 defined here) | <1/month | 90; not mutually exclusive | 70; defined as ignore or mingling; not mutually exclusive |

^aWLG = western lowland gorilla; MG = mountain gorilla ^bAs overall totals were not presented in this study, I listed the percentages of responses when a group male was involved and a solitary male was involved separately

⁷Parnell [2002b]

⁸Sicotte [1993]

⁹Robbins & Sawyer [2007]

4.4.3 Case Study - Interaction Period Involving Transfer and Return of Etefi

July represented the peak interaction period in the study year (Section 4.4.1) and involved a group of interactions associated with the transfer of Etefi (a natal recently matured female) to a suspected solitary male, and then eight days later, back to the Makumba group. The interaction that led to the temporary departure of Etefi represented the start of high level interactions that continued throughout the rest of the year, and caused a dramatic shift in the Makumba group's ranging patterns (Section 4.4.5).

Etefi transferred out of her natal group on July 6th during the first recorded high level interaction in 2007. Observations are summarized below from July 1st to July 17th, as there was evidence to suggest a build-up to the July 6th event. Each day coincides with a map (Appendix 1-17) of ranging for that day. Figure 4.3 shows cumulative ranging and nesting during July 1st-July 17th.

July 1

We found their nests 600 meters north of where they were left. Nests were difficult to find and there were traces of leopard in the area. The trackers felt that there was either an interaction with an extragroup silverback or a leopard (Appendix 1).

July 2

In the morning all seemed relatively calm, until suddenly Makumba ran directly by us stopping close to his group. I don't think it was a side charge directed at us because we were not in anyone's path and there were plenty of open trails for individuals to use since they were in *Gilbertiodendron* forest. For the next 30 minutes, Makumba kept looking behind us while sitting. Was he waiting for someone or was there a noise he was hearing? On our way back to camp, we found leopard prints and scat nearby the group (Appendix 2).

July 3

Mainly a normal day, although while Makumba was feeding in a tree in the morning several juveniles started to bark and cry and Makumba descended from the tree very quickly and immediately went towards the sounds, although the sounds soon stopped and Makumba relaxed soon after. In the afternoon, the group spent over an hour in the *Celtis adolfi frederici*

tree noted on Figure 4.3. Also solitary silverback traces were found close to the group upon leaving to return to camp (Appendix 3).

July 4

Nests were found over 1.5 km away from where the group was left yesterday. There were signs of an interaction with an extragroup male near the area we left them yesterday afternoon. The group walked quite a lot today, although the juveniles spent lots of time playing as well (Appendix 4).

July 5

A normal day (Appendix 5).

July 6

In the morning they spent a lot of their time in the same *Celtis adolfi frederici* tree noted on Figure 4.3. The afternoon started quite normally until Makumba awoke from a nap and walked off. A few minutes later we heard adult females screaming a lot. Makumba raced back and we ran off after him. When we arrived we saw a silverback male running away screaming. We moved closer and saw a silverback male about 30 meters to our right. He was screaming and ground slapping. Makumba and possibly Kunga (blackback) were on our left. The group had already moved off and we saw Makumba return, chest-beat, display and then run off. We followed Makumba and the solitary male followed behind and screamed a lot at us. There were continuous chest-beats and tree breaks from both males. Makumba and possibly Kunga kept returning to the solitary male, chest-beating, displaying and then running off. We saw Makumba a few times but no females. The continuous screaming, chest-beating, ground slapping, tree slapping and tree breaking continued for hours. We had lost Makumba and were closer to the solitary male but at 1608 we heard Makumba chest-beat from farther away. We then saw Kunga or Etefi and another juvenile, possibly Silo, with the solitary male. Soon after, the solitary male screamed and charged us. Shortly after the charge, we saw Kunga or Etefi sitting nearby with someone else behind the solitary male hooting. Then the solitary male charged us again. We then saw Silo walking off. The three individuals were hooting a lot and moving slowly off and the solitary male followed them, still screaming at us. We haven't heard Makumba in over

half an hour and have not seen any of the younger juveniles or females. Why are these juveniles with the solitary male? (Appendix 6). Note: the other individual with the solitary male was likely to be Etefi not Kunga, since he was seen supporting Makumba earlier.

July 7

We spent the morning on traces today. We think we found the solitary silverback nest with two other juvenile nests and no faeces, indicating the nests may have been used as a rest spot only. We found the Makumba group nests with no faeces a long way from where we left them yesterday. The nests were very oddly positioned and somewhat broken up. We also saw diarrhoea while on group traces. The size of the diarrhoea seemed like it came from Makumba. We spent several hours getting lost on traces and sidetracked by elephants but then somehow we found fresh traces, and not long after finding the traces, we found the group. In fact we bumped into them while they were eating. They were DEAD SILENT. We bumped into Mio feeding. She noted our presence but didn't react. Mai sat with us and watched us quietly for a while but they all moved very cohesively and quietly. There was no play, no vocalisations, and when Makumba belched, it was very quiet. Etefi is missing. We left soon after to return to camp (Appendix 7).

July 8

We found traces and then soon after solitary silverback nests with one other nest that appeared to be from an adult female (Etefi?). The nests were very close to each other. We found the Makumba nests with normal faeces and normal nest patterns about 600 meters south of where we left them. We basically spent the rest of the morning going around in circles, constantly finding fresh traces but the group was not making a sound. At one point the trackers said they saw solitary silverback traces going in one direction and Makumba going in another direction, as if they were passing each other or circling each other. But all morning there was silence, nothing! We knew the gorillas had to be close by due to the traces. Eventually we bumped right into Makumba because we kept circling the fresh traces completely confused. Just as we were about to move on, he jumped out of the Marantaceae and *silent* charged us without a sound. He just jumped out of the bushes and quietly stared us down. The whole group was very silent

and moved in unison until late afternoon. At one point we bumped into Malui and she just sort of jumped, looked at us and quickly walked off without charging or barking. Near the end of the day once they hit some *Gilbertiodendron* forest, things slowly seemed to normalize. The kids started playing and Makumba was belching normally. We even had a bark and light charge from Bombe and Malui by the end of the day (even though Malui charged us silently earlier). They were still moving a lot but they settled into their nest spot quite early. As the afternoon went on, the group spread out slightly (moved from cohesive to midrange at points), although Makumba was 'question mark' vocalizing a fair bit at the end of the day (this is a type of vocalisation that appears to be directed to group members out with of his range of vision, almost as if a question of whereabouts is being asked; hence the name 'question mark' vocalisation). Normally the question mark vocalisation is used in combination with a hoot, although this time it stood alone and remained quiet in strength. Etefi is still missing (Appendix 8).

July 9

In the morning the group was found quite quickly. Two minutes later we heard Makumba angry whinny (a very short, loud, hoarse whinny calling group members to him with immediacy; see Table 4.1 for definition) and they turned right around to go north. They moved as a very tight group not making much noise. Makumba chest-beated in front of Malui (guarding?) and then it started to rain and we lost the group. Nests were close together in an open area but faeces were normal. During the rain, traces from the group were moving quickly and cohesively north towards the first interaction site? I am beginning to wonder if Makumba is the one following the solitary silverback now? Then we started hearing chest-beating and screaming and we saw diarrhoea and smelled a strong gorilla odour, although I think it was coming from the solitary male as it was an unfamiliar smell. We heard a lot of screaming. Then Makumba showed up, looked at us and then angrily ate Djele (*Haumonia danckelmaniana*) and looked directly at the solitary silverback who was about 10 meters away. Silo was watching and Kunga was there, and I think Etefi was there as well although I am not certain. When Kunga left, Makumba moved closer to the solitary silverback and displayed by strutting whilst making no noise, even though the solitary male was screaming. Then Makumba turned his back on the solitary male and left,

strutting with Silo and Etefi(?) in tow, while the solitary silverback continued to scream and scream. Was it at us? Is Etefi back? Eventually the solitary male bypassed us screaming and then continued on following the group. We kept trying to catch up to Makumba who had bolted away and instead we ended up in the back with the solitary male who continued to scream whilst searching for Makumba. Then as the Makumba group moved south we stopped hearing the solitary male. It seemed as if he had disappeared. There were traces of fresh feeding at the same *Celtis* tree (Figure 4.3). We found Makumba who was hooting and chest-beating, and several individuals were in trees (definitely Mopambe, Mai, Malui and Mossoko Abuli). It was very silent again. We kept running into elephants everywhere probably because the group was being so quiet and not alerting the elephants to their presence (Appendix 9).

July 10

We ran into the group quite quickly. Makumba was displaying at Malui and blocking her from taking other paths. Also at one point he was sex vocalising at Malui. Is he mate guarding? (We later found out she was pregnant at the time). The nests were very difficult to find. We found the nests in an open area, close together, generally without faeces. Likemo (tracker) said there had been a lot of fighting the night before based on the traces and the ground disturbance. The group was still walking a lot, but not as far as the other days and we were able to keep up with them. They would move, stop, rest, eat, and then move on. It didn't seem that the group was more spread out today, but Makumba was whinnying A LOT! I wonder if it was because he is tense and wants the group close by. He was question mark vocalising as well (see July 8 for my definition). I did see him falling asleep at one point. Poor guy, he must be exhausted. There didn't seem to be much play (if any) either. We also ran into leopard scat where the group was sitting but Makumba didn't appear to react. They then spent some time in Bai Debwe where we saw the whole group and can confirm that Etefi is still missing. They then started to move towards the first interaction site again, and suddenly abruptly turned and went back towards Bai Debwe where they nested. Why the quick turn? Why does it seem like Makumba is returning to the initial interaction site again? He was whinnying and chest-beating and hooting all afternoon even when the group was close. I even heard a few hoots from the juveniles. Were they calling Etefi? Was he looking for her? Or was he just tense? (Appendix 10)

July 11

The nests were in a more open area but otherwise were normal. We found them in the regular *Celtis adolfi frederici* tree (Figure 4.3). They then abruptly turned and moved south west at which point we lost the group. When we caught up to them they were moving, and Malui, Bombe and Mopambe were close to Makumba with all the children nearby playing. They then spent the next two hours sleeping. Makumba seemed very tired. It was very quiet and there were individuals close to Makumba. Although it was hard to tell how many, I think they were quite cohesive. The afternoon seemed fairly normal, except they were still moving a fair bit and Makumba was whinnying more than usual, but not as much as yesterday. There was no hooting from the other members today. Makumba did chest-beat once. At one point an adult female screamed and several individuals barked. Makumba did go to investigate, although it appeared to be an intragroup argument (Appendix 11).

July 12

No new interaction today, although the group was definitely very cohesive all day (Appendix 12).

July 13

On our way to find the nests we heard a chest-beat about 200-300 meters away. We found the nests shortly after, and they were all normal. The morning was okay, although the group stayed cohesive. Some of the kids were playing. Makumba rested while the group fed in the same *Celtis adolfi frederici* tree (Figure 4.3). At one point near the end of the morning, Bombe and Mopambe (with their infants) suddenly got up and walked south. Makumba seemed to hear something and walked off quickly in the same direction as the females and then turned and walked back north looking across the river at something. He kept starrng across the river for a long time and then he sat down. We kept hearing an elephant banging against a tree but we were not sure what he was hearing. The adult females seemed to be acting a bit fidgety also, walking back and forth, although I'm not sure where Malui was. Then about 30 minutes later we heard an extragroup silverback chest-beat. At this point, Makumba started chest-beating and went into the river and used the water in display, presumably to make more noise. He then left

his group to go in the direction of the extragroup male chest-beat. We heard him tree slapping and chest-beating. He soon returned and then went off again chest-beating. He returned again to the group and we could still hear the solitary male chest-beating several hundred meters away. The group remained dead silent during this period and when Makumba was with the group he did not make a sound either (not even a belch). The group remained very cohesive and moved back towards their nesting spot from yesterday. What is Makumba doing hanging around the same spots? Does he want Etefi? Does he want to meet the solitary male? These seem like definite intentional ranging patterns. By the end of the day, the juveniles were playing again and Makumba was belching a lot (Appendix 13).

July 14

The group returned to the same area as yesterday again. In the early afternoon we saw Makumba leave the group and chest-beat and tree slap several times. After that, he returned and they basically moved very quickly down south west. They moved over 2 km in 20 minutes. As they were moving, we saw the entire group walk by in a single file line, with ETEFI! They kept moving and resting for the rest of the afternoon. Makumba I'm noticing seems to be losing weight. His face seems very long and he is spending more and more time resting or moving, but I don't see him eating as much as normal. He is definitely more jumpy when he rests. At one point while he was sleeping he literally whipped around because he heard something behind him. It was only Kunga. Another time Makumba reacted similarly to Beakoko (tracker) who was just quietly coming back from a wee. We left them while they were still moving (Appendix 14).

July 15

They had kept moving when we left them last night because we found their nests about 800 meters from where we left them. They then kept moving south throughout the morning. They continued to move cohesively, and alternated moving with resting; but on the whole things seemed less tense. The juveniles were playing a lot and Makumba was feeding today but still spent more time resting. No one seems to be paying any attention to us at the moment. Makumba actually played a little with Kunga today. Until 15:43 the afternoon progressed as the morning had. Ngombo (tracker) said he saw a scar on Etefi's right palm. Just as I thought they

were going to settle down for the night, we heard a solitary silverback scream about 50 meters away. The group just went dead silent and hid in a Marantaceae patch. A few minutes later, we saw Kunga come out of the Marantaceae patch, patrol in a circle and then I think he went back in to the patch. After the scream, we heard the solitary male move to the other side of us within 10 meters and then Kunga came back out of the forest patch and moved in the same direction as the solitary male. At this point I'm not sure if Kunga went back to the group or kept patrolling, but it seemed like he walked back to the group. Then it was silent. About 20 minutes later we heard the silverback scream about 500 meters away. Makumba and the group remained hidden in the forest patch and stayed dead silent, except for the odd fart here and there. I heard him belch twice from 1543-1625, but they were incredibly quiet belches. No one else made a sound. We don't know who this male was? (Appendix 15)

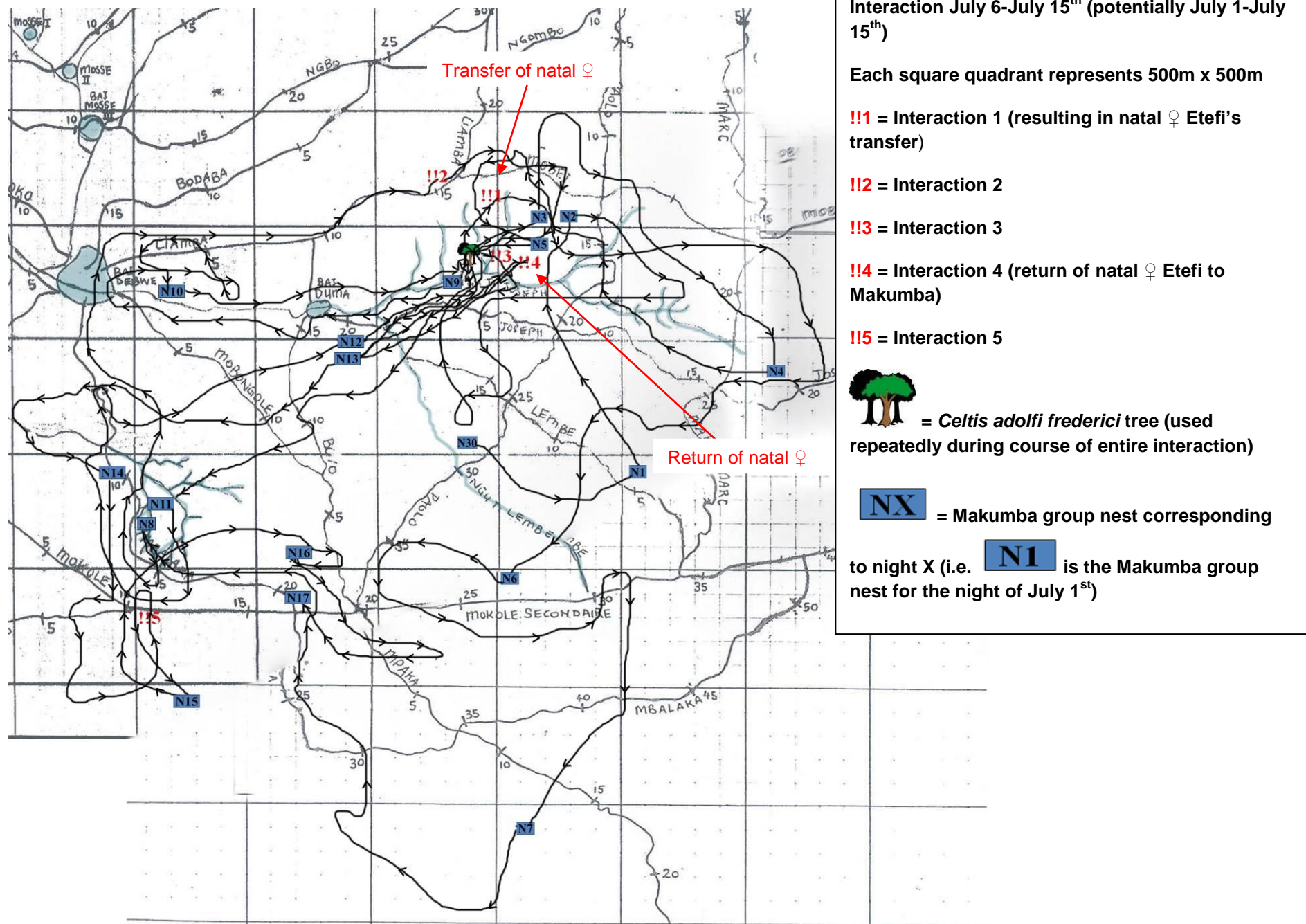
July 16

They rested a lot today and didn't move far (Appendix 16).

July 17

They are still staying south, but otherwise this was the most normal day we've had in weeks (Appendix 17).

Figure 4.3 Interaction Resulting in the Temporary Transfer of a Natal Recently Mated Adult Female



Interaction July 6-July 15th (potentially July 1-July 15th)

Each square quadrant represents 500m x 500m


!!1 = Interaction 1 (resulting in natal ♀ Etefi's transfer)

!!2 = Interaction 2

!!3 = Interaction 3

!!4 = Interaction 4 (return of natal ♀ Etefi to Makumba)

!!5 = Interaction 5

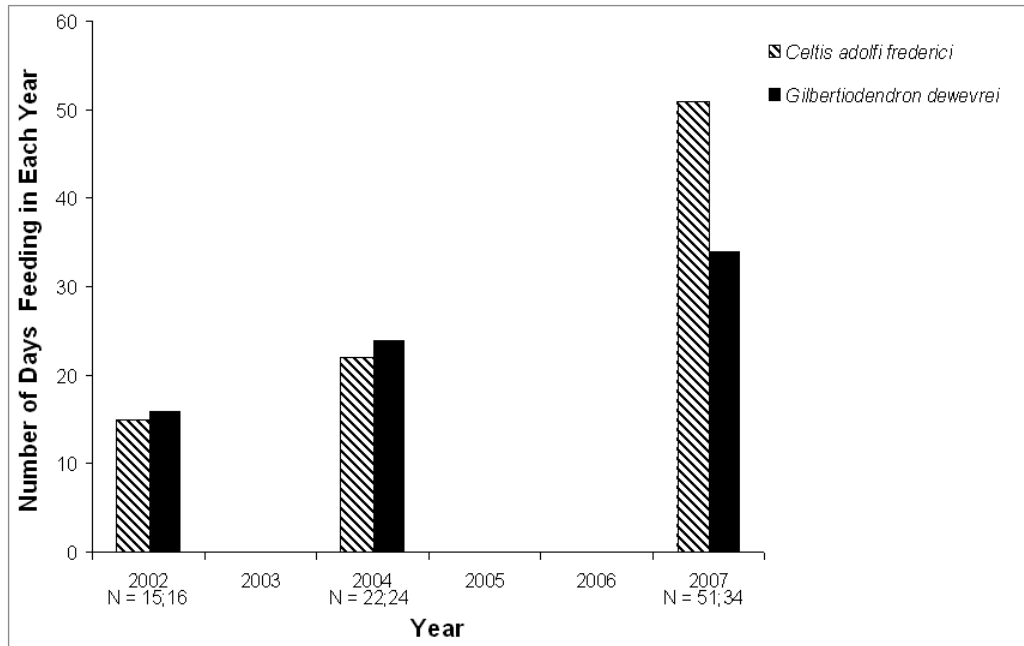
 = *Celtis adolfi frederici* tree (used repeatedly during course of entire interaction)

NX = Makumba group nest corresponding to night X (i.e. **N1** is the Makumba group nest for the night of July 1st)

4.4.4 High Level Interactions and Mast Fruiting

Year 2007 appear to have a double mast fruiting season, where both *Celtis adolfi frederici* and *Gilbertiodendron dewevrei* fruited simultaneously. Neither *Celtis* nor *Gilbertiodendron* fruited in 2005 or 2006 (Chapter 2). Additionally, fruiting records of the Makumba group available from 2002, suggest that 2007 represented an extraordinary fruiting year for both species, as more days were recorded feeding on either of these fruits in 2007 than in any other (Figure 4.4). Additionally, both tree types began fruiting in July. *Gilbertiodendron dewevrei* is a well known mast fruit producer in Central African rainforests, whose production cycles on a 2-6 year timeline [Blake & Fay, 1997; F. Maisels & D. Morgan pers. comm.]. Less is known about the cycling of *Celtis adolfi frederici*, however, fruiting periods at Goualougo Triangle, Nouablale-Ndoki National Park, suggest yearly fruit availability can vary with potential mast fruiting events occurring in some years [Morgan, 2006]. *Gilbertiodendron* is an important species for forest mammals, including elephants and gorillas [Blake & Fay, 1997]. This alone may have brought a large number of mammals, including gorillas, into Makumba's range (we experienced many more elephant encounters during this fruiting time period than at any other part of the year; pers. obsv.). This apparent *Gilbertiodendron* mast fruiting event, coupled with what appears to be an additional mast *Celtis* fruiting event, further justifies motives for gorilla migration into the region.

Figure 4.4 Number of Days Observed Feeding on *Celtis* and *Gilbertiodendron* from 2002-2007



Note: it was not possible to control for missing observation days in 2002-2006, as I was not able to access these data. However, daily follows began in 2002; thus the group will have been followed almost every day of the year from 2002-2006.

4.4.5 Home Range in Relation to Interactions

The total home range was assessed as 27.3 km² in 2007 with a core area of 8.4 km², based on quadrat use (Section 4.3.7). August-December core area size increased by 165% and home range by 94% when compared to January-July (Table 4.5). Additionally, both core and home range location shifted dramatically (Figure 4.5 and 4.6), where only the south west portion of the original core area remained as part of a much larger and shifted core area in August-December. Seven of the 65 cells (11%) that made up the core area in January-July were not even entered in August-December, and 60% of the January-July core area was not used as core area in August-December.

Table 4.5 Core and Home Range Area Change from January-July to August-December

| Range | January-July (km ²) | August-December (km ²) |
|------------|---------------------------------|------------------------------------|
| Core Area | 4 | 10.4 |
| Home Range | 12.6 | 24.4 |

4.4.6 Ranging and Resource Use Patterns from July 1st-July 17th

The red border on Figure 4.5a, 4.5b and 4.6a represent the outer boundaries of the Makumba group's movement during July 1st-July 17th. Most of this path was walked during four consecutive days after the interaction on July 6th until the second interaction on July 9th in the same area (Figure 4.6b). The 4 day range almost completely circles the core of the Makumba group's January-July range. There was also repeated use of one *Celtis adolfi frederici* feeding tree throughout this interaction period (Figure 4.3), and four high level interactions (two of which coincided with Etefi leaving and returning to the Makumba group) took place within 250-300m of this tree (Figure 4.3).

Figure 4.5 The Makumba Group's Core and Home Range for (a) January-July and (b) August-December

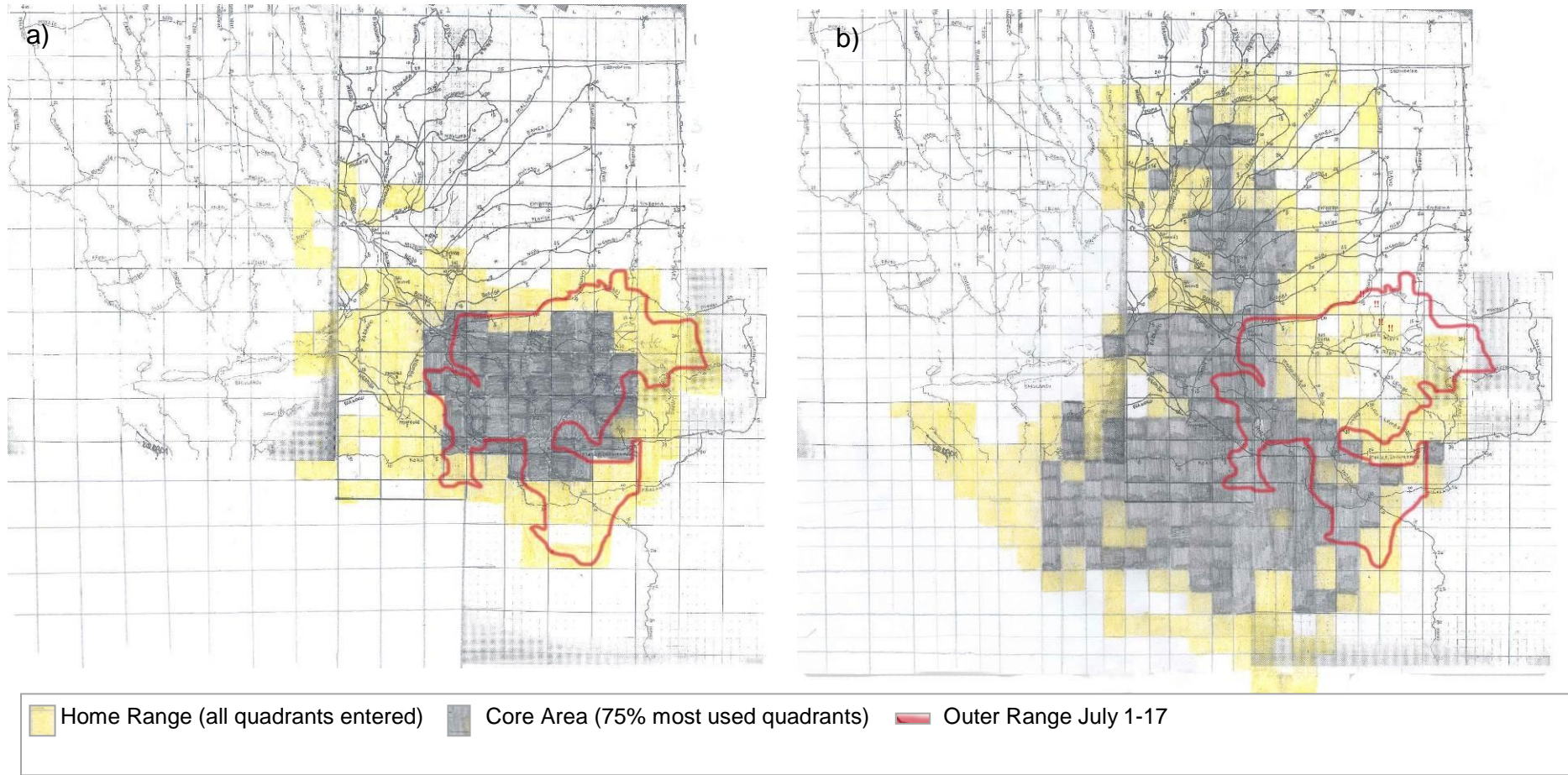
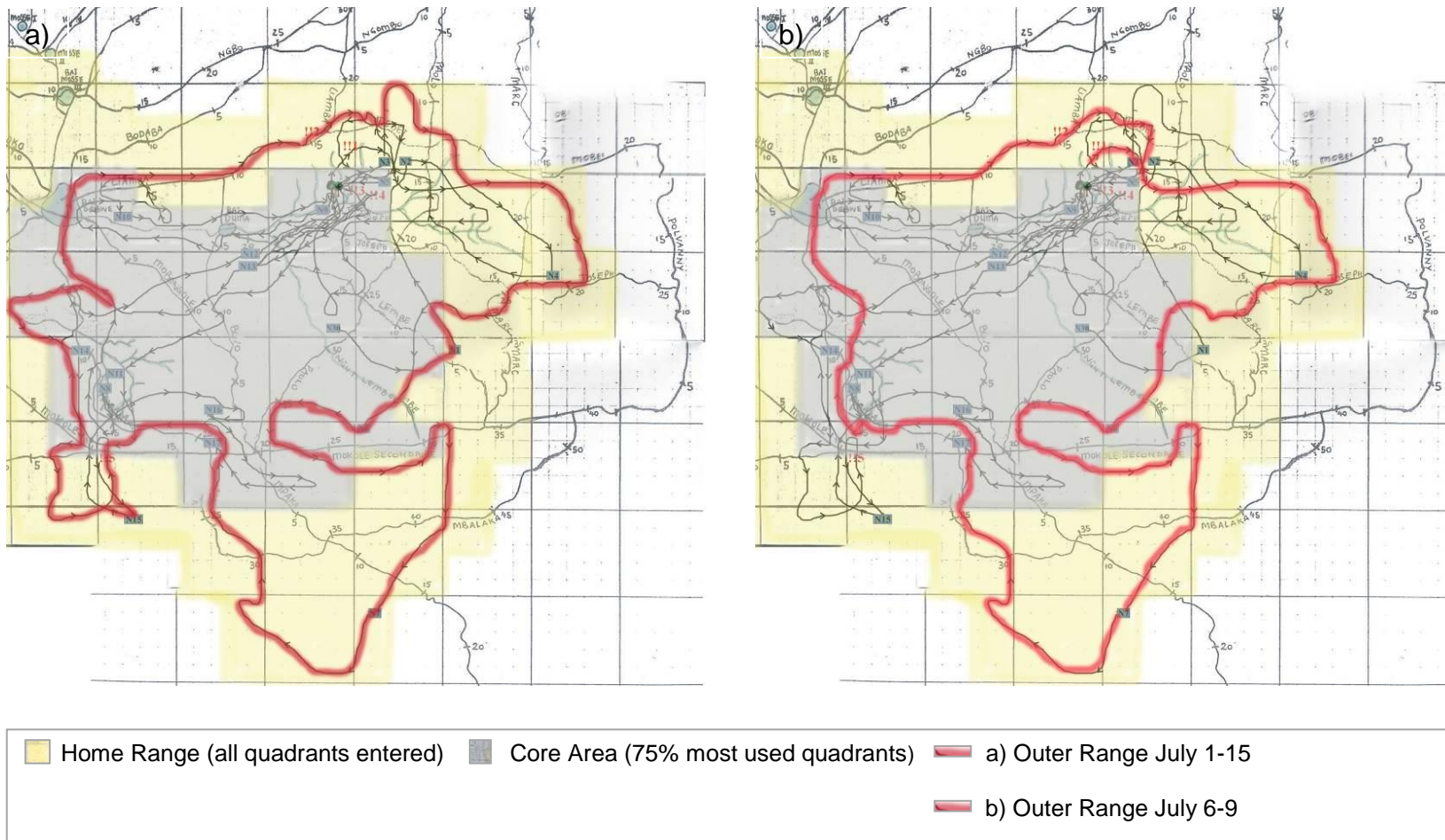


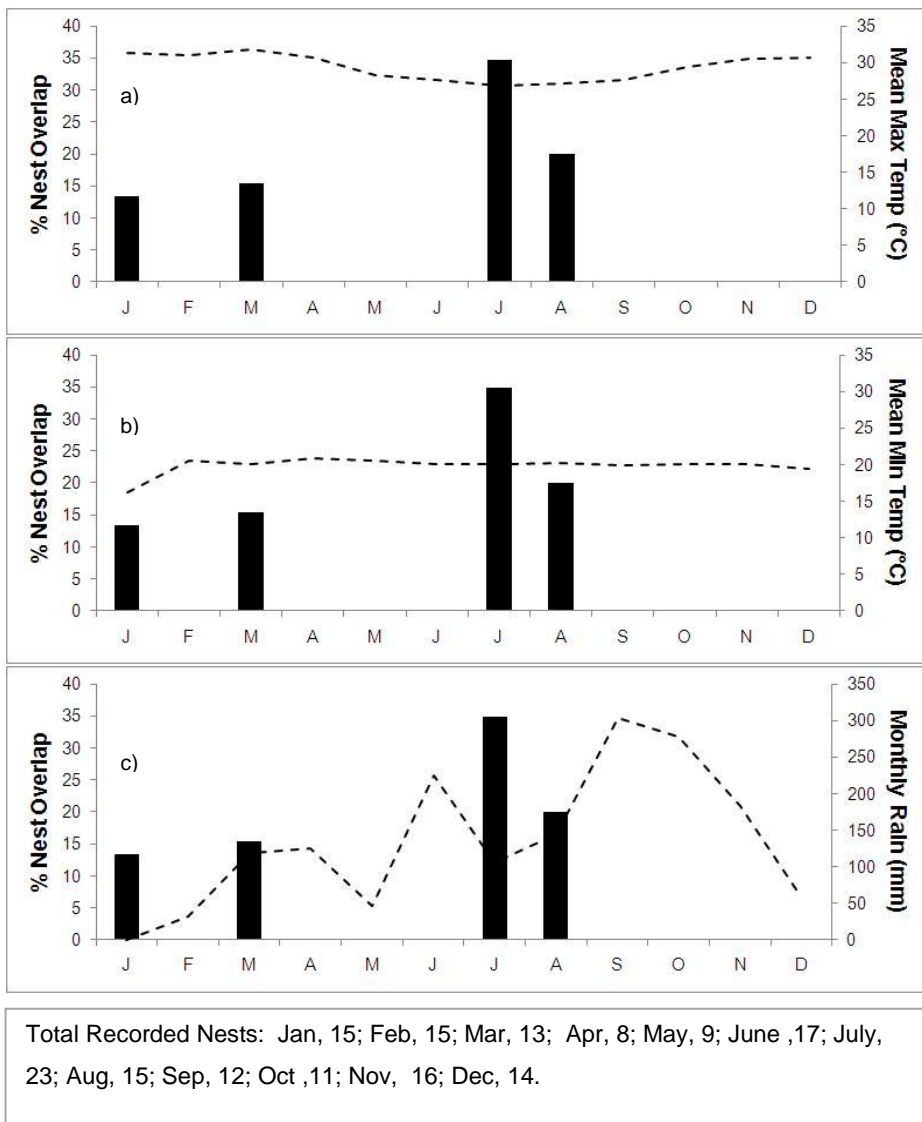
Figure 4.6 The Makumba Group's Core and Home Range for (a) January-July and (b) August-December



4.4.7 Nest Overlap

Nests that overlapped in the same quadrat occurred rarely, although nests overlapped most in July (35%) and August (20%). Additionally, 75% (N = 6) of the overlapping nests in July occurred within the July 1st-July 17th period. It is unlikely that mean maximum and minimum temperatures affected July's high nest overlap, as temperature remained relatively stable throughout the year (Figure 4.7a and 4.7b; also see Chapter 2) even though nest overlap numbers did not. Furthermore, it is unlikely that the drop in July's rain level had a significant influence on July's high nest overlap; since nest overlap was either nonexistent or seen at lower levels (compared to July) during drier parts of the year (i.e. January and March; Figure 4.7c).

Figure 4.7 Makumba Group Nest Site Overlap in Quadrats per Month



4.4.8 Interaction Level and its Effects on Forest Density Nest Choice

There was no significant difference in nest site preference as a function of forest density between interaction and non-interaction days ($F = 2.06$, $df = 1, 153$, $p = 0.153$, $N = 157$; controlled for daily rainfall and maximum temperature). Nesting in open forests only occurred during high level interactions (Figure 4.8). As interaction level increased, nesting in dense forests decreased, or to put alternatively, nesting in open forests increased, although this relationship did not reach significance ($B = -0.452$, $SE = 0.437$, $Wald 1.070$, $df = 1, 3$, $Exp(B) = 0.636$, $p = 0.301$, $N = 35$; controlled for daily rainfall and maximum temperature; Figure 4.8). Failing to reach significance may be an artefact of the small sample sizes in each category (Table 4.6). Nesting in moderate forests was likely to occur at similar percentages across all three interaction levels ($B = 0.090$, $SE = 0.435$, $Wald = 0.043$, $df = 1, 3$, $Exp(B) = 1.094$, $p = 0.836$, $N = 35$; controlled for daily rainfall and maximum temperature; Figure 4.8). On non-interaction days, dense forest nest sites were preferred over moderately dense nest sites ($X^2 = 28.855$, $df = 1$, $p < 0.001$, $N = 128$; Figure 4.9). No open forest nest sites were observed on non-interaction days

Figure 4.8 Interaction Level in Relation to Forest Density in Nesting

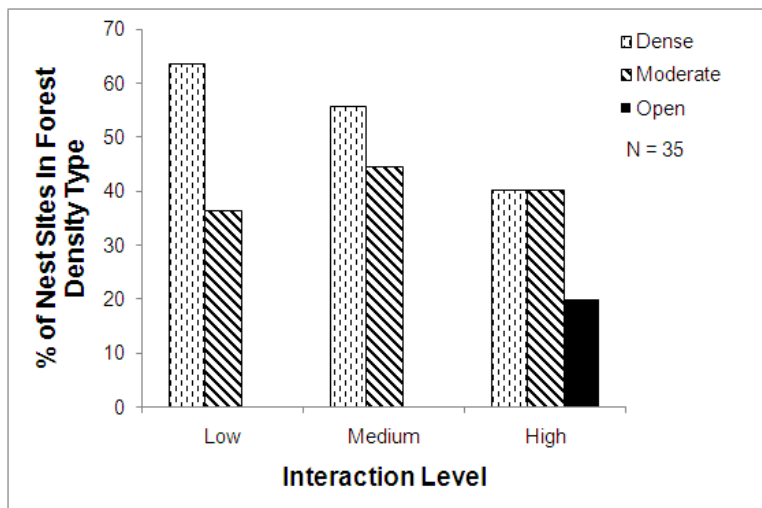


Figure 4.9 Forest Density of Nests on Non-Interaction Days

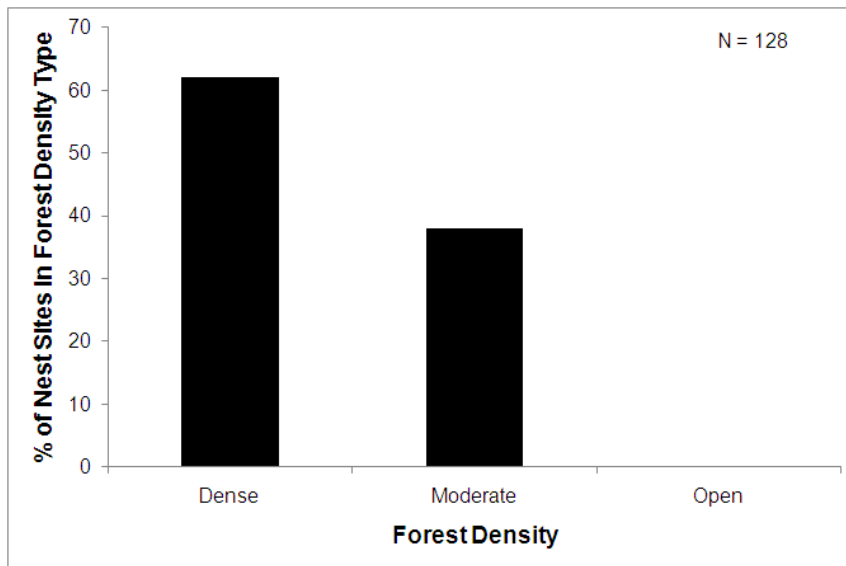


Table 4.6 Number of Nests in each Forest Density Type by Interaction Level

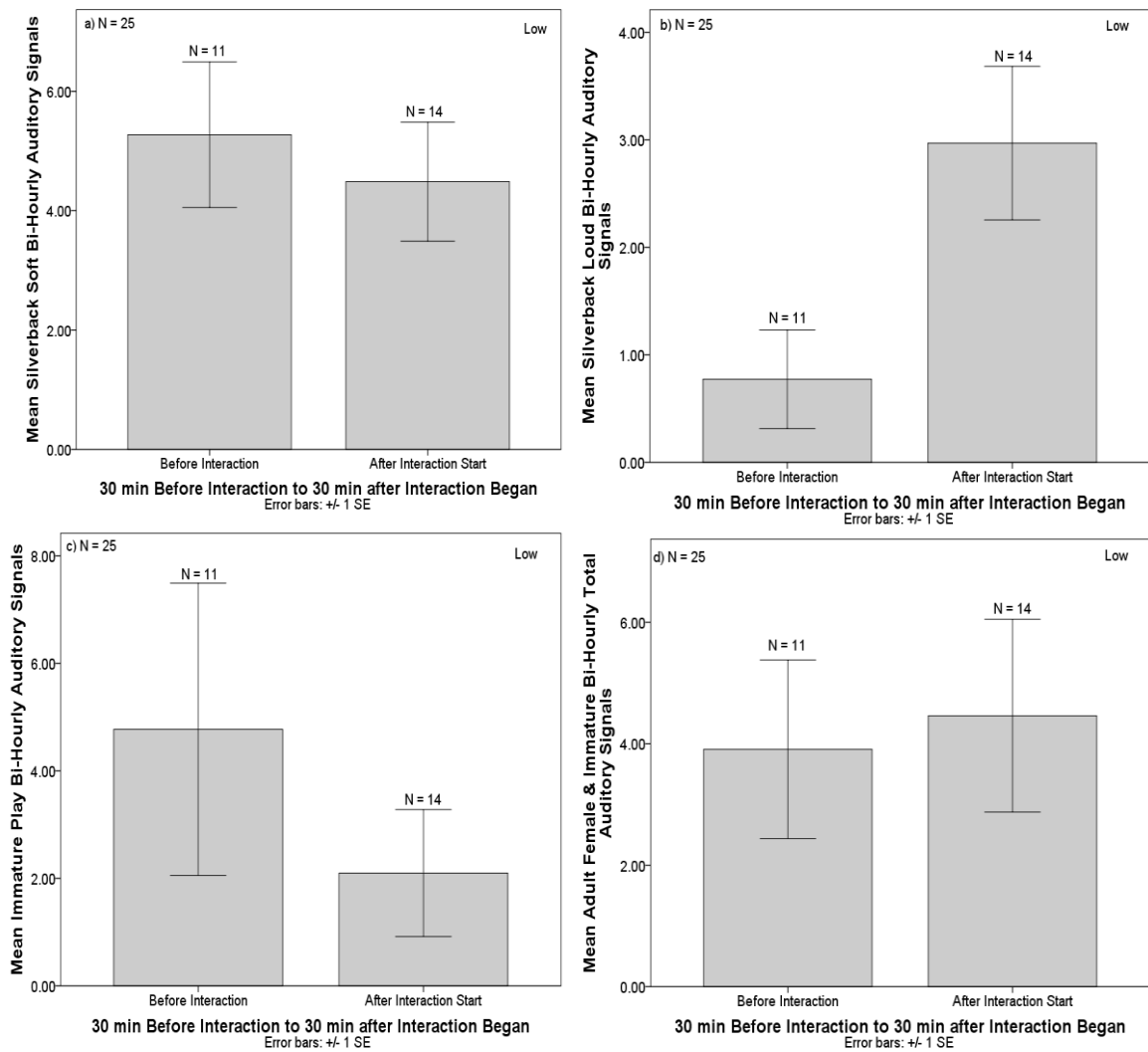
| N | Dense | Moderate | Open |
|--------|-------|----------|------|
| Low | 7 | 4 | 0 |
| Medium | 5 | 4 | 0 |
| High | 6 | 6 | 3 |

4.4.9 Vocalisation Rates in Relation to Interaction Level

4.4.9.1 Low Level Interactions

Rain, temperature and season were controlled for in ANOVA models of vocalisation rates and interactions. Rates of silverback soft auditory signals did not significantly change after interactions began ($F = 0.23$, $df = 1, 19$, $p = 0.635$, $N = 25$; Figure 4.10a), however rates of silverback loud auditory signals did significantly increase after interactions began ($F = 11.12$, $df = 1, 19$, $p = 0.003$, $R^2 = 0.289$, $N = 25$; Figure 4.10b). Immature rates of play auditory signals did not significantly change after interactions began ($F = 1.49$, $df = 1, 19$, $p = 0.238$, $N = 25$; Figure 4.10c). Total adult female and immature auditory signal rates (not including play) did not significantly change after interactions began ($F = 0.72$, $df = 1, 19$, $p = 0.406$, $N = 25$; Figure 4.10d).

Figure 4.10 Auditory Signals in Relation to Low Level Interactions¹



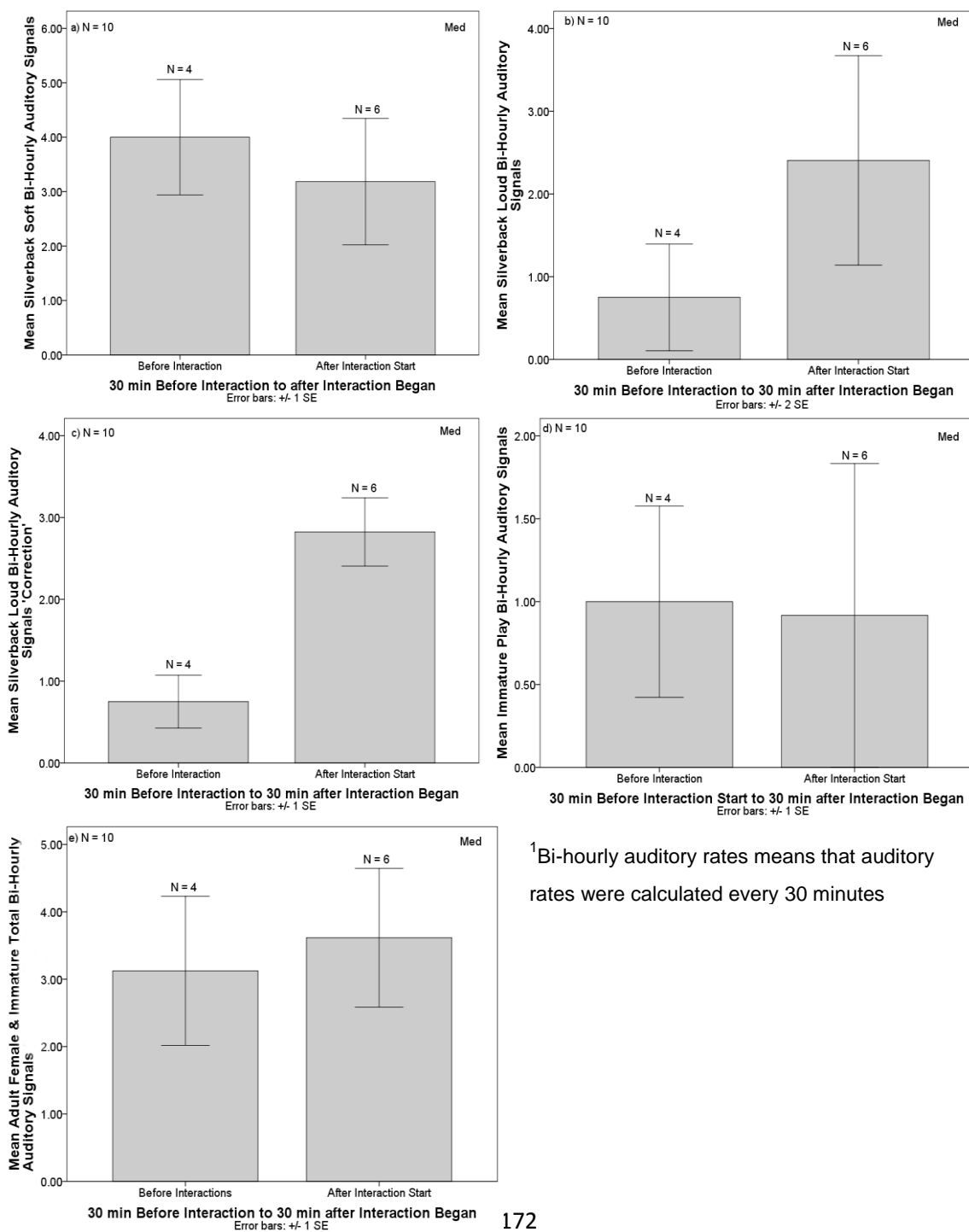
¹Bi-hourly auditory rates means that auditory rates were calculated every 30 minutes

4.4.9.2 Medium Level Interactions

Rain – the most influential factor on rates of auditory signalling – was the only control factor used here, as the model would flood otherwise. Silverback soft auditory signal rates did not significantly change after interactions began ($F = 0.42$, $df = 1, 7$, $p = 0.536$, $N = 10$; Figure 4.11a), nor did loud auditory signals ($F = 1.41$, $df = 1, 7$, $p = 0.274$, $N = 10$; Figure 4.11b). However, in one interaction on March 3rd, it was unclear whether the loud auditory signals belonged to an extragroup silverback or to Makumba. The above analysis assumed that the loud auditory signals belonged to the extragroup silverback. If these same signals belonged to Makumba, then rates of silverback loud auditory signals significantly increased after interactions

began ($F = 8.433$, $df = 1, 7$, $p = 0.023$, $R^2 = 0.42$, $N = 10$; Figure 4.11c). Rates of immature play auditory signals did not significantly change after interactions began ($F = 0.58$, $df = 1, 7$, $p = 0.471$, $N = 10$; Figure 4.11d). Total adult female and immature auditory signal rates (not including play) did not significantly change after interactions began ($F = 0.03$, $df = 1, 7$, $p = 0.866$, $N = 10$; Figure 4.11e).

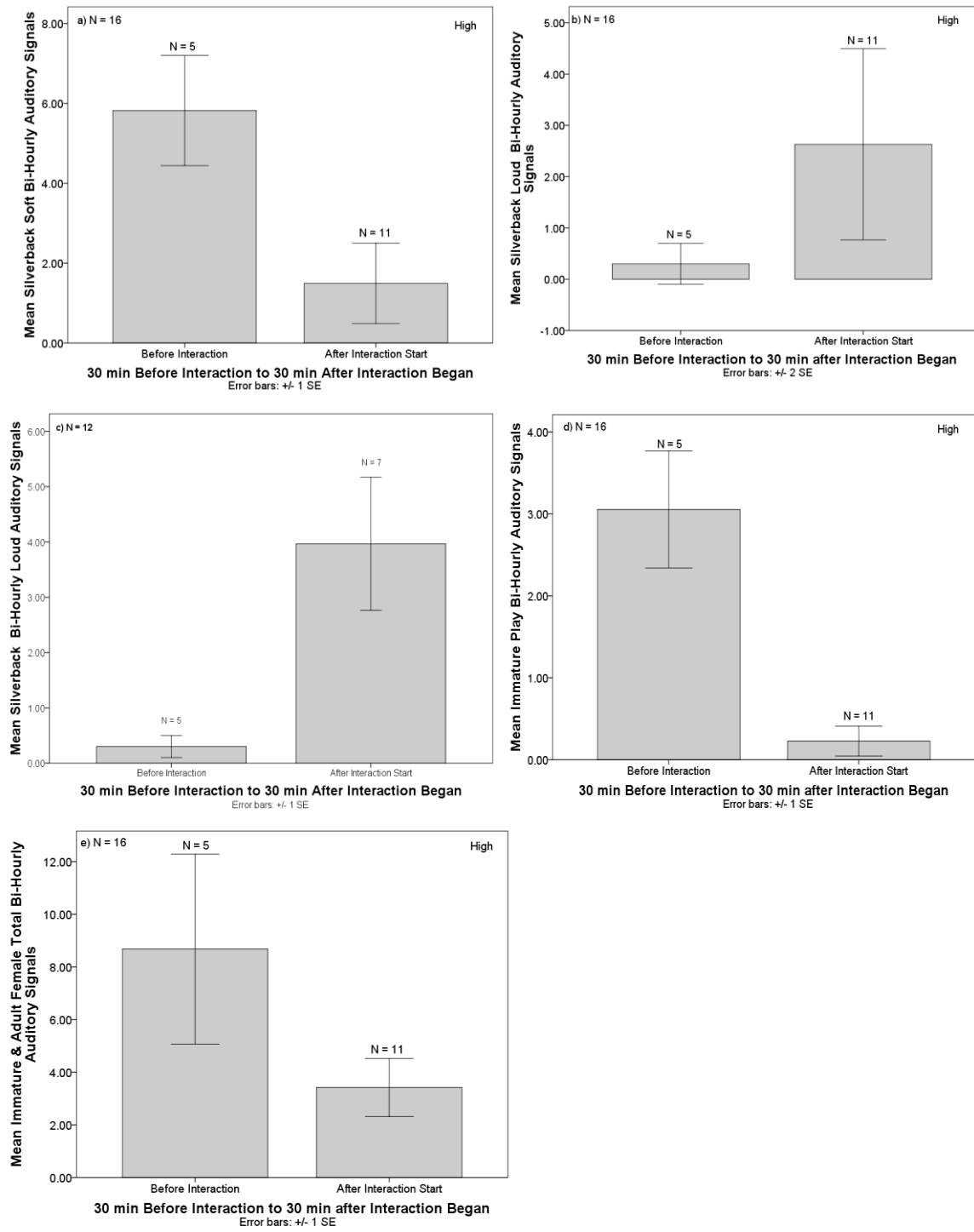
Figure 4.11 Auditory Signals in Relation to Medium Level Interactions¹



4.4.9.3 High Level Interactions

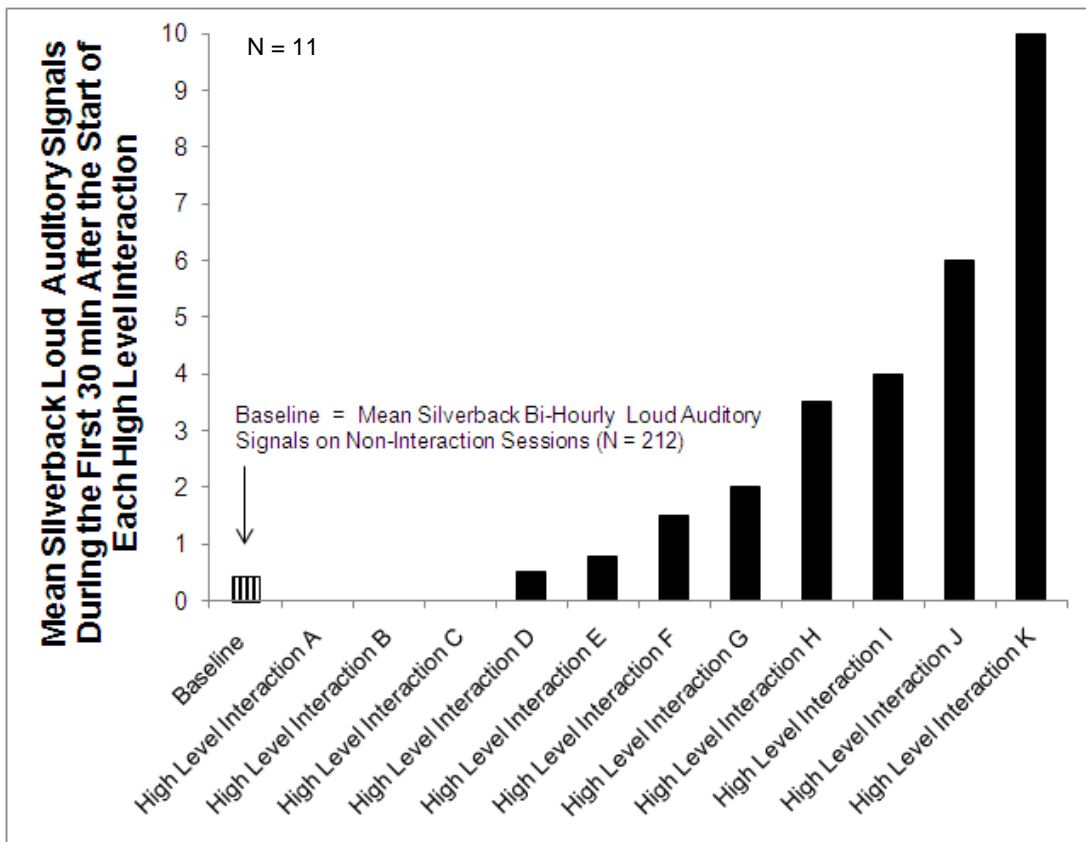
Rain and temperature were controlled for in ANOVA models of rates of signalling during high level interactions. Controlling for season was not necessary as all high level interactions recorded during observation sessions occurred in the fruiting season. Rates of silverback soft auditory signals significantly decreased after interactions began ($F = 21.98$, $df = 1, 12$, $p = 0.001$, $R^2 = 0.48$, $N = 16$; Figure 4.12a). Rates of silverback loud auditory signals did not significantly change after interactions began ($F = 1.88$, $df = 1, 12$, $p = 0.196$, $N = 16$; Figure 4.12b). However, Figure 4.13 illustrates that during four high level interactions, Makumba's loud auditory rates decreased from baseline of 0.5 loud auditory signals per 30 minutes on non-interaction days, to zero on three occasions whilst remaining the same on one occasion. It was not possible to do a before-after comparison of vocalisations for these four interactions, as rates of loud auditory signals before the start of the interactions were unknown for three of the above occasions. On the 4th interaction, loud auditory rates decreased from 0.5 thirty minutes before the interaction to 0, up to 30 minutes after the interaction began. Upon exclusion of these four 'silent' responses, silverback loud vocalization rates significantly increased after the interaction began ($F = 10.57$, $df = 1, 8$, $p = 0.012$, $R^2 = 0.48$, $N = 12$; Figure 4.12c). Immature rates of play auditory signals significantly decreased after interactions began ($F = 34.70$, $df = 1, 12$, $p < 0.001$, $N = 16$; Figure 4.12d). Even though adult female and immature rates of total auditory signals decreased during the first 30 minutes after a high level interaction began as opposed to the increase in rates seen in both low and medium level interactions, changes were not significant ($F = 1.34$, $df = 1, 12$, $p = 0.270$, $N = 16$; Figure 4.12e).

Figure 4.12 Auditory Signals in Relation to High Level Interactions¹



¹Bi-hourly auditory rates means that auditory rates were calculated every 30 minutes

Figure 4.13 Silverback Loud Auditory Signalling Responses During the First 30 Minutes After a High Level Interaction Began, in Comparison to Baseline Silverback Loud Auditory Signalling Rates on Non-Interaction Sessions



Note: Interactions are in order of strength of response, not in order of occurrence

Also see Section 4.4.9.3 for a justification of why baseline rates on non-interaction sessions were used to graphically represent the silent responses instead of graphing a 'before high level interaction - after high level interaction' comparison of auditory rates

4.4.10 Makumba's Responses (in Addition to Auditory Responses) According to Interaction Level

Makumba responded to interactions by: (a) communicating with extragroup males through loud auditory signals (as analysed in detail in Section 4.4.9); (b) silence (see Section 4.4.9.3); (c) patrolling a given area while the group stayed behind and waited or moved off [Fossey, 1974]; (d) fleeing; (e) hiding with the group in a thicket [Fossey, 1972].

Auditory responses were the silverback's most frequent response type in low level interactions, with some patrolling and to a lesser extent movement (Figure 4.14). Again, auditory responses

were the silverback's response in medium level interactions, although patrolling now occurred in 71% of the interactions and movement also increased from 27% in low level interactions to 42% in medium level interactions (Figure 4.14). Even though auditory responses were still frequent during high level interactions, they decreased by 27% from those in medium and low level interactions. Movement also increased from 43% in medium level interactions to 73% in high level interactions. Additionally, high level interactions represented the only time where silent responses and hiding were observed (Figure 4.14 and Table 4.7).

Figure 4.14 Makumba's Responses According to Interaction Level

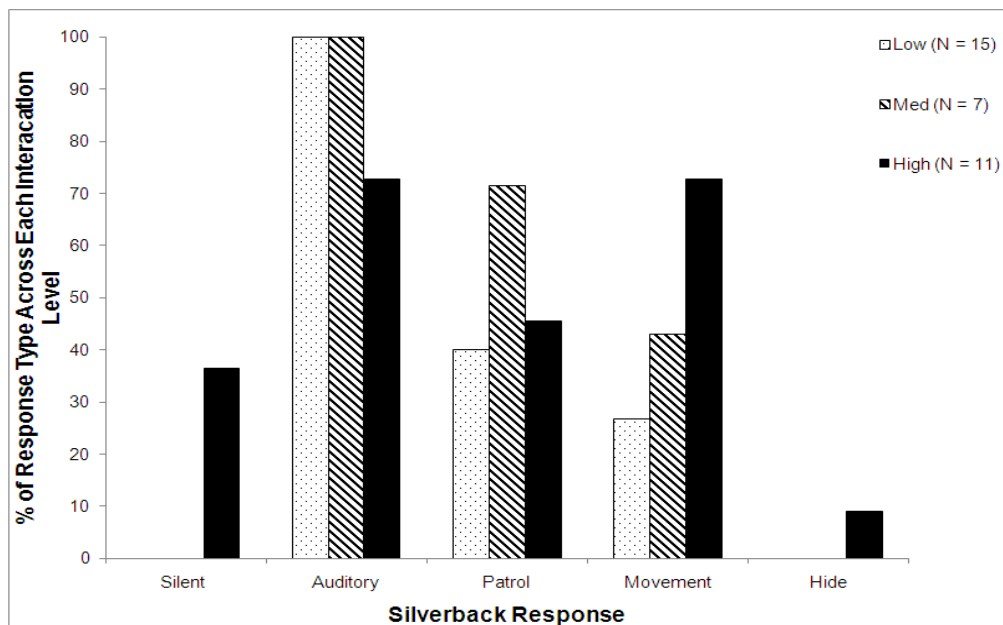


Table 4.7 Makumba Responses According to Interaction Level Sample Sizes

| N | Silent | Auditory | Patrol | Movement | Hide | Total |
|--------|--------|----------|--------|----------|------|-------|
| Low | 0 | 15 | 6 | 4 | 0 | 15 |
| Medium | 0 | 7 | 5 | 3 | 0 | 7 |
| High | 4 | 8 | 5 | 8 | 1 | 11 |

Makumba's responses were not necessarily mutually exclusive and could be grouped into: (a) auditory responses only; (b) auditory response with or without patrol, with or without movement/fleeing; (c) silence and fleeing; (d) silence and hiding.

'Auditory only' responses were used primarily in low level interactions, with a complete lack of this response type during high level interactions (Figure 4.15). The 'mixed' auditory category was frequent in medium level interactions (Figure 4.15). In high level interactions, the silverback used a combination of 'mixed' auditory and silent with flee or hide responses, which as stated previously, were observed only during high level interactions (Figure 4.15 and Table 4.8).

Figure 4.15 Grouped Makumba Responses According to Interaction Level

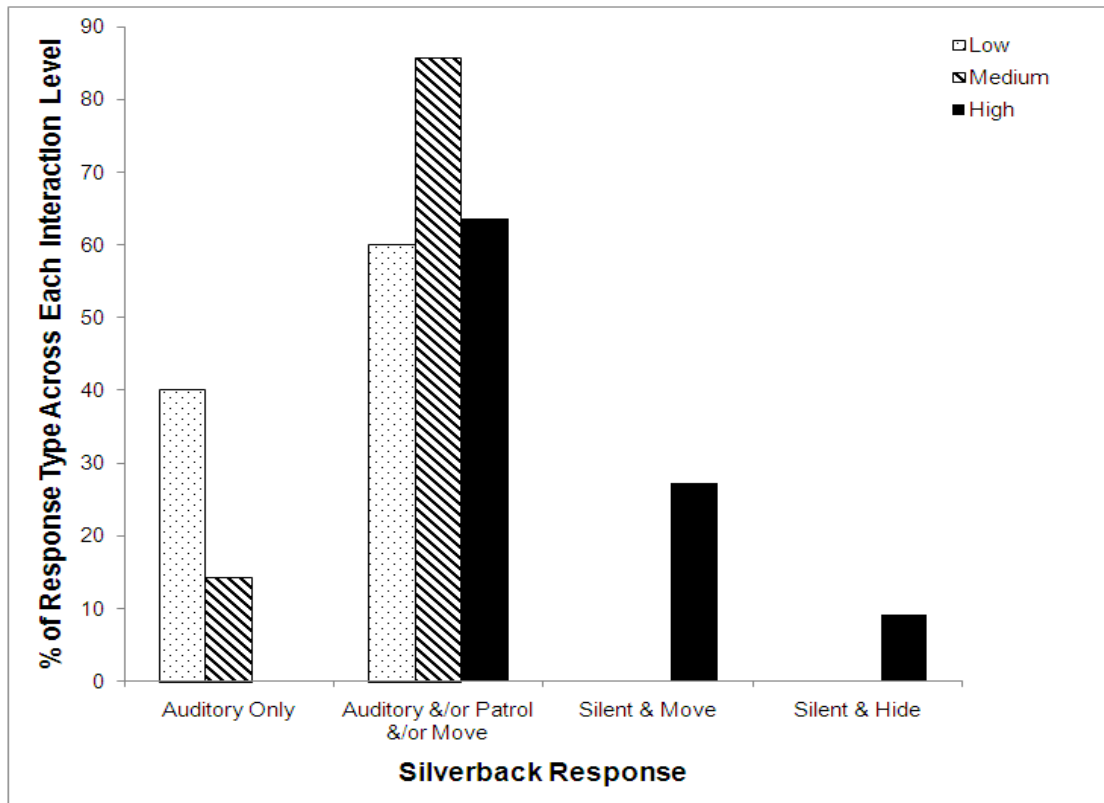


Table 4.8 Grouped Makumba Responses According to Interaction Level Sample Sizes

| N | Auditory Only | Auditory &/or Patrol &/or Move | Silent & Move | Silent & Hide | Total |
|--------|---------------|--------------------------------|---------------|---------------|-------|
| Low | 6 | 9 | 0 | 0 | 15 |
| Medium | 1 | 6 | 0 | 0 | 7 |
| High | 0 | 7 | 3 | 1 | 11 |

Several unique observations regarding Makumba's response to high level interactions were recorded. These observations are set into context and briefly described in Section 4.4.3. Here I describe the observations in more detail.

Displaying using Food

During two interactions, Makumba ate herbaceous vegetation very aggressively, once in front of an extragroup silverback on July 9th, and once upon hearing an extragroup male on August 23rd. On July 9th this can best be described as angry eating, where he grabbed as much herbaceous vegetation as possible, stood in a stiff stance, stared the extragroup male down and very quickly and very angrily tore off the leaves in his teeth, eating some and spitting some to the floor. On August 23rd the same situation occurred, except the extragroup male was not in visual presence. On this occasion he stripped a sapling and left it on the ground.

Displaying using Water

This method of display has been shown to occur during interunit interactions at Mbeli Bai [Parnell & Buchanan-Smith, 2001]. Section 4.4.3 describes the July 9th water display event in full detail.

Whispering

This vocalisation sounded exactly like a 'belch' used in intragroup communication, yet the volume of the vocalisation was extremely quiet, almost inaudible. These quiet belches occurred only during silent responses in high level interactions, and appeared to be the equivalent of a 'whisper'. On July 7th, Makumba whisper belched 14 times, while the adult females and immatures whisper belched four and two times respectively. On July 8th, Makumba, the adult females and the immatures whisper belched twice each. On July 15th during an interaction, an unknown individual whisper belched once. As these 'whispers' were unlike any other vocalisation used throughout the year, occurred infrequently, and were almost inaudible, they were excluded from the analyses, but still appear to contain information in the signal.

Silent Charges

Parallel to the whisper belch, human observers received two silent charges on July 8th. Section 4.4.3 describes these events in full detail.

4.4.11 Influences of Interactions on Group Spread with Focus on Cohesive

Groupings

Group spread differed significantly among months ($F = 13.79$, $df = 11, 1967$, $p < 0.001$, $R^2 = 0.049$, $N = 2407$; controlled for visibility, season, group activity, total human observers, observer-silverback distance; Figure 4.16). Post-hoc analysis reveals that the Makumba group was significantly more cohesive in July – the peak interaction month – than any other month apart from August (Table 4.9).

Figure 4.16 Group Spread Changes per Month

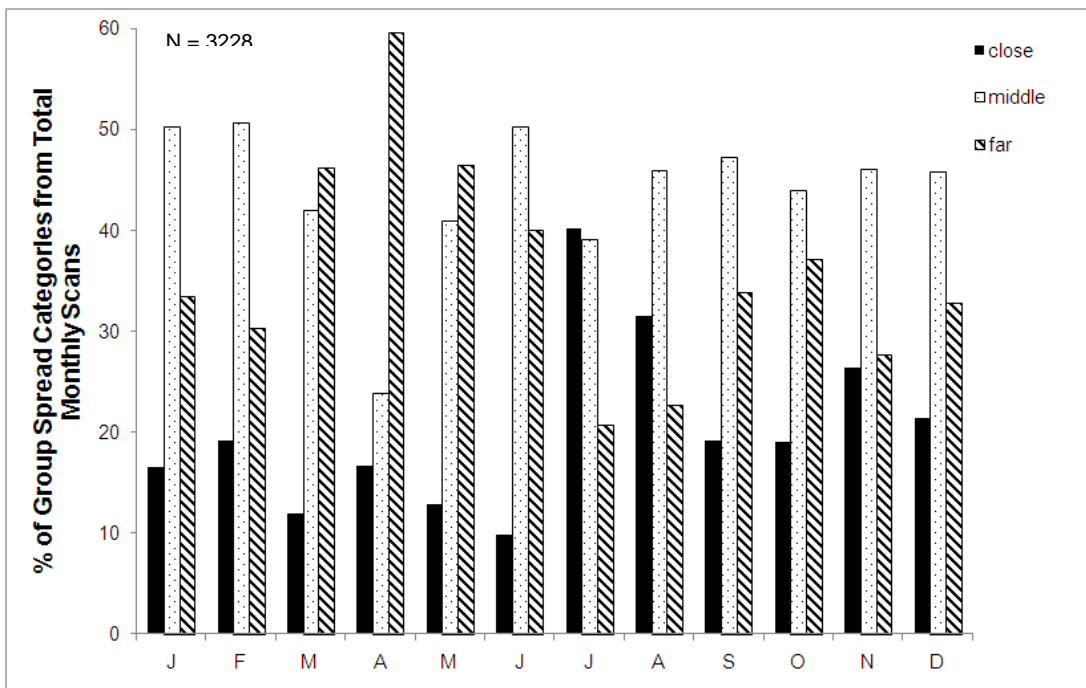


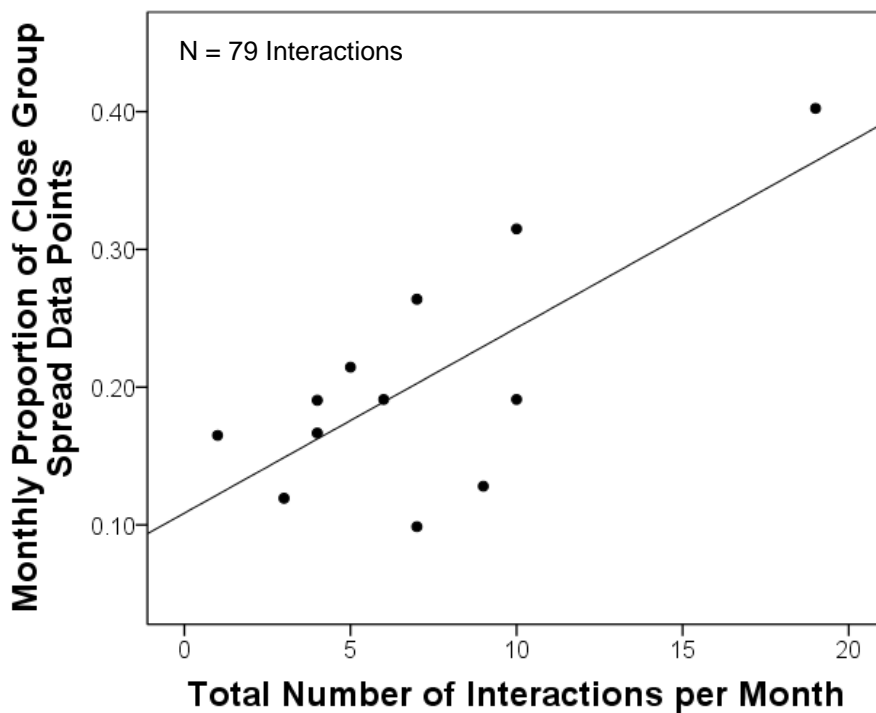
Table 4.9 July Post-Hoc Results on Group Spread Changes per Month^a

| July vs. | Sig. | Standard Error | N |
|----------|---------|----------------|-----|
| Jan | < 0.001 | 0.06187 | 297 |
| Feb | < 0.001 | 0.5675 | 492 |
| Mar | < 0.001 | 0.6446 | 243 |
| Apr | < 0.001 | 0.7552 | 168 |
| May | < 0.001 | 0.07196 | 164 |
| Jun | < 0.001 | 0.06322 | 233 |
| July | - | - | 256 |
| Aug | 0.945 | 0.07214 | 181 |
| Sep | < 0.001 | 0.07410 | 157 |
| Oct | < 0.001 | 0.06360 | 294 |
| Nov | 0.028 | 0.06000 | 398 |
| Dec | < 0.001 | 0.06147 | 345 |

^aLevene's Test $p < 0.001$; Games Howells Results Reported

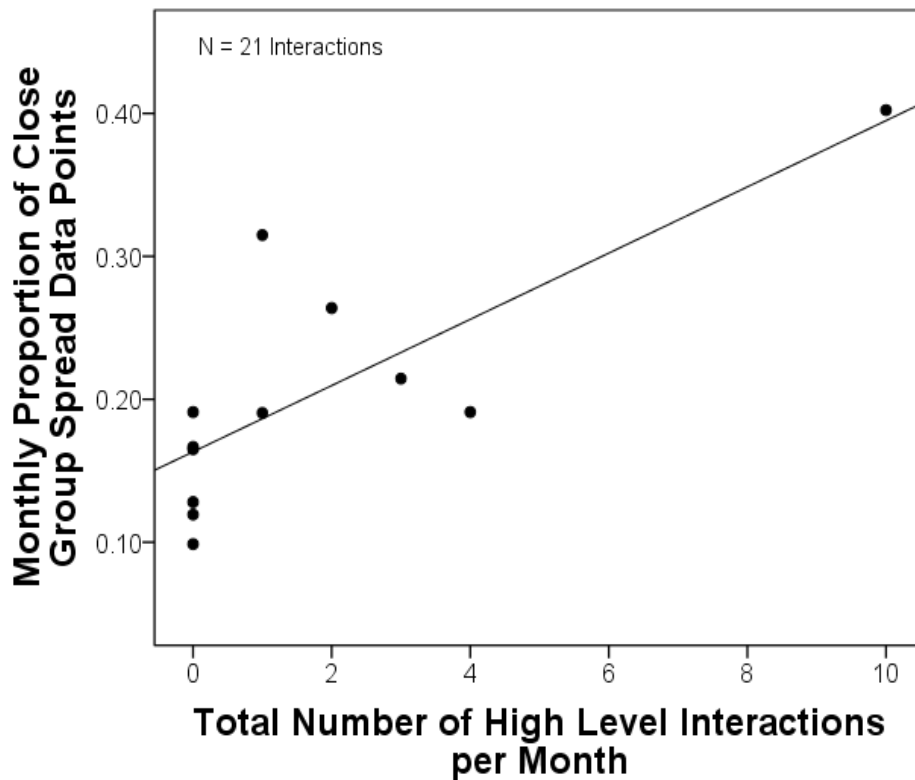
Cohesive or close group spread was predicted by the total number of interactions in each month ($B = 0.013$, $SE = 0.004$, Standardised Beta = 0.725, $df = 1, 11$, $p = 0.008$, $R^2 = 0.479$, $N = 12$; controlled for month to take into effect habituation, season and density as these were the strongest predictors in the previous analyses; Figure 4.17).

Figure 4.17 Mean Proportion of Close Group Spread in Relation to Total Number of Interactions per Month



Close group spread was predicted by the total number of high level interactions per month ($B = 0.023$, $SE = 0.006$, Standardised Beta = 0.782, $df = 1, 11$, $p = 0.003$, $R^2 = 0.572$, $N = 12$; controlled for month to take into effect habituation, season and visibility as the strongest predictors in the previous analyses; Figure 4.18). Close group spread was not predicted by the number of low level interactions per month ($B = -0.004$, $SE = 0.017$, Standardised Beta = -0.071 , $df = 4, 11$, $p = 0.839$, $N = 12$) nor by the number of medium level interactions per month ($B = 0.008$, $SE = 0.019$, Standardised Beta = 0.146, $df = 4, 11$, $p = 0.705$, $N = 12$).

Figure 4.18 Makumba Group Close Group Spread in Relation to Total Number of High Level Interactions per Month



4.4.12 Silverback-Neighbour Changes (within 5m)

4.4.12.1. Monthly Changes Using Only Interactions Recorded During Observation Sessions

Numbers of individuals scored as neighbours to the silverback differed significantly among months ($F = 15.47$, $df = 11, 1960$, $p < 0.001$, $R^2 = 0.058$, $N = 2399$; controlling for visibility,

season, group activity, total human observers, observer-silverback distance; Figure 4.19). Post-hoc analysis showed that Makumba had significantly more neighbours in July than other months, apart from January, February, May, June and August (Table 4.10). Mean monthly neighbour counts could have been skewed by the large number of 'zero' neighbour scans in the data set (Chapter 3). When all 'zero' scans were excluded from analysis, neighbour numbers to the silverback still significantly varied by month ($F = 7.08$, $df = 11$, 994 , $p < 0.001$, $R^2 = 0.047$, $N = 1346$; controlling for visibility, season, group activity, total human observers, observer-silverback distance; Figure 4.20); and, post hoc analyses now showed that Makumba had significantly more neighbours in July than any other month except April, August and September (Table 4.11).

Even though August and September have lower numbers of neighbours to the silverback than July, this difference was not significant. This "bunching" of neighbours in August and September may have been an ongoing response from July's peak interaction period. April however, was not a high interaction period and was not significantly different from July. While Games Howell post hoc results for mean daily rainfall and mean maximum temperature did not differ significantly between April and July (mean monthly rainfall: $p = 1.00$, $SE = 0.793$, $N = 12$ months, 258 sessions; mean maximum monthly temperature: $p = 0.055$, $SE = 1.064$, $N = 12$ months, 258 sessions), April represented the first month that the Makumba group was observed feeding on *Gambeia lacourtiana* (the most fed on fruit between April-June; Chapter 2), and the only month where the group was observed feeding on *Ficus* sp. (Chapter 2). While tree productivity and location was not assessed in this study, it is possible that when this species began fruiting in April it may have been limited to only certain patches, increasing spatial clumping. Additionally, since the gorillas fed on *Ficus* in April only, it is also possible that it too was found in a few non-uniform patches. Thus April's silverback-neighbour numbers may have been influenced by an unusually clumped fruiting distribution.

Figure 4.19 Mean Neighbours to the Silverback (within 5m) by Month

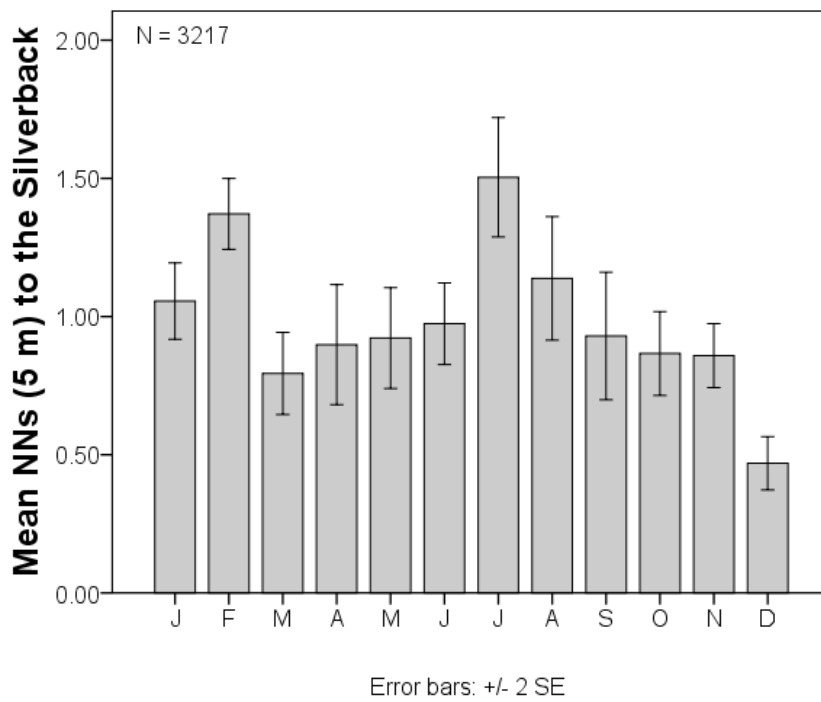


Table 4.10 July Post-Hoc Results for Neighbours to the Silverback (within 5m) by Month^a

| July vs. | Sig. | Standard Error | N |
|----------|---------|----------------|-----|
| Jan | 0.401 | 0.0664 | 303 |
| Feb | 1.00 | 0.0666 | 487 |
| Mar | < 0.001 | 0.6806 | 243 |
| Apr | 0.002 | 0.7851 | 167 |
| May | 0.084 | 0.07486 | 167 |
| Jun | 0.198 | 0.06899 | 233 |
| July | - | - | 258 |
| Aug | 0.482 | 0.07860 | 181 |
| Sep | 0.021 | 0.07914 | 156 |
| Oct | < 0.001 | 0.06715 | 292 |
| Nov | <0.001 | 0.06293 | 389 |
| Dec | < 0.001 | 0.06117 | 341 |

^aLevene's Test p <0.001; Games Howells Results Reported

Figure 4.20 Mean Neighbours to the Silverback (within 5m) by Month Excluding 'Zero' Neighbour Scans

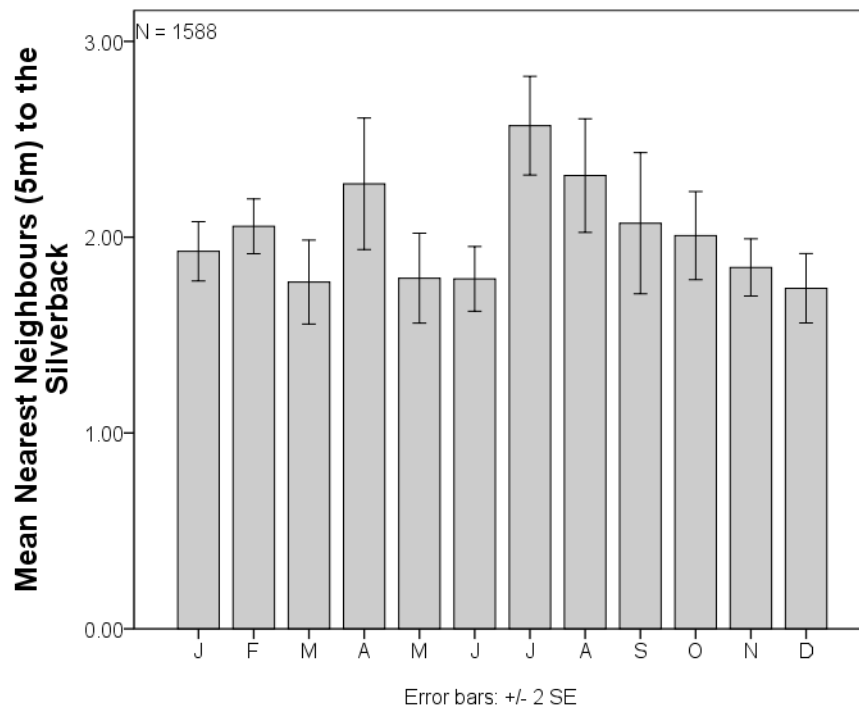


Table 4.11 July Post-Hoc Results for Neighbour Numbers to the Silverback (within 5m) by Month Excluding 'Zero' Neighbour Scans^a

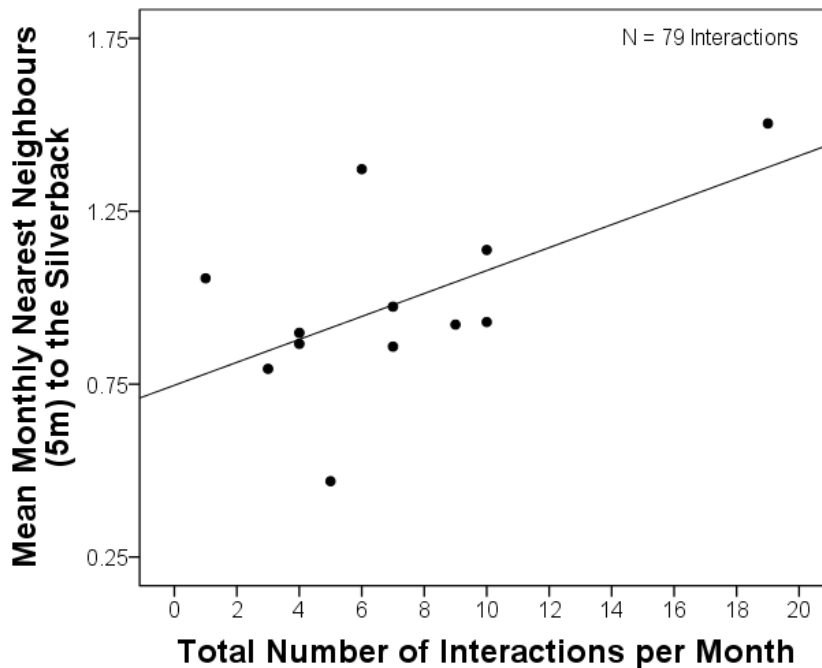
| July vs. | Sig. | Standard Error | N |
|----------|---------|----------------|-----|
| Jan | 0.001 | 0.04327 | 166 |
| Feb | 0.002 | 0.03789 | 325 |
| Mar | < 0.001 | 0.04836 | 109 |
| Apr | 1.000 | 0.05678 | 66 |
| May | < 0.001 | 0.05198 | 86 |
| Jun | <0.001 | 0.04643 | 127 |
| July | - | - | 151 |
| Aug | 1.00 | 0.05142 | 89 |
| Sep | 0.221 | 0.05564 | 70 |
| Oct | < 0.001 | 0.04643 | 126 |
| Nov | <0.001 | 0.04241 | 181 |
| Dec | < 0.001 | 0.05089 | 92 |

^aLevene's Test p <0.001; Games Howells Results Reported

4.4.12.2 Monthly Changes Using Total Number of Interactions per Month

Numbers of neighbours to the silverback (within 5m) were predicted by the total number of interactions per month ($B = 0.044$, $SE = 0.011$, Standardised Beta = 0.761, $df = 1, 11$, $p = 0.002$, $R^2 = 0.579$, $N = 12$; controlled for month to take into effect habituation, season and visibility as they were the strongest predictors in the previous analyses; Figure 4.21).

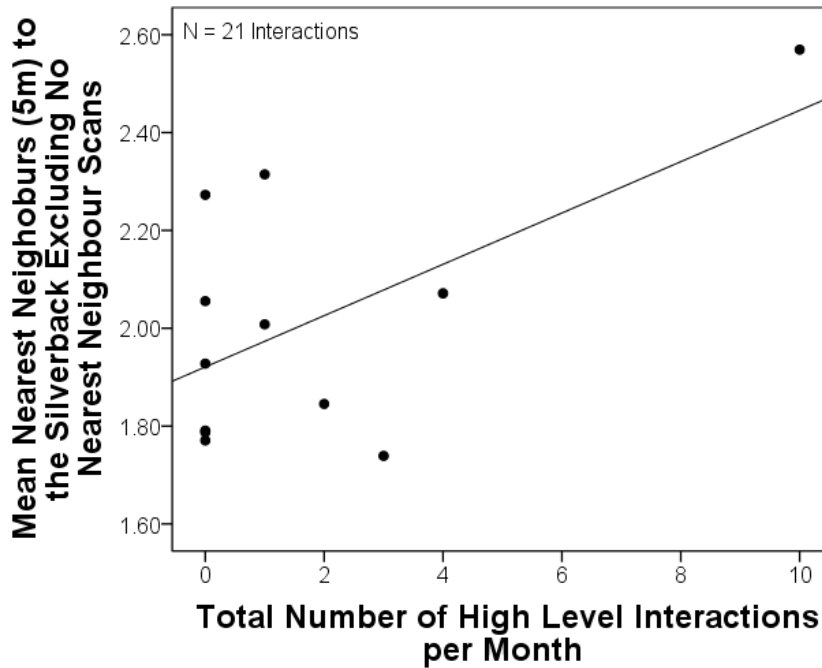
Figure 4.21 Mean Monthly Number of Neighbours to the Silverback (within 5m) in Relation to Total Interactions per Month



Numbers of neighbours to the silverback (within 5m) were not significantly predicted by the total number of high level interactions per month, although a positive trend was detected ($B = 0.054$, $SE = 0.025$, Standardised Beta = 0.584, $df = 4, 11$, $p = 0.066$, $N = 12$). As above, when 'zero' neighbours scans were excluded, neighbour numbers to the silverback significantly increased as the total number of high level interactions per month increased ($B = 0.043$, $SE = 0.023$, Standardised Beta = 0.591, $df = 1, 11$, $p = 0.043$, $R^2 = 0.284$, $N = 12$; Figure 4.22). Again, neighbour numbers to the silverback were not significantly predicted by the total number of medium ($B = 0.050$, $SE = 0.047$, Standardised Beta = 0.311, $df = 4, 11$, $p = 0.319$, $N = 12$) or low level interactions per month ($B = 0.027$, $SE = 0.044$, Standardised Beta = 0.169, $df = 4, 11$, $p = 0.557$, $N = 12$). When 'zero' neighbours scans were excluded, results remained insignificant

(medium: $B = 0.030$, $SE = 0.054$, Standardised Beta = 0.194, $df = 4, 11$, $p = 0.594$, $N = 12$; low: $B = 0.023$, $SE = 0.049$, Standardised Beta = 0.148, $df = 4, 11$, $p = 0.652$, $N = 12$).

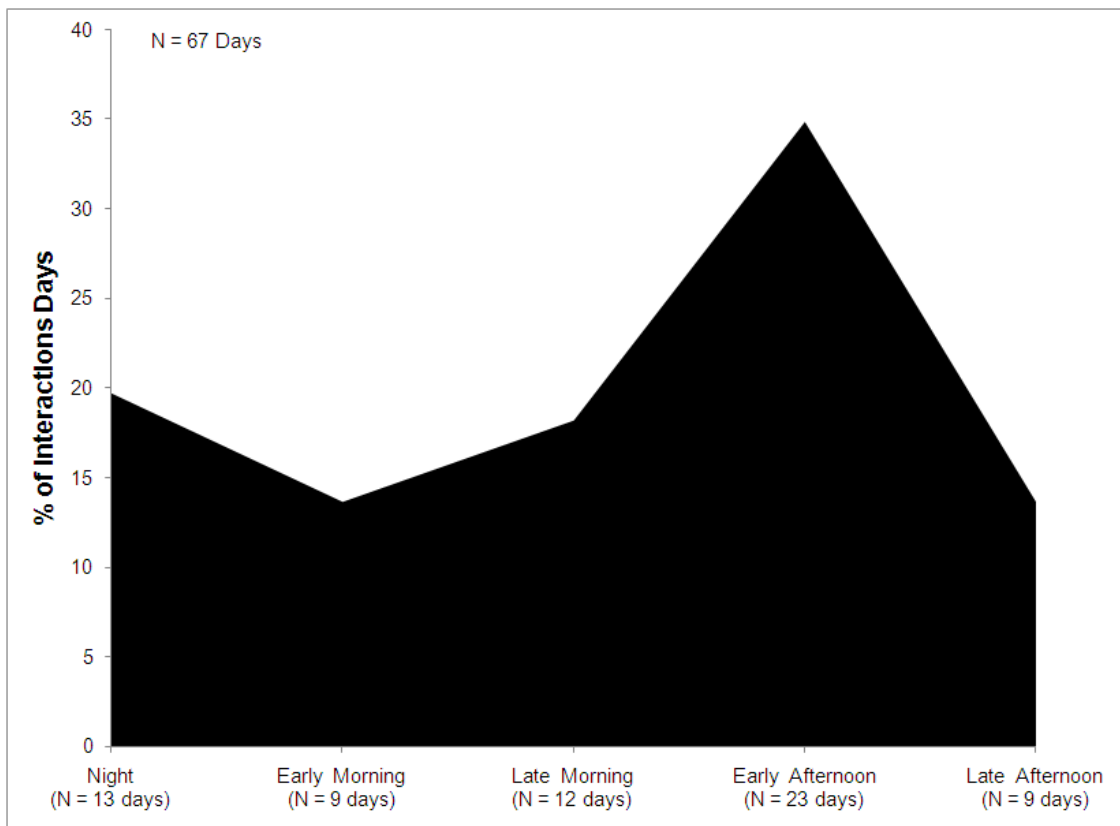
Figure 4.22 Mean Neighbour Numbers to the Silverback Excluding 'Zero' Neighbour Scans in Relation to Total Number of High Level Interactions per Month



4.4.13 Interactions, Group Spread, and Time of Day

Interactions were differentially distributed across times of the day ($X^2 = 9.940$, $df = 4$, $p = 0.041$, $N = 67$; Figure 4.23). They were significantly more likely to occur in the early afternoon than in the early morning or late afternoon ($X^2 = 6.125$, $df = 1$, $p = 0.013$, $N = 32$). Interactions tended to be more likely to occur in the early afternoon than the late morning, although not significantly so ($X^2 = 3.457$, $df = 1$, $p = 0.063$, $N = 35$). While interactions were more likely to occur in the early afternoon than during the night or dawn, again results did not reach significance ($X^2 = 1.087$, $df = 1$, $p = 0.297$, $N = 36$).

Figure 4.23 Number of Interactions by Time Block



Group spread differed significantly according to time of day ($F = 16.69$, $df = 3$, 3220, $p < 0.001$, $R^2 = 0.015$, $N = 3228$). When time of day was controlled for, group spread still differed significantly according to interaction presence or absence ($F = 2.88$, $df = 1$, 3220, $p = 0.024$, $R^2 = 0.026$, $N = 3228$) as shown in previous analyses (Section 4.4.11); although there was an interaction between time of day and interunit interaction presence or absence ($F = 2.88$, $df = 3$, 3220, $p = 0.035$, $N = 3228$). No other control variables were used in this analysis because of the minimal effect that other factors had on previous analyses. Group spread on non-interaction days differed significantly by time block ($F = 18.60$, $df = 3$, 2640, $p < 0.001$, $R^2 = 0.020$, $N = 2644$; Figure 4.24) but did not differ significantly by time block on interaction days ($F = 1.04$, $df = 3$, 580, $p = 0.375$, $N = 584$; Figure 4.24). Post-hoc analysis showed that group spread on non-interaction days was significantly greatest in the early afternoon compared to any other time of day apart from the late morning (Table 4.12). While interaction presence or absence

significantly decreased group spread on interaction days (Figure 4.24 and see Section 4.4.11), post-hoc analysis found no significant differences according to time of day (Table 4.13).

Interactions were more likely to occur in the early afternoon (and to an extent in the late morning), when the Makumba group was the most spread out (see above). The group's response was to become more cohesive during an interaction. There was also a peak in interactions at night or dawn (N = 14), and although there were more interactions in early afternoon (N = 23), chi square analysis did not reveal a significant difference (see above). While this may partly be due to small sample sizes, it also suggests that the Makumba group may have been targeted secondarily during periods where they were most cohesive (i.e. nesting). Note that while night/dawn interunit interactions are noted on Figure 4.23, information was gained through traces. Therefore night/dawn is not noted as a category in Figure 4.24 because researchers began collecting data in the early morning only. However, it is reasonable to assume that the gorillas would be nesting during the night/dawn and would be equally or perhaps even more cohesive during this time period in comparison to the early morning.

Figure 4.24 Mean Group Spread in Relation to Time Block

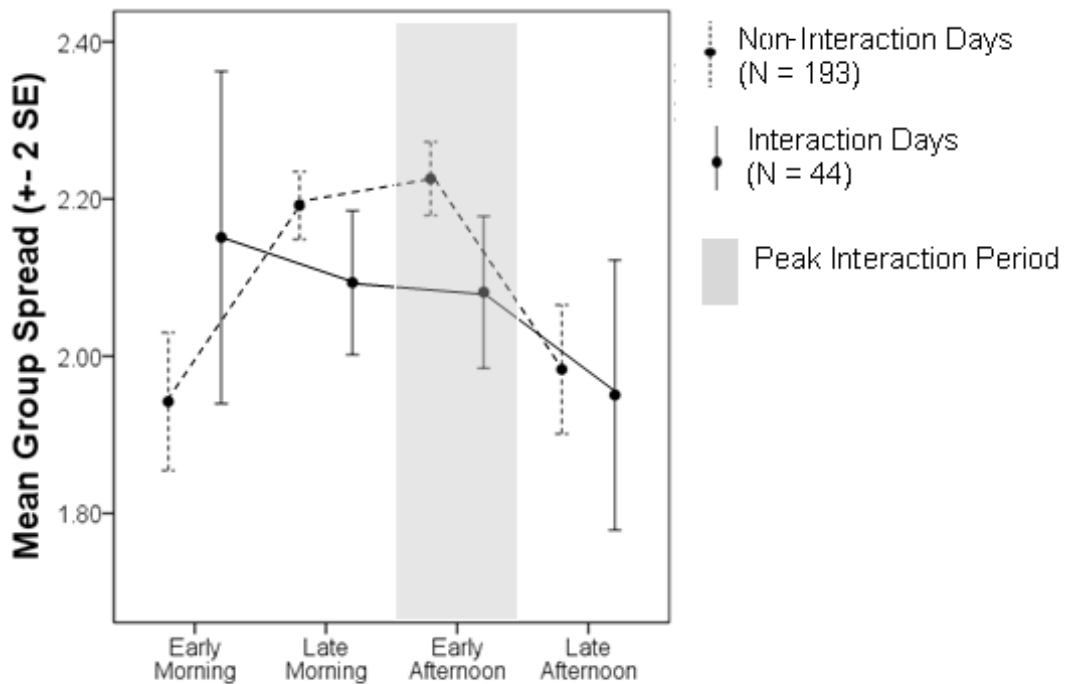


Table 4.12 Post Hoc Analysis of Group Spread by Time of Day on Non-interaction Days^a

| | Early Morning (N = 277) | Late Morning (N = 1090) | Early Afternoon (N = 921) | Late Afternoon (N = 356) |
|-----------------|----------------------------|----------------------------|------------------------------|-----------------------------|
| Early Morning | - | p <0.001, SE = 0.049 | p <0.001 SE = 0.049 | p = 0.980 SE = 0.058 |
| Late Morning | p <0.001 SE = 0.049 | - | p = 0.0873 SE = 0.323 | p < 0.001 SE = 0.044 |
| Early Afternoon | p <0.001 SE = 0.495 | p = 0.873 SE = 0.323 | - | p <0.001 SE = 0.045 |
| Late Afternoon | p = 0.980 SE = 0.058 | p < 0.001 SE = 0.044 | p < 0.001 SE = 0.045 | - |

^aLevene's Test p = 0.422; Hochberg's Results Reported**Table 4.13** Post Hoc Analysis of Group Spread by Time of Day on Interaction Days^a

| | Early Morning (N = 53) | Late Morning (N = 278) | Early Afternoon (N = 172) | Late Afternoon (N = 81) |
|-----------------|---------------------------|---------------------------|------------------------------|----------------------------|
| Early Morning | - | p = 0.959, SE = 0.115 | p = 0.932 SE = 0.116 | p = 0.458 SE = 0.136 |
| Late Morning | p = 0.959 SE = 0.115 | - | p = 0.998 SE = 0.666 | p = 0.460 SE = 0.097 |
| Early Afternoon | p = 0.932 SE = 0.116 | p = 0.998 SE = 0.666 | - | p = 0.548 SE = 0.9858 |
| Late Afternoon | p = 0.458 SE = 0.136 | p = 0.460 SE = 0.097 | p = 0.548 SE = 0.098 | - |

^aLevene's Test p <0.001; Games Howell Results Reported

4.5 DISCUSSION

The Makumba group experienced approximately seven interunit interactions per month in one year alone, more than any other published study based on one focal unit. A total of 21 (27%) high level, 27 (34%) medium level and 31 (39%) low level interactions occurred during the study period. However, high level interactions only started in the peak interaction month of July, and then continued at decreased rates for the next five months of the study.

The multisite comparison suggested that Makumba's tolerance of other units resembled the avoidance - aggression seen in mountain gorillas. However, multisite comparisons should be approached with caution, as definitions across sites were not standardised. For example, had I chosen to define tolerant responses as displays without movement or patrols [as in Tutin, 1996] instead of a simple 'ignore' reaction, then Makumba group 'tolerance' would rise to 21%, which approaches levels seen at Bai Hokou during a previous study on another focal group [Cipolletta, 2006]. Tolerance rates may have been under-represented since low level interactions may have occurred without being detected by the observer.

Lone silverbacks are rarely tolerated by group males and are viewed as the most dangerous neighbours to silverbacks with fertile females. They will track other groups silently for days in the pursuit of potential females (Section 4.2.1). The exceptional number of interactions experienced by Makumba in 2007 may have been a reflection of the extra unit type involved; solitary males may have been involved in more interactions and in more high level interactions than were group males. While this is not unexpected, especially given the fact that western lowland gorilla solitary males comprise 46% of the population in bai study sites (Section 4.2.7), the mast *Gilbertiodendron dewevrei* and *Celtis adolfi frederici* fruiting events beginning in July 2007 may have brought even more lone males into Makumba's home range during the 2007 study period [Tutin 1996; Robbins & Sawyer, 2007; Section 4.4.4]. These fruiting events in combination with the high potential losses for Makumba and the high potential gains for extragroup males may have been the catalyst for high level interactions. Makumba was faced with protecting two females with dependent infants and one pregnant female. Even if the extragroup units were only interested in the recently matured female, Etefi and potentially Mio

(another natal female nearing adulthood), extragroup males could commit infanticide to coerce one or several of Makumba's adult females away, placing much of Makumba's group in jeopardy during any high level interaction (Section 4.2.1). As stated earlier (Section 4.2.1), infants in single male units will face higher chances of infanticide, due to the potential inability of a single male to protect a large group and a high possibility of group disintegration during fatal encounters. Interactions in western lowland gorillas pertaining to the acquisition of females will be very risky for all individuals involved. Thus the complete lack of tolerance exhibited by Makumba to interactions throughout the year may reflect the possibility that most involved encounters with lone males.

All extragroup traces during the period where Etefi transferred out of and then back to her natal group, appeared to implicate one extragroup adult male. The day after Etefi left the Makumba group, extragroup male traces were followed and a new nest count indicated that he had acquired a female. Could this nest have belonged to Etefi? Additionally, visual matching confirmed that the same silverback was involved in both the interactions that took place on July 6th and July 9th. It was not possible to confirm identity during the other interactions in this period, due to the dense forest habitat and the dangerous nature of the encounter which meant that we kept our distance. Additionally, while we heard auditory signals from several members of our group during these encounters, we only ever heard the extragroup silverback vocalise. While his group may have been hiding elsewhere, this scenario is unlikely given the evidence listed above. Observations and Makumba's responses support the involvement of at least one solitary male during many of the high level interactions, especially those that took place in July.

Active resource defence does not appear to be a major contributing factor in encounters with different mountain gorilla units, due to the relatively uniform distribution of folivorous plants within their habitat (Chapter 1). However, Fossey [1974, p 578] states that a solitary silverback's method of area defence may involve *“over-use of the area: circuitous routing, prolonged feeding, and nests, both day and night, built close together, all resulting in nearly total destruction of the foliage. This repels the silverback's former group. The vegetation damage may extend over 0.5 km and has always preceded a visit by the group of which the silverback was formerly a member. Such defence of the core area by over-use has been documented for*

three lone silver-backs, each from different groups and in different regions of the study area.” Resource defence does appear to occur in western lowland gorillas (Section 4.2.5 and 4.2.6) and the clumped distribution of fruit may allow dominant units to actively defend smaller areas with highly sought after resources (Section 4.2.4). During the July interaction period involving Etefi’s transfers, the Makumba group responded by immediately circuiting a large proportion of their core January-July range. If the extragroup unit was simply chasing Makumba, then one would not expect such predictability to Makumba’s movements. Instead, he clearly circuited the majority of his January-July core range in four days, with repeated use of one *Celtis adolfi frederici* tree throughout this interaction period. Four of the high level interactions that occurred during this period (two of which coincided with Etefi leaving and returning to the Makumba group) took place within 250-500m of this tree.

Were these behaviours related to active resource defence as seen in lone silverback mountain gorillas [Fossey, 1974]? While this seems likely, it is also possible that more complex factors were at play. *Celtis* trees were clearly abundant across the range, since the group was seen to be feeding on this fruit throughout the entire month of July (25 days where *Celtis* feeding was observed at least once; see also Chapter 2) and August (20 days where *Celtis* feeding was observed at least once; see also Chapter 2). In July, five *Celtis* feeding days were spent in the aforementioned tree, and of those five days, three led to a high level interaction. However, encounters due to resource defence have not been reported as highly aggressive for any other western lowland sites (Section 4.2.5). Additionally, in the latter half of July and August the group moved down to the southernmost edge of their range but were still observed to be eating the fruit 10 out of the 12 remaining days in the month and 65% of the days in August (Chapter 2; see also Figure 4.3). While exact tree locations cannot be calculated, ranging patterns and personal observations indicate that the only *Celtis* tree visited repeatedly was the main tree involved in the July 6-17th interaction period. After Etefi returned to Makumba, the group moved swiftly out of the area. If the tree held primary resource importance, the group would be expected to stay on longer to protect their food source. While they may have depleted their food source during their time spent at the tree, Etefi’s return combined with the immediate vacation of the area and the obvious availability of this fruit in other areas across the region strongly

suggests that resource defence was not the overriding factor in the repeated visits to the *Celtis* tree. Nonetheless, territory defence could underlie Makumba group's 'patrol' around the outer boundary of their core range immediately following the start of high level interactions. Nest area overlap was highest in July and in particular, through the July 6th-17th interaction period. Makumba's ranging and nesting reaction appears similar to Fossey's [1974] description of lone silverback area defence, previously unreported in group males or western lowland gorillas. While she suggested that this only occurs from lone silverbacks trying to repel their former groups, my data suggest that such active defence may occur in varying contexts with group or lone silverbacks, and across gorilla subspecies.

With Etefi's return, Makumba dramatically shifted his home and core range for the rest of the year, as has been seen in mountain gorillas and some western lowland gorilla groups (Section 4.2.2 and 4.2.6). What remains unclear is why the group's home range expanded so extensively instead of merely shifting location. When a similar expansion was observed in a previously habituated group at Bai Hokou [Cipolletta, 2004; Section 4.2.5], it was a result of the focal silverback's attempts to find and acquire females. The larger range in Makumba's case might have been a combination of extraunit avoidance, the potential lack of resource location knowledge, and longer distances between fruiting resources. Although it is possible that the Makumba group moved out of their core area to take advantage of certain fruiting patterns, all evidence presented here strongly implicates extraunit interactions as the causal factor in the study group's range shift.

Given that females disperse from their natal group at sexual maturity, the behaviours exhibited by Makumba and his group in response to Etefi's dispersal were unexpected. After the first interaction when Etefi emigrated, Makumba circled his core range, went directly back to the same interaction area and had another high level interaction. He and his group stayed in that area even though they faced further high level interactions and his group's safety was at risk. As soon as Etefi returned to her natal family, the Makumba group silently fled the area and didn't return for the remainder of the year. While only speculation is possible, it appears as if the group returned and waited for Etefi. Once Etefi apparently decided to leave the chosen male and return, there was no reason for the group to remain in the area.

Mountain gorilla females who leave their natal group for the first time often transfer back before leaving again at a later point. This is suggested to reflect female sampling of extragroup males [Harcourt, 1978a; Stewart & Harcourt, 1987; Watts, 1990b]. The high genetic relatedness of males at some western sites [Bradley et al., 2004, 2005] may help explain the greater tolerance seen in many western gorilla units, assuming that gorillas from different areas individually identify and recognize each other. If this is true, then it is equally possible that 'unfit', close kin or 'poor protector' males are recognizable throughout the range as well. While Yamagiwa [1987b] states that the direction of travel is usually determined by the dominant silverback in the group, frugivorous western lowland gorillas who often forage far from their leader silverback may show a different pattern entirely. Adult females within the Makumba group can influence the group's daily direction of travel (Chapter 3). Therefore, it is possible that the choice to return to, and remain in the interaction area during Etefi's absence, was not Makumba's decision but that of one of his females, such as Etefi's mother. If this were the case, he would have no choice but to follow and protect the group. A similar situation occurred in an all-male group of mountain gorillas when they acquired a new member during a high level interaction. The new member chose not to leave the area for two weeks, thus the other members were also forced to stay and as a result the group had several further high level interactions. The new member's movements had a considerable effect on other group members, even if the longer tenure of more senior group members made them dominant to the new immigrant [Yamagiwa, 1987a].

Although the sample size was small, the group only nested in open areas during high level interactions. This preference might represent the need to be fully aware of their surroundings so they can better hear and see any approaches by extragroup males. Dense habitats were preferred mainly during low level interactions which was similar to non-interaction days. Dense habitats may be the most comfortable as they provide lots of foliage to make warm nests, and they are more secluded and therefore better hidden from predators and elephants. Dense habitat preferences during low level interactions are suggestive of the minimal threat involved in this interaction type.

The Makumba group reacted according to the threat of each encounter. Data on auditory responses showed that Makumba increased his loud signals after a low level interaction began.

However, there was no significant change in his rate of soft signals, in the immature play signals or in the group's rate of total auditory signals. The same effect was found in medium level interactions. During high level interactions, Makumba exhibited two contrasting vocal responses; silence or loudness [Fossey, 1972]. Additionally, the immatures' rate of play signals decreased abruptly after a high level interaction began and group auditory totals (which does not include Makumba auditory or immature play signals) tended to decrease. The threat of high level interactions appeared to silence group members, so that they remained vigilant to any cues given by Makumba. By contrast, lower intensity interactions meant that the rest of the group could generally continue with daily activities while Makumba drove off the extragroup male. In those lower level interactions where Makumba felt the need to move out of the area, this was done without much urgency and without a change in the groups' auditory signalling, possibly reflecting lower tension levels.

When auditory replies were combined with other response types such as patrolling, movement, and hiding, a pattern of response choice according to interaction level emerged. While auditory replies without movement or patrol were predominant in low level interactions, medium level interactions showed a mixture of auditory replies with patrol and/or movement. Although this 'mixed' response type was used during high level interactions as well, the group also silently fled or hid in dense thickets [Fossey, 1972]. These latter responses were only seen in high level interactions and may reflect the extreme risk involved in intense interactions [Fossey, 1972]. Even though detailed analyses of response type to interaction levels are not yet available for other sites, the term 'avoidance' was most often used when a gorilla unit left an area to avoid an encounter (Section 4.3.6); this definition could include silent fleeing or hiding. Yamagiwa [1987a] provided anecdotal evidence of silent avoidance by an all-male group encounter with a mixed group. During one such encounter they came within 20 meters of each other, when one group slapped the ground and the other gathered silently and then rapidly moved away from the encounter site. Fossey [1972] described a similar reaction to extremely risky situations. The protector male of any group must weigh up the costs and benefits of pursuing each encounter. In some situations, avoidance by silence and fleeing or hiding may be the most effective defensive strategy.

Other strategies used by Makumba were only observed a few times, but still deserve mention. Displaying using food occurred on two occasions, and could be best described as 'angry' eating. It might be suggested that this acts as a tension releasing mechanism, as seen in classical ethological studies of birds engaging in displacement pecking [Hinde, 1970]. Alternatively, these acts may enhance displays, making them more intimidating. Using water in displays has been seen in bai environments (Section 4.4.10), but water displays in forested environments have not yet been reported. It appears that these displays are not only used when in visual presence of other rival males as suggested by Parnell & Buchanan-Smith [2001], but also in their absence. Additionally, when the group responded with silence during an interaction they would rarely utter a sound. Yet if they did, the belch vocalizations they produced were extremely quiet; like a 'whisper', suggesting considerable social and cognitive control over utterances.

Makumba was also aided in several interactions by his eldest son, Kunga, a young blackback. Kunga was observed to patrol a given area during several high level interactions. On one occasion I witnessed him patrolling while Makumba took his group and hid in dense thickets (Section 4.4.3; July 15th). Such helping behaviour has been observed in mountain gorillas [Fossey, 1983; Harcourt, 1978; Watts, 1996; K. Fawcett pers. comm.]. Kunga and Makumba appeared to have a close bond, since the few occasions which involved silverback play also involved Kunga (pers. obsv.). Kunga's mother left the group in early 2006, leaving her son behind; the loss of his mother may have brought him closer to the silverback. While the Makumba group cannot be considered multimale, decisions to stay in a mountain gorilla group throughout adulthood are partially based on the bond formed between the dominant silverback and an adolescent (Chapter 3). Group spread around the silverback and neighbours within 5m of the silverback were both influenced by the number of interactions per month and their intensity. The group was significantly more cohesive in July, the peak interaction period, than in any other month, although this difference was not significant for August. They may have been exhibiting a lag in the decrease of tension as a result of interactions in July, and they were also shifting into newer, potentially less well known ranges.

Since an extragroup male's best strategy to acquire females is to lure and coerce one or a few females in a group (instead of all females) by gaining her trust (Section 4.2.2), he should approach females when they are least likely to be close to their protector silverback. This would most likely occur in the late morning to early afternoon, when the group was most spread out. Additionally, interactions that occurred throughout the night or dawn may represent an alternative strategy to attack a group in 'surprise' while sleeping and unalert at their nest. Similar "midnight raiding" tactics have been described for baboons during consort takeovers [Packer, 1977]. In certain situations the benefits of luring females away from their current group by successfully killing one of the female's infants may outweigh the costs of a potentially severe violent battle. In these circumstances, a surprise attack may be the less costly strategy. After experiencing infanticide, the female might be more likely to leave Makumba for this solitary male (Section 4.2.2). Extragroup silverbacks may even target the Makumba group on days where they were more spread out in the early morning than would be normally expected, which may explain the large variation in early morning group spread on interaction days.

It is likely that our presence affected the nature of these interactions, since extragroup males were unhabituated to our presence and thus may have avoided approaching the Makumba group. Additionally, extragroup units who did approach may have reacted differently as a result of human presence. During several high level interactions, it appeared that the extragroup male was not only screaming at Makumba but also at us. Over the years of following the group, we may have also unintentionally habituated some extragroup males to our presence. These extragroup males may have been more likely to interact with the Makumba group, potentially changing the dynamics of interunit interactions in the region. Regardless of the human influence, it is clear that 2007 represented an extraordinary year for the Makumba group.

These results illustrate the intricate nature of interunit interactions in western lowland gorillas. They indicate that (a) western lowland group gorillas react according to the perceived threat of an extragroup unit; (b) the high ratio of solitary males observed at western gorilla bais (Section 4.2.8) appears to be the largest threat to group males; (c) interunit interactions involve an

extremely complex, highly strategic framework of responses and approaches, and; (d) infanticide, which has only been suspected or inferred in western lowland gorillas [Stokes, et al., 2003] is an important consideration in the decisions of adult males whose group contains females with dependent infants.



CHAPTER 5

*TOURIST & RESEARCHER
IMPACTS ON SILVERBACK
– GROUP DYNAMICS*



CHAPTER 5

TOURIST AND RESEARCHERS IMPACTS ON SILVERBACK-GROUP DYNAMICS¹

5.1 ABSTRACT

Gorilla tourism, widely perceived as a lucrative industry, is propelled by strong market demand with programs in five countries and for three of four gorilla subspecies. Human presence may negatively affect wild gorillas, potentially lowering immunity and increasing the likelihood of acquiring human borne disease. Yet, behavioural impacts of humans on wild gorillas remain largely unexplored, particularly for western lowland gorillas. We evaluate the impact of tourist presence, human observer numbers (tourists, trackers, and researchers), and human observer distance on the behaviour of one habituated gorilla group at Bai Hokou, Central African Republic. Of silverback aggressive events, 39% (N = 229) were human directed, but 65% were low level soft barks. Adult females, and one in particular, were responsible for the highest number of aggressive events toward humans. Humans maintained closer proximity to the silverback when tourists were present, although tourist numbers had no significant impact on overall group activity budgets or rates of human directed aggression. However, as research team size increased, group feeding rates decreased. Close observer–silverback distance correlated with a decrease in his feeding rates and an increase in human monitoring. He directed less aggression toward observers at distances greater than 10m, although observers spent 48.5% of time between six and 10m of the silverback. I discuss gorilla personality as a factor in human directed aggression. I explore whether the current

¹Data from this chapter were published in (1) Klailova M, Hodgkinson C, Lee PC. 2010. Behavioral responses of one Western Lowland Gorilla (*Gorilla gorilla gorilla*) Group at Bai Hokou, Central African Republic, to Tourists, Researchers and Trackers. *American Journal of Primatology* 72: 897-906 (Appendix 18)

7m distance limit governing gorilla tourism, based on disease transmission risks, is sufficient considering the potential behavioural stressor of close human presence. I recommend increasing minimum observation distance to 10m where possible, decreasing observer group sizes, particularly after a visit consisting of maximum numbers, and restricting tourist access to one visit per day.

5.2 INTRODUCTION

5.2.1 Wild Gorilla Tourism

Wild gorilla groups have been visited by tourists since 1955, and deliberately habituated for that purpose since the 1970s [Butynski & Kalina, 1998]. Gorilla tourism has since developed into a lucrative industry fuelled by a strong market demand, with programs currently operating in five countries for three out of four gorilla subspecies (*Gorilla berengei berengei*, *G. beringei graueri*, *G. gorilla gorilla*). The high earning potential of gorilla tourism, evidenced by mountain gorilla programs, combined with its assumed non-extractive nature, has proved popular with governments promoting successful conservation partnerships that protect threatened habitats and the species they contain [Adams & Infield, 2003; Plumptre et al., 2002]. In theory, ecotourism should represent a win-win situation for both the country in which it occurs and for the vulnerable places and animals that it protects. One of the key tenets of ethnoprimateology—integrating the needs of human and non-human primates—seems to be met by the non-consumptive alternative of primate tourism. Yet, human impacts on gorilla populations and the sustainability of these programs remain largely unexplored [Butynski & Kalina, 1998; Goldsmith, 2000, 2005a; McNeillage & Thompson-Handler, 1998; Williamson & Feistner, 2003; Woodford et al., 2002]. If we wish to pursue the aims of human–non-human primate coexistence, then a thorough assessment of our impact on primates and especially the threatened ape species, is needed.

Risk of disease transmission from humans to gorillas is a major concern of ape tourism [Butynski & Kalina, 1998; Cranfield, 2008; Homsy, 1999; Muelhenbein & Ancrenaz, 2009; Travis et al., 2008;

Werikhe, 1991]. Habituated gorillas face a risk of disease from tourists, who may be carrying foreign illnesses from their home country, who can suffer high rates of illness owing to the stress of travel and exposure to air-borne diseases on airplanes, and who are themselves potentially lacking in immunity to local endemic infections [Adams et al., 2001; Muelhenbein & Ancrenaz, 2009; Ostroff & Kozarsky, 1998; Wilson, 1995]. Chronic stressors may act to lower gorilla immunity and thus increase their susceptibility to disease [Hofer & East, 1994; Hudson, 1992; Meder, 1994; Woodford et al., 2002]. To help alleviate some of these risks, most gorilla tourist sites have rules designed to minimize threats, including 1 hr maximum visits and a minimum distance to gorillas of 7m [Homsy, 1999]. However, the efficacy of these measures could be compromised by the behavioural impact of human presence on gorilla behaviour.

Habituating gorillas to human presence is known to be a highly stressful process, typically involving altered activity budgets, frequent displays of aggression toward humans, and altered ranging patterns [Anon, 1996–1997; Blom et al., 2004; Cipolletta, 2003; Doran-Sheehy et al., 2007; Fossey, 1983; Goldsmith, 2005b; Williamson et al., 1997]. Habituation, defined as the acceptance of human presence as a neutral element in their environment [Tutin & Fernandez, 1991], is assumed to occur when humans are tolerated, but few studies have explored the impact of human presence on gorillas that are already considered to be habituated. Before the advent of organized tourism, researcher presence was suggested to affect natural ranging patterns, intergroup transfer, and reproduction [Veder, 1989]. Current data on mountain gorilla groups found increased monitoring of humans and less time spent feeding when in the presence of tourists rather than researchers [Steklis et al., 2004]. Muyambi [2005] reported similar findings for Bwindi mountain gorillas, additionally noting increased frequency of disturbed behaviour, such as charging, fleeing, and self-directed behaviours.

5.2.2 Western Lowland Gorilla Tourism

Western lowland gorilla tourism programs exist on a reduced scale compared with those for the high-profile mountain gorillas. Only four places in Central Africa are currently open to gorilla tourism. Two offer sightings from fixed platforms (Mbeli Bai, Republic of Congo; Langoué Bai, Gabon) and two offer visits to habituated western lowland gorilla groups (Mondika, Republic of Congo; Bai Hokou, Central African Republic). Lowland gorillas are difficult to habituate, attributed to their long daily path lengths, large home ranges, infrequent vocalizations, and dense habitat in which they live (Chapter 1). Quality of the tourist experience may also be impeded by poor visibility in the dense tropical forest that makes up much of the western lowland gorilla habitat. Tourism is further hampered by the generally poor accessibility of these sites, paucity of tourist infrastructure, and political instability of host countries. Yet, demand from international tourists and expectations of local governments for revenue generation, combined with the successful habituation of several western lowland gorilla groups, have resulted in the expansion of tourist programs and increasing researcher presence.

The Bai Hokou Primate Habituation Camp is host to tourists, film crews, and independent researchers. This chapter details results from the second stage of a longer-term study aimed at evaluating the impact of tourism and human presence on gorilla behaviour. A preliminary study conducted in 2006 with the same gorilla group at an earlier stage in their habituation process, found that the presence of tourists and film crews resulted in a number of significant behavioural alterations, including a decrease in silverback resting and an increase in group aggressive behaviour [Hodgkinson & Cipolletta, 2009]. During this assessment, the group was “semihabituated” and it was only possible to approach the group comfortably at 15m, although they were followed daily from nest-to-nest.

5.2.3 Chapter Aims

Here, I provide an in-depth evaluation of the impact of humans, both of the research team (researcher and trackers) and tourist groups, on the same gorilla group in later stages of the habituation process. We assess the effects of human group type (trackers, researchers, and tourists), size and distance on gorilla behaviour, measured in terms of activity budgets, visual monitoring of people by the silverback, frequency of aggressive behaviour, and individuality in aggression. I also discuss whether the current 7m distance limit governing gorilla tourism, based on mountain gorilla disease transmission risks, is sufficient considering the potential behavioural impact of close human presence. To date, only scientists at Bai Hokou, Mondika [Doran-Sheehy et al., 2007], Lopé [Tutin & Fernandez, 1991] and Moukalaba-Doudou National Park in Gabon [Ando, 2009; Ando et al., 2008] have attempted to document behavioural responses of western lowland gorillas to human presence.

5.3 METHODS & ANALYSIS

5.3.1 Definitions and Sampling Independence

Makumba group was followed from nest to nest by a team of trackers (range 2-4) and researchers (range 1-3), and tourists (391 in 2007) would join the main team in either session and stay for a maximum of 60 minutes of visibility (not necessarily consecutively) or until they expressed a wish to return to camp. Only one tourist visit (with a maximum of three tourists per visit) was allowed per session. Stringent effort was made to limit total observer group size (trackers and researchers and tourists) to seven people (Chapter 2).

As described in Chapter 2, scans taken a minimum of ten minutes apart were considered to be independent. However, in these analyses given that tourists were only present for 60 minutes of viewing time (effectively a single bout), all scans at intervals of less than 20 minutes apart were excluded, leaving an average interscan interval of 29 minutes.

Gorillas were grouped into age–sex classes, as per Chapter 2, however the ‘immature and infant’ category was simply termed ‘immatures’ for analyses in this chapter. As per Chapter 2, auditory signals were categorised by age–sex class and defined as any sound made by a gorilla, either vocally or via other signals (ground slapping, tree breaking, chest beating, displaying, and hand clapping). Aggressive auditory signals directed toward humans (bark, soft bark, charge, display, scream) are the focus of the analyses here (see Chapter 4 for definitions). Human directed aggression was divided into low, medium and high levels (Table 5.1). As younger or more fearful gorillas might also emit human directed distress signals (i.e. scream, cry) rather than overt aggression, these were also included in the analyses. For all other definition used in this chapter, see Chapter 2.

Table 5.1 Aggression Levels with Associated Auditory Signals^a

| Low Level | Medium Level | High Level |
|-------------|-------------------------|---------------------------|
| -Soft Barks | -Barks Only | -Charges |
| | -Displays | (with or without Barking) |
| | (Ground & Tree Slaps or | -Contact |
| | Breaks, Chest-Beats) | -Scream |

^aSee Chapter 4 for more detail

5.3.2 Analysis Overview

Final analyses were conducted on 1, 885 silverback scans, over 258 observation sessions. Where auditory rates were included in analysis, data were grouped by session to limit any effects of dependence.

5.3.3 Human Directed Aggression

- (1) Does distance between human observers (hereafter ‘observers’ or ‘humans’) and the silverback change when tourists are present compared with when only researchers and trackers are present?
- (2) How much group and silverback aggression is directed at humans, and what type of human

directed aggression (i.e. soft barks, screams, etc) is most common? (3) Is silverback aggression to humans affected by human-silverback distance?

With regards to the other group members, I asked (1) does human group type and size affect human directed aggression by gorilla age-sex class and by individual?

Finally, I examined whether human group type and size affected gorilla group and silverback activity budgets? Does silverback monitoring of humans affect his activity budget?

Analyses were separated into research team (trackers and researchers) and tourist groups for comparison. Total numbers of observers (research teams and tourist groups) were used in distance analyses. Human groups (regardless of type and number) always stood in the smallest possible clump so as not to intimidate the gorillas; each person within the observer unit stood at approximately the same distance to the gorillas as another person in the same observer unit. Thus it would only be appropriate to analyse the distance related measurements using total number of observers instead of separate groups.

As outlined in Chapter 2, aggression rates were calculated relative to the number of minutes of observation in each session, computed hourly, and normalized (where necessary) using square root or log transformations. Data were primarily analysed using hierarchical ANOVAS, and stepwise regressions (both linear and logistic) to control for potential influences of other factors (Chapter 2). The median distance to the silverback was calculated per session from scan data. Median scores were used to control for the influence of tree heights affecting distance records where human directed aggression was unlikely to occur (Chapter 2). Modal scores for silverback activity budget were calculated per session. Corrected silverback-human monitoring scores were calculated (defined as: 1 ignore, 2 low, 3 medium, 4 high), as per Chapter 2. Mean team and tourist numbers were calculated for each session and corrected for the number of minutes that different team sizes were present (Chapter 2). Research team size was categorized from the distribution of all observer group sizes as small (2.5-3.49), medium (3.5-4.49), large (4.5-5.49), very large (5.5+).

Activity budgets and monitoring were analysed using logistic regressions, where zero represents the activity occurring, and one represents the activity not occurring; results were based on the activity not occurring. Individual gorilla comparisons of human directed aggression were analysed using chi square analyses and where data was unable to be normalized, non parametric Mann-Whitney tests were used.

5.4 RESULTS

5.4.1 Overview

Tourists were present in 63 of the 258 observation sessions (24.4%) and in 320 of the 1,885 silverback scans. A total of 135 tourists visited the group during these recording sessions, with mean tourist numbers per visit of 2.14 ± 0.981 (range: 1–4). Mean total group size when tourists were present was 6.22 ± 1.325 (range: 4–9). Mean research team size over the study period was 3.95 ± 0.704 (range: 3–7). Total observer group size, encompassing both tourists and team members, stayed within the seven person limit on all but seven occasions (35 scans); for these, the total group size did not exceed nine and tourist numbers did not exceed four.

5.4.2 Human Directed Aggression and Human-Silverback Distance

Distance between human observers and the silverback was significantly lower when tourists were present compared with when only researchers and trackers were present. More time was spent at distance category of 6-10m from the silverback when tourists were present (N = 63), whereas more time was spent at 11-15m when only researchers and trackers (N = 191) were following the silverback (Mann Whitney: $U = 5104.5$, $p = 0.046$). To determine whether human distance to the silverback was affected by the number of tourists, distance categories were grouped at 1-10 m (N = 40) or 11-20 m (N = 23). The number of tourists present did not significantly affect mean human distance to the silverback (Mann Whitney test: $U = 396.5$, $p = 0.396$).

Of the 22,343 auditory signals recorded, 2,009 were aggressive in context. Furthermore, 23% (460) of all aggressive events were directed toward human observers. Because data were collected on the silverback and only those individuals in his presence (within human earshot), total group auditory signals will be underrepresented. The silverback was responsible for 593 of all aggressive events, and 39% (229) of those events were directed towards observers. However, low level aggression (soft barks) was the most common form of aggression directed at humans by the silverback (Table 5.2).

Table 5.2 Silverback Aggressive Events toward Observers (N = 229)

| Low Level | Medium Level | High Level |
|-----------|--------------|------------|
| 148 | 57 | 24 |
| 65% | 25% | 10% |

Rate of silverback aggression to observers was significantly affected by human-silverback distance (controlling for time of day, season, silverback activity, and human group size) ($F = 5.34$, $p = 0.001$, $df = 4$, 249 , $R^2 = 0.077$, $N = 250$). When observers were further from the silverback, his rates of aggression towards humans significantly decreased ($B = -0.011$, $SE = 0.004$, Standardised Beta = -0.159 , $df = 1$, 252 , $p = 0.011$, $R^2 = 0.025$, $N = 254$; Figure 5.1).

Observers spent 48.5% of their time within 6-10 m of the silverback (Figure 5.2). A cumulative rate of change plot shows a reduction in silverback aggression towards observers at 6-10 m (Figure 5.2), as seen by the break in the slope (Chapter 2). Aggression continues to decrease with distance, until it distinctly plateaus at 16-20 m. A cumulative rate of change plot calculated for the median total session (ungrouped) distances (Figure 5.3) shows that aggression rates decreased most markedly at 10 meters, but also at six and 15m, ceasing after 18 meters.

Figure 5.1 Silverback Aggression to Humans in Relation to Observer-Silverback Distance

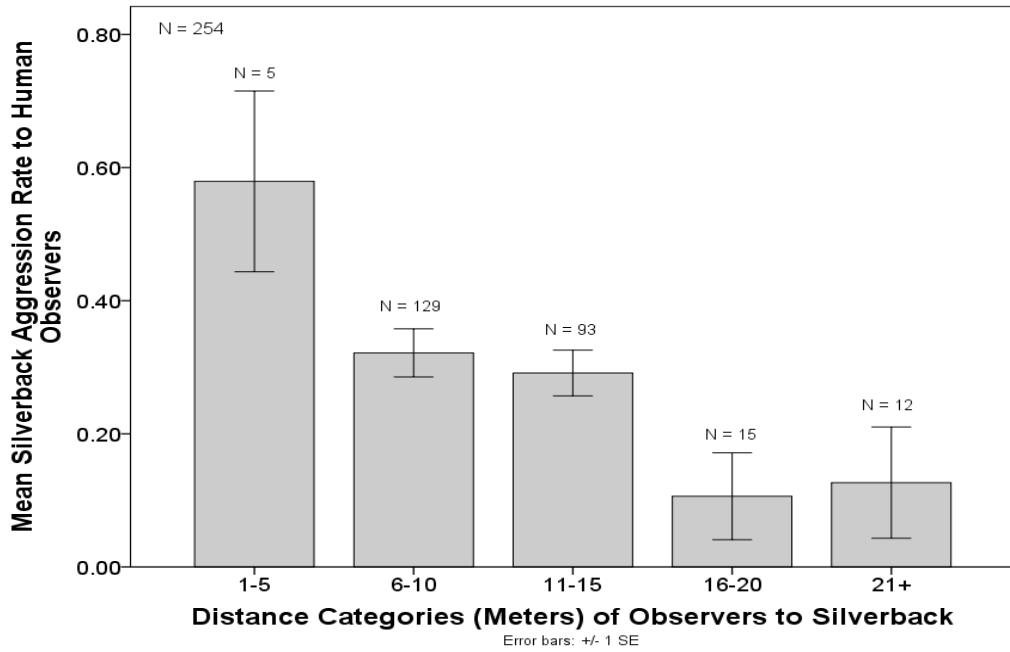


Figure 5.2 Observer Time at Different Human-Silverback Distance categories and a Cumulative Rate of Change in Human Directed Aggression by the Silverback in Relation to Human-Silverback Distance Categories

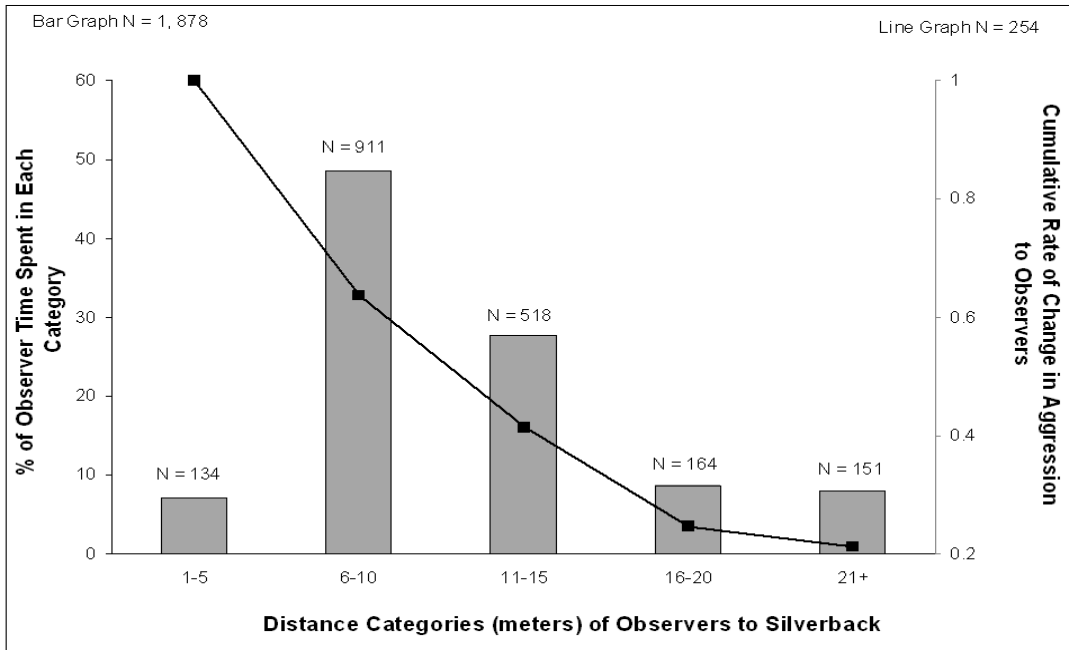
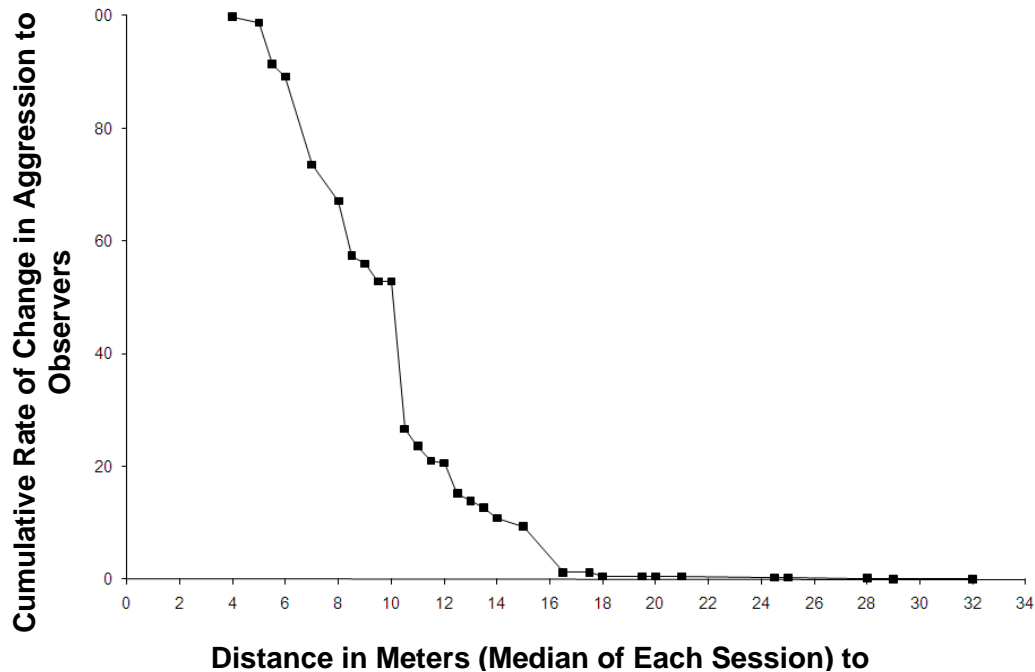


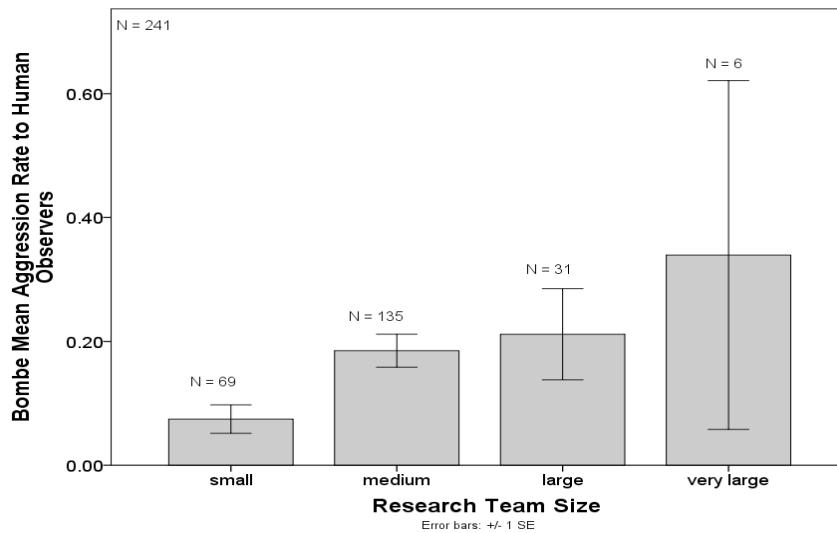
Figure 5.3 Cumulative Rate of Change in Human Directed Aggression by the Silverback in Relation to Human-Silverback Ungrouped Distances



5.4.3 Effect of Human Group Type and Size on Aggression towards Observers

Rates of aggression towards observers were not significantly affected by the presence or absence of tourists (controlling for time of day, season, group activity and observer-gorilla distance). This lack of effect was similar for all age-sex classes. Likewise, in all but one case, rates of aggression were not significantly affected by the number of people in either the research team or tourist groups. When considering individual females, research team size had a significant effect on the rates of aggression towards humans from one female (Bombe) ($F = 3.10$, $p = 0.029$, $df = 3, 236$, $R^2 = 0.041$, $N = 238$). As researcher and tracker numbers increased, Bombe's rates of aggression towards people also significantly increased ($B = 0.081$, $SE = 0.031$, Standardised Beta = 0.168, $df = 1,239$, $p=0.009$, $R^2=0.028$, $N = 241$; Figure 5.4).

Figure 5.4 Bombe's Aggression to Humans in Relation Research Team Size



Of the 460 human directed aggressive events, the silverback was responsible for 229 events, adult females for 185 (Bombe, 122; Malui, 61; Mopambe, 2), immatures for 25, where 21 aggressive event instigators were unknown. Although the silverback seemed to be responsible for the largest number of aggressive events directed towards humans, when correcting for the proportion of time other individuals were seen within 5m of Makumba (since he was followed by humans 100% of the time), adult females were the most likely age-sex class to direct aggression towards observers ($X^2 = 52.02$, $df = 2$, $p < 0.001$; expected values and proportions of aggression for adult females = 36 (0.12), for the silverback = 232 (0.78), for immatures = 31 (0.10); Figure 5.5)². One female in particular, Bombe, was more likely to direct aggression to humans in comparison to any other gorilla within the group including Makumba (see Figure 5.6 for statistics).

²In order to achieve a 1:1:1 ratio (i.e. instead of '1 silverback: 3 adult females: 8 immatures not including mobangui' ratio) to ensure accuracy for analysis across age-sex class categories, I divided the total number of adult female aggressive events ($N = 199$; 185 events + 14 events where exact female instigator was unknown but age-sex class was known) into 3, and the total number of immature aggressive events ($N = 25$) into 8. This then allowed me to fairly compare using a 1:1:1 ratio, where total aggressive events equalled 299. Regardless, when analyzing results using a 1:3:8 ratio, using the full 453 'known' aggressive events by age-sex class (7 aggressive events were of unknown age-sex class and therefore omitted from analysis), results are very similar, where expected values and proportions are: adult females 54.4(0.12), silverback 353.3(0.78), and immatures 45.3(0.10). Adult females aggressed humans 199 times though they were expected to aggress humans only 55 times; the silverback aggressed humans 229 times but though he was expected to aggress humans 359 times, and immatures aggressed humans 25 times though they were expected to aggress humans 46 times. Again, when using the full 453 'known' aggressive events by age-sex class, adult females were the most likely age-sex class to direct aggression towards observers ($X^2 = 429.47$, $df = 2$, $p < 0.001$).

Figure 5.5 Corrected Proportion of Human Directed Aggression by Age-Sex Class

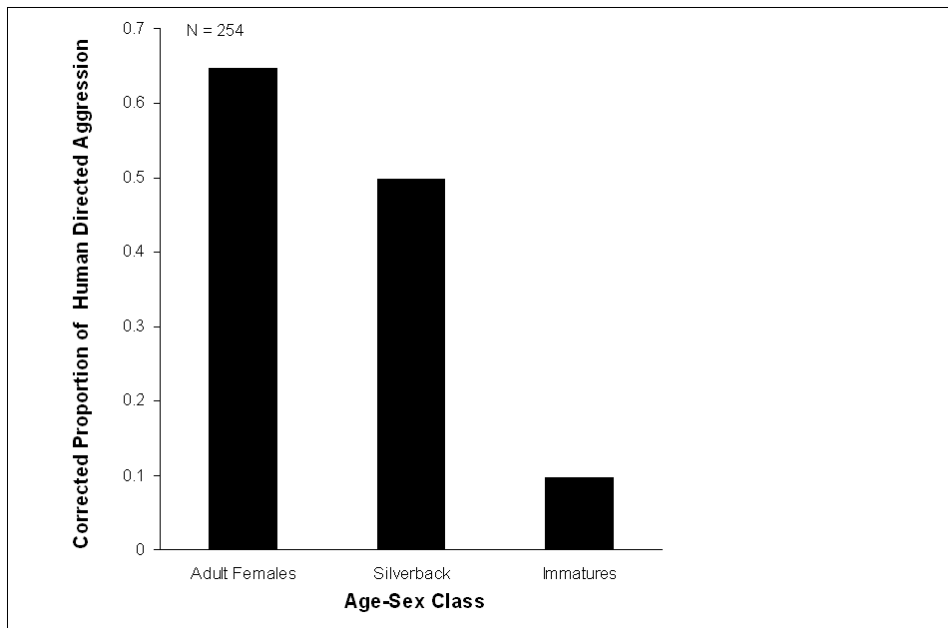
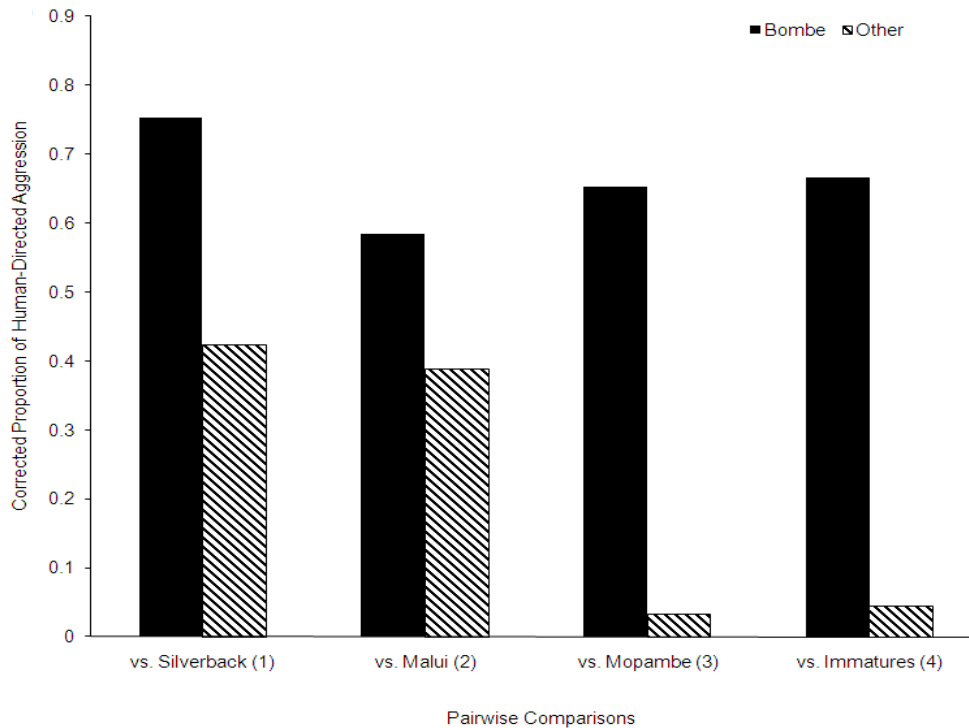


Figure 5.6 Corrected Proportion of Pairwise Comparisons of Bombe's Human Directed Aggression with that of Other Individuals and Age-Sex Classes^a



^aBlack bars represent Bombe and lined bars represent other individuals or age-sex classes as listed on the figure: (1) $X^2 = 189.72$, $df = 1$, $p < 0.001$, (2) $X^2 = 26.84$, $df = 1$, $p < 0.001$ (3) $X^2 = 104.88$, $df = 1$, $p < 0.001$, (4) $X^2 = 119.14$, $df = 1$, $p < 0.001$

Bombe's high rates of human directed aggression may be the result of partial or delayed habituation [Doran-Sheehy, 2007]. However, if this was the chief cause of aggression towards observers, Bombe should be seen less often than were the other females and as the study (habituation) progressed, she should have spent more time with Makumba (and thus humans). Rates of aggression should therefore decrease over time as the level of habituation increases. Bombe spent similar proportions of time within 5m of the silverback as did Mopambe, and even though Malui spent slightly more time next to Makumba, this difference was minimal (3%). Bombe did not differ significantly from the other females in time spent within 5m of Makumba (Table 5.3). In addition, Bombe's human directed aggression did not significantly decrease as the year progressed ($B = 0.100$, $SE = 0.006$, Standardised Beta = 0.108, $p = 0.095$, $df = 1, 240$, $R^2 = 0.012$, $N = 241$; Figure 5.7) and her time spent with Makumba did not significantly increase as the year progressed ($B = -0.011$, $SE = 0.006$, Standardised Beta = -0.117, $df = 1,253$, $p = 0.063$, $R^2 = 0.014$, $N = 254$; Figure 5.8).

Table 5.3 Bombe-Female Comparisons of Time Spent within 5m of Makumba^a

| Mopambe/Bombe | Bombe/Malui | Occasions within 5m of SB (N = 1,090) |
|---------------|--------------|---------------------------------------|
| $X^2 = 0.04$ | $X^2 = 5.66$ | Mopambe 126 (0.116) |
| $df = 1$ | $df = 1$ | Bombe 129 (0.118) |
| $p = 0.835$ | $p = 0.018$ | Malui 162 (0.149) |

^aBonferroni Correction $p < 0.017$

Figure 5.7 Bombe's Human Directed Aggression by Month

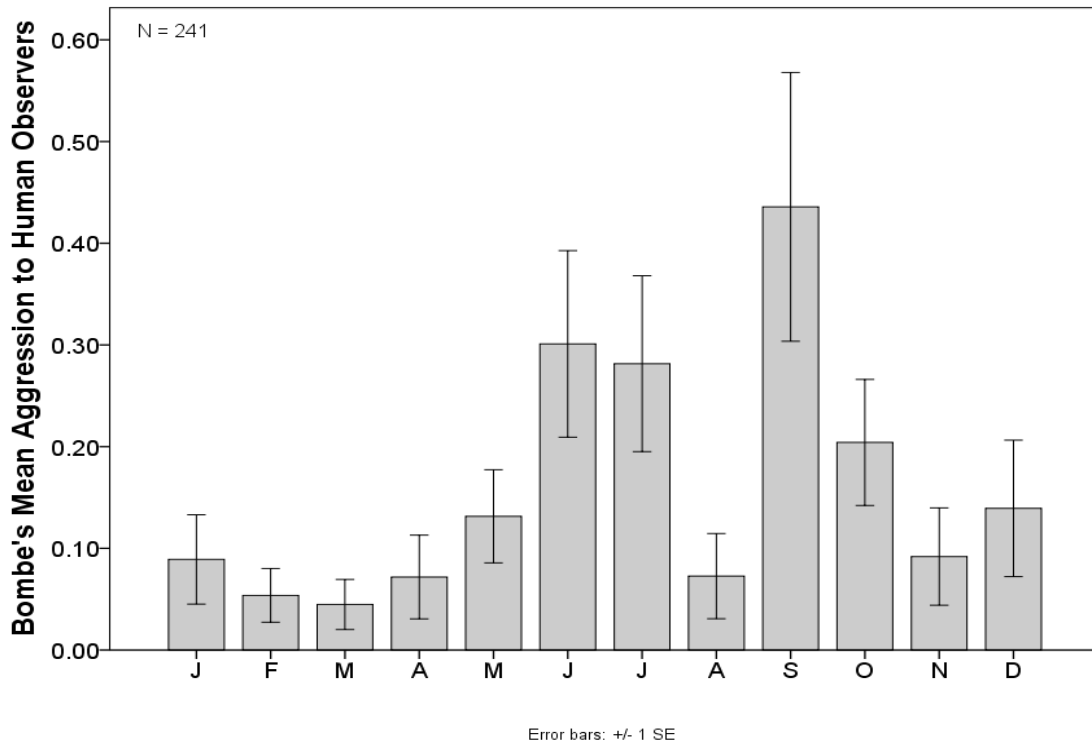
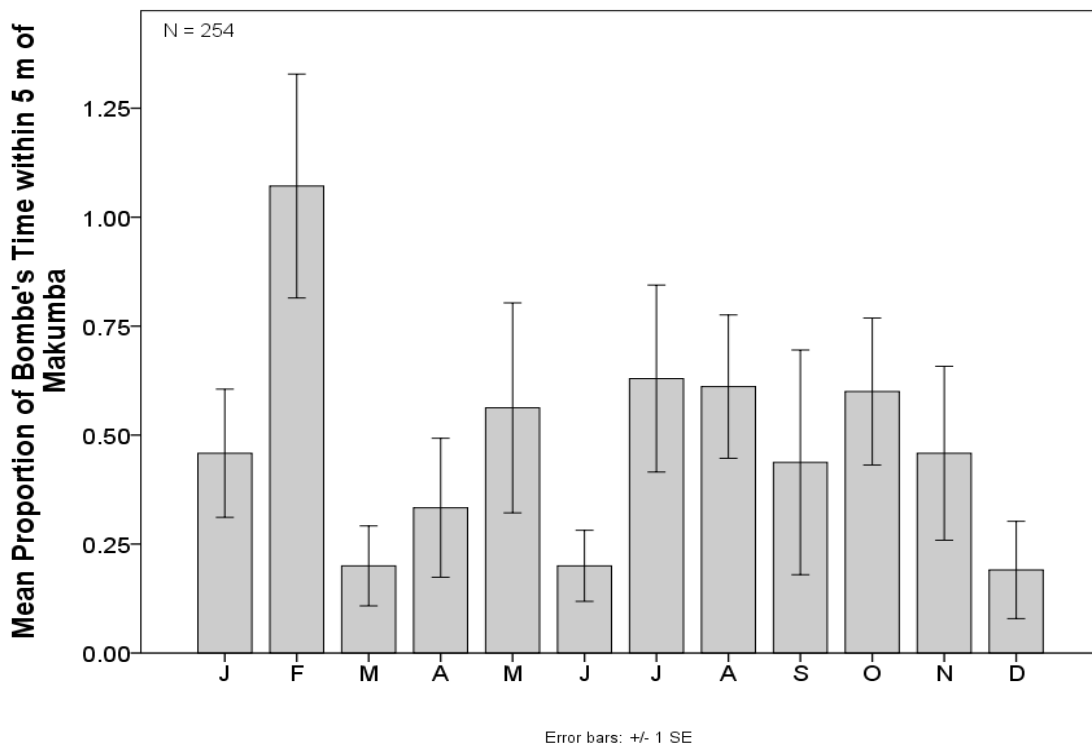


Figure 5.8 Bombe's Time Spent within 5m of Makumba by Month



5.4.4 Effect of Human Group Type and Size on Activity Budget and Silverback Monitoring

Presence or absence of tourists did not significantly affect group or silverback activity budgets (controlling for time of day, distance and season). As research team size increased, group feeding rates decreased ($B = 0.185$, $SE = 0.089$, $Wald = 4.373$, $Exp(B) = 1.203$, $df = 1, 4$, $p = 0.037$, $R^2 = 0.003$, $N = 1,532$) and mixed behaviours increased ($B = -0.284$, $SE = 0.100$, $Wald = 8.020$, $df = 1, 4$, $Exp(B) = 0.753$, $p = 0.005$, $R^2 = 0.008$, $N = 1,532$), whereas silverback activity budget remained unaffected by research team size. Tourist numbers did not have a significant effect on silverback or group activity budgets.

Observer distance did have a predictive effect on silverback activity budgets (controlling for time of day, season, group type and size). As observer-silverback distance increased, Makumba spent more time feeding ($B = -0.595$, $SE=0.053$, $Wald = 142.028$, $Exp(B) = 0.552$, $df = 1, 6$, $p < 0.001$, $R^2 = 0.081$, $N = 868$; Figure 4.11) and less time resting ($B = 0.605$, $SE=0.058$, $Wald = 110.106$, $Exp(B) = 1.831$, $df = 1, 6$, $p < 0.001$, $R^2 = 0.009$, $N = 1,868$). Because monitoring was recorded separately from activity budgets (i.e. not included as an 'activity'), it is possible that resting and monitoring behaviour might overlap. As silverback monitoring of observers (controlled for time of day, season, group type and distance) increased, resting also increased ($B = -0.280$, $SE=0.121$, $Wald = 5.366$, $Exp(b) = 0.756$, $df = 1, 6$, $p = 0.021$, $R^2 = 0.006$, $N = 1,705$) but feeding decreased ($B = 0.377$, $SE=0.132$, $Wald = 8.211$, $Exp(b) = 1.458$, $df = 1, 5$, $p = 0.004$, $R^2 = 0.006$, $N = 1,705$). These results indicate that there is an overlap between the silverback's resting and monitoring behaviours.

Furthermore, as observer-silverback distances increased, monitoring rates of humans decreased ($B = 0.291$, $SE= 0.068$, $Wald = 17.987$, $Exp(b) = 1.337$, $df = 1, 6$, $p < 0.001$, $R^2 = 0.024$, $N = 1,705$; controlling for time of day, season, group type and activity budget). However, neither group type nor size was significantly associated with monitoring rates.

5.5 DISCUSSION

Although habituation may be neatly described as the acceptance of humans as a neutral element in the environment [Tutin & Fernandez, 1991], it is not always clear when, if ever, this state is reached. The nature of observational studies means that it is not possible to compare gorilla behaviour to what might be considered 'normal,' as trackers and at least one researcher must always be present. What is possible, however, is to see if gorilla behavioural changes are associated with changes in human variables, such as the type and number of humans' present as well as gorilla–human distance.

The maximum total observer group size limit of seven was generally adhered to, other than a few exceptional circumstances where tourist time constraints and safety measures necessitated a breach of this rule. Even so, numbers never reached the 10 person maximum recommended for mountain gorillas [Homsy, 1999]. We clearly show that observers spent more time within 6–10m of the silverback when tourists were present. Although this does not necessarily represent regular breaches in the 7m rule, human–gorilla distance has certainly moved closer to this minimum recommended limit. This is made evident when compared with the Hodgkinson and Cipolletta's [2009] study on the same group, where even though humans were found to stand closer when tourists were present, distances fell well outside the 7m policy (averaging 17–18m). This increasing closeness is most likely a result of moving from a semihabituated state to a later stage in the habituation process.

Throughout the study period, 39% of silverback and 23% of total group aggressive events were directed at humans. Although these percentages represent a large effect, 65% of silverback and 47% of group human directed aggression were low level soft barks. Soft barks are warning signals that if ignored can escalate into high level aggression, and as such should be considered an important indicator of human–gorilla tension.

Even though 48.5% of observation time was spent within 6–10m of the silverback, there were distinct decreases in human directed aggression at 10m and then again at 15m, to plateau at 18m. The current 7m limit derived from mountain gorillas, is based predominantly on the risk of disease transmission and does not take into account the potential behavioural impact of close human presence.

Although several studies recommend avoiding contact with unhabituated gorillas at distances less than 10m [Ando, 2009; Blom et al., 2004], no study has explored this issue with gorillas in the later stages of habituation. Our results suggest that in order to eliminate aggression toward observers by the silverback, humans should maintain a distance of greater than 18m from Makumba. It is however, unrealistic to expect quality viewing at these distances when gorillas are on the ground. Yet, the clear drop in aggression at 10m indicates further that human directed aggression may be greatly reduced if humans avoided proximity within this distance. Again, given the dense habitats in which western lowland gorillas live, it is not always possible to optimally view them for the purpose of tourism or research at this distance. Blom et al. [2004] suggested that gorillas seem to be more comfortable with closer human approaches in dense habitats as opposed to open habitats. In more open habitats, viewing can easily be achieved when standing at greater than 10m away from the silverback. In denser habitats, this will not always be feasible and approaches to seven meters may be necessary.

The presence of tourists did not affect rates of aggression toward humans for any of the gorilla age–sex classes, nor did the number of people present in either research team or tourist groups. However, one female, Bombe, did show a significant increase in rates of aggression as research team numbers increased, although there was no additional effect of tourist numbers. Bombe was also responsible for more human directed aggression than any other gorilla in the group, and adult females were the most likely age–sex class to aggress humans.

Sex biased responses to habituation have been noted earlier in previous studies [Ando, 2009; Cipolletta, 2003; Doran-Sheehy et al., 2007; Tutin & Fernandez, 1991]. Doran-Sheehy et al. [2007] found that females tend to stay away from humans until later in the habituation process and, as a

result, move through the stages of habituation well after the silverback. This delay may present itself in the form of heightened aggression from females at a stage when the silverback is already tolerant of human presence. Individual gorilla personality may also play a role in their rates of human directed aggression, with some great ape sites still experiencing high levels of female aggression up to 15 years after group habituation began [Bertolani & Boesch, 2008; Doran-Sheehy et al., 2007]. Although it is impossible to tease apart the possible causes of Bombe's aggression (since an individual is less likely to become habituated if her personality does not readily accept human presence), she spent a similar proportion of time within 5m of the silverback as did other females, her aggression rates did not significantly change throughout the year, and the time she spent in Makumba's presence did not increase over the study period. Thus, habituation alone seems an unlikely explanation. This study suggests personality played a role in the aggression Bombe directed toward humans. In some circumstances, even when adhering to all ethical gorilla viewing guidelines, humans may receive aggression simply because certain individuals remain intolerant of their presence.

The presence and numbers of tourists did not significantly influence group or silverback activity budgets; however, as research team numbers increased, group feeding decreased while mixed behaviours increased. Research team size affected the gorillas resulting in alterations in their behaviour. Silverback activity budget was unaffected by research team size, but as human–silverback distance decreased, Makumba fed less and monitored humans more at the cost of feeding time.

Research teams may have a more pronounced effect on the behaviour of the Makumba group than do tourist groups. Although this difference may partly be owing to lower tourist pressure at this site compared with the highly visited mountain gorillas, management of the number of trackers and researchers visiting wild gorilla groups needs stricter consideration. It is also important to note that the factors analysed here explain only approximately one to 10% of the overall variance in the data.

Thus, on a biological scale, there are other important but as yet undetermined factors that affect the gorillas' behaviour far more than simply human presence. Human–gorilla distance, however, explains much more of the variance in the data than does human group type or size, further suggesting the need to reexamine the current distance rule of 7m.

Based on these results, I make the following recommendations:

1. Limit distance between observers and gorillas to greater than 10m where possible (i.e. in more open habitats where visibility can be easily achieved at distances greater than 10m).
2. Limit research team size to a maximum of five observers (two to three trackers, and one to two researchers) but make efforts to reduce researcher team size to three people as often as possible (two trackers and one researcher). Bai Hokou has decreased research team sizes as of 2008 (Todd, pers. comm.).
3. Limit total group size when tourists are present to a maximum of six observers (two trackers, one guide/researcher, three tourists). Bai Hokou has altered their policy to reflect this change as of 2008 (Todd, pers. comm.).
4. When larger team sizes cannot be avoided (i.e. tourists, training of assistants/volunteers/researchers) ensure that team size is kept to a three person maximum in the subsequent observation session(s). Bai Hokou makes every effort to minimize team sizes after larger groups visits to the gorillas. (Todd, pers. comm.).
5. Limit tourist visits to one tourist group per day. Western lowland gorilla sites are often very remote and difficult to access. As a result tourists often arrive in large groups with strict timelines, which makes adhering to the one visit per day recommendation challenging. Although in the past tourist and film crew visits remained low and with intermittent visits, numbers at this site are on the rise. Compliance will be increasingly challenging as visitor numbers continue to grow, but with careful consideration of logistics before problems arise

and an increase in the cost of gorilla visits (which is currently being phased in at Bai Hokou), this recommendation should be attainable.

Ecotourism, when conducted properly, should both conserve the environment and sustain the wellbeing of local people [Muelhenbein & Ancrenaz, 2009]. Gorilla tourism programs have been found to contribute significantly to both local and national economies [Wilkie et al., 2001], improve the attitudes of local communities and governments toward gorillas and their conservation [Archabald & Naughton-Treves, 2001; Weber, 1995], and fund the management of the gorilla parks as well as other less productive parks [Adams & Infield, 2003]. Although factors, such as high travel costs relative to other travel destinations in Africa, poor infrastructure, frequent political instability, and a deficit of other close tourist attractions, currently limit tourist numbers at western lowland gorilla sites, these programs may still benefit the gorillas, their habitat, and the local human communities.

Over 40 BaAka trackers and six local assistants are employed at Bai Hokou, with many more local residents accessing tourism revenue through craft sales or accompanying tourists on cultural trips [Hodgkinson, 2009]. As a result, local communities surrounding the Dzanga-Sangha project are generally very supportive of the tourism program [Hodgkinson, 2009] and there is a high degree of pride amongst local residents working directly with the gorilla groups, particularly amongst the BaAka trackers. Furthermore, although unquantified, there is considerable evidence that the presence of researchers and tourists in a gorilla range can act as a significant deterrent to poachers, as well as allow anti poaching units to be alerted if illegal activities are detected (pers. obsv.).

I do not purport to provide an overall analysis of the success or value of gorilla tourism, but a specific facet — that of exploring the impact of human observers on gorilla behaviour. This study forms part of a long term program at Bai Hokou, designed to monitor human impact when following western lowland gorillas and identify potential negative triggers [Blom et al., 2004; Cipolletta, 2004; Hodgkinson & Cipolletta, 2009]. In doing so, we learn how best to minimize our level of disturbance when following habituated and semihabituated western gorilla groups.



CHAPTER 6

SILVERBACK
CHEMOSIGNALLING



CHAPTER 6

WESTERN LOWLAND GORILLA SILVERBACK CHEMOSIGNALLING

6.1 ABSTRACT

Vision and audition have been perceived as the dominant modalities in great ape sociality, despite a growing body of evidence that mammals use their sense of smell in intricate ways within a social domain. Non-human great ape olfaction has received little attention due to a paucity of naturalistic olfactory observations, and a decline in relative olfactory brain size and number of olfactory receptor genes over primate evolutionary history. Thus, questions of expression and functions of olfactory signalling in complex behavioural exchanges have been explored only rarely. Here I investigate wild western lowland gorilla silverback olfactory communication. I assess the factors predicting high levels of silverback odour and I explore the relationships between arousal levels and silverback odour production, measured through a human pungency rating scale starting at zero (no smell detected) and ending at four (extreme smell detected). I suggest that olfaction in silverbacks is used as a highly flexible and context dependent signalling mechanism, whereby olfaction, vision and audition are interwoven into a complex, non-mutually exclusive and extremely elastic communicative framework. High level smells can function as acute and chronic indicators of arousal designed to intimidate extragroup males and attract adult females, indicating dominance, strength, and health. They may also provide cues for group members to increase vigilance in risky situations. Low smells appear to function in both self and intragroup reassurance. To date, this is the only detailed behavioural study to explore chemosignalling and behaviour in wild great apes. Implications are far reaching, not only because social theories have placed little importance on great ape olfactory communication but also because results suggest that olfaction in humans has evolved through adaptations present in other great ape species.

6.2 INTRODUCTION

Before discussing non-human great ape - in particular gorilla - olfaction, it is necessary to understand the mechanisms by which chemosignals operate in social dynamics. As little is known about non-human great ape chemocommunication, I first present a literature review on chemosignalling drawing from a wide variety of species.

6.2.1 Chemosignalling

Dawkins [1995, p73] defines communication as occurring “when one animal’s behaviour can be shown to have an effect on the behaviour of another”, and “signals are the means by which these effects are achieved”. By this simple definition, signals can be visual, acoustic, or, as in the topic of this chapter, chemical.

A growing body of evidence indicates that mammals use their sense of smell in subtle and intricate ways, which parallel if not surpass the complexity of odour cues used in social insect communication systems. Chemical sense is the oldest sense shared by all organisms, including bacteria, thus animals are already pre-adapted to detect and chemocommunicate with their environment [Wilson, 1970].

Olfactory communication occurs when a sender generates and transmits a chemical signal to a receiver, who then identifies, integrates and responds - behaviourally or physiologically - to the sender [Eisenberg & Kleiman, 1972]. Pheromones are combinations of molecules used in animal olfactory communication, although some prefer to use the term social chemosignal [Doty, 2010], as defining and elucidating pheromone frameworks can be a complicated process [Saxton & Havlicek, 2010]. For simplicity, the terms ‘pheromone’ and ‘chemosignal’ will be used interchangeably in this chapter.

Chemical signals have certain advantages: (1) the receiver is able to gain very specific information about its social environment via the chemosignal, and; (2) chemical signals, unlike visual and auditory signals can persist in the environment for some time, even in absence of the sender [Eisenberg & Kleiman, 1972]. The one disadvantage to chemocommunication is the

lack of directionality in the signal, making orientation difficult. Receivers must make use of the pheromone's 'active space', which is related to the sensitivity of the receiver as well as the quantity and molecular weight of the relevant chemical(s) involved [Bossert & Wilson, 1963].

Perhaps some of the most familiar chemosignals are the sex pheromones that have been shown to produce profound effects on many animals, including humans (Section 6.2.2.1). Interest in chemosignalling has mounted since androstenes were identified as pheromones in boar saliva, resulting in the classic lordosis behaviour whereby females assume mounting position when the male boar saliva containing androstenes comes into contact with the female recipient [Signoret & du Mesnil du Buisson, 1961].

Due to the diversity of communication among animals, chemical cues are emerging as one of the key mechanisms used in mate choice and resource defence. Chemosignals can be divided into various categories, such as: sex, alarm, and social organisation/identification pheromones, and are expressed through scent marking on a specific object. For simplicity, these pheromone categories and the way in which they are expressed will be discussed as separate entities in this chapter. However in reality, chemical signalling is an extremely complex and delicate, non-mutually exclusive system. This lack in mutual exclusivity will become evident when the discussion focuses on the expression of gorilla chemosignalling later in the chapter.

6.2.2 Sex Chemosignals

6.2.2.1 Mechanisms of Sexual Selection Mediated by Chemosignals

In mate selection, the most likely chemical cues detected and released in mammals are related to changes in androgen levels via androgen dependent glands (steroidal compounds) linked to testosterone production. An important internal measure of 'health' and 'viability' in vertebrates is linked to the way an individual smells; for example, illness can be detected by changes in odour and dominance status can be assessed by an individual's scent [Wyatt, 2003].

In species with high maternal investment and low paternal investment, evolution favours female choice of males, leading to the development of conspicuous male traits designed to advertise

male strengths to their female counterparts [Clutton-Brock & Vincent, 1991; Clutton-Brock & Parker, 1992]. Several mechanisms have evolved to aid selection of successful traits, such as healthy mate selection, where diseased mates are avoided through scent [Kavaliers & Colwell, 1995]; runaway sexual selection, where sexy sons inherit a desired trait (i.e. dominance) that made their fathers more attractive to females [Ryan & Keddy-Hector, 1992]; and indicator or 'good gene' traits, where viability is advertised in different ways. If males display strength of odour in proportion to their viability then females who choose males with stronger odours will produce more viable offspring. Since females are often the 'choicemakers' in mate selection, they can be exposed to several potential mates before deciding on the appropriate mate. For example, female carpenter bees (*Xylocopa fimbriata*) fly downwind of several male marked territories, briefly entering each territory before choosing a mate [Vinson & Frankie, 1990].

The selective mechanisms described above, can be expressed in intersex displays and intrasex contests: females of the scorpion fly (*Panorpa japonica*) prefer the pheromones of males that have more symmetrical wings [Thornhill, 1992] indicating that symmetry is proportionate to 'viability'; female African cockroaches (*Nauphoeta cinerea*) prefer the odour badges of dominant males [Moore & Moore, 1999]; females of the bank vole (*Clethrionomys glareolus*) prefer the odours of a dominant male over those of a subordinate [Kruczek, 1997]; only African (*Loxodonta africana*) and Asian (*Elephas maximus*) elephants in good condition enter musth - a period of elevated testosterone concentration expressed through volatile chemosignals of temporal gland secretion and strong smelling urine, along with heightened aggression and increased association with female herds - and females prefer to mate with musth over non-musth males [Poole, 1982, 1989; Poole & Moss, 1981; Rasmussen et al., 1986; Rasmussen & Schulte, 1998]. Sexual selection via intrasex contests where males fight each other for access to females or resources needed by females, can lead to marked sexual differences in traits which improve fighting ability, such as larger antlers in the male red deer [Wyatt, 2003], larger gluteal muscles and sagittal crests in western lowland gorillas [Breuer, 2008] and Caillaud et al., [2008], or an intense expression of odours which may advertise more dominant individuals [Darwin 1874, pg 809].

Other important mechanisms of sexual selection mediated by chemical communication can include: scramble competition, where males scramble to arrive at fertile females, who then choose their mate via the chemical signals of the displaying males, as seen in (*Carassius auratus*) goldfish [Sorenson & Stacey, 1999]; competition illustrated by the Bruce effect, where female mice are more likely to miscarry if they meet a novel male soon after fertilization [Brennan, 1999]; and long distance 'calling' using pheromones, as seen in many vertebrates and invertebrates; i.e. fish [Stacey & Sorensen, 1990], frogs [Wabnitz et al., 1999] and moths [Phelan, 1997]. Vertebrates also use long distance chemosignalling as a form of mate selection: hamsters leave vaginal secretion trails for males (Johnston, 1998; Meredith, 1998); female dogs release long range pheromonal attractants [Eisenberg & Kleiman, 1972; Wyatt, 2009]; and in sheep, ewes run towards rams in response to the emission of male sheep long range attractant odours [Cohen-Tannoudji et al., 1994].

6.2.2.2 Human Sex Pheromones¹.

Recent studies of humans also show sex biased patterns in chemosignalling. Humans have both eccrine and apocrine sweat glands. Eccrine glands are located throughout the body and function in thermoregulation, excretion and protection through dilution of harmful chemicals [Edgar et al., 1991]. Apocrine sweat glands are found in the genital and belly button area, areola, ear canal and eyelids, although they are most common in the axillae (armpit) region and the pubic area. The high density of apocrine glands found specifically in the underarm forms an axillary organ, which along with the other apocrine areas, becomes functional at puberty [Cleveland & Savard, 1964; Edgar et al., 1991]. These glands secrete androstene steroids (such as androstenol and androstenone) via testosterone, thus levels are much higher in males than females [Brooksbank et al., 1972; review in Havlicek et al., 2010]. Newly produced secretions from apocrine glands are odourless but transformed into its characteristically musky androstene derivatives, once acted upon by bacterial processes (Grammer et al., 2005; review in Havlicek et al., 2010).

¹Non-human primates are discussed in detail in Section 6.2.6 below and for a detailed review of human social chemosignals see Havlicek et al., [2010].

When exposed to male pheromones, women rate male faces as more attractive (Thorne et al., 2002). In addition, normally ovulating (non-contraceptive-using) women prefer the scent of symmetrical men [Gangestad & Thornhill., 1998; Thornhill & Gangestad, 1999]. Grammer [1993] showed that women perceive androstenone – which is often described as unpleasant - as less aversive when in the fertile phase of their cycle, potentially allowing advertising males to accurately and efficiently detect ovulating females. Another study found that ovulating women in stable relationships prefer males who are not their long term partners to have a psychologically dominant odour [Havlicek et al., 2005]. These results agree with the finding that during the fertile phase of a woman's cycle, they prefer men for short term relationships who display strong social presence and intrasexual competitiveness [Gangestad et al., 2004]. Tendency to dominate is a risky strategy in competitive encounters and is associated with higher levels of testosterone, which may reduce immunocompetence in weaker individuals [Folstad & Karter, 1992]; dominance can therefore reliably indicate male condition. Only individuals with strong immunocompetence can afford the high testosterone levels associated with dominance [Folstad & Karter, 1992]. Chemical preferences in female mate choice may take advantage of the 'honest-signal theory' [Zahavi, 1975] whereby the scent of symmetry, attractiveness and dominance are honest markers of good male genes [Thornhill & Gangestad, 1999].

Further evidence of human chemical communication is illustrated in the synchronization of menstrual cycles from women who live together (a phenomenon also found in rats and mice). This regulation of ovulation by pheromones has been suggested to reduce male competition and increase the chances of co-mothering [McClintock 1983, 1984; Stern & McClintock 1998; van der Lee & Boot, 1955; Wyatt, 2003].

6.2.2.3 Major Histocompatibility Complex (MHC)

The major histocompatibility complex is a large chromosomal region containing genetic information relayed through androgen-based pheromones [Jordan & Bruford, 1998]. Several studies on mice have shown that the MHC genotype influences mate choice, and body odour is responsible for the choices that are made [Potts et al., 1991]. Similar results have been found in human females who prefer the scent of men possessing different MHC alleles to themselves [Wedekind et al., 1995]. This preference for dissimilar MHC genotypes is important for

producing offspring with maximum disease protection and minimum recessive mutations [Herz & Inslicht, 2002].

6.2.2.4 Human Female and Male Olfactory Abilities

Women rank smell as the most important factor in mate selection whereas men rate looks as most important [Herz & Inslicht, 2002]. This is not surprising given the role of smell in finding genetically suitable men for successful offspring production. Predictably, women are also superior over men in detecting scent, and in many cases perform better than males in olfaction memory tasks [review in Brand & Millot 2001]. This is important from an evolutionary perspective, since these differences may have been selected for, to increase the probability of offspring and individual survival [Brand & Millot, 2001] not only through 'choosiness' for 'good genes', but also because more developed sensitivity in other areas such as 'smell' may increase survival chances as the physically weaker sex. In addition, as gatherers in traditional societies, a keen sense of smell will have been necessary to ensure safe selection and location of edible foods [Velle, 1992].

It is important to note that methodological issues have given rise to conflicting results in several human studies [Havlicek et al., 2010]. Nevertheless, the repeated findings in many experiments indicate that human olfaction is used, to some degree at least, as a chemosignal.

6.2.2.5 Alternative Mating Strategies and Olfactory Communication

Alternative mating strategies can involve sneaky eavesdropping on the chemosignals of conspecifics. In some situations it pays to stay silent (instead of advertise presence) especially if the encounter rate of predators or risk of confrontation with other more dominant males is high. In these contexts it may be more beneficial to sneakily gain access to females or resources [Wyatt, 2003]. Males of the African cockroach are able to control the release of attractant pheromones by choosing to expose or hide their chemosignalling gland. Instead of releasing pheromones, subordinates who are in contest with higher-ranking dominant conspecifics eavesdrop on nearby calling males, and as a result sometimes gain sneaky matings [Moore et al., 1995]. Another alternative mating strategy can involve the usage of mate guarding behaviours also known as consorting. A clear example of mate guarding can be seen

in elephants; dominant male elephants can detect oestrus in the urine of females and will monopolise and herd these receptive females to ensure successful insemination (Section 6.2.2.1).

6.2.3 Scent Marking

6.2.3.1 Scent Marking as a Means of Expressing Chemosignals

Scent marks play an important role in the behaviour of mammals and other terrestrial vertebrates. Scent marking with specialized glands is often sexually dimorphic, where many male species exhibit functional glands that are reduced or non-functional in females [Eisenberg et al., 1971; Lipkow 1954; Mykutowycz, 1965]. The deposited odour benefits animals, because it can act as a signal that 'shouts' at other individuals even in the absence of the marker; allowing chemical information to be exchanged between animals that live in overlapping ranges [Wyatt, 2003]. The deposited odour enables conspecifics to acquire information about the marker - such as age, sex, dominance status and reproductive condition – and the receiver's response to the scent mark will depend on the location of the mark, the mood, sex and status of the receiver, as well as the qualitative properties of the scent mark itself [Eisenberg & Kleiman, 1972]. Scent marking has traditionally been considered a means of territorial defence, although data from many animal systems indicate that this definition, while valid, is oversimplified. Scent marking should be viewed as a means of information exchange that can direct the movements and reaction of individuals, integrate social and reproductive behaviours, and provide a means of competitor assessment [Eisenberg & Kleiman, 1972; review in Gosling & Roberts, 2001].

Scent marks can be deposited on either specific or unspecific objects in the environment through scent glands, as well as through faeces and urine. For example, male European brown bears (*Ursus arctos*) will rise on their hind legs to rub their backs and necks on specific loci such as tree trunks, and they can detect female scent in urine deposits [Tschanz et al., 1970]. Some mammals use environmental disturbance as a means of rendering an area conspicuous and/or releasing odour. Scratching up of earth by cats (*Felis sylvestrus*) releases not only pedal scent but also odours from the earth itself [Eisenberg & Kleiman, 1972]. In addition,

breaking of branches or scarring of tree trunks can attract attention from the odour of the sap as well as the visual conspicuousness of the disturbance [Eisenberg & Lockhart, 1972]. Chemical compounds can also be placed on a social partner (i.e. rats will urinate or drag their ano-genital region while crawling over their partner's body), on different parts of the sender's own body in a self marking process (i.e. black tailed deer, *Odocoileus hemionus*, smear tarsal gland secretions on their own head)

Scent marking can: (1) deter potential intruders (scent fence hypothesis) [Hediger, 1949; Peters & Mech, 1975]; (2) allow receivers to match the scent of markers if met (scent matching hypothesis) [Gosling 1982, 1990]; (3) establish boundaries between competitors (border maintenance hypothesis) [Gosling, 1986a]; (4) establish territorial understandings between neighbours and higher rates of competition between unknown solitary floater males (dear enemy hypothesis) [Fischer, 1954], and; (5) allow individuals to assess characteristics of the marker through the use of androgen-dependent volatiles (i.e. dominance, health, sex, etc) [Gosling & Roberts, 2001]. While the scent fence hypothesis could act as a 'keep out' signal to individuals who mark their territory, most studies suggest that intruders do not avoid marked areas [Gosling, 1990]. In fact, the marks may even make an area more attractive as it indicates that a given location is rich in resources [Stamps, 1994]. Fighting competitors is a risky business that can have consequences for all individuals involved. Scent matching may allow both intruder and marker to identify themselves before deciding on the appropriate response (escalate versus withdrawal). Males of many species, such as the hyaena (*Crocuta crocuta*) and Coke's hartebeest (*Alcelaphus buselaphus cokeii*) will expose and allow inspection of their scent glands as they approach opponents [Gosling, 1982; Kruuk, 1972]. Receivers may associate the mark with individuals they have met or fought in the past or they may remember its properties and match it to the scent of individuals they encounter when ranging. Scent matching allows individuals to assess the costs and benefits of competitive encounters between different individuals, whereas the border maintenance hypothesis suggests that males mark along borders adjacent to their most threatening rivals, serving as a 'property line' between neighbours. A clear example of border maintenance is seen in male Klipspringers (*Oreotragus oreotragus*), who scent mark on disputed boundaries and on branch tips facing likely intruders [Roberts & Lowen, 1997]. The dear enemy phenomenon suggests that territory or resource

owners will incur greater costs by increasing time and energy spent scent marking when a rival is an unfamiliar 'floater'. If neighbours recognize and respect each other's boundaries, territory defence can focus on potentially higher-danger floaters. However, there are cases where owners have responded more aggressively towards neighbours rather than floaters [Temeles, 1989, 1990]. Perhaps a more inclusive definition of the dear enemy phenomenon is necessary; where the level of defence is based on the potential gains or losses of each competitive interaction and the importance of the resource being defended, rather than simply the familiarity of the competitors [Temeles, 1994].

Finally, animals can identify the mood, social stage, and reproductive stage of conspecifics solely based on scent marks. For example, two ways in which reproductive stage can be assessed through smell is seen in European rabbits (*Oryctolagus cuniculus*) whose chin gland odour gets stronger with age [Mykytowycz, 1970] and male dogs or cats who express the well-known patterns of leg-lifting and spraying only when sexually mature [Eisenberg & Kleiman, 1972]. Individuals can determine the mood and dominance status of conspecifics: mice avoid fearful smelling individuals and prefer the smell of a fight winner over the smell of a losing conspecific [Carr et al., 1970]; rats can distinguish stressed and unstressed conspecifics [Valenta & Rigby, 1968]; and females of many species prefer the scent of dominant individuals, often signalled through the androgen-dependent volatiles released in scent marks [Gosling & Roberts, 2001]. This is exemplified in female rodents who prefer the urine of dominant to subordinate males [Carr et al., 1982; Drickamer, 1989; Eviskov et al., 1995; Hayashi, 1990; Parmigiani et al., 1982]. In addition, female rodents prefer males with larger scent marking glands and higher marking rates, choosing males whose territories contain only owner marks [Clark et al., 1992; Rich & Hurst, 1998]. Individuals use several, non-mutually exclusive forms of assessment when detecting and releasing scent marks. The choice of release and response is determined by a balance of costs and benefits in particular social and ecological contexts [Gosling & Roberts, 2001].

6.2.3.2 *Scent Marking and Self Arousal*

Odours can contain a multitude of information about the marker, but it is also likely that the simple acts of detecting and releasing odorous stimuli may in themselves have arousal properties (i.e. increased aggression, increased scent marking, grooming, etc) for the marker and receiver [Eisenberg & Kleiman, 1972]. Brush tailed possums (*Trichosurus vulpecula*) exhibit increased aggression by threat displaying when smelling anal gland secretions of other adult males [Thomson & Pears, 1962]. When exposed to the odour of unfamiliar males, flying phalangers (*Petaurus breviceps papuanus*) show increased aggression towards males in neighbouring cages [Schültze-Westrum, 1965]. Such changes in aggression can occur during paired encounters or group situations. For example, Mackintosh & Grant [1966] demonstrated increased aggression in familiar pairs of mice when the anogenital region of one mouse was covered by the secretions of an unfamiliar male. In addition, when a group of mice were exposed to a strange male's odour, an increase of intragroup aggression was observed [Archer, 1968]. This aggressive response may be an adaptive mechanism to prepare individuals for battle.

6.2.3.3 *Scent Marking as a Form of Reassurance*

The odour each individual encounters most, is their own or that of a familiar conspecific. Both familiar (i.e. personal) and unfamiliar odours may increase the frequency of scent marking behaviour [Eisenberg & Kleiman, 1972]. These odours act to reassure the individual [Ewer, 1968].

6.2.3.4 *Scent Marking and Displays of Dominance*

While scent marking is most often documented with emphasis on 'territorial' defence, it is also commonly expressed by males in dominance mating systems. Ralls [1971] suggests that scent marking acts to intimidate and threaten opponents, by advertising virility and status. This concurs with theories discussed previously, where scent signals are suggested to advertise the costs of pursuing or withdrawing from the marker, instead of simply acting as a 'keep out' sign [Gosling, 1990; Temeles, 1994]. In order to minimize risk and prolonged fights, male mice avoid scent marked substrates from dominant males or conspecifics likely to outcompete the

receiver mouse [Gosling et al., 1996a, 1996b; Gosling & McKay, 1990; Hurst, 1993; Hurst et al., 1994; Jones & Nowell, 1989].

Furthermore in many mammals, resource holders - either territorial males or dominant males in a dominance mating system - scent mark more than non-resource holders [Allen et al., 1999; Hurst, 1990; Miller et al., 1987; Rozenfeld et al., 1987] and intrasexual dominance later in life is best predicted by the marking rates of young males [Collins et al., 1997]. In addition, the intensity of scent marking appears to correlate with the threat level of potential opponents. Thomson's gazelles (*Gazella thomsoni*) and Klipspringers mark their territories more intensely when the threat of competition is more intense [Roberts & Lowen, 1997; Walther, 1978]. In coypus (*Myocastor coypus*), the anal gland size used in scent marking is predicted by the total number of potential competitors in the population [Gosling & Wright, 1984]. In other mammals (i.e. Coke's hartebeest), males may use scent marking in territory take-over attempts (Gosling, 1974). Male aardwolves (*Proteles cristatus*) also increase scent marking behaviours prior to the start of a mating season, to challenge resource ownership or mating opportunities [Richardson, 1987, 1991].

This use of scent marking behaviours as signals in intrasexual competition is clearly illustrated in the Madagascan ring tailed lemur (*Lemur catta*): males load secretions from their shoulder and wrist glands onto their tails, which they then wave at their opponents in both intragroup dominance displays and intergroup territorial interactions. This olfactory threat is complemented through the striking visual displays of their tail and face markings [Charpentier, 2008; Jolly 1966; Knapp et al., 2006; Lewis, 2006]. In addition, African elephants ear wave towards competitor males when in musth, to deposit and communicate their 'dominant' scent in the air [Poole, 1982]. These examples illustrate the importance of olfaction to intrasexual competition, and validate the use of androgen dependent (via testosterone) glands in mammalian scent marking [Eisenberg & Kleiman, 1972].

6.2.3.5 Eavesdropping

When signals are emitted, individuals other than the intended receivers (i.e. predators) may also be able to detect them and use the information given in the signals to their own advantage.

Eavesdropping [McGregor, 1993] can occur in a variety of contexts, although has been most widely discussed in the acoustic signalling of territorial birds [Dabelsteen et al., 1997; Naguib et al., 1999; Otter et al., 1999]. Since scent marking acts as an honest signal of competitive ability, it seems likely that eavesdropping may be another tactic used in the assessment of varying odour signatures. For example, a male could eavesdrop on scent marking interactions between other males as a low cost alternative strategy of opponent assessment. Equally, females may eavesdrop on male signals to assess potential mate quality. For example, female white tailed deer (*Odocoileus virginianus*) in oestrus will travel long distances into different territories to investigate various male scent marks [Moore & Marchinton, 1974; Sawyer et al., 1989]. Do males signal via scent marking directly to females? Or do females simply gain information about the scent marks aimed at other males by eavesdropping? The answer remains unclear [Gosling & Roberts, 2001], but either way it is evident that females use information acquired through male scent marks as a means of assessing mate quality.

6.2.4 Alarm Chemosignals

6.2.4.1 Functions of Alarm Chemosignalling

Alarm signals may be the second most widespread signal, after sex pheromones [Wyatt, 2003]. This statement, however, is based mainly on social insects; clear divisions between signalling categories (i.e. sex, alarm, etc) are very complex and interwoven in vertebrates. Nonetheless, many animals including humans exhibit alarm chemosignalling in response to fear.

Alarm chemosignals have likely evolved to warn and protect kin from danger [Wyatt, 2003], although their conspicuousness could also be directed at the object of fear itself (i.e. predator or rival). Even though such a chemically “loud” signal may make an animal more obvious to predators or rivals, it can also function as an “I’ve seen you’ signal [Hasson, 1991] and may eliminate the element of surprise. In addition, alarm pheromones may attract conspecifics or other secondary predators, which can act to confuse and distract the original predator or rival [Smith, 1992].

Black tailed deer release a strong garlic-like odour by exposing the metatarsal gland on their hindleg in periods of fear [Müller-Schwarze, 1971; Müller Schwarze et al., 1984; Steiniger, 1950; Tschanz et al., 1970]. Females exposed to this odour are more likely to show vigilance behaviours (i.e. lifting of the head and scanning) and/or leave the area [Wyatt, 2003]. In addition, visual displays such as an erect tail, cocking of the ears, raising of anal hair and a stiff-legged gait accompany the release of this garlic-like odour, ensuring that kin can receive information through visual vigilance once the fear odour is detected. Similar signalling is found in the pronghorn antelope (*Antilocapra americana*) [Stoddart, 1980]. The subsocial aubergine lace bug (*Gargaphia solani*) runs towards predators fanning its wings to deter predators, but if caught releases an alarm pheromone from its dorsal gland that alerts nearby nymphs and causes them to stop feeding and run [Aldrich et al., 1991; Tallamy & Denno, 1982]. In protection of their nest, honeybees will release an alarm pheromone while attacking intruders so that workers are alerted to danger [Schmidt, 1998] and can join in defence. When attempting to intrude into Japanese honeybee (*Apis cerana japonica*) nests, giant hornets (*Vespa mandarinia japonica*) are roasted to death by heat generated from the buzzing of hundreds of bees, who upon detection of the hornet release alarm pheromones to attract workers and surround the predator as it attempts to enter their nest [Wyatt, 2003]. Many social insects and various mammals exhibit this type of aggregation or call to group defence (i.e. mobbing behaviour of some birds) when in the presence of inter or intraspecific competition over resources [Wyatt, 2003]. Other species exhibit fear and panic when exposed to an alarm pheromone: several ant species, such as *Lasius alineus*, respond by fleeing from the stimulus or dashing around erratically in order to confuse the predator [Regnier & Wilson, 1969]; when the European minnow (*Phoxinus phoxinus*) release an alarm pheromone, shoals respond by rapidly swimming away, increasing shelter use, freezing or shoaling [review in Friesen & Chivers, 2006; Von Frisch, 1938].

6.2.4.2 Human Fear Chemosignals

Fear-related chemosignals exist in humans as well. In Ackerl et al. [2002], pads were placed in the axillae region of females watching either a horror movie or a comedy. Other female subjects were then asked to categorise the worn pads as fearful (belonging to the horror) or not

fearful (belonging to the comedy). Subjects correctly identified the fearful and nonfearful pads significantly more often than predicted by chance, noting that the fearful pads were less pleasant, more intense and more aggressive than the nonfearful versions. Fear can lead to physiological responses such as increased heart rate, muscle tension, sweating and the release of cortisol. Even though fear is often measured via cortisol levels, there was no direct correlation between changes in cortisol, smell ratings, and induced fear in this experiment. Cortisol may be acting as an indicator of arousal - both positive and negative - and does not appear to be the inducer of the 'scent of fear' in humans.

Zhou and Chen [2009] found that the presence of fearful sweat led women to interpret ambiguous facial expressions as more fearful. This finding has evolutionary implications since ambiguity in dangerous situations can threaten survival. Prehn et al. [2006] also found that anxiety related chemosignals increased the startle reflex in humans, and Pause et al. [2004] found that women were less likely to see a neutral face as happy (after being exposed to a subliminal happy face), when in the presence of fear related chemosignals. Finally, Chen et al. [2006] illustrated that women showed increased cautiousness on a word-association task to ambiguous word pairs, when exposed to anxiety related chemosignals.

6.2.4.3 Chemosignals as Cues for Vigilance

The avoidance of predators, rivals and dangerous situations is likely to be very costly, as energy involved in fitness related behaviours (i.e. foraging) are sacrificed at the cost of these avoidance behaviours [Brown 2003; Lima & Bednekoff, 1999; Wisenden, 2000]. Chemical cues as signals can increase vigilance during lower level threats; that way individuals can continue to perform the necessary fitness related behaviours while remaining cautious towards any potential dangers. Glowlight tetras (*Hemigrammus erythrozonus*) use a mixture of visual and chemical cues to detect and respond to predators. When exposed to subthreshold concentrations of alarm pheromones from conspecifics, they do not disrupt their fitness related activity, but instead increase vigilance towards detecting additional sensory information (i.e. visual alarm signals such as fin-flicking). In doing so, cost-benefit trade-offs regarding fitness can be maximized when in the presence of lower level threats [Brown et al., 2003].

6.2.5 Identification Pheromones

6.2.5.1 Functions of Identification Pheromones

Chemosignalling is clearly a means of communication, and is also associated with individual identification. For example: in the eusocial paper wasp (*Polistes eucatus*), adult wasps particularly the queen, deposit scent marks from their glands onto the surface of the nest. Thus, the odour template contains the queen's signature and odour cues from the surrounding environment as well as other wasps in the colony. When young wasps emerge from the pupa, they learn to identify intruders and nestmates by resting on the comb of their nest, where they are exposed to the specific odour template created by their colony [Singer et al., 1998]. Experiments on the dwarf and Indian mongoose (*Helogale undulate*; *Herpestes auropunctatus*) show that they are able to identify individuals simply through anal gland secretions [Gorman, 1976; Rasa, 1973]. In addition, individual recognition is important for pair bonding in monogamous species such as prairie voles and monogamous lizards, who track their partners by following their scent trail, which indicates that recognition is imperative to the maintenance of their long lasting relationships [Carter & Roberts, 1997; Olsson & Shine, 1998].

6.2.5.2 Human Individual Recognition

Some of the most compelling evidence for human scent recognition is found in newborns: babies will turn their head towards a pad carrying odours of their mothers only three days after birth and will move less and suckle more when exposed to these odours [Porter & Wineberg, 1999; Schaal et al., 1980; Schaal & Porter, 1991]. Additionally, fathers were correctly able to identify t-shirts worn by their own infants only 72 hours after birth, and aunts as well as grandmothers were able to detect neonatal relatives through scent [Porter et al., 1986]. Humans can even match the odour of twins [Roberts et al., 2005]. In fact, even young children were able to correctly identify t-shirts worn by similarly aged siblings [Porter et al., 1986].

6.2.6 Olfaction and Non-Human Primates

6.2.6.1 Olfactory Communication of Non-Human Primates

Until recently, vision and audition have been perceived as the dominant force moderating social behaviours in great apes and other primates [Dominy et al., 2004; Heymann, 2006; King & Forbes, 1974]. As a result, olfaction has received little attention and its relevance to social behaviours has been questioned.

Smells are processed in two brain pathways. Simplistically, the main olfactory system processes environmental odours (i.e. food, predators, etc) and the accessory olfactory system processes social odours (i.e. pheromones, etc) [Barton, 2006]. Decreases in size of both systems over primate evolutionary history and lack of accessory olfactory bulbs in some higher primates (i.e. catarrhines) has led to olfaction receiving little attention in primate sociality [Barton 2006].

The anatomical structures of the brain involved in great ape olfaction are even smaller by comparison to other primates and thus perceptually 'less important'. The relative size of the area in the brain dealing with olfaction when compared to overall brain size is 8.88% in insectivores, 1.75% in strepsirrhines, 0.07% in great apes and 0.01% in humans [Stephen et al., 1970]. Furthermore, studies have revealed that the number of functional olfactory receptor genes in humans (350) have decreased significantly from numbers in Old World (700) and New World (1000) primates (Gilad et al., 2004). This decline in anatomical and olfactory receptors combined with the general paucity of evidence regarding olfactory influences on behaviour in natural settings have, unsurprisingly, led great apes to be labelled as microsomatic (poor smellers). As a result, little attention has been given to olfactory stimuli and their moderating effect on great ape sociality [Hepper et al., 2008].

However, several human and non-human primate studies suggest that communication via odour stimuli may involve alternative pathways for processing social odours [review in Barton, 2006]. Thus, olfaction in primates may be more important to behaviour than previously thought. Since human chemosignalling was described in detail above, this section will mainly focus on the usage of olfaction in non-human great apes and other non-human primates.

Laska et al. [2005d] demonstrated that Old World pigtail macaques (*Macaca nemestrina*), and New World squirrel and spider monkeys (*Saimiri sciureus*; *Ateles geoffroyi*) were able to detect androstenone and androstenol at very similar threshold values despite catarrhine and platyrrhine differences in relative olfactory bulb size and numbers of functional olfactory receptor genes. While the tested primates appeared to be at least as sensitive to androstenone as human subjects, humans were more sensitive to androstenol despite the fact that humans have fewer olfactory receptor genes and a smaller relative brain area devoted to olfaction. Furthermore, the old world pigtail macaques did not perform any worse than the New World primates. Interestingly the three non-human primates were more sensitive to androstenone, a steroid-based ketone, over androstenol, an alcohol, despite the structural similarity of these odorants and the fact that other studies show monkeys are more sensitive to aliphatic alcohols compared to aliphatic ketones (Laska & Seibt, 2000b; Laska et al., 2005a, 2005b). This reversal in sensitivity suggests that an important determinant of sensitivity to odour stimuli may be related to the behavioural relevance of the odorant (Laska et al., 2005a, 2005b). Conclusions regarding the olfactory sensitivities of species should not be based solely on comparisons of olfactory brain structure or differences in the numbers of functional olfactory receptor genes [Laska et al., 2005d].

Non-human primates use olfaction as an important means of communication and individual identification: lemurs, marmosets, tamarins, and galagos are able to recognize individuals via odour cues [Clark, 1982; Epple, 1974; Mertl, 1975; Palagi & Deporto, 2006; Smith, 2006]. Dominant saddleback tamarin (*Saguinus fuscicollis*) and common marmoset (*Callithrix jacchus*) females use odour to suppress the reproductive facilities of subordinate females [Barrett et al., 1990; Epple & Katz, 1984]. In wild woolly monkeys (*Lagothrix lagotrica*) scent marking increased on copulatory days and during intergroup encounters even though male-male competition is rare, suggesting that odour plays a role in advertising male quality and competitive ability [Di Fiore, 2006]. Scent marking behaviour is also seen in the white saki (*Pithecia pithecia pithecia*) [Brumloop et al., 1995], callitrichids [Epple et al., 1993; Heymann, 2003] and many strepsirrhines [Schilling, 1979] such as the ring tailed lemurs, who defend territories and females and advertise male genetic quality via ritualised tail-waving 'stink fights' (detailed explanation in 6.2.3.4). Recent studies of mandrills (*Mandrillus sphinx*) [Feistner,

1991; Setchell et al., 2010a, 2010b], also demonstrate that odour profile potency and production signals identity, age, genetic quality and dominance rank of adult males; where high ranking males are more likely to produce increased secretions as a function of higher testosterone levels.

Several captive studies have investigated the effects of various olfactory stimuli on great ape behaviour. Struthers and Campbell [1996] reported an increase in captive chimpanzee activity when peppermint was diffused throughout the enclosure. Another study on chimpanzee odour preferences suggests that infants preferred strawberry and lavender odours but disliked pyridine [Oeda et al., 2002]. However, Ostrower & Brent [2000] found that captive chimpanzees did not react differently to pleasant or aversively scented cloths when compared to unscented control cloths.

Much of the argument against the importance of olfaction in great apes has evolved in the absence of naturalistic observations [Hepper et al., 2008]. While great ape studies of communication via odour stimuli are completely lacking in wild settings, there are anecdotal reports of orangutans [Rijksen, 1978] and chimpanzees [Blackmann, 1947] smelling their fingers after touching objects, each other's hands, and conspecifics' genitals. There are also some anecdotal and very recent captive studies, which explore the importance of odour in the gorilla.

6.2.6.2 Captive Gorilla Olfaction

The importance of olfaction to great apes has recently been examined in three studies on captive western lowland gorillas. Hepper et al., [2008] demonstrated that when one group of captive western lowland gorillas was exposed to almond, ck1 (perfume) and control scented cloths, they held and sniffed the almond scented cloth significantly more than the ck1 and control scented cloths. Furthermore, after one trial they exhibited aversion to tasting the ck1 scented pads for up to seven weeks (the periods between all the trials), which indicates that they associate smell with taste and have a long term memory for aversive stimuli. A previous study on the same group of gorillas investigated the use of scents as enrichment tools [Wells et al., 2006]. The introduction of orange, peppermint, vanilla, almond and unscented cloths had

little effect on their behaviour. However, the animals were still able to differentiate between the novel odours as they once again held the almond scented clothes more than any other cloth, and spent more time (although not significantly) sniffing the odour impregnated cloths compared to the unscented flannels. Although these studies did not find the clear olfactory reactions seen in other captive non-primate macrosomatic species – such as the African lion, *Panthera leo* [Powell, 1995], the black footed cat, *Felis nigripes* [Wells & Egli, 2004], and dogs, *Canis familiaris* [Graham et al., 2005] – results from these studies still indicate that gorillas have a functioning olfactory system which is used in exploration of their environment. The lack of reaction seen in the Wells et al. [2006] study may be due to the methods used in the experiment (scented cloths instead of enclosure diffusion) or the choice of odours, which perhaps held little biological relevance to the gorillas.

Gorillas have both eccrine and apocrine sweat glands and have a functional axillary organ whose general histochemical properties and structure are very similar to that of humans [Ellis & Montagna 1962; see Section 6.2.2.2 for a detailed definition of sweat glands]. Given the close similarity in hormone physiology and steroid metabolism between humans and other great apes, non-human apes, like humans, should have individually identifiable odours. It also seems reasonable to assume that androstenone and androstenol (Section 6.2.2.2) may be compounds used in non-human great ape chemical communication [Laska et al., 2005d]. Additionally, gorilla-human similarities in (1) physiology; (2) relative brain size dedicated to olfaction, and; (3) number of olfactory receptor genes, clearly suggest that a gorilla's sense of smell is very similar to, if not more sensitive than a human's sense of smell.

Hepper and Wells [2010] exposed humans to the scent of six different gorillas of varying age-sex classes (one silverback, one 11 year old castrated male, two adult females, one 5 year old male, and one 4 year old female). If humans can identify individual gorillas, then gorillas should also be able to discriminate between each other. Human participants correctly identified all individuals through their odours significantly better than by chance for both experiment one, where a target odour was matched to one of two possible samples, and experiment two, where a target odour was matched to all six possible samples. The silverback's odour was easiest to recognize, and in experiment two, he was identified without error in all occurrences. In

experiment one, the castrated blackback male was correctly identified against the silverback 85% of the time, and in experiment two, the castrated male was never misidentified as the adult silverback. Further exploration of multimale groups and assessment of individually identifiable odours between silverbacks would be an interesting and biologically relevant extension of this captive study. Interunit interactions between gorilla groups and solitary males must rely on the ability of individuals to recognize each other so approach and response strategies can be accurately assessed (Chapter 4). The high accuracy of individual discriminations across all age-sex classes, combined with the general lack of confusion when identifying the adult male and the blackback suggest that humans (and thus gorillas) would be able to distinguish different silverbacks from each other. It must be noted however, that since the blackback was castrated he would not have been producing hormones typical of pubertal males.

This study strongly suggests that gorilla odours are individually identifiable, especially when comparing the silverback to other gorillas. In addition, participants reported the silverback's odour as being 'intense', a word not associated with the scent of other group members. This indicates that intensity of odour may act as an advertiser of traits, such as dominance.

6.2.6.3 Wild Gorillas

Several anecdotal observations of odour communication in both wild mountain and western lowland gorilla adult males exist:

(1) Schaller [1963, p 91]: "The most potent and unmistakable odor of gorillas 'is rather like a combination of very pungent human sweat, manure, and charred wood' [Donisthorpe, 1958]. I compared it to the smell of distant burning rubber in my notes. When this odor was discerned, I knew that gorillas were within 100 feet of me, although on occasion I noted it as far as 150 feet. I think the strong odor is emitted primarily by silverbacked males, but I was unable to prove this point to my satisfaction. The odor becomes especially noticeable when the group is excited. On some days I smelled it when the group fed or rested leisurely, but on others I was unable to perceive it even though a breeze blew in my direction. I was unable to determine the source of the odor. Although gorillas were observed to sweat while lying peacefully in the sun, the odor was not apparent at that time, suggesting that sweat alone is not the cause."

(2) Donisthorpe [1958, p 202]: "Gorillas have a very strong smell which is difficult to describe but unmistakable. It is rather like a combination of very pungent human sweat, manure and charred wood. "

(3) Cousins [1990]²:

(a) When Lomie (female gorilla) was introduced to Guy (male gorilla) at Chessington Zoo in Greater London, the following reaction was recorded: "When they were finally put together in October, 1971, with keepers standing by with hosepipes, the reaction of Guy was far from being one of aggression. He rushed to Lomie, grasping her and smelling her while she submitted. This was followed by a prolonged period of rough play, the animals making vocalizations of pleasure the whole time" [p 246].

(b) "The Fang (African tribe) also came to the astute conclusion that the gorilla's sexual drive is less pronounced than the chimpanzee's and this gave rise to the belief that as he moves about, the gorilla detects everything from odour and he will first attack a man who has been with a woman beforehand" [p 201].

(c) "Scent appears to play an important part in initiating the mating act, as captive males have been observed sniffing the female's vagina and armpits prior to copulating, suggesting that odour from scent glands in these areas may stimulate the male to mate" [p 141; also cited in Dixson, 1981].

(4) Williamson [1988, page is missing from published version of thesis so Williamson provided me with the following quote; Williamson pers. comm.]: "When aroused, adult males (western lowland gorilla) bark or scream and emit a pungent odour before charging, thumping the ground and breaking vegetation to intimidate human observers."

(5) Fossey [1983, p 45]: "Traces of a silverback's (mountain gorilla) pungent odour, resembling human non-deodorized sweat smell, permeated vegetation the gorilla had travelled through some twenty four hours previously. Had I been walking after the lone silverback that day rather than crawling, I never would have realized the importance of olfactory clues existing at ground

² Although several papers have reported Cousins mentioning that silverbacks emit pungent odours in a state of excitement, fear or stress, I was unable to find any such anecdotal reports. However, I did find the quotes which suggest that odour stimuli is a potentially important means of gorilla communication.

level.... The axillary region of the adult male contains four to seven layers of large apocrine glands responsible for the powerful fear odour of the silverback, an odour only weakly transmitted by the adult female...and appears to be an evolutionary adaptation for olfactory communication, particularly for adult male gorillas.

(6) In BBC News Gorilla Diary [<http://news.bbc.co.uk/1/hi/sci/tech/7251261.stm>:Friday November 30th] park rangers were quoted as saying: "Their (mountain gorillas) sense of smell is probably more developed (than humans); dominant males may make crucial decisions to move on or stay put on smell alone. When silverbacks sense strangers in their midst, they also let off a very particular odour from the glands in their armpits. It is this scent that is the first thing that hits you when you visit a family of gorillas in the forest – it is pungent. We hope this smell will ward off any unwanted visitors into the sector."

These reports, along with evidence presented earlier, suggest that olfaction may not be as irrelevant in great apes as previously thought and that olfactory chemosignals may play an important role in the regulation of gorilla (and great ape) social communication.

6.2.7 Chapter Aims

Here I investigate the functions and importance of wild western lowland gorilla silverback olfactory communication. I assess which factors predict high level western lowland silverback odour, with a particular focus on interunit interactions. I explore the intricate relationship of varying arousal levels and silverback odour production, measured in terms of a pungency rating scale starting at zero (no smell detected) and going to four (very strong smell detected; see also Chapter 2). To date, this is the only detailed study to explore chemosignalling in wild non-human great apes. Implications are far reaching, not only because social theories have placed little importance on great ape olfactory communication but also because results suggest that olfaction in humans has evolved through adaptations present in other great ape species.

6.3 METHODS & ANALYSIS

6.3.1 Definitions and Sampling Independence

As outlined in Chapter 2, a subjective silverback odour intensity rating was defined as: (0) no odour was detected; (1) slight odour detected but not stronger than the smell of surrounding vegetation; (2) odour detected at the same level as the smell of surrounding vegetation; (3) odour detected was stronger than the smell of surrounding vegetation; (4) odour detected was overpowering and was the first or only element smelled in the surrounding air (similar to the smell of burned coffee). Odour ratings were recorded at each scan (Chapter 2). If an odour was detected outside scan times, its intensity rating was recorded as *ad libitum* data along with silverback activity, silverback body positioning, group activity, group spread, forest density and type, human-silverback distance (m), silverback-neighbour presence or absence, and wind presence or absence (see Chapter 2 for definitions). If an odour was detected within one minute of scan time, the odour was included in the scan (not as *ad libitum* data). Once an odour was recorded (any odour greater than zero), five minutes must have elapsed before a new odour (greater than zero) recording could be made. This was designed to minimize the lingering effects of a previously recorded smell. An exception to the five minute rule occurred when a new *ad libitum* odour was detected and recorded less than five minutes to the next scan, where a smell rating was taken regardless. This occurred only 199 times out of the 4,305 recordings (Section 6.3.3). Smell data collection was therefore essentially a continuous data set of no generally no less than five minutes between each smell recording. As shown in Chapter 2, smells recorded a minimum of five minutes apart from each other can be considered independent and were used in analyses. When a scent was detected, the recorder would wait one minute before recording its intensity to ensure that the scent was recorded at its strongest point.

For hourly identity record or roll call, interunit interaction (termed 'interaction'), group spread definitions, auditory sampling data collection specifications, and any other definitions and specifications in the chapter, see Chapter 2. Gorillas were grouped into age–sex classes, as per Chapter 2, however the 'immature and infant' category was simply termed 'immatures' for

this chapter. Auditory signals and the presence and intensity of interactions were matched with ratings of odour (Section 6.3.3)

As described in Chapter 2, interobserver reliability was maintained by regularly visiting the Makumba group, collecting data at the same time, and checking for inconsistencies in the collection process. Humans who are anosmic (not able to smell) to the scent of androstenone are able to detect its odour after repeated exposures to the compound [review in Havlicek et al., 2010; Wysocki et al., 1989]. In addition, those who were not anosmic at first detection, exhibited lower detection thresholds to androstadienone (a low odour androstene) after repeated exposures [Jacob et al., 2006].

Androstene sensitisation can occur in anosmic humans in as little as three days [<http://www.physoc.org/publications/pn/subjectcollections/pncollectionspdfs/Integrative/2004/Jacob.PDF>]. Additionally sensitisation to non-androstene compounds (citraiva and benzaldehyde) have also been shown to occur in women of reproductive age [Dalton et al., 2002]. If anosmia was an issue for observers during data collection, sensitisation would have likely taken place within three days, which on a biological timescale would not have been long enough to bias the study. It might also be argued that due to sensitisation, recorder thresholds to silverback odour might lower (thus increasing detection ability) throughout the recording period and bias the results. However, a logistic regression (controlling for the number of interunit interactions), showed that observer time spent temporally (by month) in the presence of the silverback did not affect the likelihood of recording low (level 1 & 2), high (level 3) or extreme (level 4) smells (also see Section 6.3.3). Similar patterns emerged when both data recorders were considered separately (Table 6.1).

Table 6.1 Recorder Non-Sensitisation to Silverback Odour (N = 255)

| Recorder Type | Odour Level | B | S.E. | Wald | df | Exp(B) | Sig |
|-----------------------------|-------------|--------|-------|-------|-----------------------|--------|-------|
| | Recorded | | | | (predictor, model) | | |
| Combined | Extreme | 0.061 | 0.048 | 1.597 | 1,2 | 1.062 | 0.206 |
| Recorders | High | -0.064 | 0.041 | 2.382 | 1,2 | 0.938 | 0.123 |
| | Low | -0.075 | 0.055 | 1.834 | 1,2 | 0.928 | 0.176 |
| Recorder One: | Extreme | 0.038 | 0.070 | 0.294 | 1,2 | 1.039 | 0.888 |
| Sessions | High | -0.006 | 0.062 | 0.010 | 1,2 | 0.994 | 0.919 |
| Recorded = 201 ^a | Low | -0.064 | 0.082 | 0.602 | 1,2 | 0.938 | 0.438 |
| Recorder Two: | Extreme | 0.438 | 0.403 | 1.180 | 1,2 | 1.550 | 0.277 |
| Sessions | High | 0.253 | 0.307 | 0.708 | 1,2 | 1.288 | 0.400 |
| Recorded = 57 | Low | -0.454 | 0.450 | 1.015 | 1,2 | 0.635 | 0.314 |

^athree sessions were omitted for this analysis due to missing information

6.3.2 Auditory Categories

For this chapter, auditory rates were grouped into categories listed in Table 6.2. For my definitions of auditory signals, see Chapter 3.

Table 6.2 Auditory Categories with Associated Arousal Levels

| Age-Sex Class And Category | Auditory Signals | Arousal Levels |
|-----------------------------------|--|---|
| Silverback Anger and Distress | Bark, Soft Bark, Charge, Display, Scream | Very High |
| Adult Female Anger and Distress | Bark, Soft Bark, Charge, Display, Scream | |
| Immature Anger and Distress | Bark, Soft Bark, Charge, Display, Scream, Cry | |
| Silverback Excitement | Talking Belch, Play Grunt, Sex Whinny/Neigh, Singing Belch | Medium (These Auditory Signals Appear to be Generally Positive but Represent an Excited State) |
| Adult Female Excitement | Talking Belch, Play Grunt, Singing Belch | |
| Immature Excitement | Talking Belch, Play Grunt, Singing Belch | |
| Silverback Long-Call | Chest-Beat and/or Hoot | Very High |
| Adult Female Long-Call | Chest-Beat and/or Hoot | |
| Immature Long-Call | Chest-Beat and/or Hoot | |
| Silverback Soft | Belch, Soft Whinny/Neigh | Low |
| Adult Female Soft | Belch | |
| Immature Soft | Belch | |
| Immature Chest-Beat or Hand-Clap | Chest-Beat, Hand-Clap | Medium (These Auditory Signals are Generally Positive but Represent an Excited State) |

6.3.3 Analyses Overview

Final analyses were conducted on 4,305 silverback scans. This number includes both original data (3,252 scans with an average interscan interval of 16 min) where each scan is associated with one smell record, and 1,053 *ad libitum* smell data points with the associated behavioural and environmental information (with an average intersmell interval for all 4,305 smell data points of 12 min). As described in Section 6.3.1 and in Chapter 2, smells ratings were considered as independent of each other. Even though the associated information for *ad libitum* smells was taken at intervals of less than ten minutes apart, it was essential to include behaviours directly associated to each 'non-zero' smell recording and as such were all included in the final analysis. Data were grouped by session, to match auditory data analyses where session groupings were necessary to limit any effects of dependence.

As described in Chapter 2, proportion of each odour rating (zero, one, two, three, four) was calculated out of total smell recordings for each session. Odours one and two were grouped together to represent low level smells, but odours three and four were analysed separately since one of the main aims of this study was to determine which factors predict high (level 3) and extreme (level 4) smells. For wind presence or absence grouping and calculation, and for any other analysis groupings and justifications used here, see Chapter 2.

The forward stepwise logistic regression was the primary analytical tool used, given the main aim of this chapter relates to predicting factors involved in the presence and absence of low, high and extreme odours. As described in Chapter 2, the first two months of scan collection (N = 66 sessions) were dropped from logistic regressions that included an individual(s) hourly roll call as one of the final predictors in the model (hourly roll call collection began in March). This form of recording was the most accurate way to determine presence of individuals within Makumba's vicinity, as individual hourly roll call captured hourly movements of each gorilla, whereas session presence noted only if each individual was spotted once during the entire session (Chapter 2). The addition of roll call into logistic regressions resulted in a stronger model which predicted more of the variance in the outcome smell variables. Logistic models based on individual session presence or absence were also calculated to take into account the

full range of available data points, including the first two months. The resulting model predictors were very similar to those of the hourly individual roll call logistic models.

6.3.4 Factors Predicting Changes in the Presence of Extreme (Level 4), High (Level 3) and Low (Levels 1 & 2) Level Silverback (SB) Odour

As there is no *a priori* knowledge for which factors may affect or predict silverback odour production and detection, the logistic regression models contained 43 predictors (Table 6.3; also see Chapter 2), all of which could potentially affect silverback scent production or bias observer scent detection. Final analyses were based on a sample size of 175-258 sessions (this large difference was mainly due to the elimination of 66 sessions when individual hourly roll call was one of the final variables in each stepwise model – see Section 6.3.3). These sample sizes fall within those necessary for analysis of 43 predictors (Chapter 2). After initial analyses using the 43 predictors, the logistic models were re-run using only the final variables included in stepwise models; results were very similar and were reported here. A Bonferroni correction (N-1 design for repeat tests of different hypotheses on the same data set) has been applied to all overall logistic models, which after correction, are considered significant when $p < 0.025$.

Table 6.3 Predictors included in initial forward stepwise regressions^a

| Predictors | |
|---|--|
| 1. Daily rainfall | 21. Adult female human directed aggression |
| 2. Daily maximum temperature | 22. Juvenile human directed aggression |
| 3. Silverback-human monitoring | 23. Grouped observer-silverback distance |
| 4. Group spread | 24. Mopambe roll call |
| 5. Corrected forest density | 25. Bombe roll call |
| 6. Corrected number of neighbours (within five m) to silverback | 26. Malui roll call |
| 7. Silverback anger and distress | 27. Kunga roll call |
| 8. Silverback excitement | |

| | |
|--|---|
| 9. Silverback long-call | 28. Etefi roll call |
| 10. Silverback soft | 29. Mio roll call |
| 11. Adult female anger and distress | 30. Silo roll call |
| 12. Adult female excitement | 31. Mai roll call |
| 13. Adult female long-call | 32. Mosoko abuli roll call |
| 14. Adult female soft | 33. Essekerende roll call |
| 15. Juvenile anger and distress | 34. Interaction presence or absence (categorical) ^b |
| 16. Juvenile excitement | 35. Wind presence or absence (category) |
| 17. Juvenile long-call | 36. Silverback behaviour (category) |
| 18. Juvenile soft | 37. Silverback position (category) |
| 19. Juvenile hand-clap and chest-beat | |
| 20. Silverback human directed aggression | |

^aAs detailed in Chapter 2, all data averaged over the session were corrected for observation minutes and turned into an hourly rate/ corrected score)

^bInteraction presence or absence was substituted by other relevant predictor variables depending on the aim

There was no effect of session (afternoon or morning) on any odour level (Table 6.4) so 'session' was not included as a predictor in subsequent logistic regression models.

Table 6.4 Influence of Session on Silverback Odour Levels (N = 255)

| Smell Level | Spearman's Correlation (Morning or Afternoon Session Correlated with Smell Level) |
|--------------|---|
| None (0) | $r_s = -0.090, p = 0.154$ |
| Very Low (1) | $r_s = 0.027, p = 0.663$ |
| Low (2) | $r_s = -0.003, p = 0.967$ |
| High (3) | $r_s = 0.077, p = 0.223$ |
| Extreme (4) | $r_s = 0.051, p = 0.418$ |

Where time lags and the decrease of extreme or high level silverback odour were investigated, interaction presence or absence was substituted for the 'number of (non interaction) sessions since previous interaction' (categorical variable). Post interaction sessions were grouped for analysis as: (1) 1-5, (2) 6-10, (3) 11-15, and (4) 16-30 sessions post interaction.

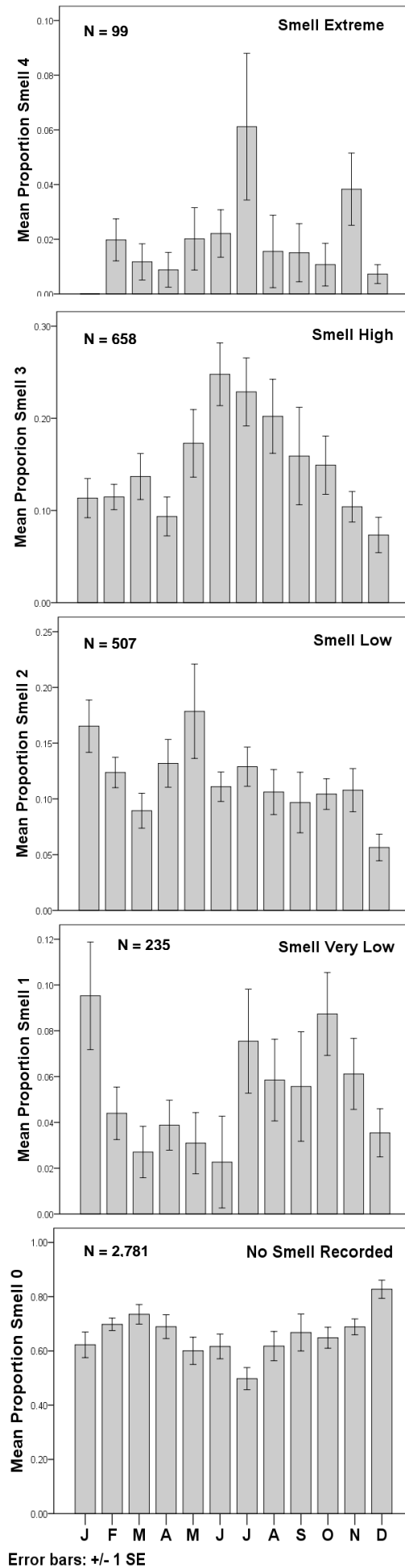
Total number of interactions per month in relation to silverback odour were analysed using Hierarchical ANOVAS, partial and bivariate correlations, and non-parametric Spearman correlation coefficients for non-normal data. Likewise, context dependent changes in the presence of extreme level silverback odour were analysed using the Hierarchical ANOVA (Chapter 2).

6.4 RESULTS

6.4.1 Overview

Of the 4,305 silverback odour data points, each smell rating was recorded in the following number of scans: (0) 2,781 scans; (1) 235 scans; (2) 507 scans; (3) 658 scans; (4) 99 scans; (unknown) 25 scans. The unknown smell rating scans were omitted from analysis. Figure 6.1 illustrates the changes in the relative proportions of smell levels by month during the recording period. The largest change took place in July, where the proportion of extreme smell level increased dramatically, while the proportion of high level smell remained very high, and the proportion of 'no smell' recordings were lowest. As described in Chapter 4, a total of 79 inter-unit interactions were documented throughout the study period and 44 of these interactions occurred on recording sessions (Chapter 4). More interactions were recorded in July (N = 19) than in any other month during the recording period. Additionally, high level interactions were absent in the first half of the study year, starting in July, and then continued at decreased rates until the end of the recording period.

Figure 6.1 Changes in the Relative Proportion of Smell Levels by Month (N = 4,280)



6.4.2 Factors Predicting Changes in the Presence of Extreme (Level 4), High (Level 3) and Low (Levels 1 & 2) Silverback Odour

6.4.2.1 Extreme Smells (Level 4)

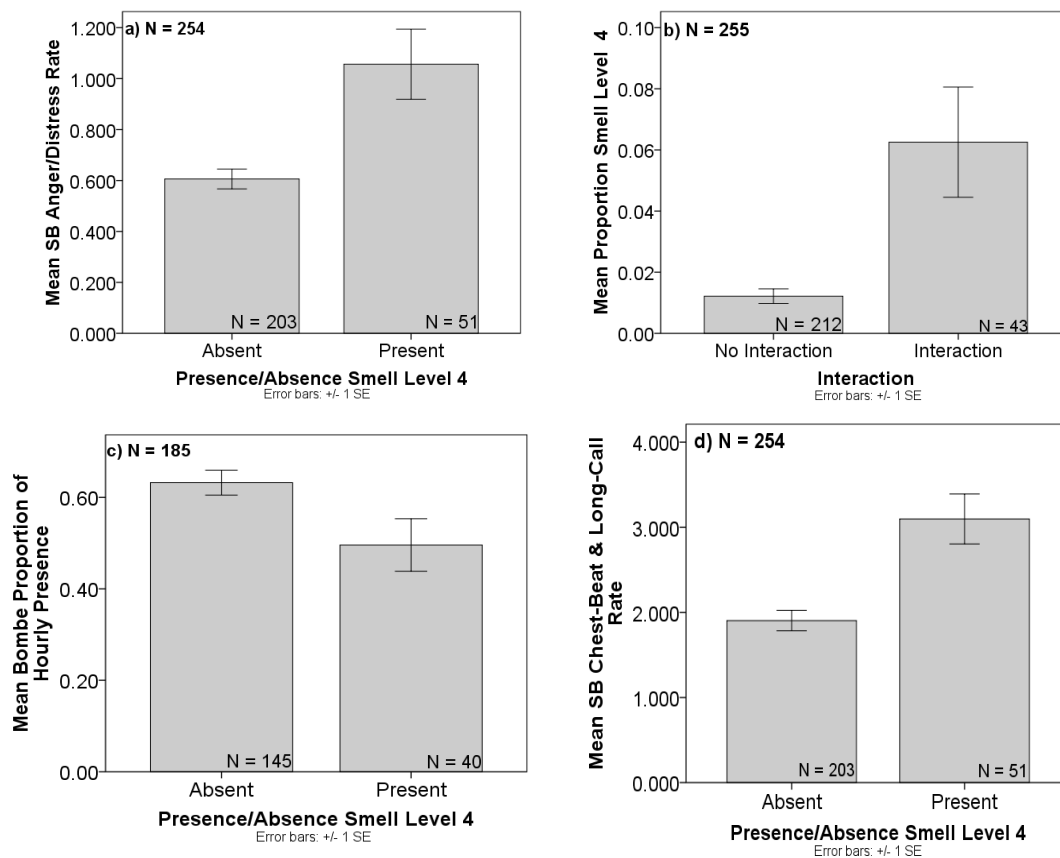
As Makumba's anger and distress rate ($R^2 = 0.11$), interaction presence ($R^2 = 0.06$), and Makumba's chest-beat and/or long-call rate increased ($R^2 = 0.034$), the presence of extreme level odour significantly increased. As the female Bombe's hourly presence close to Makumba increased, the presence of extreme level odour significantly decreased ($R^2 = 0.054$). Bombe exhibited more human directed aggression than any other gorilla in the group, including the silverback (Chapter 5). She was also the mother of Mobangui, the youngest infant in the group during the study period (Chapter 2). See Table 6.5 and Figure 6.2.

The increase in the presence of extreme smell levels when Bombe was absent may have been due to the silverback's concern over human-related factors (i.e. protecting her from accidentally encountering a human group). However Makumba's monitoring rate of observers and human directed aggression were not significantly correlated with proportional changes in Bombe's hourly presence (monitoring rate: $r_s = 0.086$, $p = 0.244$, $N = 188$, human-directed aggression: $r_s = 0.027$, $p = 0.715$, $N = 188$). Bombe's presence or absence per session (which encompasses almost all data points) confirms non-significant results (monitoring rate: $|r| = 0.069$, $p = 0.270$, $N = 254$; human directed aggression: $|r| = 0.109$, $p = 0.082$, $N = 257$).

Table 6.5 Logistic Regression of Factors Predicting Extreme (Level 4) Smell; Overall model $X^2 = 33.83$, $df = 4$, $r^2 = 0.258$, $p < 0.001$, $N = 185$

| Predictors | B | S.E. | Wald | df | Model R^2 at each step | Exp(B) | Sig |
|--|--------|-------|--------|----|--------------------------|--------|--------|
| Constant | -2.023 | 0.500 | 16.372 | 1 | - | 0.132 | <0.001 |
| Silverback(SB) anger and distress rate | 0.922 | 0.257 | 12.811 | 1 | .11 | 2.177 | 0.008 |
| Interaction presence | 1.327 | 0.457 | 8.434 | 1 | .17 | 3.770 | 0.004 |
| Bombe hourly presence by proportion | -1.489 | 0.607 | 6.014 | 1 | .224 | 0.226 | 0.014 |
| SB chest-beat and/or long- call rate | 0.778 | 0.108 | 4.606 | 1 | 0.258 | 1.260 | 0.032 |

Figure 6.2 Factors Predicting Extreme (Level 4) Smell in Order of Importance^a



^aSince interaction presence/absence and extreme smell presence/absence are both categorical variables I reversed Figure 6.2b for visual purposes only, so that the format of all four graphs could remain similar.

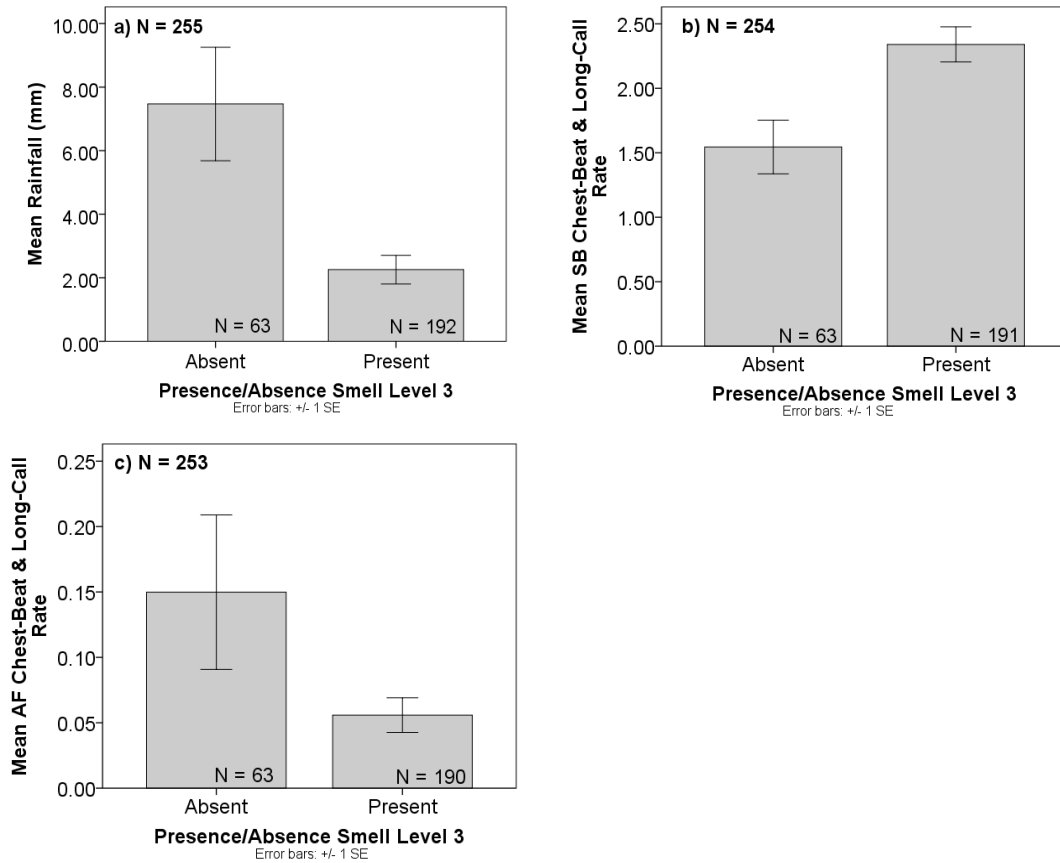
6.4.2.2 High Smells (Level 3)

As Makumba's chest-beat and/or long-call rate increased, the proportion of high level 3 odour significantly increased ($R^2 = 0.085$). As adult female chest-beat and/or long-call rates increased, the proportion of high level smell significantly decreased ($R^2 = 0.03$). As rain levels increased, the proportion of high level smell significantly decreased ($R^2 = 0.077$). See Table 6.6 and Figure 6.3.

Table 6.6 Logistic Regression of Factors Predicting High (Level 3) Smell; Overall Model $X^2 = 33.79$, $df = 3$, $R^2 = 0.192$, $p < 0.001$, $N = 250$

| Predictors | B | S.E. | Wald | df | Model R^2 at each step | Exp(B) | Sig |
|---|--------|-------|--------|----|--------------------------------|--------|---------|
| Constant | 0.714 | 0.237 | 9.061 | 1 | - | 2.043 | < 0.001 |
| Rain | -0.070 | 0.018 | 15.550 | 1 | 0.077 | 0.932 | < 0.001 |
| SB chest-beat and/or long-call rate | 0.418 | 0.114 | 13.585 | 1 | 0.162 | 1.519 | 0.027 |
| Adult female chest- beat and/or long- call rate | -1.269 | 0.572 | 4.922 | 1 | 0.192 | 0.281 | 0.003 |

Figure 6.3 Factors Predicting High (Level 3) Smell in Order of Importance



6.4.2.3. Low Smells (Levels 1 & 2)

As the forest became less dense ($R^2 = 0.068$), as wind presence increased ($R^2 = 0.077$) and as the female Mio's hourly presence close to Makumba increased ($R^2 = 0.063$), the presence of low level odours significantly decreased. However, as the corrected number of neighbours to Makumba (within 5m) score increased, low level odours significantly increased ($R^2 = 0.039$). See Table 6.7. In addition, Makumba's soft call rates significantly increased, as the presence of high numbers of 'no odour' scans increased ($B = 0.096$, $SE = 0.034$, $Wald = 7.792$, $Exp(B) = 1.100$, $df = 1$, $p < 0.001$, $R^2 = 0.064$, $N = 180$).

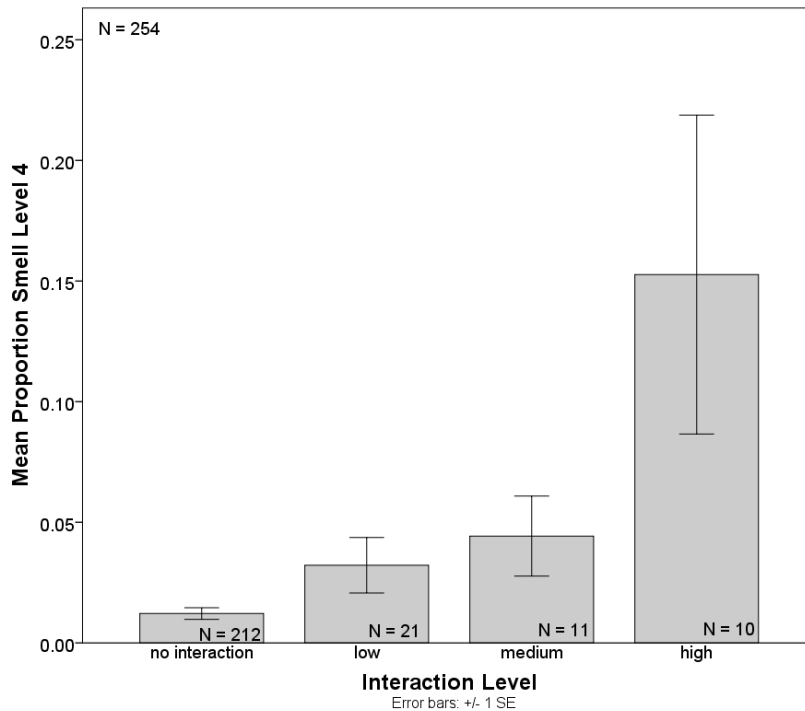
Table 6.7 Logistic Regression of Factors Predicting Low (Levels 1 & 2) Smell; Overall Model $X^2 = 26.96$, $df = 4$, $R^2 = 0.247$, $p < 0.001$, $N = 186$

| Predictors | B | S.E. | Wald | df | Model R ² at each step | Exp(B) | Sig |
|--|--------|-------|--------|----|---|---------|---------|
| Constant | 4.759 | 0.794 | 35.952 | 1 | - | 116.634 | < 0.001 |
| Corrected forest density score | -0.913 | 0.515 | 13.803 | 1 | 0.068 | 0.148 | 0.024 |
| Corrected # of neighbours (five m) to SB score | 1.939 | 0.857 | 5.116 | 1 | 0.107 | 6.951 | 0.013 |
| Wind presence | -1.381 | 0.554 | 6.217 | 1 | 0.184 | 0.251 | 0.021 |
| Mio hourly presence proportion | -1.093 | 0.474 | 5.307 | 1 | 0.247 | 0.335 | < 0.001 |

6.4.2.4 Interaction Level as a Predictor for the Presence of Extreme (Level 4) and High (Level 3) Silverback Odour

As interaction level increased from low, to medium, to high, the presence of extreme level odour significantly increased ($B = 0.778$, $SE = 0.778$, $Wald = 9.811$, $Exp(B) = 2.177$, $df = 1, 8$, $p = 0.002$, $R^2 = 0.061$, $N = 184$; Figure 6.4). While interaction level was a predictor of extreme odour, it was not a significant predictor of high odours.

Figure 6.4 Interaction Level as a Predictor for Extreme (Level 4) Smell



6.4.3 Time Lag in the Decrease of Extreme (Level 4) and High (Level 3) Silverback Odour after Interactions

The median number of observation sessions between interactions was seven (range 1-30 sessions), representing about 3.5 days. Post interaction sessions were grouped on the basis of sequential observation sessions for analysis: (1) 1-5, (2) 6-10, (3) 11-15, and (4) 16-30 sessions post interaction. The presence of extreme level odours was significantly likely to decrease over the maximum of 30 sessions post interaction (Table 6.8).³ The largest drop in the presence of extreme odours occurred 1-5 sessions (2.5 days) post interaction. The presence of extreme level smell dropped again at 6-10 sessions (3-5 days) post interaction, but remained at this baseline level for subsequent days (Figure 6.5). The presence of extreme level smell

³While original tests of intersmell intervals found that samples taken five minutes apart were statistically independent, the long time lag discussed here suggests that different behavioural or physiological factors were at play – as these were of specific interest in relation to the silverback’s long term levels of arousal, I have analysed these as a distinct phenomenon. Though time lags discussed here show long term influences on arousal levels, these should not be confused with short term five minute statistically independent ratings which do not demonstrate, nor are they meant to demonstrate, the overall behavioural phenomena at play.

decreased the most within the first 1-10 sessions (5 days) post interaction, while the presence of high level odour did not significantly decrease over the maximum of 30 sessions (15 days) post interaction (Table 6.9). These results suggest that there was an extended time lag before a decrease in high level odours, which lasted longer than 30 sessions (Figure 6.6).

Table 6.8 Logistic Regression of Duration to Decline in Extreme Smell; Overall Model $X^2 = 43.90$, $df = 7$, $R^2 = 0.094$, $p < 0.001$, $N = 254$ (only post interaction predictors by session are noted here)

| Predictor (categorical) | B | S.E. | Wald | df | Exp(B) | Sig |
|--|---------|-------|--------|----|--------|---------|
| Sessions 1-5 Post | -1.307 | 0.428 | 9.312 | 1 | 0.27 | 0.002 |
| Interaction | | | | | | |
| Sessions 6-10 Post | -2.097 | 0.578 | 13.146 | 1 | 0.123 | <0 .001 |
| Interaction | | | | | | |
| Sessions 11-15 Post | -2.194 | 0.738 | 8.827 | 1 | 0.112 | 0.003 |
| Interaction | | | | | | |
| Sessions 16+ (16-30) ^a Post | -0.1524 | 0.612 | 6.200 | 1 | 0.218 | 0.013 |
| Interaction | | | | | | |

^a16+ sessions were grouped to account for large variation in the data

Table 6.9 Logistic Regression of Duration to Decline in High Level Smells; Overall Model $X^2 = 35.18$, $df = 3$, $p < 0.001$, $df = 3$, $N = 253$ (sessions post interaction were excluded as a predictor in the final model)

| Predictor (categorical) | df | Sig |
|----------------------------|----|-------|
| Sessions 1-5 Post | 1 | 0.084 |
| Interaction | | |
| Sessions 6-10 Post | 1 | 0.545 |
| Interaction | | |
| Sessions 11-15 Post | 1 | 0.071 |
| Interaction | | |
| Sessions 16+ (16-30)* Post | 1 | 0.762 |
| Interaction | | |

Figure 6.5 Time Lag in Decline of Extreme Smell Post Interaction

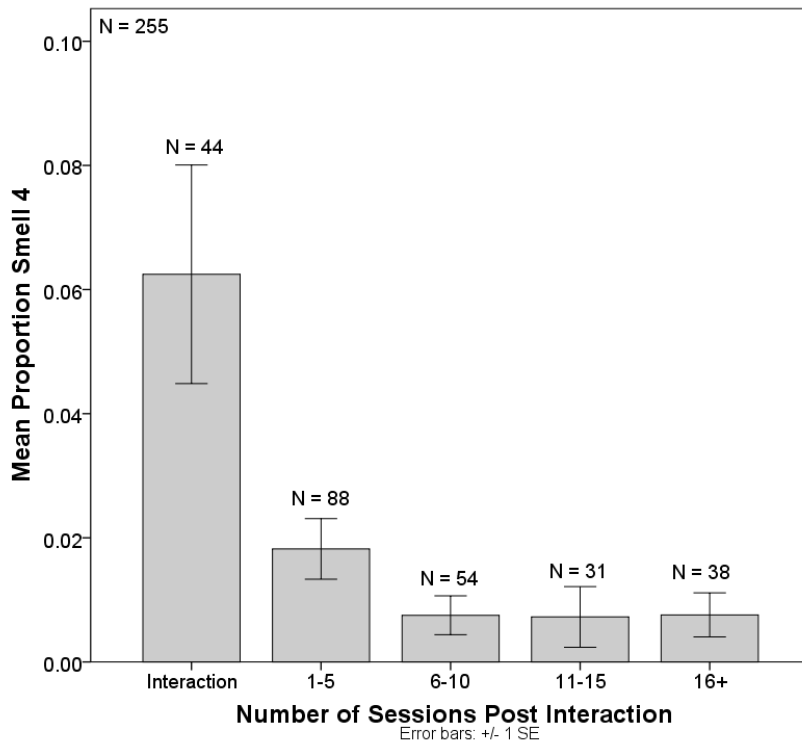
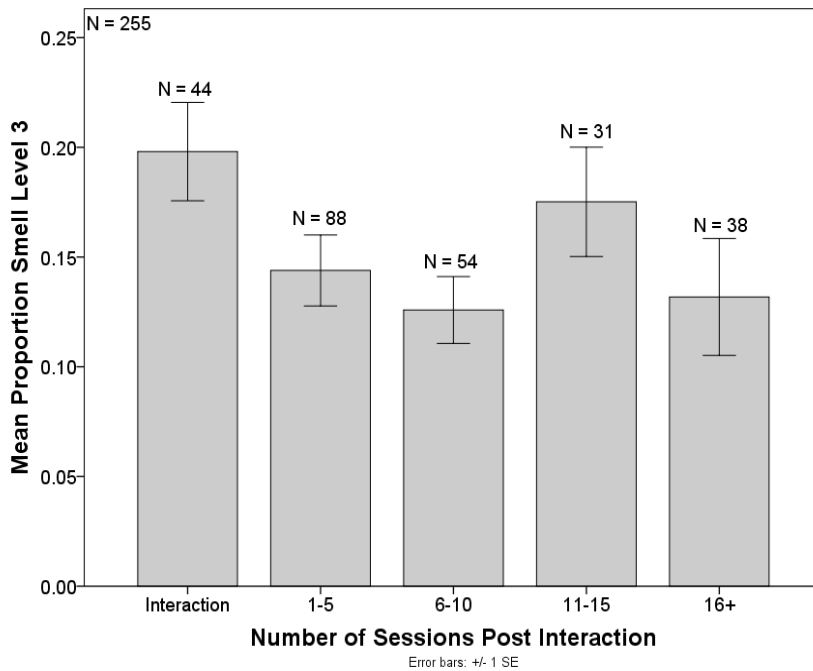


Figure 6.6 Time Lag in Decline of High Level Smell Post Interaction



6.4.4 Relationship between Total Number of Interactions per Month and Extreme (Level 4) and High (Level 3) Silverback Odour

Only 44 out of the total 79 interactions during the entire study year occurred during data recording sessions (Chapter 4). All previous logistic analyses focused solely on these 44 interactions. Figure 6.7 shows the relationship between extreme, high, and combined high and extreme (Levels 3 & 4) smell levels for all 79 interactions grouped by month.

6.4.4.1 Extreme Smell (Level 4) and Total Number of Interactions per Month

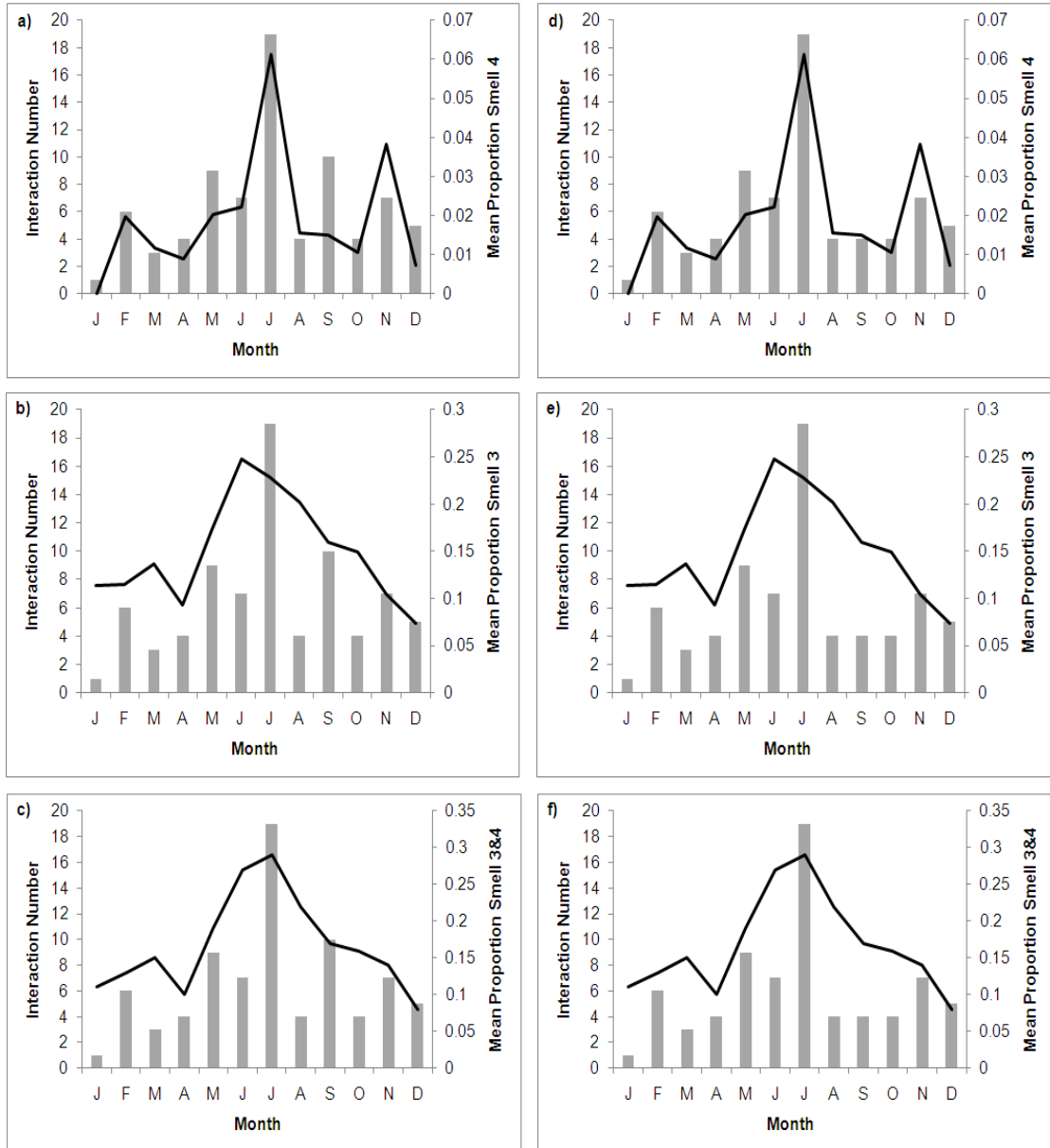
Extreme smell increased as the number of total monthly interactions increased ($r = 0.889$, $p = 0.001$, $N = 12$, controlling for silverback total auditory signals and daily rainfall; Figure 6.7a). The rationale for control choice was based on sample size constraints and results from Section 6.4.2. Total interactions per month now explained 79% of the monthly variance in extreme smells. The lack of an increase in extreme smells during September, a high interaction period, was most likely due to missing data points; during this month more interactions occurred on non-recording days ($N = 6$) than on recording days ($N = 4$). Excluding the six interactions that occurred on non-recording days in September, total interactions per month explained 88% of the monthly variance in extreme) smell ($r = 0.936$, $p = <0.001$, $N = 12$, controlled for silverback total auditory signalling and daily rainfall rates; Figure 6.7d and Figure 6.8).

6.4.4.2 High Smell (Level 3) and Total Number of Interactions per Month

Total monthly interaction rates were not significantly correlated with high level odours. However, Figure 6.7b shows that high level odours continued to increase until peak interaction during July and then gradually decreased to baseline levels. This gradual decrease continued throughout the rest of the year, even though interaction levels dropped considerably in months after the July peak (i.e. August, October, etc); and more so when the six September interactions that occurred on non-recording days were excluded (Figure 6.7e). These data may represent a 'buildup' of high level odours, followed by a lag period prior to their decrease.

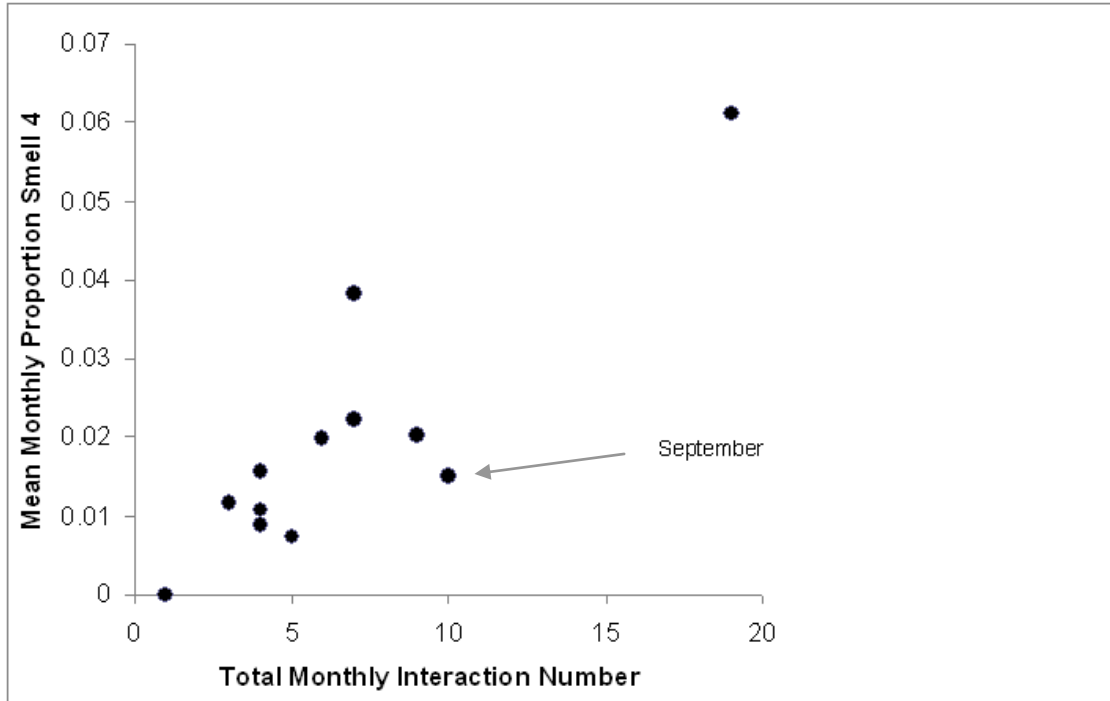
Figures 6.7e and 6.7f illustrate how combined extreme and high silverback smell (Level 3 & 4) changed in relation to the total number of interactions per month.

Figure 6.7 Total Monthly Interaction Rates in Relation to Smell Level^a



^aTotal Interaction Numbers = 79. In figures d), e) and f) six September interactions that occurred on non-recording days are excluded from the graph (N = 73) and N for extreme (level 4) smell = 99; N for high level (level 3) smell = 658; N for combined extreme and high level (level 3 & 4) smell = 757.

Figure 6.8 Scatterplot of Mean Monthly Extreme Smell by Total Monthly Interaction Rate



6.4.5 Context Dependent Changes in the Presence of Extreme (Level 4), High (Level 3) and Low (Levels 1 & 2) Silverback Odour

Eleven high level interactions occurred throughout the course of the study period (Chapter 4). During these interactions Makumba responded by staying (a) 'quiet,' where he exhibited a reduced level of loud auditory signalling (Chapter 4) and fled with the group or hid in dense thickets, or he responded by being; (b) 'loud,' where he would make his position known through 'loud visual and auditory threat displays that sometimes escalated into physical contact with the extragroup male (see Chapter 4 for details, definitions and justification of groupings). There were clear significant differences in the proportion of extreme level silverback odour when the high level interactions were separated into quiet (N = 4) and loud (N = 7) responses ($F = 27.35$, $df = 1, 7$, $p < 0.001$, $R^2 = 0.739$, $N = 10$, controlling for Makumba total auditory rates; one interaction was dropped from analysis due to missing data). Extreme level of silverback smell was not detected during any of the quiet responses (Figure 6.9). Figure 6.10 illustrates a similar (although insignificant) trend regarding high level smells, where proportionally fewer high level smells were recorded in the quiet versus the loud response categories ($F = 0.39$, $df = 1, 7$, $R^2 = -$

0.198, $p = 0.549$, $N = 10$, controlling for Makumba total auditory rates). Figure 6.11 indicates that significantly more low level smells were recorded in the quiet response category than the loud ($F = 6.91$, $df = 1, 7$, $p = 0.034$, $R^2 = 0.353$, $N = 10$, controlling for Makumba total auditory rates). However, when adding rain as a covariate to low level smells, the effect just failed to reach significance ($F = 5.15$, $df = 1, 7$, $p = 0.062$, $R^2 = 0.256$, $N = 10$).

Figure 6.9 Extreme Level Smells in Relation to Silverback Response to High Level Interaction Threats



Figure 6.10 High Level Smells in Relation to Silverback Response to High Level Interaction Threats

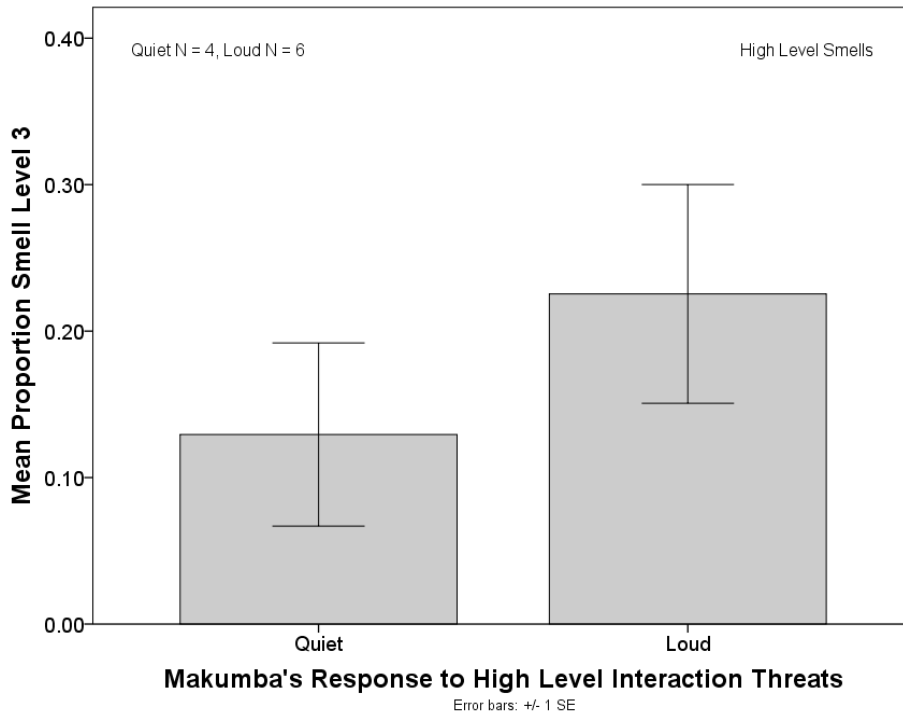
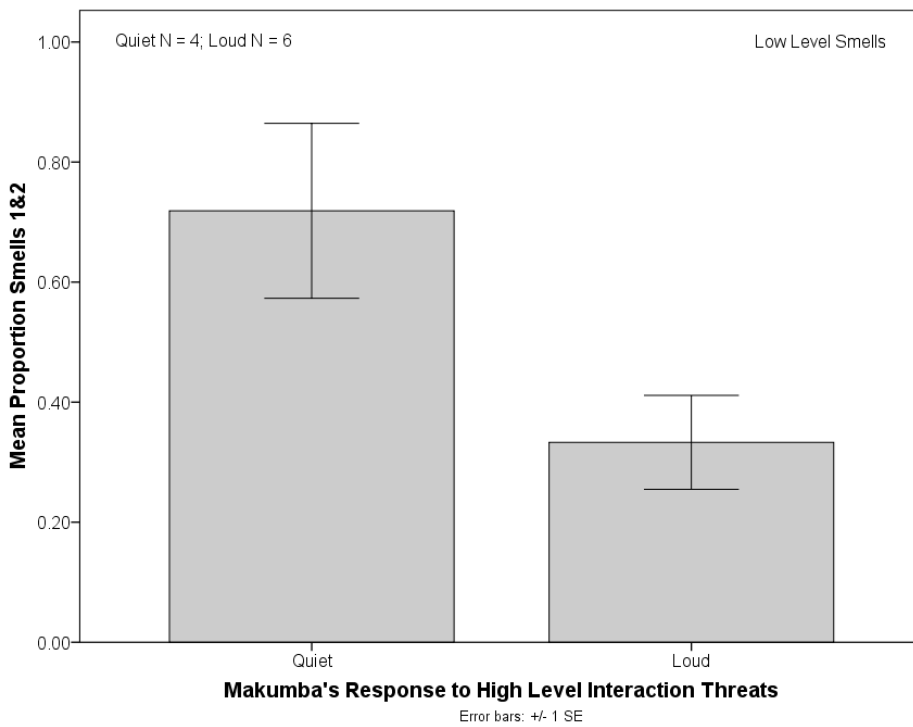


Figure 6.11 Low Level Smells in Relation to Silverback Response to High Level Interaction Threats



6.4.6 Changes in Silverback Odour Levels and their Effect on Group Activity Budgets

Mean proportional presence of low level and high level silverback odours did not significantly affect group activity budget (low; $F = 0.88$, $df = 5, 241$, $p = 0.496$, $R^2 = 0.017$, $N = 249$, high; $F = 0.74$, $df = 5, 241$, $p = .597$, $R^2 = 0.045$, $N = 249$), but mean proportional presence of extreme level smells did significantly affect group activity budget, although post-hoc analysis did not reveal directionality ($F = 2.34$, $df = 5, 241$, $p = 0.043$, $R^2 = 0.028$, $N = 249$). Analyses were controlled for rain and temperature. Group activities for this analysis were analysed as separate entities: feed, move, rest, mixed, social, and stand. In the rest of the thesis, I used group activity definitions as described in Chapter 2 (i.e. feed, move which included stand, and rest which included social). When this analysis was run on the larger groupings for activities (as in Chapter 2), all effects failed to reach significance. Regardless, figures from both grouped (Figure 6.12a, 6.12c, 6.12e) and ungrouped (Figures 6.12b, 6.12d, 6.12f) activity budgets show overall similar patterns. The greatest amount of variation in activities occurs in extreme smells (Figure 6.12a, 6.12b).

Figure 6.12 Activity Budget in Relation to Silverback Odour

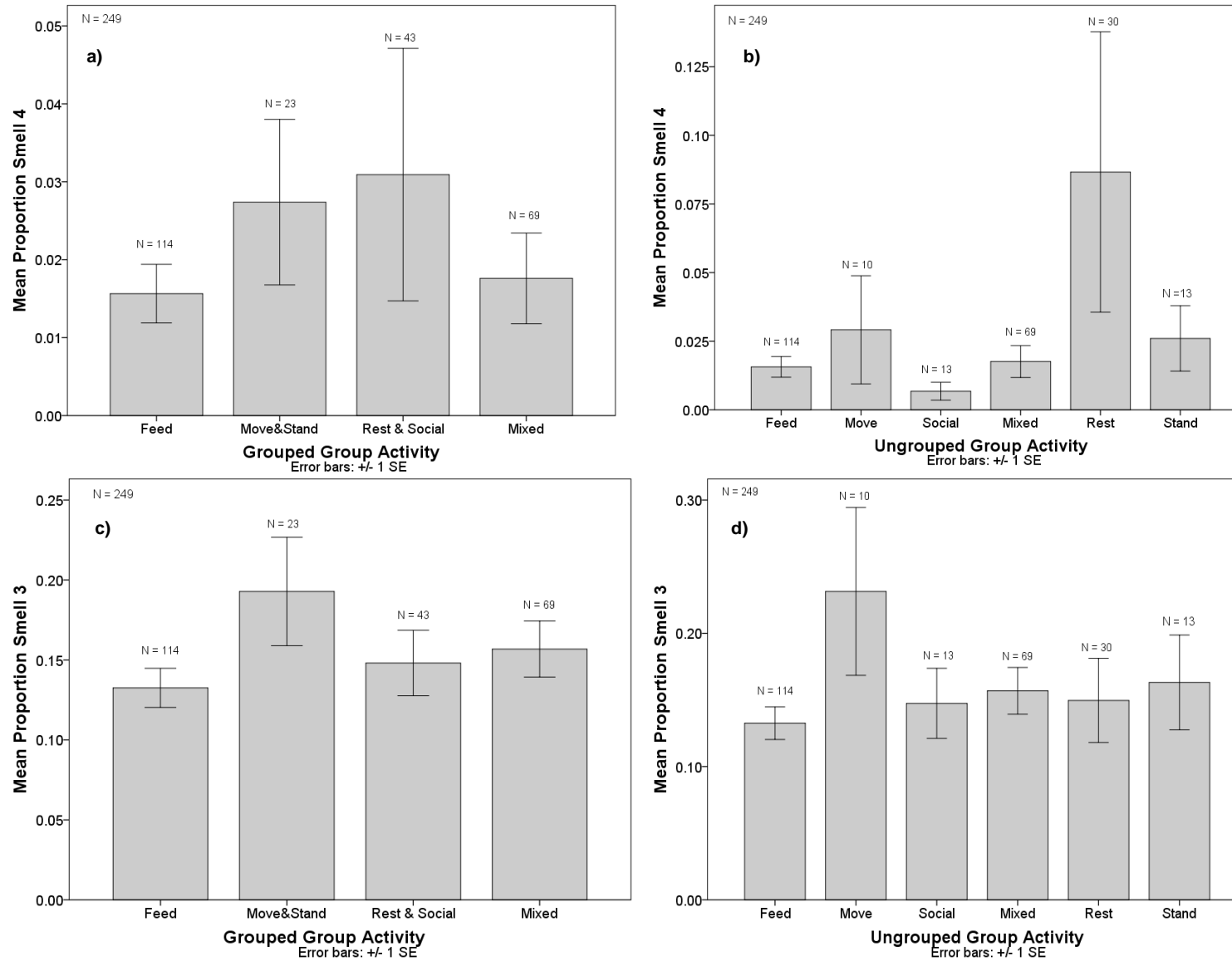
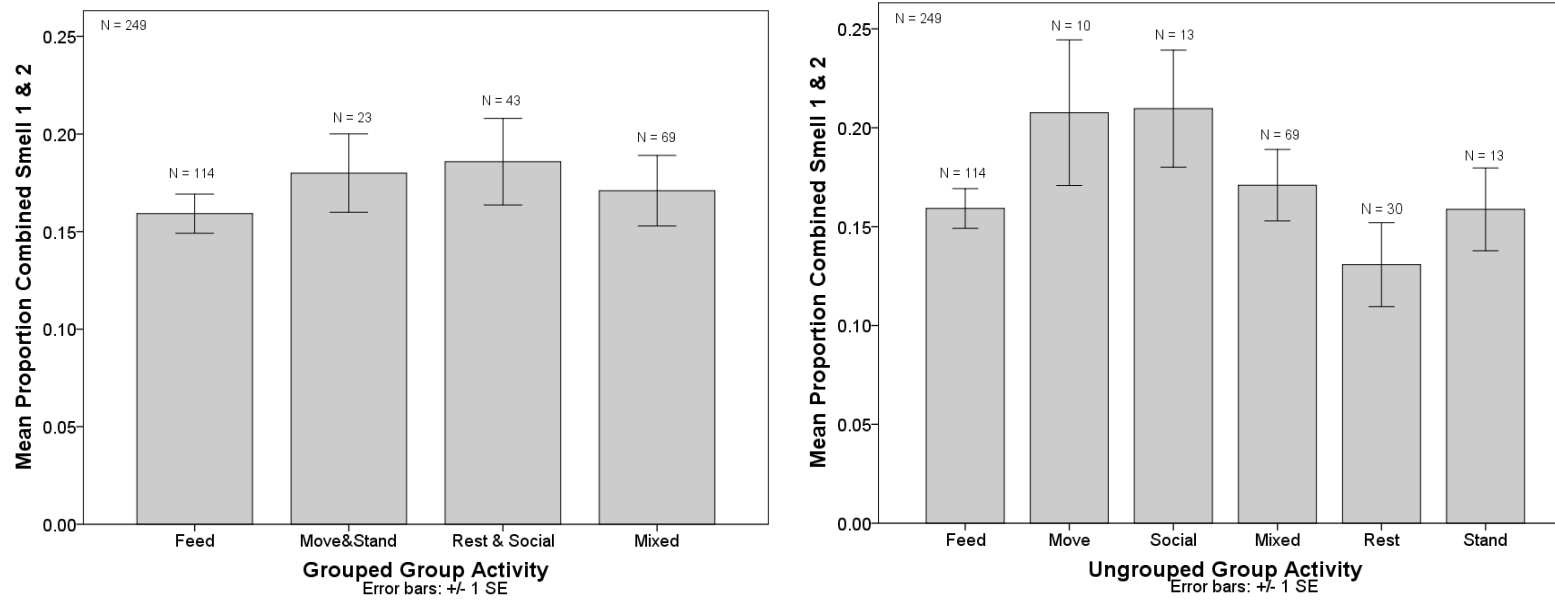


Figure 6.12 Activity Budget in Relation to Silverback Odour (Continued)



6.5 DISCUSSION

Olfactory communication appears to play a larger role in moderating western lowland gorilla sociality than has been previously thought. Results from 4,305 silverback scans collected over 258 observation sessions illustrate the complicated nature of silverback olfactory signalling.

Pheromone diffusion models demonstrate that a chemosignal can be thought of as having an 'active space' related to the quantity of chemical production, the threshold of the receiver, and the weight of the odorous molecules [Bossert & Wilson, 1963]. Intense odours, such as alarm signals, have a lower molecular mass and are therefore less persistent than other potentially less intense scent marks [Alberts, 1992].

The factors that predicted combined low level smells suggest that these less intense odours act as 'baseline' signals where detection (by the observer or another extragroup male) may be more strongly influenced by local or immediate conditions (i.e. wind, forest density, distance to silverback, etc). Low level smells may encompass a smaller active space than higher level odours, and may not be easily detected unless at very close range to the producer, although it is possible that gorilla detection thresholds may be better than human thresholds and that these less intense smells may persist in the environment for long periods of time

Only one external environmental factor – rain – that can quickly degrade odours [Alberts 1992], predicted a lack of high level smells. This suggests that detection of high level smell is less strongly influenced by environmental situations compared to low level odours. Instead, high level smells suggest higher stages of arousal as indicated by silverback and adult female chest-beating and long-calling. These auditory signals are used in longer distance intra and intergroup communication. Makumba may chest-beat and long-call to communicate with extragroup males or with other member of his group, in particular, females who may be foraging hundreds of meters away from him (western lowland group spread can be > 500 m, see Chapter 1). As auditory signalling rates noted above increase (and thus arousal levels), so do the proportions of high level smells. Both interactions with extragroup males and lack of knowledge regarding group member whereabouts can result in potentially risky situations; females transfer to other

males through choice and as a result, solitary males may try to build trust by approaching females more when they are at a distance from their silverback (Chapter 4). These risky contexts may explain why an increase in adult female chest-beating/long-calling also predicted a decrease in Makumba's high level odour; he is being informed of his females' whereabouts and can better assess the level of risk in the situation.

All external factors were excluded as predictors from the extreme level smell model. The exclusion of environmental variables such as wind, temperature or forest density suggests that extreme level smells were intense, and as a result, detection, or lack thereof due to local conditions was no longer an issue. These odours were predicted by interaction numbers, silverback chest-beating/long-calling rates, as well as silverback anger and distress signals, representing very high arousal social situations. If loud auditory signals used in long distance communication predict high level smells as arousal level increases, then quiet auditory signals used in close intragroup communication may predict low level or a complete lack of smell due to calm or very low arousal situations. Unsurprisingly, an increased presence of 'no odour' scans was associated with high rates of Makumba's soft calling (i.e. belching). Makumba's increase in extreme level smell during Bombe's absence (mother to the group's youngest infant) was not related to Bombe's strong dislike of people (Chapter 4), but instead, due to factors that reflect the social structure and dynamics of the group such as the potential risk of infanticide. As stated in Chapter 4, infanticide, while highly suspected, has yet to be directly observed in western lowland gorillas [Stokes et al., 2003]. The above result suggests that infanticidal risks in western lowland gorillas are real and contribute to silverback heightened arousal in potentially risky situations.

The strong positive relationship between total monthly interaction rates and extreme smell levels (explaining over 75% of the variance in presence of extreme smells) suggests that interactions are risky and involve high silverback arousal. It was interesting that the presence of extreme odours in May, although still high, lacked the characteristic peak present during other high interaction months (excluding September; Section 6.4.4). This is likely due to the almost total lack of high level interactions during the first half of the study year, resulting in fewer olfactory reactions to risks or challenges from other males. However, in November extreme

level odour peaked even though only six low/medium level interactions occurred. By November, the silverback had been involved in four continuous months of numerous high level interactions, thus it is possible that he had simply become hyper-responsive to all interactions by this point. It must be restated that interactions, while very important, were not the sole predictor of fluctuations in the presence of extreme level smells; other defence and cohesion behaviours were also significant predictors of this level of silverback odour.

While interunit interactions and the risks associated with these, played a major role in extreme level smell production, neither number, rate, nor the intensity of interunit interactions predicted high level smells. This lack of an association was surprising considering that high level smells can also represent high arousal situations (albeit not extreme). However, underlying this apparent lack of a relationship was more complicated, interlinked likely explanation whereby the slow build up of arousal over a long time period was associated with the cycles of decrease and increase of high level smell relative to interactions. This association suggests that interaction rates did in fact play an important role in high level as well as extreme smells.

Extreme level smells appeared to act as 'acute' indicators of arousal, which increased or decreased in response to immediate circumstances, whereas high level smells may have acted as a general chronic indicator of some overall high level arousal, which were not driven by immediate changes in the social environment. Extreme level smells dropped very quickly to baseline levels on non-interaction days, whereas high level smells did not significantly decrease over the maximum non-interaction period of 30 sessions. While high level smell continued to increase in June, a surprisingly sharp drop off occurred just before the peak interaction period of July. At this point, high level odours were substituted by acute extreme level smells, which replaced the lesser smells into July. High level smells started to decrease after July, as interaction numbers after this month dropped substantially.

Finally, and perhaps most interestingly, extreme level smell responses to high level threats confirmed the flexible and strategic nature of silverback chemosignalling. The highest interaction level predicted the greatest proportion of extreme odours from Makumba. But, when his responses during these high level interactions were categorised as quiet (silence) or loud, extreme level smells were only present in the loud response category even though all high level

interactions represented high risk situations. If smells were simply a by-product of arousal, then extreme level smells would be expected in both quiet and loud situations. The 'silence' associated with the quiet response extends to smell production as well, suggesting that silverback odour production is a signalling mechanism to other individuals both close and distant. The lack of extreme level smells in the quiet response may partially be due to the minimized (or absent) usage of auditory signals, which also predicted extreme level smells. However, Makumba's auditory signalling rate was entered as a covariate in this analysis and thus its effect was controlled for; and the lack of smell was still significantly associated with a quiet response to high level threats. These results illustrate the interlaced nature of olfactory, auditory and visual communication mechanisms.

As detailed in Chapter 4, competition between extragroup males can be fierce, especially when involving the acquisition and defence of females. The study's data collection period represented an extraordinary year for the Makumba group, as the group faced an average of close to seven interactions per month (Chapter 4), more than in any other published study based on one focal group only. This high number may have been due to the high potential gains of pursuit by extragroup males and as a result, the high potential cost of interaction withdrawal by Makumba. As a result, many interactions during the study very likely represented higher risk situations and thus played a large role in predicting extreme level smells.

Hepper et al. [2010] showed that individual gorillas produce unique odours, identifiable to humans and by extension, identifiable to gorillas. Darwin [1874, pg 809] states that the "development of elaborate odour glands in male mammals is intelligible through sexual selection if the most odoriferous males are the most successful in winning the females, and in leaving offspring to inherit their gradually perfected glands and odours." Makumba's extreme and high level odour production may have been used as a chemosignal [Eisenberg & Kleiman, 1972] in conjunction with other physical and auditory signals. While the mechanisms by which he is signalling (release into the air) may be different from that of scent marking, the information transmitted in the signal could be analogous to ring-tailed lemur 'stink fights' (Section 6.2.3.4) or to mandrills whose odour profile potency and production signals identity, age and dominance rank of adult males; high ranking males are more likely to produce increased secretions as a

function of higher testosterone levels [Setchell et al., 2010a; Setchell et al., 2010b]. Setchell et al. [2010b] suggest that such adaptations may be particularly relevant in Central African rain forests - the home of both the mandrill and the western lowland gorilla - where visibility is often limited.

As noted in the introduction, dominant males scent mark more than their subordinate counterparts, and females of many species prefer the scent of dominant males although uncertainty remains over whether males scent mark directly to attract females or whether females eavesdrop on male-male chemocommunication [Gosling & Roberts, 2001]. Since the interunit interactions observed in this study appeared to be related to acquisition or defence of females, it is likely that both rivals were not only chemodisplaying (in addition to auditory and visual displaying) as an act of intimidation towards one another, but also as an advertisement of health, strength, dominance and protective skills towards females. If dominance favours more intense odours as Darwin suggests, then greater levels of arousal and thus stronger odour production would be advantageous in riskier situations where advertisement of dominance is key. In addition, health can be signalled through individual odour as only individuals with strong immunocompetence can afford to produce the high testosterone levels needed to produce high androstene levels, which when acted upon by bacteria, are the compounds involved in producing the characteristic musky odour in mammal chemo communication. Females and competing males can determine the 'status' of their potential counterpart through their individual scent, which takes advantage of the honest signal theory (Section 6.2).

Could observers have confused silverback smells during the high level interactions, since the active chemical detection space could at times be very large (>100 m)? Makumba's scent was unique and individually recognizable, even to the human nose. In those rare situations where odour identities may have been confused, the extreme smells would have been emanating from both silverback gorillas with similar probabilities of detection. Since we were primarily considering the 'strength' of the odour, data collection should not have been biased if we unintentionally confused unknown silverback identities and both individuals were emitting powerful smells.

One of the main benefits of chemosignalling is that the signal can remain in active space long after the signaller has left. In gorillas, chemosignalling appears to be communicated mainly by release into the surrounding air. Environmental disturbance may also signal to receivers by releasing odours from the site of the disturbance (i.e. sap flow from broken branches) [Eisenberg & Lochart, 1972: Section 6.2.3.1]. Gorillas often break branches, ground slap, tree slap and trample vegetation as a means of potential resource defence and intimidation [Fossey, 1974]. In doing so, their presence is made more conspicuous by visual, auditory and olfactory mechanisms. These signals could be used to obtain information about rivals or potential mates, allowing for a more accurate assessment of the costs and benefits of withdrawing or pursuing their competition (Section 6.2.3.1).

Western lowland gorilla populations tend to have many 'floaters' or solitary males ranging across territories, whose primary goal is to acquire females. The "dear enemy" hypothesis, suggests that these floaters will be tolerated less than those neighbours who respect each other's boundaries (Section 6.2.3.1). For Makumba, floater males appeared to be involved in all high level and thus the most costly interactions (Chapter 4) suggesting some validity to the dear enemy phenomenon. Yet it is also likely that interaction levels will be based on the potential gains or losses of each interaction and the importance of the resource being defended, rather than simply the identity of the competitor (Section 6.2.3.1; see also Chapter 4). In this situation, floater males appeared to be the riskiest competitors.

Fossey [1983] suggested that pungent extreme odours released by the silverback during high arousal situations are similar to the 'fear' odour of many other species (Section 6.2.6.3). If this were the case, we would expect to see this odour of fear produced in every high level interaction. However, extreme level smells were not recorded during the high level interactions where Makumba's response tactic was one of silent flight, although arousal and fear levels must have been very high in all contexts. The existence of these two divergent tactics are compelling evidence that alarm signalling is not the adaptive function of extreme level smells. Silverback extreme smells appear not to be as much a function of fear, but rather a form of chemical communication that acts as a signal of intimidation, advertisement of location

presence (for kin who are not in the immediate vicinity as well as for extragroup individuals) and virility.

However, the functions of gorilla olfactory communication are not mutually exclusive. It is also possible that silverback scent is not only produced as a threat but also as a reassurance (and confidence builder) to the signaller and his kin (Section 6.2.3.2). Indeed, none of the interactions during the year resulted in the death or successful emigration of any non-kin adult females (Chapter 4). Perhaps Makumba's low level smells function more to reassure and remind group members of his virility, dominance, paternity and health, rather than to communicate with extragroup silverbacks. This communication context of reassurance may explain why Makumba exhibited more low level smells as numbers of neighbours within five meters of him increased, and why he exhibited more low level smells in the 'quiet' response versus the loud response. That environmental factors affected low level smells more than other odours may be irrelevant as these low level smells were used in close contact intragroup signalling and thus attenuation over distance due to wind or forest density was irrelevant. In fact environmental factors which mask detection of low level smells could be beneficial, since it will then be more difficult for other silverbacks to 'eavesdrop' on these signals.

Mio's role as a predictor of low level smells was unexpected. As one of the eldest natal adolescent females close to emigration, her absence might have caused elevated levels of arousal in Makumba since extragroup males would be more likely to approach her when he was not nearby. Even though Mio's eventual emigration is to be expected, extragroup male approaches can lead to fierce contact interactions especially when other higher risk females are involved (Chapter 4). However, Etefi, who was of emigration age and was implicated in July's high interaction period, did not have a similar effect on Makumba's low level smells. Thus, it seems likely that there were other specific although unknown circumstances which affected Makumba's arousal level (albeit low) in regards to Mio's absences (i.e. personality type, health issues, a potential tendency to be more distant from the silverback than individuals, etc).

High level smells may also function as a cue to increase vigilance in risky situations. Perhaps - as has been shown in glowlight tetras (Section 6.2.4.3) - high level smell functions as a sub threshold indicator of maximum arousal, which acts as a signal for individuals to maintain

vigilance to silverback visual and auditory cues, while continuing to perform their regular daily activities. Time spent on each activity were not significantly different from each other in the low and high level smell categories, but were significantly different in the extreme level smell category. Chronic high level smells may be used, at least in part, as a vigilance cue so individuals can continue to perform daily activities in riskier situations. In extreme risk situations, the cost of continuing daily activities in a 'normal' fashion is clearly greater than the benefits, resulting in behavioural shifts focused on short term responses rather than long term survival.

The study of western lowland gorilla chemosignalling can have important applications for captive enclosures, where silverback odour intensity could be used as an indicator of his arousal level and thus his, as well as the group's, emotional state. This measurement of anxiety through odour intensity would provide keepers and zoo management with another tool to detect and thus attempt to reduce situations of negative arousal.

I have presented here the first study to explore chemosignalling in non-human great apes. I offer compelling evidence of the highly flexible usage of chemosignals in western lowland gorillas, which points to the important role that great ape olfactory communication plays in moderating social behaviours. Past research has focused on the supposed primacy of vision and audition in great ape communication. Instead, we suggest that olfaction, vision and audition are delicately interwoven into a complex, non-mutually exclusive and extremely elastic communicative framework. This study not only reveals the potential flaws involved in judging the significance of smell solely by relative olfactory brain size and the number of olfaction receptor genes, but also suggests that olfaction in humans has evolved through adaptations present in other great ape species.



CHAPTER 7

SUMMARY & CONCLUSIONS



CHAPTER 7

SUMMARY & CONCLUSIONS

“On the other side of a small clearing a female is playing with a small baby. Everything seemed perfect for a good shot. The gorilla wasn’t fifty yards away and was unconscious of our presence. But I couldn’t help thinking of the other gorillas that we could hear, and couldn’t see...But there was nothing for it, I had to shoot. I took plenty of time and when I stopped shaking, I made a clean hit through the skull, killing her instantly. The male rushed up. I fired and hit him in the shoulder. He staggered for a second, but kept going. I fired again, and again he staggered...” [Westley, 1951 in Schaller, 1963, p 321]

“I sit on a steep slope while the animals feed 90 feet distant. A female spots me and slaps her chest; a juvenile too looks up and beats its chest. The silverbacked male, who feeds about 150 feet away, suddenly moves toward the female. When he sees me, he roars about 5 times, and the whole group crowds around him. He continues to roar and beat his chest intermittently for about 10 minutes, but the other gorillas show little excitement – none vocalize and only a few beat their chests. Abruptly the male turns and descends into a narrow ravine and out of my sight. All members of the group follow him...” [Schaller, 1963, p 309]

“It was a regular afternoon and all seemed fairly relaxed whilst the adult females rested and the juveniles played in the same area for several hours. Then in the distance an odd rasping sound was heard. Upon hearing this, Makumba looked in the direction of the noise, sat up immediately, strutted to the centre of his group and stood there for several seconds while the group gathered closer to him. Taking the lead position, he then quickly moved out of the area with all other individuals following single file behind. Later upon looking for the source of the noise, we found leopard scat and prints not far from where the group was resting earlier.” [Van der Wyde, pers. comm.]

7.1 Data Collection

I have critically evaluated the western lowland silverback's role as the protective leader of his group. I followed one habituated group in the forests of the Bai Hokou Primate Habituation Camp, Central African Republic, comprised of one silverback (Makumba), three adult females (two with dependent offspring and one pregnant female), and seven immatures of varying age and sex. Researchers (two in this study) accompanied gorilla trackers during morning (7 am–12 pm) and/or afternoon (12–6 pm) sessions. Tourists – 391 over 158 visits in 2007 - joined the main team in either the morning or the afternoon session and stayed for a maximum of 60 minutes of visibility (equivalent to one visit).

Data collection focused on the silverback, and those individuals in his immediate proximity. Instantaneous scans [Altmann, 1974] were taken on the silverback at a minimum of every 10 minutes. Silverback behaviour, spatial location, neighbour (within 5m) behaviour and identification, group spread, progressions, silverback odour, and human directed aggression were the focus of scan data collection.

Continuous written records of all auditory signals were also made for Makumba and gorillas in his presence (within human earshot). On observation mornings, a written record of nest spatial patterns was also collected. Detailed *ad libitum* notes on all interunit interactions were made and compiled along with Bai Hokou 2007 camp data (Chapter 2). Analyses were conducted on 3,252 silverback scans (plus 1,053 smell scans) over 258 sessions, 22,343 auditory signals and 166 nests.

7.2 Thesis Aims

The socioecological model predicts that animal social groupings vary based on a complex network of predation, ecological factors, competition, habitat saturation and infanticide avoidance (Chapter 3). Since the dominant adult male gorilla assumes the control function, providing protection and leadership, he is the crucial element moderating and managing the way groups respond in situations of high perceived risk or disturbance (Chapter 3). While a

major benefit of female-male associations is protection from infanticidal males, a silverback is also responsible for providing overall group stability and protection from predation (i.e. humans, leopards) or other environmental risks (i.e. elephants or getting lost/left behind) (Chapter 3). A silverback's reproductive success will be a function of his group's survival, of his females' reproductive rates and the survival of his progeny.

Due to difficulties of habituation and observation, no previous western lowland gorilla study has been able to document and quantify the mechanisms by which western lowland males interact with and protect their group in forested environments, where they spend 99% of their time [Parnell, 2002b]. Studies that have taken place in bai environments have naturally focused on demography, comparative intergroup interactions and only overall general behaviour [Brueur, 2008; Nowell, 2005; Parnell, 2002b]. But Nowell [2005] in particular, provided the first real insight into immature development and silverback-group behaviour in western lowland gorillas. She found that the silverback played a minimal interactive role in western lowland groups when in bais. However both Nowell [2005] and Parnell [2002b] emphasized that gorillas not only spend just 1% of their time in bais, but that most of this time is spent feeding, not socializing. It is essential to quantify relationship dynamics from a holistic perspective in order to obtain a more complete picture.

Brueur [2008] and Caillaud et al., [2008] studied male reproductive success from a phenotypic perspective rather than a behavioural one, and their results will be discussed in relation to gorilla olfaction (Section 7.6). In the absence of long term research on habituated western lowland groups, the study of one habituated western lowland male's role represents the first attempt to quantify the mechanisms by which western lowland silverbacks interacted with their group throughout their environment. As the mechanisms by which he protects his group in situations of perceived risk or disturbance are crucial to (1) his safety, (2) his group's safety, and (3) his ultimate tenure as group leader and hence his reproductive success, I focused on intergroup, environmental, and interspecific risks or disturbances.

7.3 Silverback-Group Spatial Relationships (Chapter 3)

While Makumba spent half of his overall time without 'neighbours within 5m' (hereafter 'neighbours'), results strongly suggest that he still played a commanding and strong protective role within his group:

(1) The silverback was significantly more likely to have a neighbour than no neighbour in potentially riskier bai environments.

(2) In forests, young immatures were the most likely neighbour (NN1-NN4) to the silverback. While young immatures were again the age class most likely to be the closest neighbour to the silverback in bays, this effect disappeared for those neighbours (within 5m) furthest from the silverback, potentially due to (a) an increase in competition for the 'further' neighbour positions, causing a tug of war situation resulting in equalisation across age-sex classes, and; (b) a potential preference in infants to remain closer to their mothers when they were not able to be the 'closest' neighbour to the silverback.

(3) The age-sex class preferences for being a neighbour to the silverback in both forest and bai environments followed the patterns discussed in Stewart [2001], Harcourt [1979a, 1979b], and Watts & Pussey [1993], among others: (a) the older the infant was, the more likely he/she was to be a neighbour to the silverback; (b) the more juvenile the young immature (i.e. the 'younger' young immature) was, the more likely he/she was to be a neighbour to the silverback, and; (c) adolescent females were more likely to be a neighbour to the silverback than were adolescent males. Infants were seen alone as neighbours of the silverback in forest environments in all but one scan; perhaps they were more likely to be near or in contact with their mother in riskier bai environments.

(4) Similar to mountain gorilla silverbacks (Chapter 3), Makumba appeared to babysit young immatures and infants, but in small groups only; this protective role may be particularly important for western lowland gorilla mothers who often forage hundreds of meters away from their leader male (Chapter 1).

(5) Each female spent approximately the same proportion of time as a neighbour to Makumba, however, females at high risk (i.e. pregnant, etc) increased their time as a neighbour to the silverback or spent more time in the vicinity¹ of the silverback, relative to their level of risk. Makumba was significantly likely to have only one adult female neighbour at any given time. This sharing of access may minimize potential conflicts of interest amongst adult females and maximize silverback reproductive success by allowing him to retain as many adult females as possible (Chapter 3). Although speculative in the absence of proximity matrices and measures of responsibility for proximity, the fact that adult females shared 'sole' access to Makumba suggests that like Harcourt's [1979b] and Yamagiwa's [1983] study on mountain and eastern lowland gorillas respectively, adult females may have been more attracted to the silverback than to each other.

(6) A silverback's location in the middle of his neighbour unit may reflect a protective spatial response in situations of higher perceived risk or at times where individuals are competing for access to the dominant adult male. Additionally although insignificant, a strong trend indicated that Makumba was more likely to be on the periphery of his neighbour group as the number of human observers increased. Habituation was controlled for in the analysis, thus it is possible he was acting as a barricade between larger numbers of human observers and other gorillas.

(7) As the group became more dispersed, which occurred in the late morning and early afternoon when the group was most likely to engage in mixed behaviours (and therefore difficult to keep track of), Makumba was more likely to be at the back of the entire group, perhaps ensuring that all individuals kept up and passed by safely (Chapter 3). During periods of higher perceived risk (i.e. high level interunit interactions, rainfall, etc) and as the number of neighbours to the silverback increased, Makumba was more likely to be nearer the front of the group (a potential leading position).

On the basis of evidence presented here, I suggest that western lowland silverbacks in single male groups are responsible for, or at least play a strong role in determining the initial feeding

¹Outside of the 5m neighbour demarcation, but still in the vicinity of the silverback (see Chapter 2 for roll call definition)

direction of their groups. While adult females forage, the silverback may wait in the rear (a potential protective position) until they return to him, or until he moves to them. Once the group has reconvened, he may then determine the group's next movement. During periods of higher perceived risk, he may take a more forward position and move his group out of danger.

(8) Makumba was significantly more likely to nest closest to the largest trail, suggesting that he placed himself in areas where he could monitor trail usage and alert group members to danger or disturbance. Makumba may be selecting areas with better visibility so he is able to watch over his group, whilst other group members prefer the safety and comfort of denser patches for nesting.

Unlike Nowell's [2005] and Parnell's [2002b] findings from bais, analyses here reveal many behavioural similarities with mountain and eastern lowland gorillas. Most importantly, my results stress the protective nature of the silverback-group relationship and reveal the often subtle mechanisms by which an adult male uses proximity and spatial position to protect and interact with his group.

7.4 Silverback-Group Dynamics During Interunit Encounters (Chapter 4)

Little is known about silverback social and protective roles and silverback-group dynamics during interunit interactions in western lowland gorillas. Since the Makumba group experienced more interunit interactions in 2007 (N = 79) than in any other published work, this study provided a unique opportunity to quantify the mechanisms by which Makumba protected and stabilized his group during very high risk periods. As the group contained one natal recently matured female potentially ready for dispersal, the Makumba group may have been an attractive option for extraunit males. Makumba's unit also faced considerable risk of infanticide as his group contained two non-natal adult females with dependent lactating offspring, one pregnant female, and three other young immatures. While infanticide has not yet been observed in western lowland gorillas, it is strongly suspected to occur [Stokes et al., 2003]. Infants in single male units may face higher probabilities of infanticide than those in multi male units (Chapter 4). A total of 21 (27%) high level, 27 (34%) medium level and 31 (39%) low level interunit interactions occurred during the study. High level interactions only started in the peak

interaction month of July, and then continued at decreased rates for the final five months of the study. Western lowland gorilla silverbacks appear to exhibit an intricate and strategic framework of response and attack during interunit interactions; extragroup males should seek out encounters that may attract females to their unit, whereas males with fertile females may seek to avoid or drive away extragroup units, thereby decreasing the risk of female emigration.

Results from this study indicated:

(1) Makumba's tolerance levels were more similar to those seen in mountain gorillas than at other western lowland gorilla sites (i.e. during feeding in bais) [Nowell, 2005; Parnell, 2002b]. The lack of tolerance exhibited by Makumba may reflect the possibility that most interactions appeared to involve encounters with lone males.

(2) It is likely that the mast *Gilbertiodendron dewevrei* and *Celtis adolfi frederici* fruiting events in 2007, which began in July, brought a higher than average number of gorillas into and surrounding Makumba's home range (Chapter 4). These fruiting events in combination with the high risk of losses (infants and/or females) for Makumba and the high potential gains for extragroup males may have been the catalyst of high level interactions.

(3) During interactions in July, the recently matured female Etefi, transferred out of, and then eight days later, back into the Makumba group. In this period, Makumba patrolled the group's core area, continuously reused the same resource patches - specifically one *Celtis* tree - and the group nested at overlapping sites more often during this period than any other time of the year. Four of the high level interactions that occurred during this period (two of which coincided with Etefi leaving and returning to the Makumba group) took place within 250 - 500m of this tree. Fossey's [1974] description of lone male defence responses during interunit interactions seem very similar to Makumba's reactions during July's interaction events, however, resource defence does not appear to be the only factor in the Makumba group's movement patterns or in the repeated visitations to the noted *Celtis* tree. After the first interaction when Etefi emigrated, Makumba circled his core range, went directly back to the interaction area and had another high level interaction. He and his group stayed in that area even though they faced exposure to further high level interactions and his group's safety was at risk. It is possible, given that

western lowland females may have some power in group directional control (Chapter 3), that Makumba was forced to return to this area to protect his group due to the action of one or several of his adult females. When Etefi returned to Makumba, the group dramatically shifted their core and home range area for the remainder of the year.

(4) Makumba's preference to nest in open environments during high level interactions (although sample size was small), may represent the need to be fully aware of his surroundings. Dense nest sites, preferred during low level interactions and non interaction days, may be more comfortable and better hidden from predators or elephants.

(5) (a) During low and medium level interactions Makumba increased his loud auditory signalling rates, although no change occurred in immature play or group auditory signalling rates. The rest of the group appeared to continue with their typical daily activities while Makumba drove off the extragroup male; (b) during high level interactions, Makumba either increased his loud auditory signalling rates or alternatively, decreased them to such an extent that he remained silent; whilst immature play auditory signals decreased abruptly and group auditory signalling rates also tended to decrease - the threat of high level interactions appeared to silence the group members, perhaps allowing them to remain vigilant to any cues given by Makumba; (c) while auditory replies without movement or patrol were favoured in low level interactions, medium level interactions favoured a mixture of auditory replies with patrol and/or movement; (d) during high level interactions, a 'mixed' response type was used as well, but the group also chose to silently flee or hide in dense thickets.

The protector male of any group must weigh up the costs and benefits of pursuing each encounter. In some situations, avoidance by silence and fleeing or hiding may be the most effective defensive strategy.

(6) Other strategies were: (a) spitting and blowing leaves, termed 'angry' eating; used as a potential intimidation tactic and tension release; (b) water displays used as a potential intimidation tactic; (c) the 'whisper' belch used during silent responses only; where group members appeared to communicate by almost inaudible belches, and; (c) recruiting the

blackback (who may have had a stronger bond to the silverback as a result of his orphaned status) to patrol an area while Makumba moved his group to safety.

(7) As high level interaction rates increased, numbers of neighbours to the silverback increased, and the group became more cohesive. This effect was most evident in peak interaction month July.

(8) Extragroup units appeared to target the Makumba group either during the early afternoon when the group was most spread out or in the night/dawn when the group was most cohesive. Since an extragroup male's best strategy to acquire females is to lure and coerce one or a few females in a group (instead of all females) by gaining her trust (Chapter 4), he should approach females when they are least likely to be close to their protector silverback. Interactions that occurred throughout the night or at dawn may represent an alternative strategy to attack a group in 'surprise' while sleeping and not alert at their nest. If the attacker male feels that the benefits of successfully killing one of the female's infants outweigh the costs of a potentially severe violent battle, then he may prefer to attack in surprise. After suffering infanticide, the female might be more likely to leave Makumba for this extragroup male (Chapter 4).

These results reflect the threatening nature of high level interactions and quantify some of the mechanisms by which the western lowland gorilla silverback protects his group during interunit encounters. They suggest that (a) western lowland group gorillas react according to the perceived threat of an extragroup unit; (b) the high ratio of solitary males observed at western gorilla bays appears to be the largest threat to group males; (c) interunit interactions involve an extremely complex, highly strategic framework of responses and approaches; and (d) infanticide is likely to be an important consideration in the decisions of adult males whose group contains females with dependent infants.

7.5 Silverback-Group Dynamics in Relation to Tourist and Researcher Presence (Chapter 5)

One underlying factor in the gorilla socioecological framework is the presence of humans, not only as risks (e.g. hunters) but also as observers (possible threats) and protectors. Early in the habituation process humans are seen as high risk, evidenced by group fleeing and extremely

threatening silverback charges. In the later stages of habituation, constant human presence is at best, only a minimum disturbance to habituated groups. Additionally, humans may impede the natural course of interunit interactions.

Makumba, whose group was in the later stages of habituation, was forced to remain attentive to the safety of his group when in the constant presence of observers. How a silverback, in this case Makumba, reacts to tourist and researcher groups not only permits continued quantification of the manner in which western lowland silverbacks protect their group, but also can help us learn how to best minimize any negative impacts of human presence. Results from this study indicated:

- (1) Observers spent more time within 6–10m of the silverback when tourists were present.
- (2) Thirty-nine percent of silverback and 23% of total group aggressive events were directed at humans. Although these percentages might represent a large effect, 65% of silverback and 47% of group human-directed aggression were low level soft barks.
- (3) Even though 48.5% of observation time was spent within 6–10m of the silverback, there were distinct decreases in human-directed aggression at 10m and then again at 15m, which plateaued at 18m.
- (4) The adult female, Bombe, was responsible for more human-directed aggression than any other gorilla in the group, including the silverback. Adult females were the most likely age–sex class to aggress humans. Personality appeared to play a role in the aggression that Bombe directed toward humans. Therefore in some circumstances even when adhering to all ethical gorilla viewing guidelines, humans may receive aggression simply because certain individuals remain intolerant of their presence.
- (5) The presence of tourists did not affect rates of aggression toward humans for any of the gorilla age–sex classes, nor did the number of people present in tourist groups. However, as research team size increased, Bombe’s rate of aggression towards humans increased.
- (6) The presence and numbers of tourists did not significantly alter group or silverback activity budgets; however as research team numbers increased, group feeding decreased while mixed

behaviours increased. Silverback activity budget was unaffected by research team size or the number of tourists, but as human–silverback distance decreased, Makumba fed less and monitored humans more at the cost of feeding time.

(7) Factors analysed in this study explained only approximately 1-10% of the overall variance in the data. On a biological scale, there are other important but as yet undetermined factors that affect the gorillas' behaviour far more than simply human presence. Human–gorilla distance explains much more of the variance in the data than does human group type or size, further suggesting the need to re-examine the current distance rule of 7m based on mountain gorilla disease transmission risks [Homsy, 1999].

(8) Based on the results presented here and elsewhere [Klailova et al., 2010], the following recommendations were made: (a) limit distance between observers and gorillas to greater than 10m where possible; (b) limit research team size to a maximum of five observers but make efforts to reduce researcher team size to three people as often as possible; (c) limit total group size when tourists are present to a maximum of six observers; (d) when larger team sizes cannot be avoided ensure that team size is kept to a three person maximum in the subsequent observation session, (e) limit tourist visits to one tourist group per day.

It was evident that Makumba was more tolerant of our presence compared to some adult females. He clearly remained watchful and intervened when needed, but did not always support human-directed aggression from other group members. By remaining vigilant and intervening where necessary (i.e. where the safety of an individual in his group may have been perceived to be at risk), he was able to minimize his and his group's costs when under human observation. By constantly reacting to human presence he would not only lose valuable time resting and feeding but the stress could directly impact his group, potentially affecting both silverback and group activity budgets to even greater levels than recorded in this study. Regardless, human observers did alter group behaviour and the silverback behaved protectively in many circumstances. The silverback was somewhat more likely to act as a barricade between humans and his group (Chapter 3; see also Section 7.3). Additionally as human-silverback distance decreased, the silverback was more likely to be located at the rear of his group, where

humans were more likely to be standing; although it is difficult to disentangle whether humans were responsible for moving closer to the silverback when he was already at the back of the group and thus more approachable, or whether Makumba purposely moved to the back of the group as a result of human presence. While we must continue to identify and control the triggers which negatively impact gorillas when following habituated and semihabituated western gorilla groups, gorilla ecotourism and research have many benefits which can outweigh these costs.

7.6 Silverback Chemosignalling (Chapter 6)

Breuer [2008] assessed phenotypic traits in western lowland gorillas in relation to male reproductive success and found that body length, crest and gluteus muscle size were positively correlated with harem size and siring rate in western lowland adult males. He thus illustrated a clear correlation between some morphological traits and male reproductive success. Caillaud et al., [2008] found similar results. Males of many species, including many male primates also use olfaction as a chemosignal to advertise dominance, health, good genes, location and presence, not only to intimidate other males but also to attract females (Chapter 6). The decline in relative olfactory brain size and number of olfactory receptor genes over primate evolutionary history, combined with a paucity of great ape naturalistic observations regarding olfactory influences on behaviour have led to little attention directed towards the potential for great ape olfactory signalling.

Gorilla silverbacks emit a pungent odour that has been anecdotally communicated in several documents (see Chapter 6). I provided evidence to suggest that olfaction in silverbacks is a highly flexible, intricate and context dependent signalling mechanism used to intimidate rival males and advertise location, health, strength and dominance to females. Silverback chemosignalling provides silverbacks with another mechanism by which he may increase his reproductive success; which is ultimately affected by his ability to attract and retain females, and protect group members. I assessed which factors predicted high level western lowland silverback odour and explored the intricate relationship of varying arousal levels and silverback odour production, measured in terms of a pungency rating scale starting at zero (no smell detected) and ending at four (extreme smell detected).

Results from this study indicated:

(1) Extreme smells (a) may function as acute indicators of arousal designed to intimidate extragroup rival males and attract adult females by expressing dominance, strength, health; (b) were not influenced by environmental conditions (wind, rain, temperature) since their primary goal may be to ensure quick and immediate communication with rival males, potential immigrant females or group females; (c) were predicted by interaction numbers, silverback chest-beating/long-calling rates, silverback anger and distress levels, and Bombe's presence close to Makumba which - as the mother with the youngest infant - was probably due to a potential risk of infanticide; (d) appeared to act as 'acute' indicators of arousal, which increased or decreased in response to immediate circumstances, and; (d) were not simply a by product of arousal but a purposeful signalling mechanism to other individuals both close and distant, as evidenced by the lack of extreme smell recorded in all 'silent' responses during high level interactions.

(2) High level smells (a) may function as chronic indicators of arousal not driven by immediate changes in the social environment and as in extreme level smells may be designed to intimidate extragroup rival males and attract adult females by expressing dominance, strength, health; (b) may have been used at least in part, as a vigilance cue so individuals could continue to perform daily activities in riskier situations; (c) were not easily influenced by environmental conditions; and (d) decreased when Makumba was informed of adult female whereabouts (via chest-beating and long-calling) when foraging far from the silverback.

(3) Low level smells (a) may function as a baseline identification marker and provide both self and intragroup reassurance in the silverback's protective abilities, which may explain why Makumba exhibited more low level smells as silverback-neighbour numbers increased and why he exhibited more low level smells in the 'quiet' high level interaction response versus the 'loud' high level interaction response, and; (b) were used in close intragroup signalling, thus attenuation due to environmental factors may be irrelevant or even beneficial to the signaller and intended receiver, making it more difficult for extragroup males to 'eavesdrop'.

These adaptations may be particularly relevant in Central African rain forests, where visibility is often limited [Setchell et al., 2010b]. To date, this is the only detailed work to explore chemosignalling in wild non-human great apes. This study not only reveals the potential flaws involved in judging the significance of smell solely by relative olfactory brain size and the number of olfaction receptor genes, but also suggests that olfaction in humans has evolved through adaptations present in other great ape species. It provides compelling evidence to indicate that olfaction is used extensively in a delicate, interwoven, and non-mutually exclusive, extremely elastic communicative framework that may ultimately increase male reproductive success in dominant, and therefore immunocompetent silverbacks.

7.7 Limitations

Like any gorilla study conducted in wild environments there are limitations on the nature and amount of data that can be collected. This is especially true for western lowland gorillas who live in dense and dark habitats, and as previously mentioned are very difficult to habituate. Due to the tireless habituation efforts of the Bai Hokou team over eight years, the Makumba group represented one of the few western lowland groups where such data collection and analyses were even possible. As a result, I was able to provide the first detailed account of silverback-group dynamics for one western lowland group. Regardless, several limitations to this study need to be mentioned.

As in all research that involves humans following non-human primates regularly, our presence will, to at least some extent, affect the behaviour of the 'habituated' animals. While extreme care was taken to ensure observers acted as neutrally and noninvasively as possible when following the Makumba group, Chapter 5 clearly indicates that human presence does impact on their behaviour. It is also likely that our presence affected the nature of interunit interactions since extragroup males were unhabituated to humans, and thus may have also avoided approaching the Makumba group when we were present. Extragroup units who did approach may have reacted differently as a result of our presence; during several high level interactions, it appeared that the extragroup male was not only screaming at Makumba but also at us. Conversely it is also possible that we have unintentionally habituated some extragroup males to

our presence over the years of following the group. These extraunit males may have been more likely to interact with the Makumba group, potentially affecting the dynamics of interunit interactions in the region. Regardless, it was clear that 2007 represented an extraordinary year for the Makumba group, since they experienced 79 interactions compared to the 15 that occurred in 2006.

Due to the limited visibility as a result of forest density and intolerance of observer proximity within 10m by certain individuals or in certain contexts, it was not possible to collect complete neighbour matrices or approach-leave matrices. Therefore responsibility for proximity to the silverback remains unknown as does the possibility that certain individuals may have sat closer to the silverback because they were seeking proximity with another individual rather than to Makumba. Still, the cumulative results of this thesis in conjunction with past research on mountain gorillas suggest that individuals (particularly NN1 to Makumba) were generally seeking proximity to the silverback rather than other group members.

Since a formal study on non-human great ape chemosignalling has never been attempted in the wild, I was only able to use simplistic methods of olfactory data collection based on a subjective rating scale. While all effort was made to collect the data as neutrally and consistently as possible, there is no doubt that technical devices to actually capture and measure scent would have provided more precise measurements. However, the very assessment of scent as a means of communication was serendipitous, as the role of olfaction in gorilla social signalling had not been systematically tested before. Regardless, results showed very clear patterns indicating that while perhaps somewhat simplistic, my subjective scale was still very effective.

This thesis was based on only one silverback from only one focal single-male western lowland group. More comparisons are necessary, although the lack of habituated groups in wild contexts (to my knowledge there are only two other western lowland groups far enough along in the habituation process to allow for detailed behavioural studies) makes this a difficult task. Although I have generalized to some extent in the absence of these comparisons, I must stress that a silverback's individual character plays a role in his overall behaviour and therefore in silverback-group dynamics.

7.8 Future Directions

Future directions in the study of gorilla chemical communication would be to examine olfactory signals in conjunction with cortisol levels as indicative of heightened arousal, both positive and negative [i.e. Ackerl et al., 2002; Chapter 6]. Additionally, capturing wild chemosignals with more technical devices would present a natural extension to the silverback chemosignalling theories resulting from my thesis. The study of western lowland gorilla chemosignalling may have important applications for captive enclosures, where silverback odour intensity could be used as an indicator of his arousal level and thus his, as well as the group's, emotional state. This measurement of anxiety through odour intensity would provide keepers with another tool to detect and thus reduce situations of negative arousal.

Additionally, complete neighbour matrices and approach-leave matrices, responsibility for proximity, and multisite comparisons, are all necessary future avenues of study to further quantify silverback-group dynamics.

Plans are currently underway to formally investigate non-human great ape-cat interactions for the first time in wild environments. As described in detail in the introduction, leopards could be an important cause of mortality in some ape populations. Due to the evasive nature of the forest leopard and challenges in western lowland gorilla habituation, it has not been possible to systematically assess non-human related predation risks to gorilla groups. In order to assess western lowland gorilla behaviour in relation to leopard predation risks, leopard presence, abundance and density must be quantified within a gorilla group's home range. Protocols for assessing forest leopard populations have only recently been developed [Henschel, 2008; Henschel & Ray, 2003] and demonstrate excellent potential for estimating the density of secretive animals that are individually recognisable. A new project will use similar camera-trapping methodologies to estimate leopard presence, abundance, density and factors that determine preferred area use (i.e. habitat type, distance to water, distance to gorilla groups) within 80-100km² of the DSPA. The survey area is large enough to meet leopard home range requirements and is home to three of the site's focal gorilla groups. Presence or absence, density information and leopard area preference factors will be assessed in relation to the

ranging of the sympatrically occurring gorilla groups. We hope to expand research to include a survey of leopard density and movement in relation to a fourth gorilla group that ranges into hunting and buffer zones within the Dzanga Sangha Forest Reserve.

7.9 Conclusions

The protective functions of western lowland silverbacks may be even more vital for this species than for mountain gorilla silverbacks, who can often rely on the support of other adult male members in their group. Consequently, western lowland silverback-group relationships appear to be centred on providing a strong protective – rather than socially interactive – and stabilizing role to ensure group cohesion and safety. In doing so, he can ultimately increase certainty of his reproductive success. Results from this thesis suggest the following overarching findings:

(1) Silverback-group dynamics represent complex, strategic spatial and social strategies to cope with perceived risk in rainforest environments. Flexible responses to environmental variables and the behaviour of other individuals (i.e. extragroup males) shows that gorillas, like other great apes, do possess complex problem solving abilities [Byrne, 1996a, 1996b; Byrne & Byrne, 1993; Patterson, 1981; Whiten & Byrne, 1988]. Gorillas have been considered less ‘intelligent’ than the orangutan and chimpanzee [Byrne, 1996b; Cousins, 1990; Gallup 1998; Whiten & Byrne, 1988]. Recent evidence of tool use in the wild [Breuer et al., 2005] and evidence of environmental exploitation [Parnell & Buchanan-Smith, 2001] has helped change this perception. My results further indicate the need to re-examine the contexts in which we view gorilla intelligence [Byrne, 1996a, 1996b; Cousins, 1990; Warren, 1973].

(2) Human observers affect group behaviour, although on a biological scale there are other important but as yet undetermined factors that affect the gorillas’ behaviour more than simply human presence. The silverback takes steps to ensure his group’s safety in situations of high perceived human disturbance. Results from this study have been used to initiate ecotourism guidelines designed to minimize the negative behavioural impact of human presence on habituated western lowland gorilla groups.

(3) Silverbacks may potentially use chemosignalling to advertise dominance, health, good genes and location; not only to intimidate other males but also to attract and retain females. High and extreme level smells may function as acute and chronic indicators of arousal designed to intimidate extragroup rival males and attract adult females by expressing dominance, strength, health and providing cues for group members to increase vigilance in risky situations. Low level smells may function as a baseline identification marker and provide both self and intragroup reassurance. To date, this is the only detailed study to explore chemosignalling in wild non-human great apes. Results suggest that human chemosignalling has evolved through adaptations present in other great ape species.

In our race to protect a fast dwindling western lowland gorilla subspecies, it is important to learn as much about western lowland gorilla socioecology and sociality as possible. Not only is this imperative in order to achieve a better understanding of a behaviourally understudied species but the conservation of this endangered species requires in depth knowledge of their behaviour so effective protective measures can be implemented, and captive groups can be better managed. Researchers work with local communities and governments, fostering pride, educating and helping to develop monetary sources of income for host countries and communities, which in turn encourages host countries to further invest in protecting their vulnerable species and the habitats in which they live. In learning more about the gorilla, one of humans' closest ancestors, our findings can engage public interest, raise awareness and bring in much needed funds to protect a species on the brink of extinction. What better place to start, than the most vital core of any western lowland gorilla group – the silverback.

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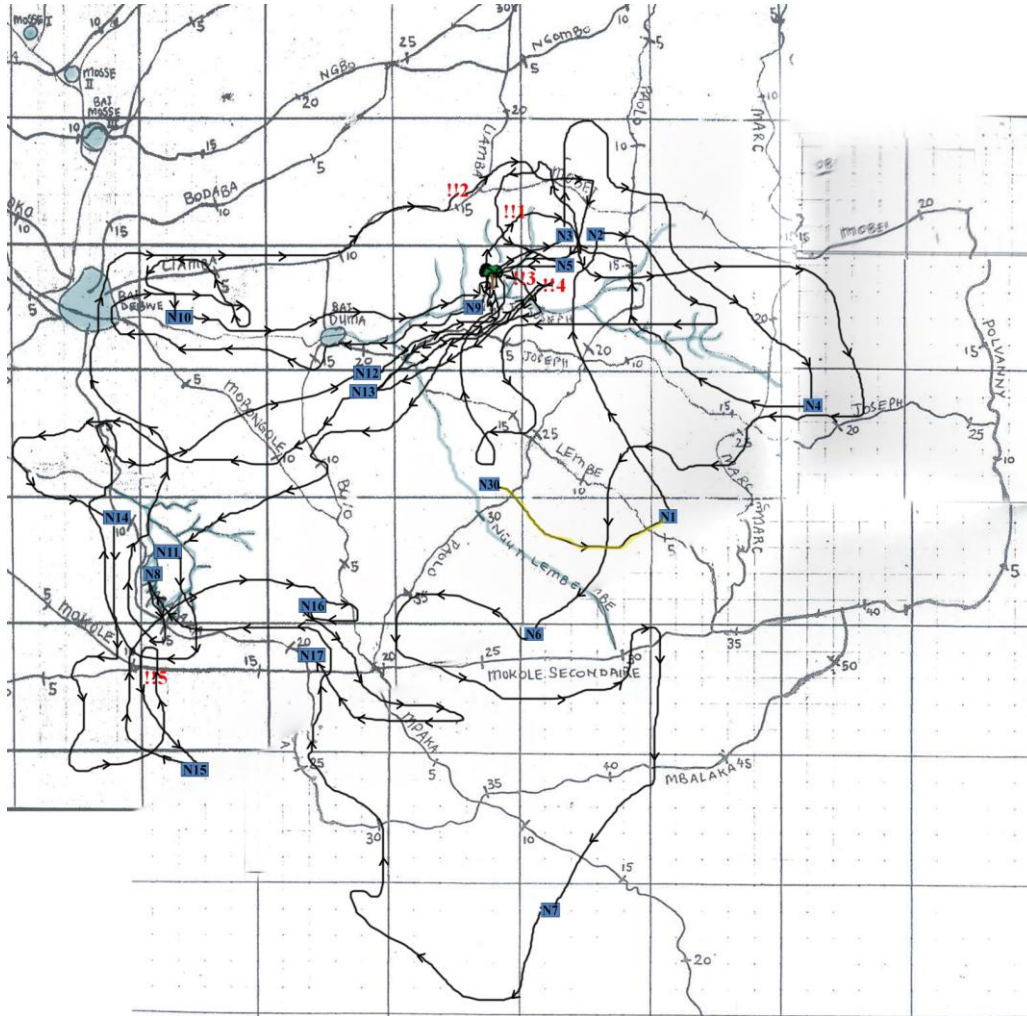
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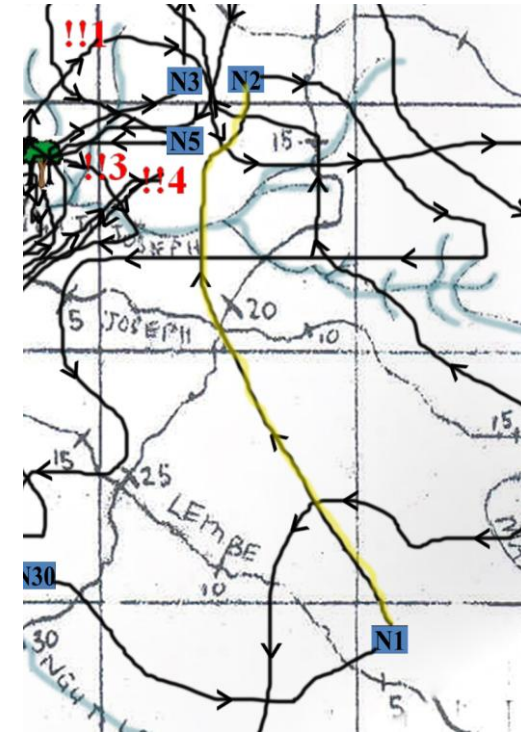
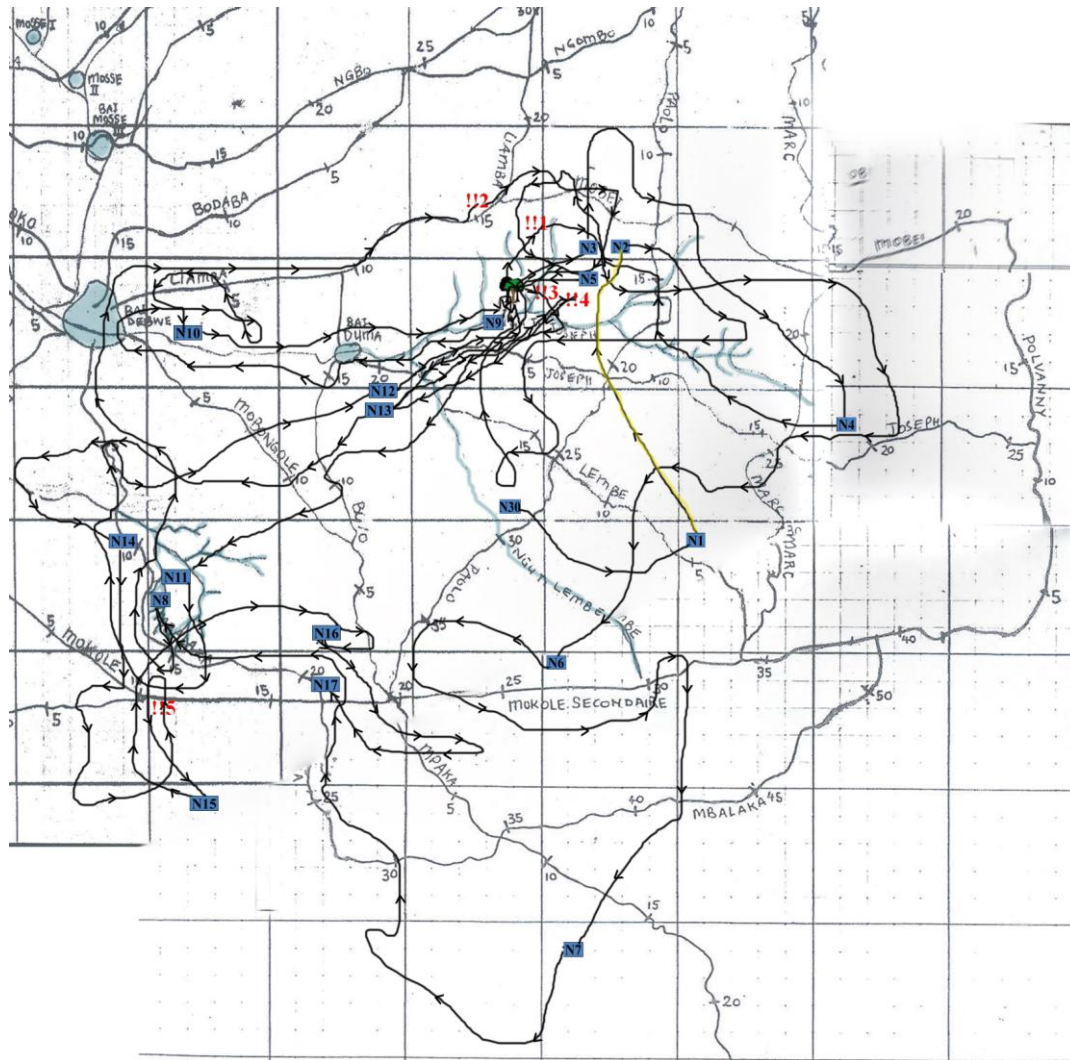
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APPENDIX

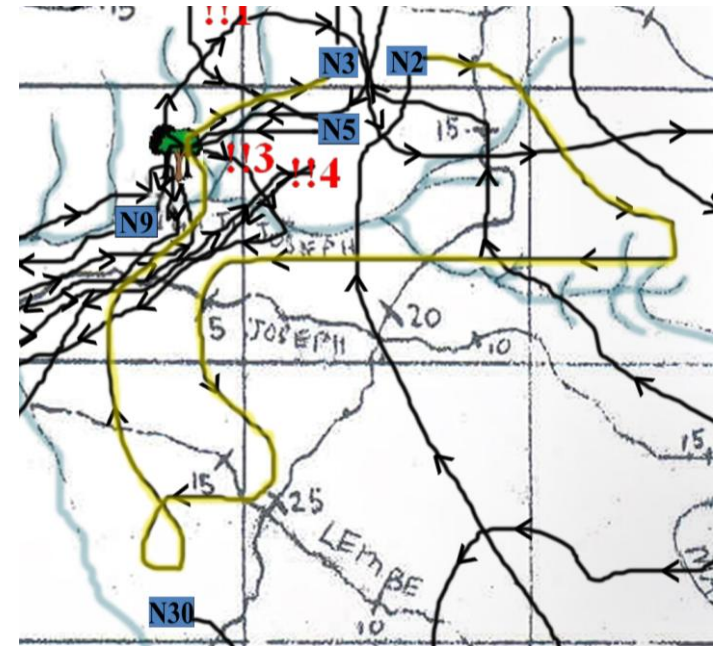
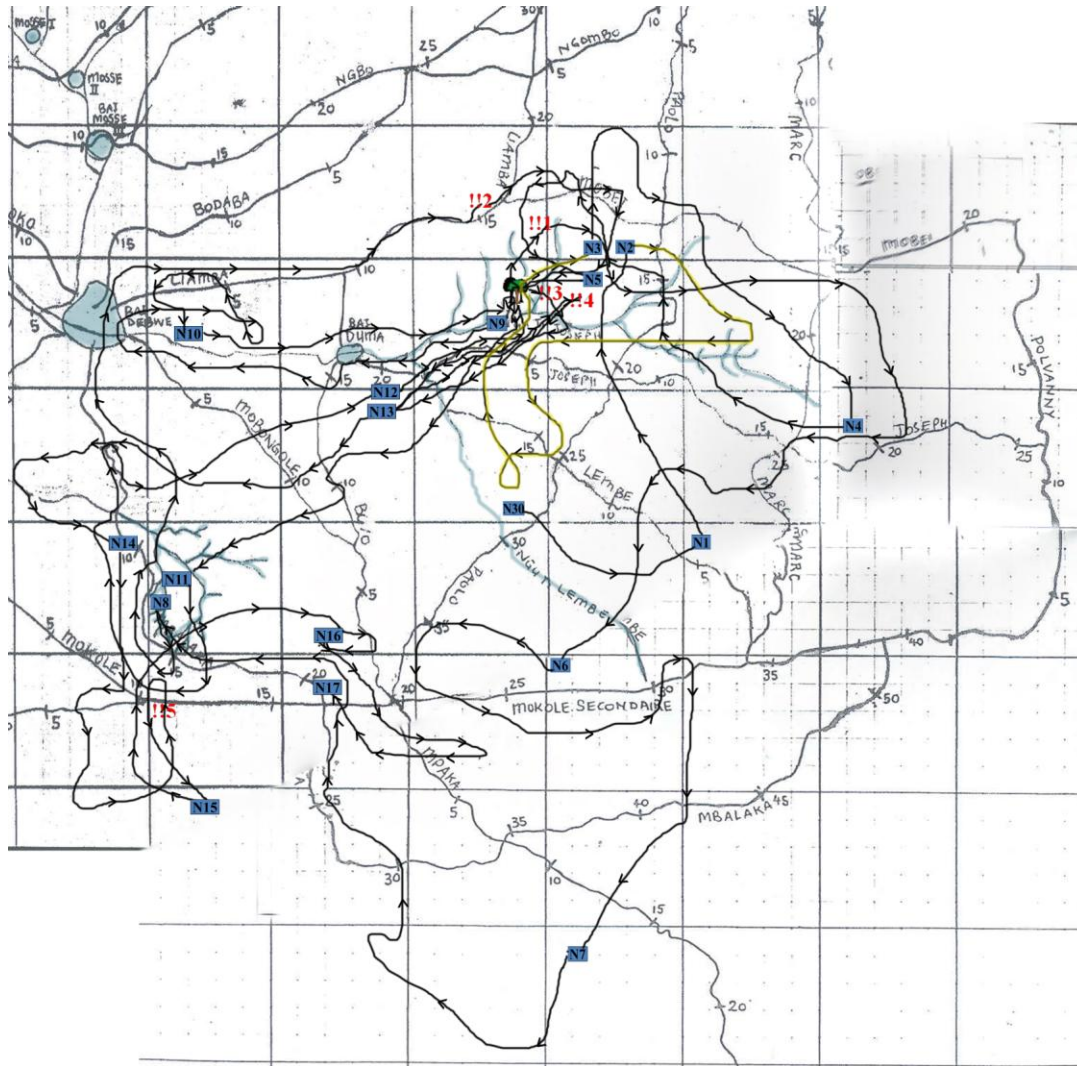
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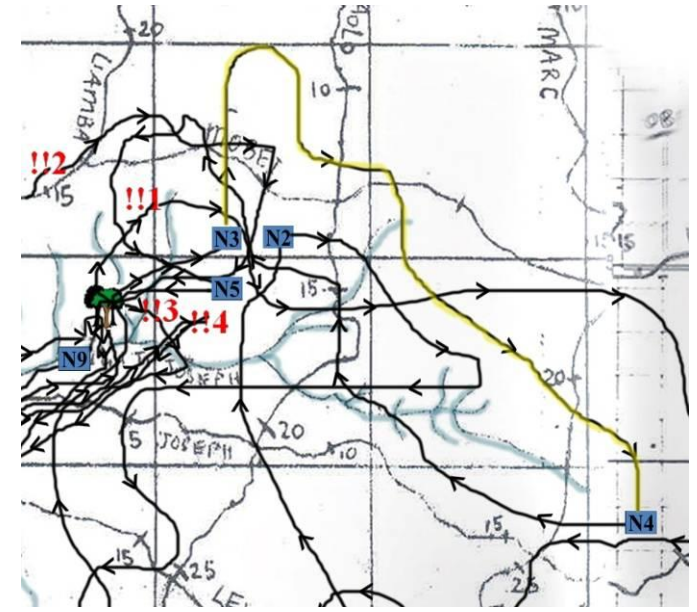
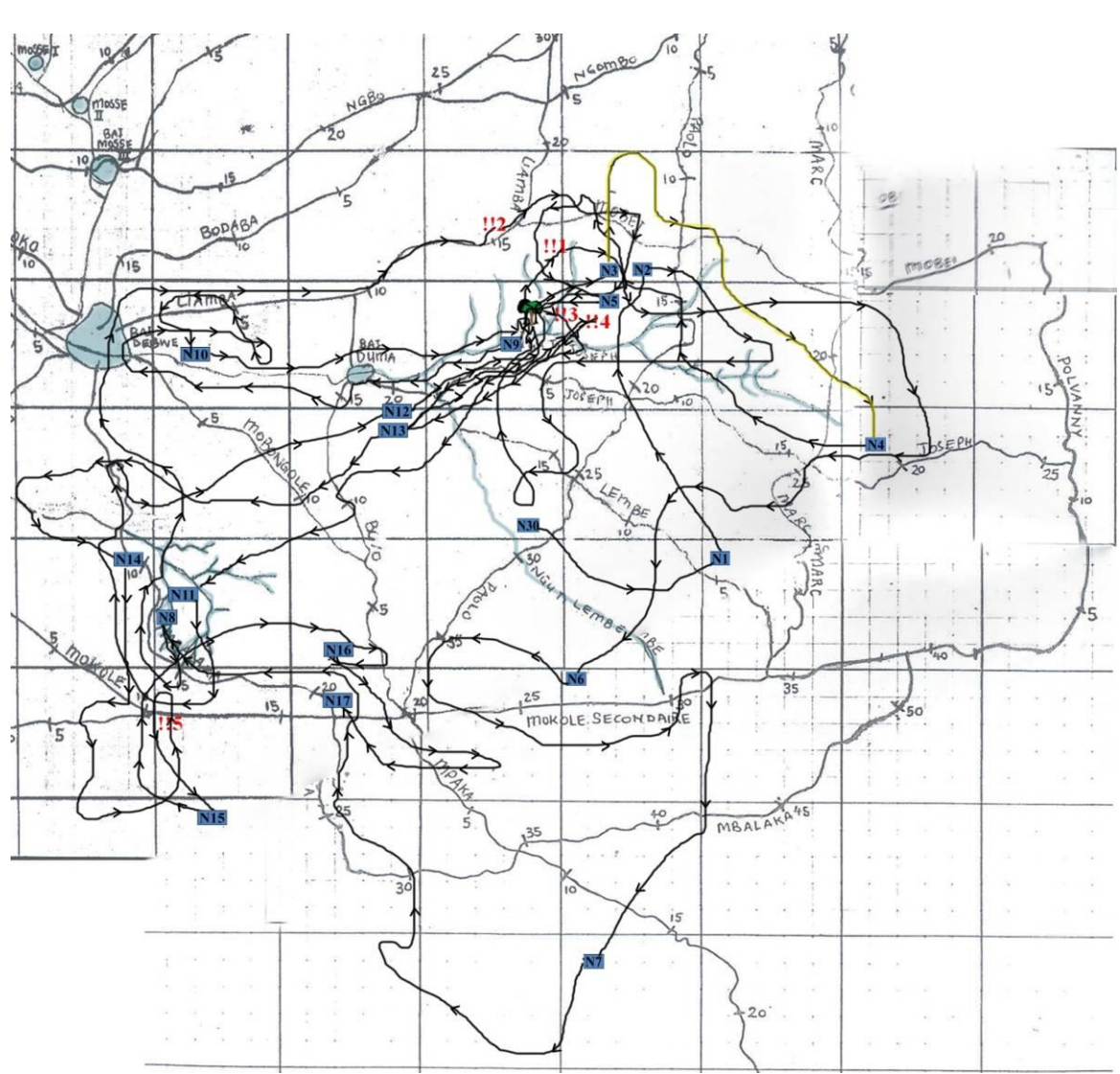
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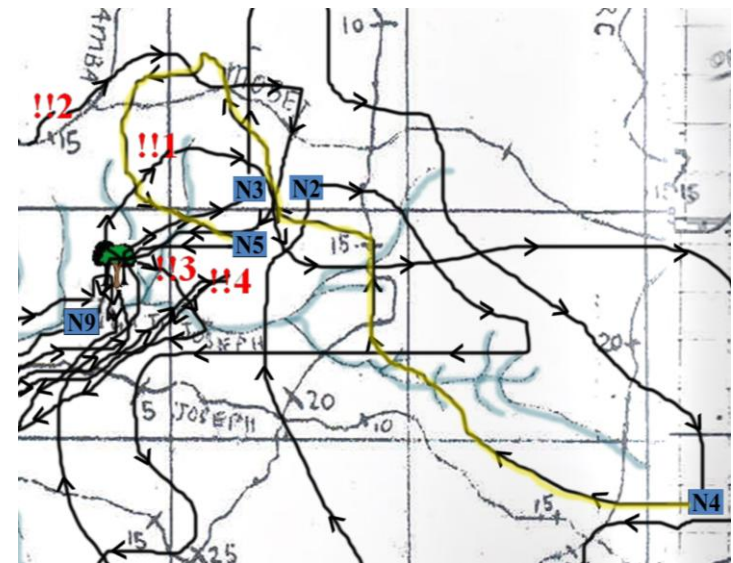
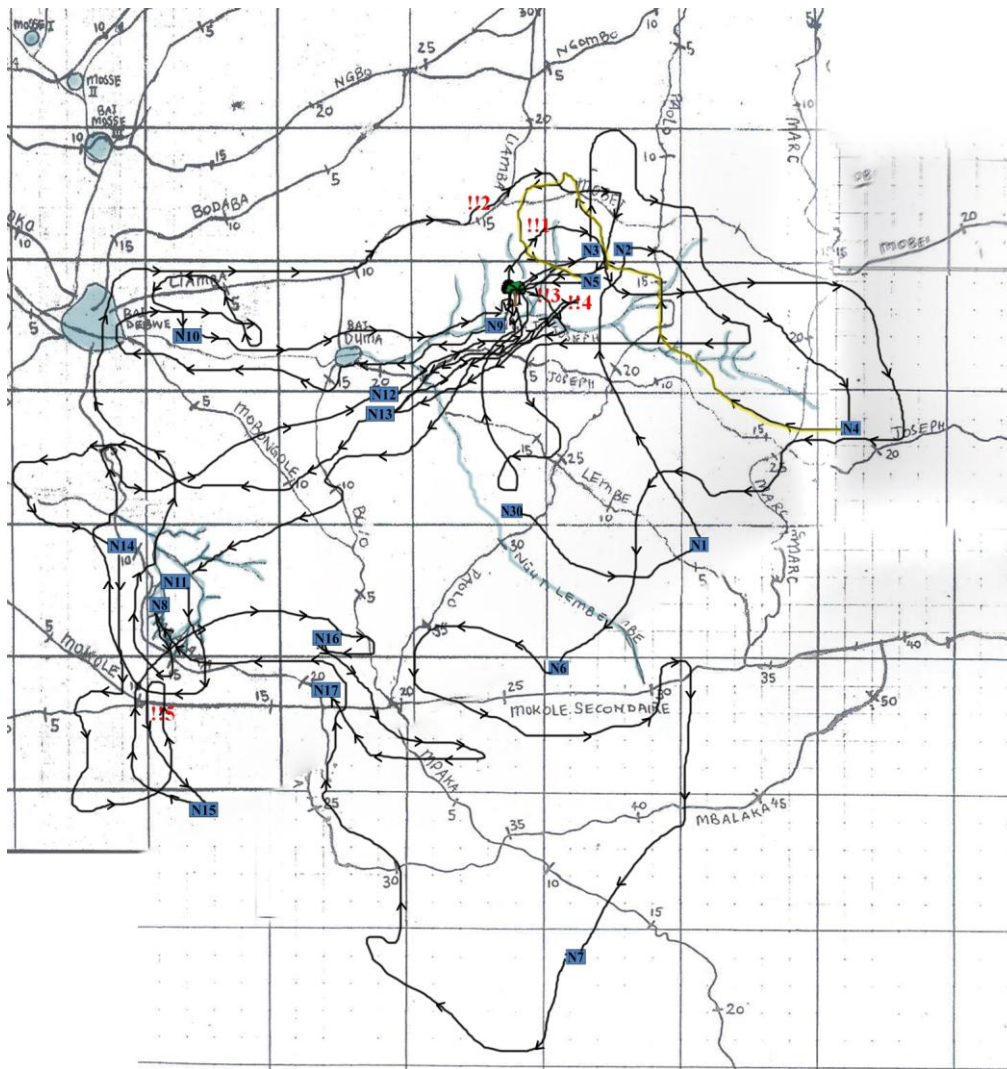
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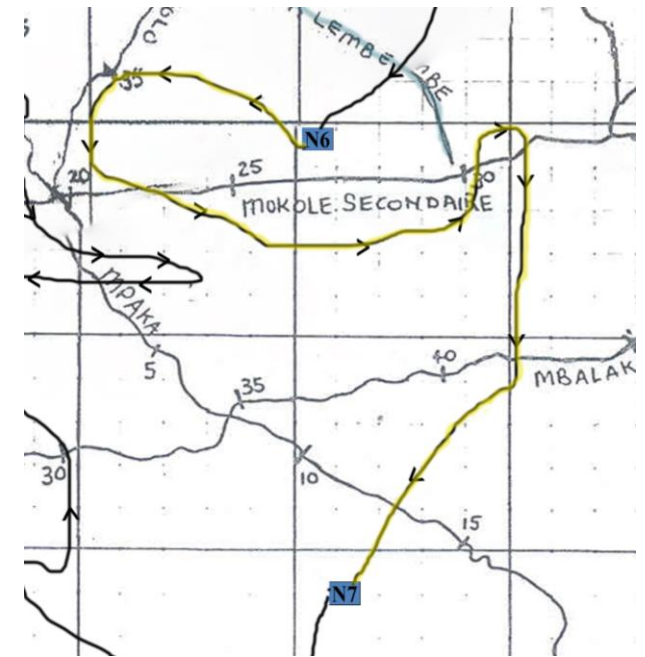
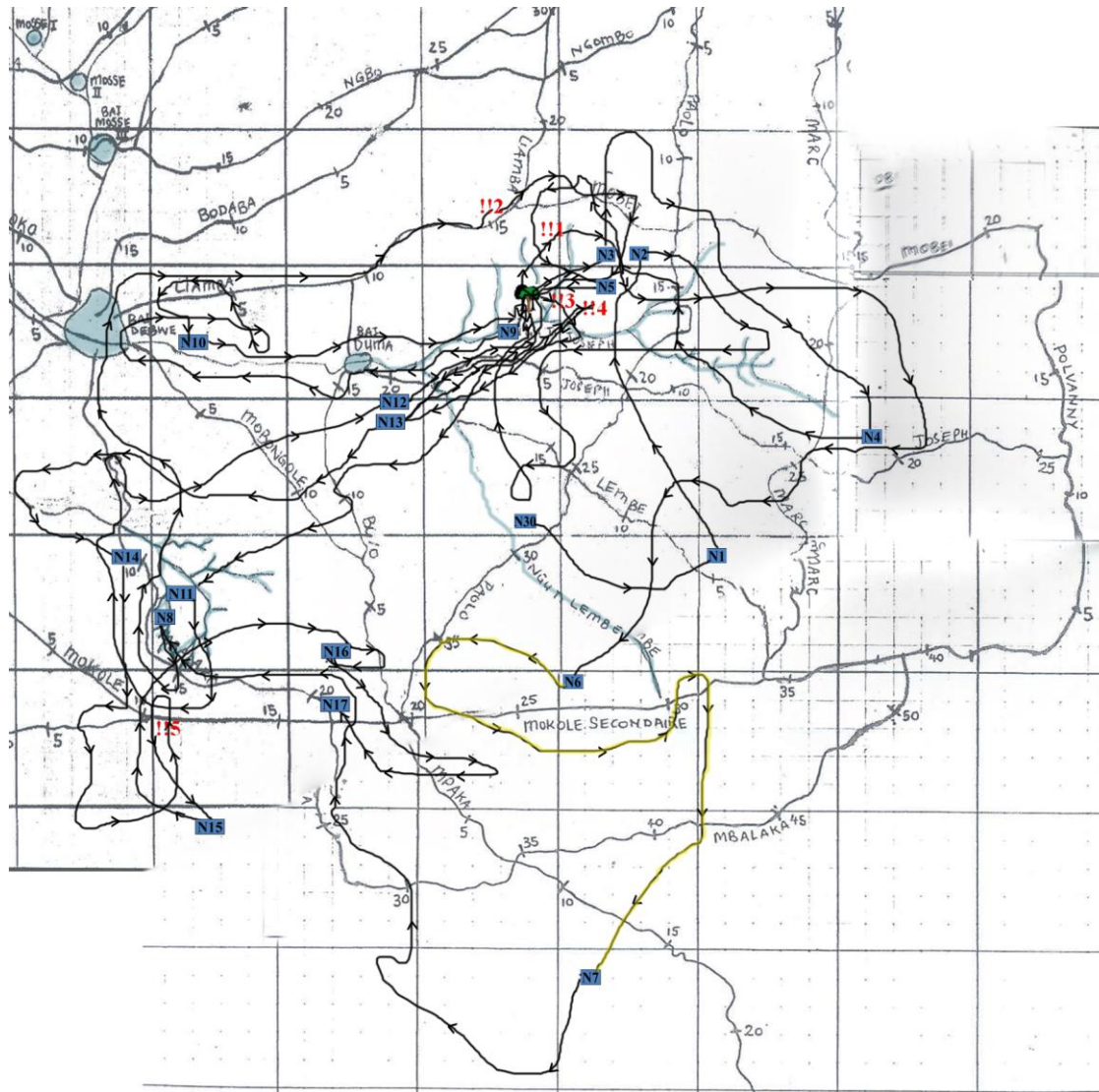
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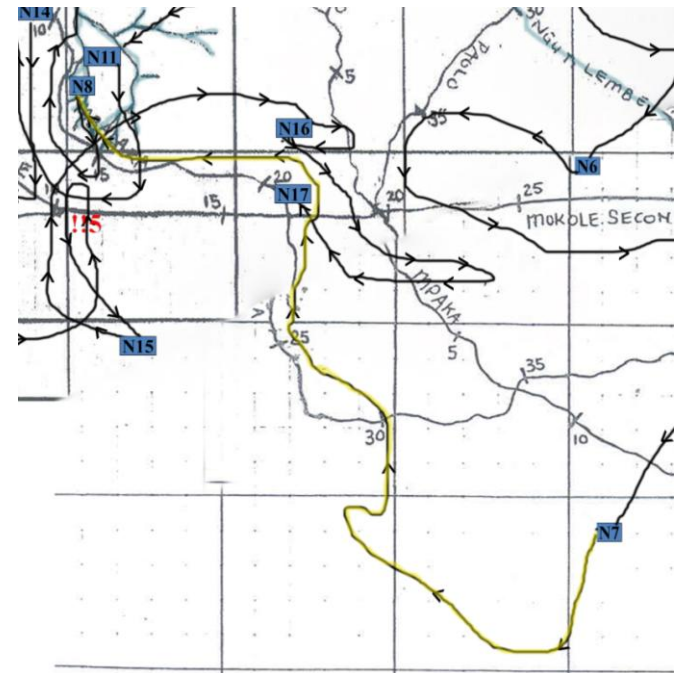
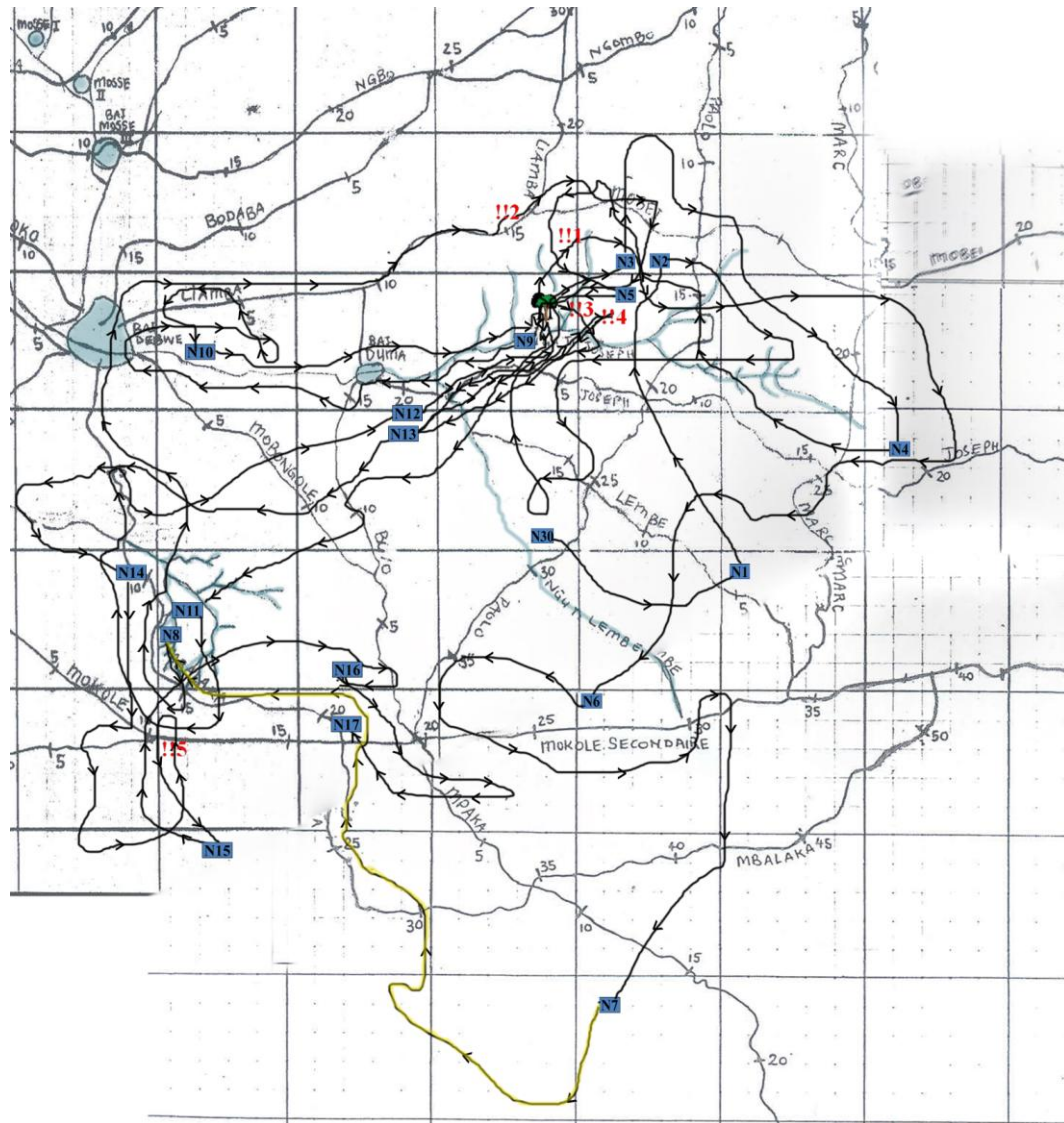
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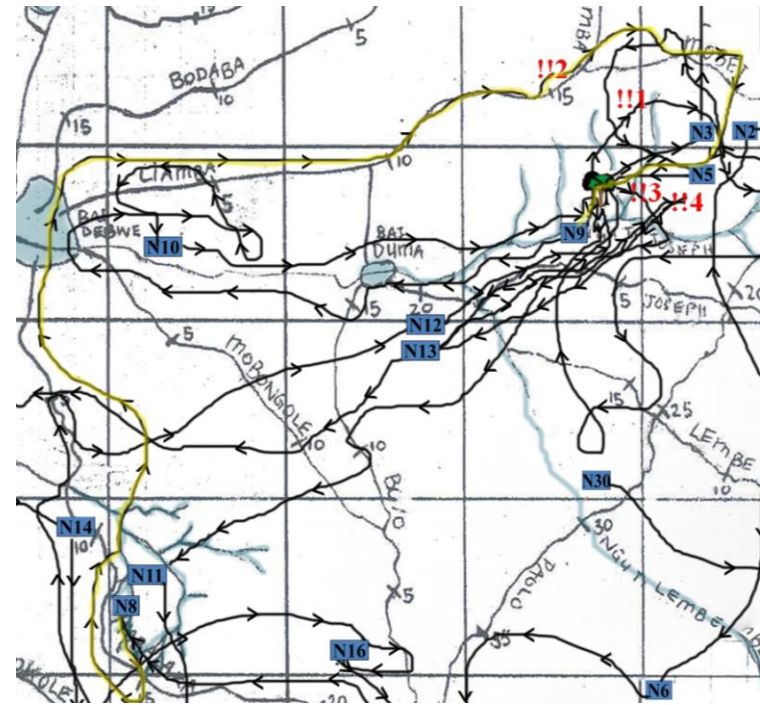
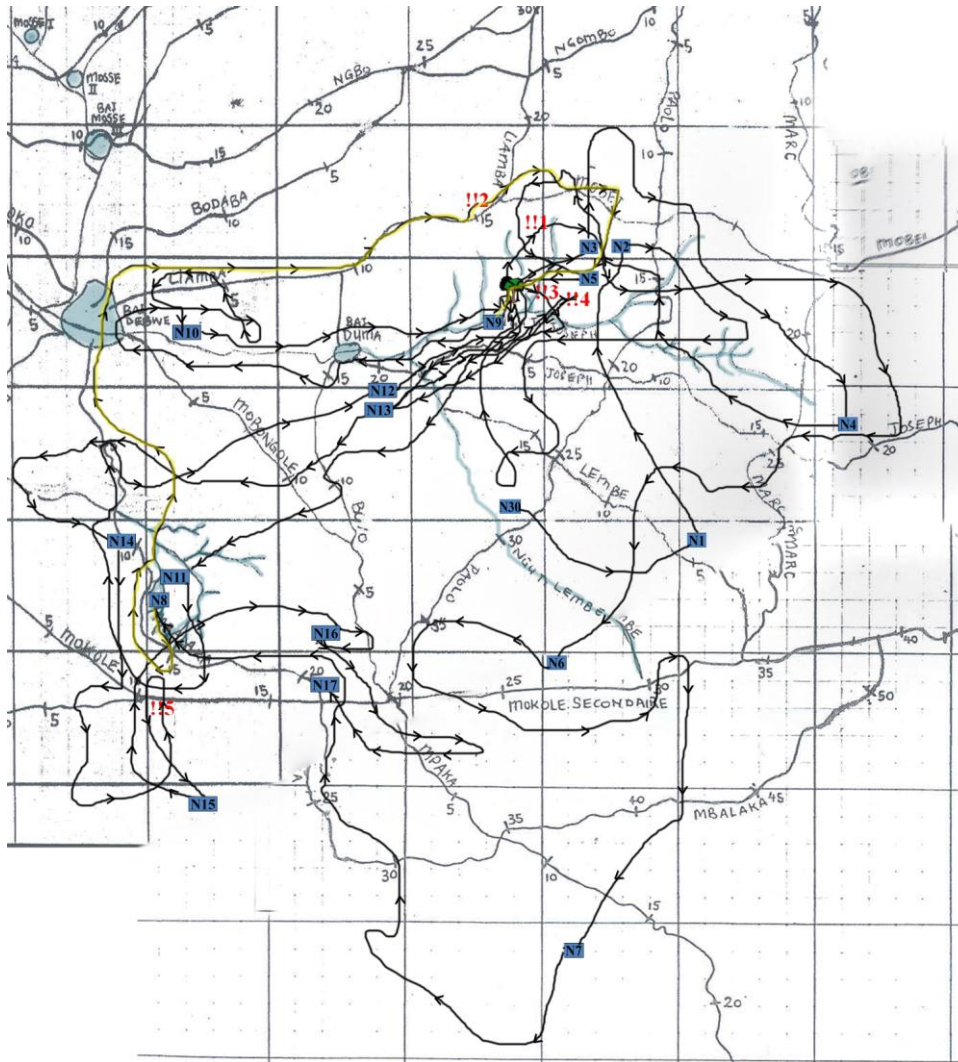
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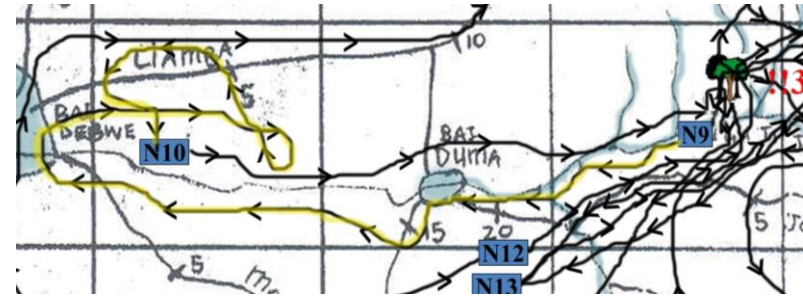
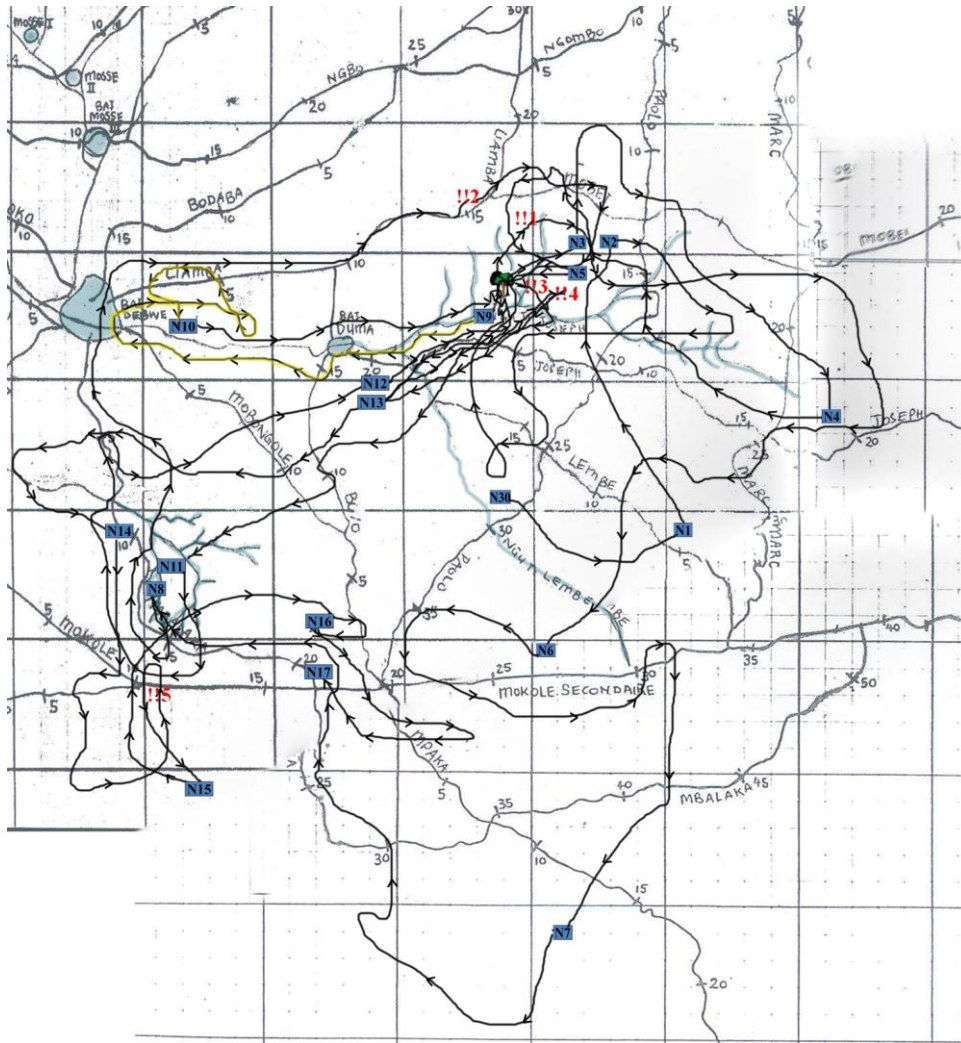
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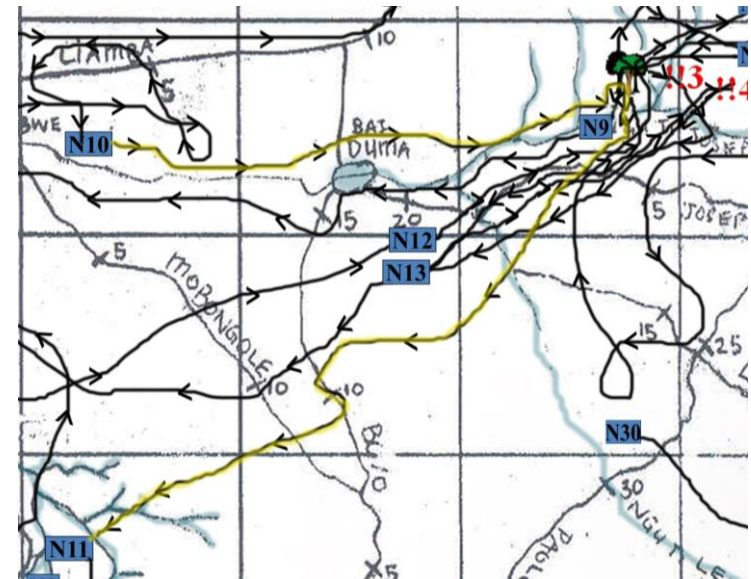
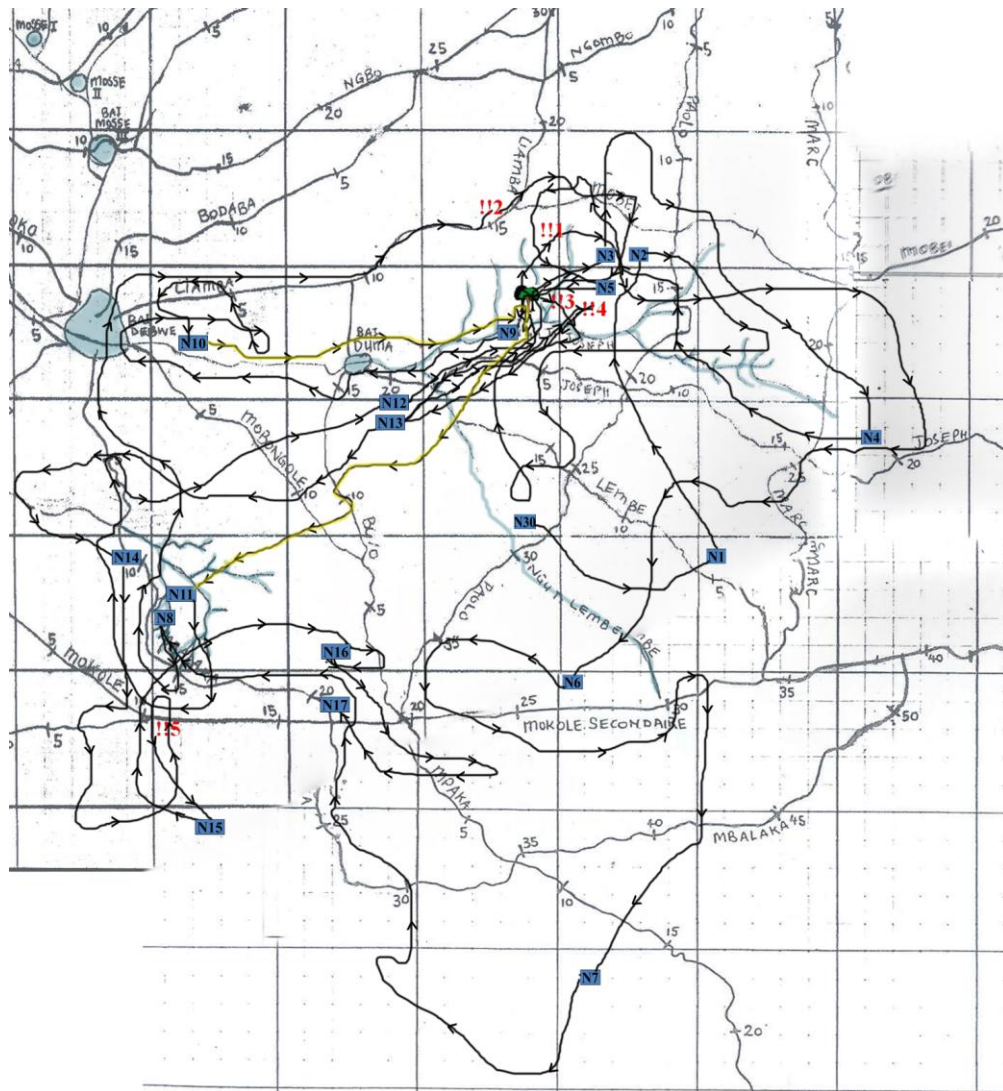
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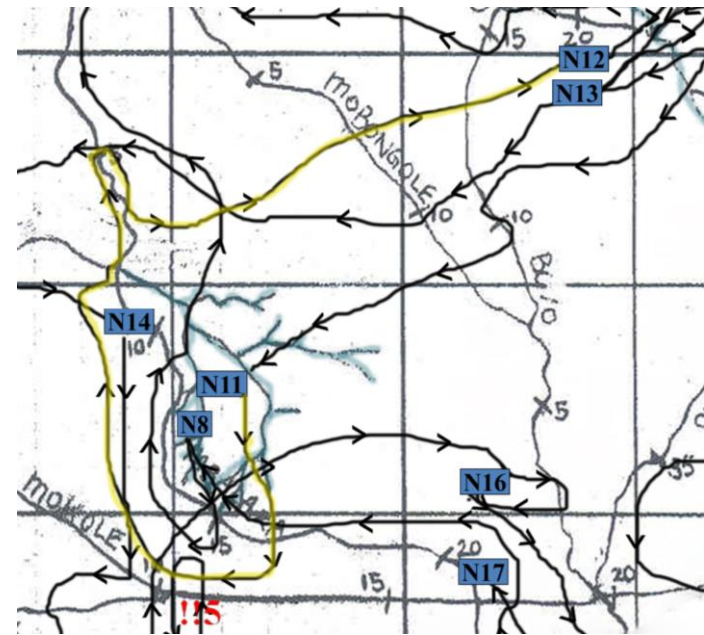
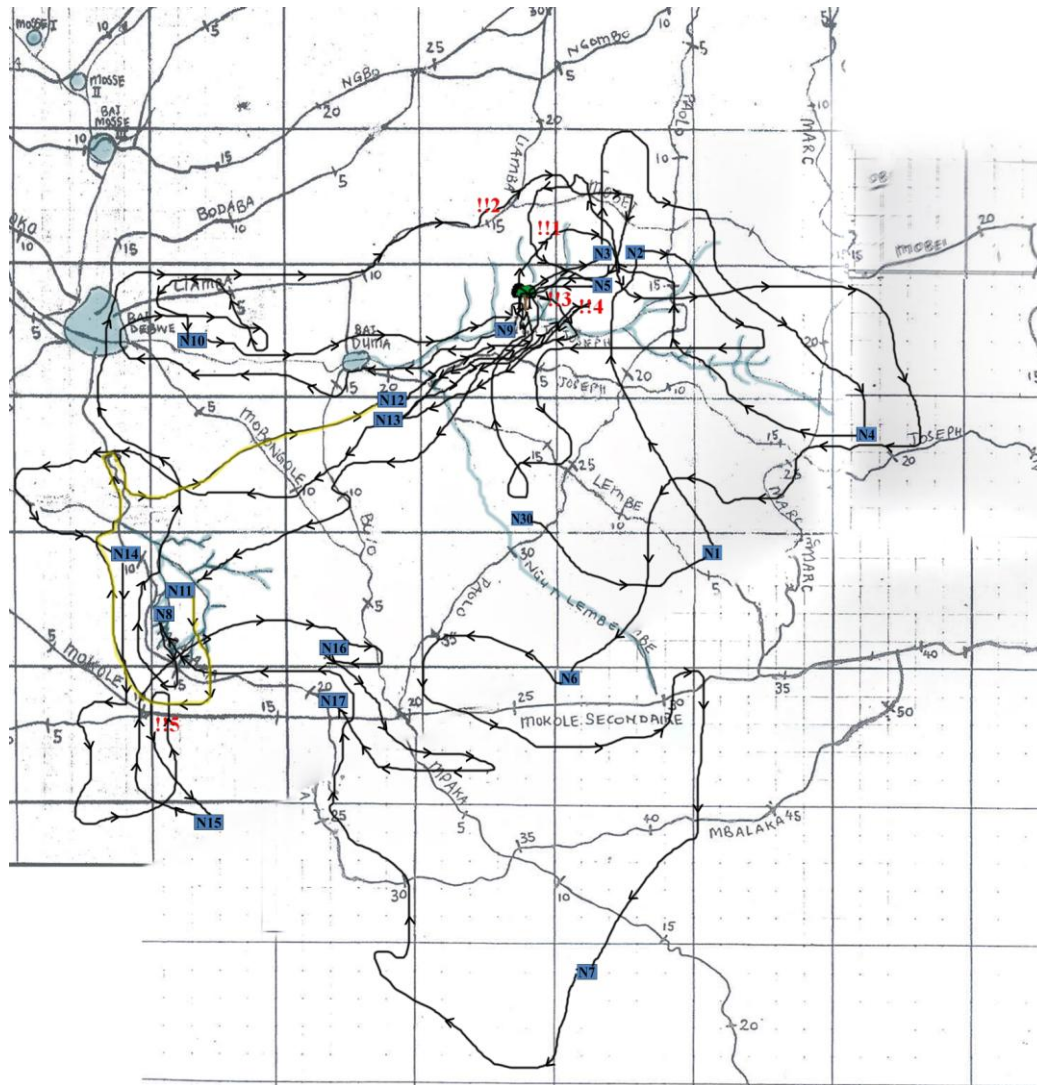
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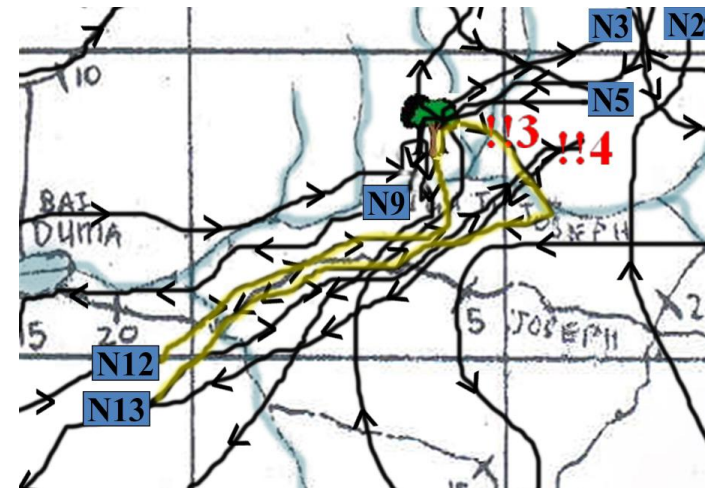
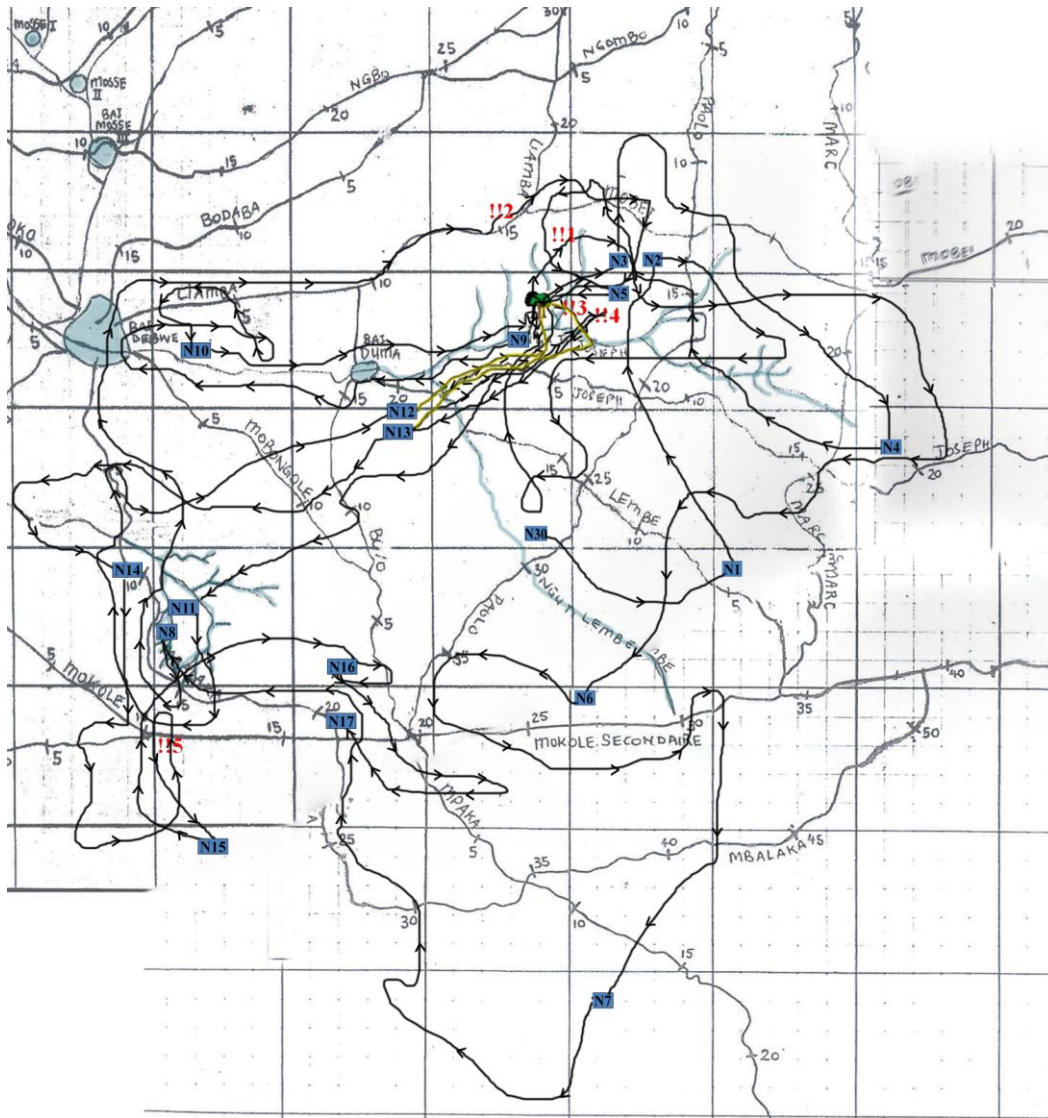
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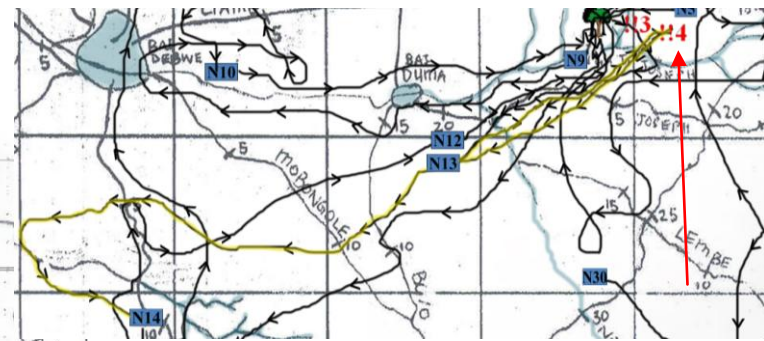
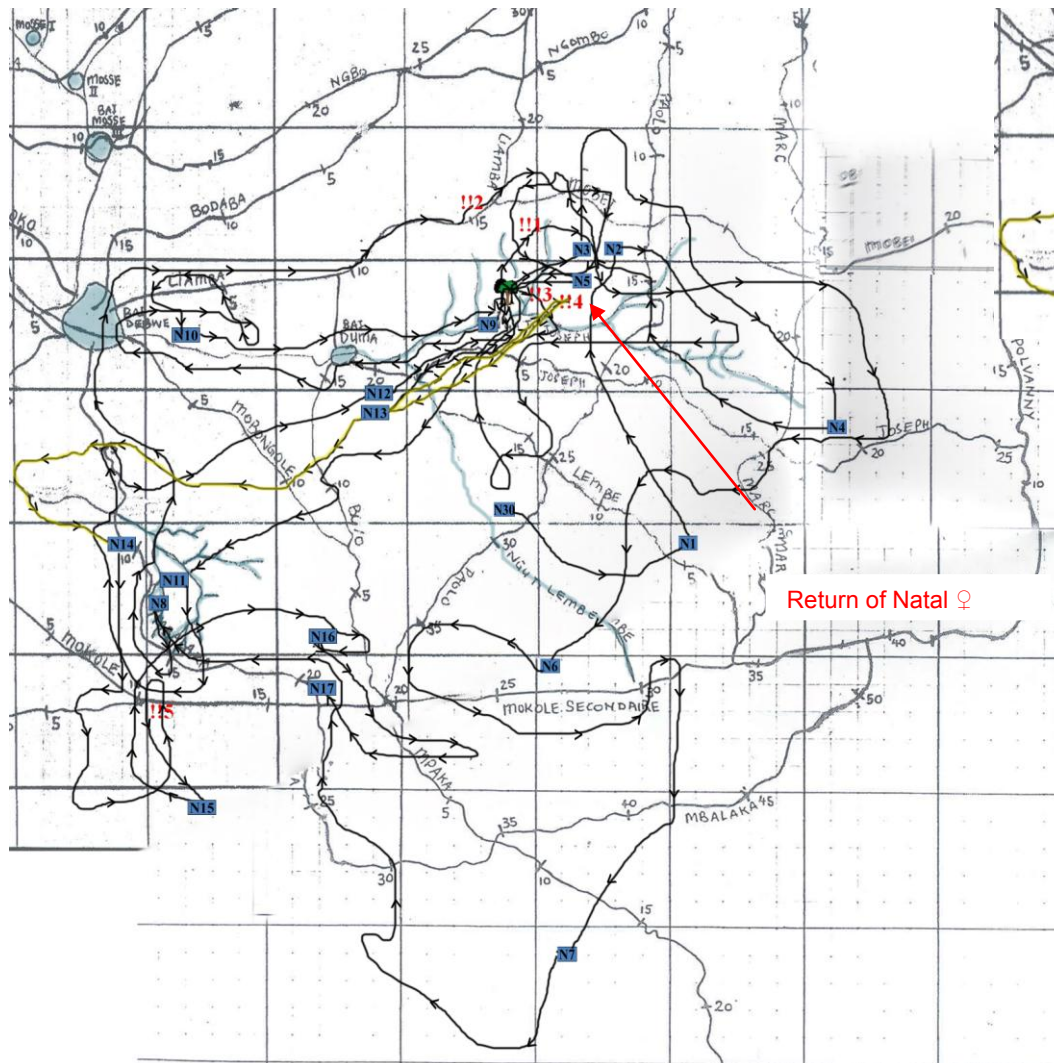
Appendix 12 July 12 Makumba Group Ranging



Appendix 13 July 13 Makumba Group Ranging



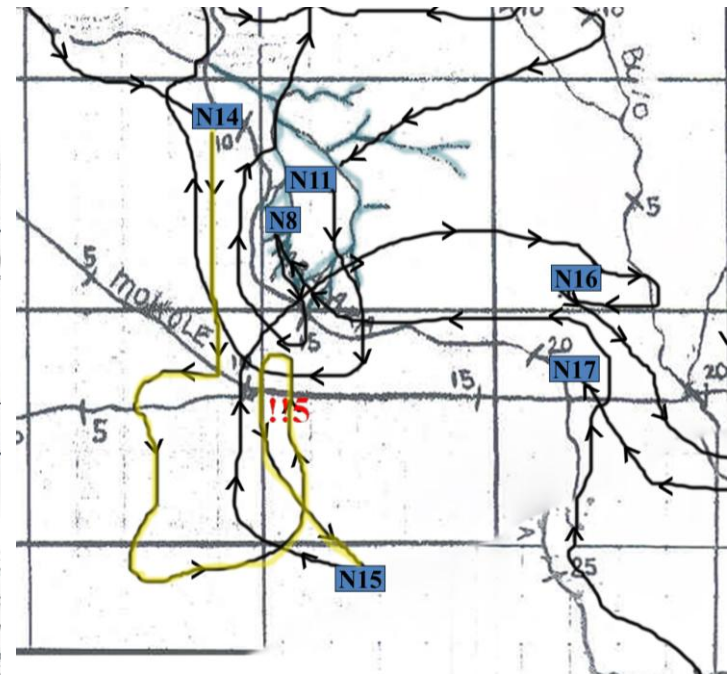
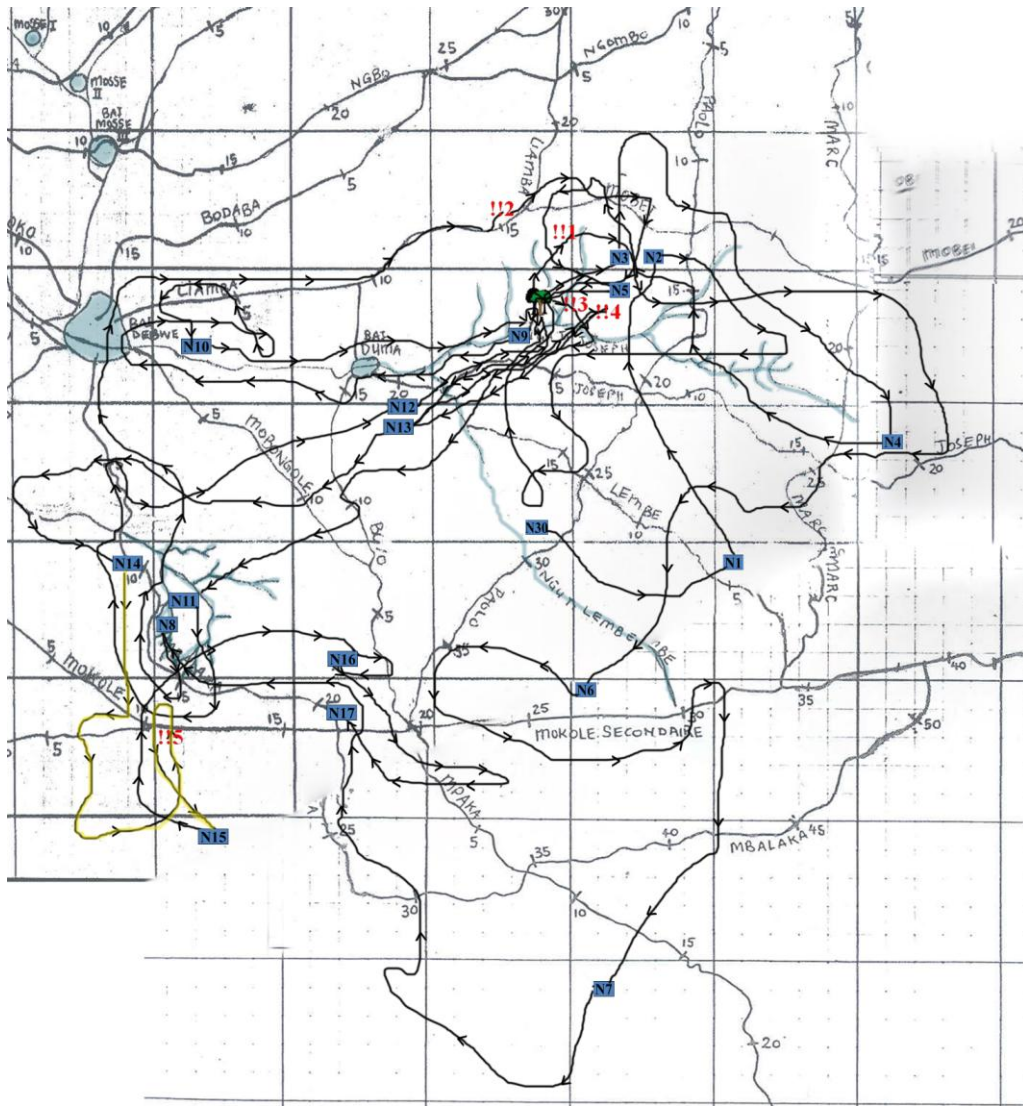
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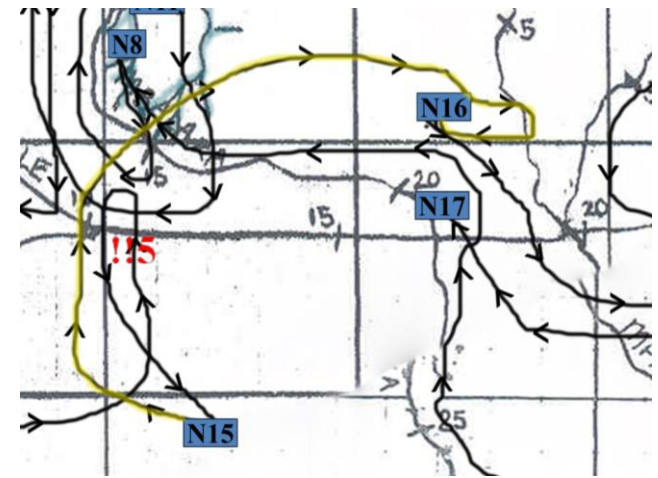
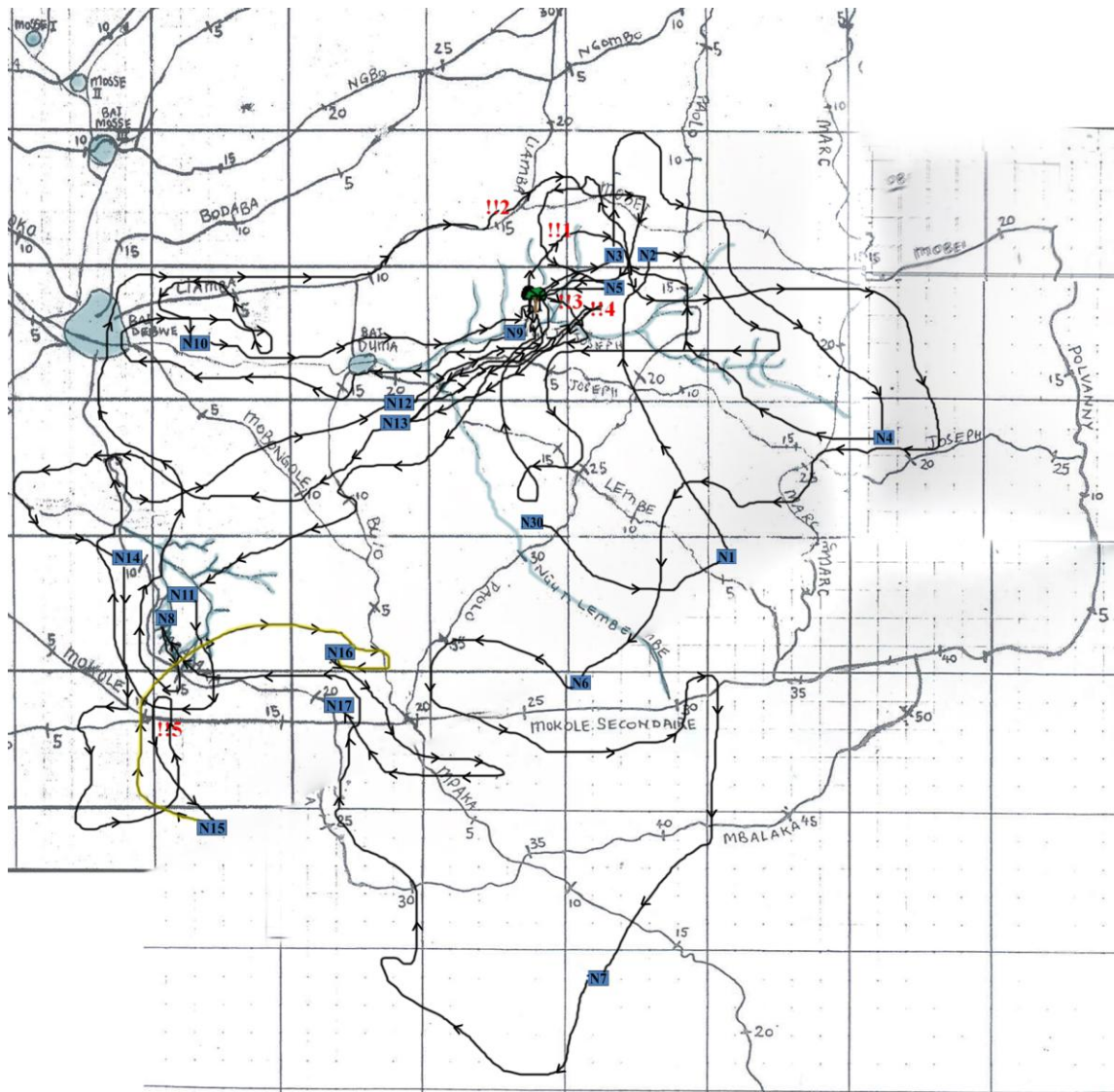
Return of Natal ♀

Return of Natal ♀

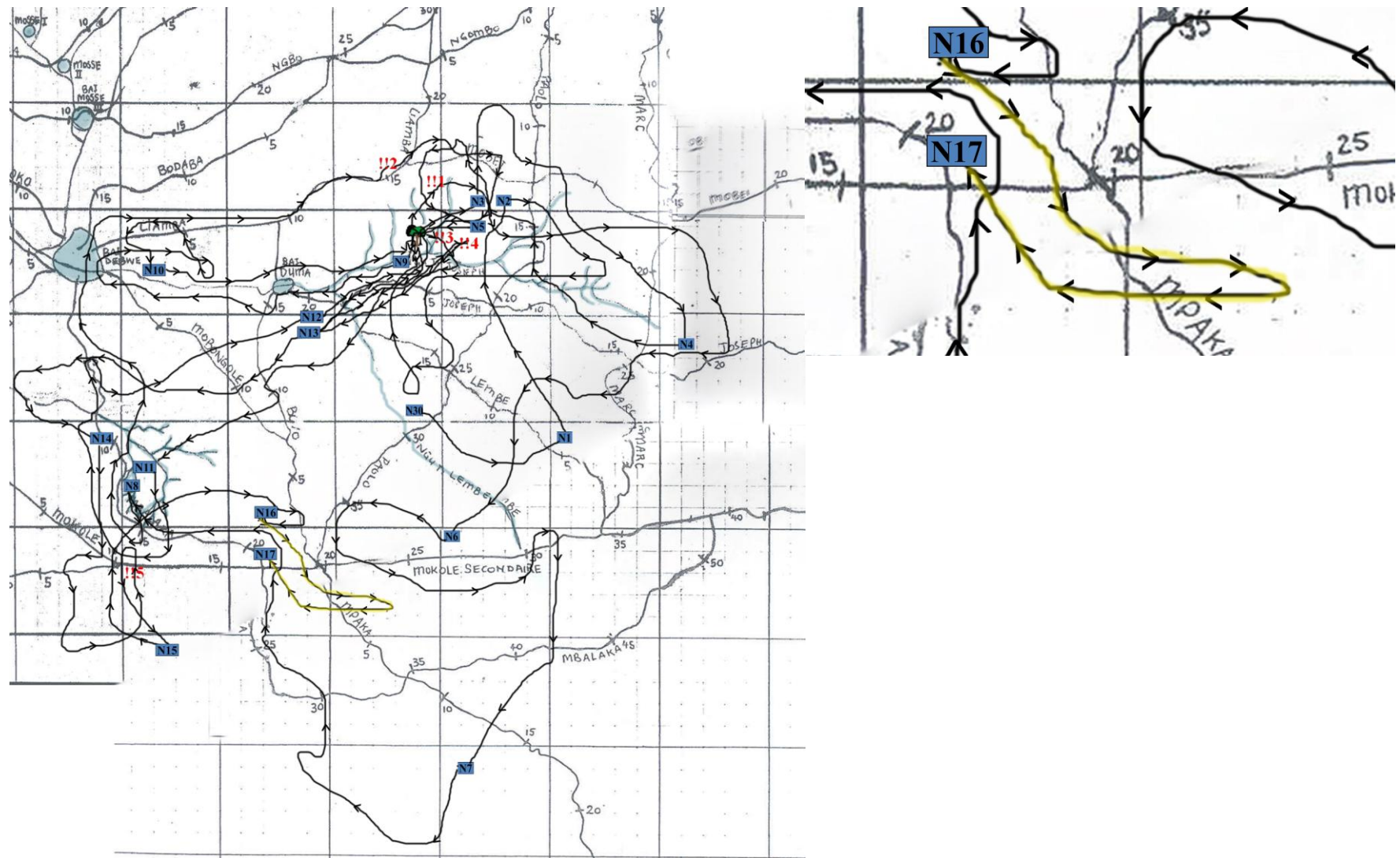
Appendix 15 July 15 Makumba Group Ranging



Appendix 16 July 16 Makumba Group Ranging



Appendix 17 July 17 Makumba Group Ranging



RESEARCH ARTICLE

Behavioral Responses of One Western Lowland Gorilla (*Gorilla gorilla gorilla*) Group at Bai Hokou, Central African Republic, to Tourists, Researchers and TrackersMICHELLE KLAILOVA^{1*}, CHLOE HODGKINSON², AND PHYLLIS C. LEE¹¹Behaviour and Evolution Research Group, Department of Psychology, University of Stirling, Stirling, United Kingdom²Department of Anthropology, University College London, Taverton Street, London, United Kingdom

Gorilla tourism, widely perceived as a lucrative industry, is propelled by strong market demand with programs in five countries and for three of four gorilla subspecies. Human presence may negatively affect wild gorillas, potentially lowering immunity and increasing the likelihood of acquiring human-borne disease. Yet, behavioral impacts of humans on wild gorilla behavior remain largely unexplored, particularly for western lowland gorillas. We evaluate the impact of tourist presence, human observer numbers (tourists, trackers, and researchers), and human observer distance on the behavior of one habituated gorilla group at Bai Hokou, Central African Republic. Behavioral data were collected for more than 12 months from January 2007. Of silverback aggressive events, 39% ($N = 229$) were human directed, but 65% were low-level soft barks. Adult females, and one in particular, were responsible for the highest number of aggressive events toward humans. Humans maintained closer proximity to the silverback when tourists were present, although tourist numbers had no significant impact on overall group activity budgets or rates of human-directed aggression. However, as research team size increased, group feeding rates decreased. Close observer–silverback distance correlated with a decrease in his feeding rates and an increase in human monitoring. He directed less aggression toward observers at distances > 10 m, although observers spent 48.5% of time between 6 and 10 m of the silverback. We discuss gorilla personality as a factor in human-directed aggression. We explore whether the current 7 m distance limit governing gorilla tourism, based on disease transmission risks, is sufficient considering the potential behavioral stressor of close human presence. We recommend increasing minimum observation distance to > 10 m where possible, decreasing observer group sizes, particularly after a visit consisting of maximum numbers and restricting tourist access to 1 visit/day. *Am. J. Primatol.* 71:1–10, 2010. © 2010 Wiley-Liss, Inc.

Key words: western lowland gorilla; tourism impacts; distance limits; activity budgets; aggression

INTRODUCTION

Wild gorilla groups have been visited by tourists since 1955, and deliberately habituated for that purpose since the 1970s [Butynski & Kalina, 1998]. Gorilla tourism has since developed into a lucrative industry fuelled by a strong market demand, with programs currently operating in five countries for three out of four gorilla subspecies (*Gorilla berengei berengei*, *G. beringei graueri*, *G. gorilla gorilla*). The high earning potential of gorilla tourism, evidenced by mountain gorilla programs, combined with its assumed non-extractive nature, has proved popular with governments promoting successful conservation partnerships that protect threatened habitats and the species they contain [Adams & Infield, 2003; Plumptre et al., 2002]. In theory, ecotourism should represent a win–win situation for both the country in which it is held and for the vulnerable places and

animals that it protects. One of the key tenets of ethnoprimateology—integrating the needs of human and nonhuman primates—seems to be met by the nonconsumptive alternative of primate tourism. Yet, human impacts on gorilla populations and the

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sustainability of these programs remain largely unexplored [Butynski & Kalina, 1998; Goldsmith, 2000, 2005a; McNeillage & Thompson-Handler, 1998; Williamson & Feistner, 2003; Woodford et al., 2002]. If we wish to pursue the aims of human–nonhuman primate coexistence, then a thorough assessment of our impact on primates and especially the threatened ape species, is needed.

Risk of disease transmission from humans to gorillas is a major concern of ape tourism [Butynski & Kalina, 1998; Cranfield, 2008; Homsy, 1999; Muelhenbein & Ancrenaz, 2009; Travis et al., 2008; Werikhe, 1991]. Habituated gorillas face a risk of disease from tourists, who may be carrying foreign illnesses from their home country, who can suffer high rates of illness owing to the stress of travel and exposure to air-borne diseases on airplanes, and who are themselves potentially lacking in immunity to local endemic infections [Adams et al., 2001; Muelhenbein & Ancrenaz, 2009; Ostroff & Kozarsky, 1998; Wilson, 1995]. Chronic stressors may act to lower gorilla immunity and thus increase their susceptibility to disease [Hofer & East, 1994; Hudson, 1992; Meder, 1994; Woodford et al., 2002]. To help alleviate some of these risks, most gorilla tourist sites have rules designed to minimize threats, including 1 hr maximum visits and a minimum distance to gorillas of 7 m [Homsy, 1999]. However, the efficacy of these measures could be compromised by the behavioral impact of human presence on gorilla behavior.

Habituating gorillas to human presence is known to be a highly stressful process, typically involving altered activity budgets, frequent displays of aggression toward humans, and altered ranging patterns [Anon, 1996–1997; Blom et al., 2004; Cipolletta, 2003; Doran-Sheehy et al., 2007; Fossey, 1983; Goldsmith, 2005b; Williamson et al., 1997]. Habituation, defined as the acceptance of human presence as a neutral element in their environment [Tutin & Fernandez, 1991], is assumed to occur when humans are tolerated, but few studies have explored the impact of human presence on gorillas that are already considered to be habituated. Before the advent of organized tourism, researcher presence was suggested to affect natural ranging patterns, intergroup transfer, and reproduction [Veder, 1989]. Current data on mountain gorilla groups found increased monitoring of humans and less time spent feeding when in the presence of tourists rather than researchers [Steklis et al., 2004]. Muyambi [2005] reported similar findings for Bwindi mountain gorillas, additionally noting increased frequency of disturbed behavior, such as charging, fleeing, and self-directed behaviors.

Western lowland gorilla tourism programs exist on a reduced scale compared with those for the high-profile mountain gorillas. Only four places in Central Africa are currently open to gorilla

tourism. Two offer sightings from fixed platforms (Mbeli Bai, Republic of Congo; Langoué Bai, Gabon) and two offer visits to habituated western lowland gorilla groups (Mondika, Republic of Congo; Bai Hokou, Central African Republic). Lowland gorillas are difficult to habituate, attributed to their long daily path lengths (>2,000 m in some western lowland gorilla groups), large home ranges (11–15+ km²), infrequent vocalizations, and dense habitat in which they live [Bermejo, 2004; Cipolletta, 2004; Doran-Sheehy et al., 2004, 2007; Mitani, 1996; Remis, 1997; Tutin, 1996; Tutin & Fernandez, 1991]. Quality of the tourist experience may also be impeded by poor visibility in the dense tropical forest that makes up much of the western lowland gorilla habitat. Tourism is further hampered by the generally poor accessibility of these sites, paucity of tourist infrastructure, and political instability of host countries. Yet, demand from international tourists and expectations of local governments for revenue generation, combined with the successful habituation of several western lowland gorilla groups, have resulted in the expansion of tourist programs and increasing researcher presence.

Bai Hokou camp, Central African Republic (CAR), is host to tourists, film crews, and independent researchers. This article details results from the second stage of a longer-term study aimed at evaluating the impact of tourism and human presence on gorilla behavior. A preliminary study, conducted in 2006 with the same gorilla group at an earlier stage in their habituation process, found that the presence of tourists and film crews resulted in a number of significant behavioral alterations, including a decrease in silverback resting and an increase in group aggressive behavior [Hodgkinson & Cipolletta, 2009]. During this assessment, the group was “semi-habituated” and it was only possible to approach the group comfortably at 15 m, although they were followed daily from nest-to-nest.

Here, we provide an in-depth evaluation of the impact of humans, both of the research team (researcher and trackers) and tourist groups, on the same gorilla group in later stages of the habituation process. We assess the effects of human group type (trackers, researchers, and tourists), size and distance on gorilla behavior, measured in terms of activity budgets, visual monitoring of people by the silverback, frequency of aggressive behavior, and individuality in aggression. We also discuss whether the current 7 m distance limit governing gorilla tourism, based on mountain gorilla disease transmission risks, is sufficient considering the potential behavioral impact of close human presence. To date, Bai Hokou in CAR, Mondika in Republic of Congo [Doran-Sheehy et al., 2007], Lopé [Tutin & Fernandez, 1991] and Moukalaba-Doudou National Park in Gabon [Ando, 2009; Ando et al., 2008] are the only study sites that have attempted to document

alterations of western lowland gorilla behavior in response to human presence.

METHODS

Study Site

Research was conducted at the Bai Hokou study site (2°50'N, 16°28'E), part of the Dzanga-Sangha Protected Areas (DSPA) and the Sangha Tri-National complex of protected areas (Lobeke in Cameroon, Nouabale-Ndoki in Republic of Congo, and DSPAs in CAR). The study site covers an approximate area of 35 km², which is located within the Dzanga Sector (495 km²) of the Dzanga-Ndoki National Park (1,220 km²), and is buffered by multiple use zones of the Dzanga-Sangha Forest Reserve (3,159 km²) in the southwestern portion of CAR. The gorilla habituation project works in collaboration with the government of CAR, World Wildlife Fund for Nature, and the German Technical Co-operation. The Bai Hokou study site was selected in 1997 to develop a long-term gorilla habituation project for ecotourism and to monitor the impact of ecotourism on gorilla groups [Carroll, 1997], although gorillas have been studied intermittently at the site since the 1990s [Blom et al., 2001; Carroll, Goldsmith, 1999; Remis, 1995, 1997, 1999].

Study Subjects

Behavioral data were collected from one gorilla group, Makumba, over a 12-month period from January 2007. The group consisted of 13 individuals: 1 silverback (Makumba), 3 adult females (Bombe, Malui, Mopambe), 2 subadults (1 female and 1 male), 1 blackback, 4 juveniles, and 2 infants (plus 1 birth in December 2007, bringing the group to 14 individuals). Habituation began in 2000 and the group was opened to tourists in September 2004. The group consisted of four adult females in 2000, but one emigrated in early 2006 after the death of her infant. The remaining three adult females observed in this study were residents from the onset of habituation. For analyses, gorillas were grouped into age-sex classes: adult male (one silverback), adult females (three individuals), immatures (seven individuals) and infants (two to three individuals).

Observational Methods

Data were recorded by two researchers with interobserver reliability tests conducted regularly to ensure accuracy. The Makumba group was followed from nest-to-nest by a team of trackers (range = 2-4) and researchers (range = 1-3). Research team size was not allowed to exceed seven people, and every effort was made to keep researcher and tracker numbers well below this limit. Researchers accompanied gorilla trackers during morning (7 am-12 pm) and/or afternoon (12-5pm) sessions.

Tourists (391 in 2007) would join the main team in either the morning or the evening session, and stay with the gorillas until a maximum 60 min of visibility had been achieved (not necessarily consecutively) or earlier, if they expressed a wish to return to camp. Only one tourist visit (with a maximum of three tourists per visit) was allowed per session. Total observer group size (trackers, researchers, and tourists) was also not allowed to exceed seven people.

Data collection focused on the silverback, Makumba, and those individuals in his immediate proximity; he was the focus of an in-depth study and most tolerant of constant focal follows. Instantaneous scans [Altmann, 1974] were taken on the silverback every 10 min. If visibility of the silverback was lost for more than 10 min, scanning restarted at the point of recontact. To ensure independence, all scans at intervals of less than 20 min apart were excluded, leaving an average interscan interval of 29 min. Analyses were conducted on 1,885 silverback scans, with tourists present in 320 of these. The following information was recorded during each scan:

- 1. Silverback activity: feeding, moving, or resting (including social).
- 2. Silverback visual monitoring of observers: ignore, low, medium, and high.
- 3. Group activity defined as the predominant activity of all visible group members: feeding, moving, resting (including social), or mixed.
- 4. Identification of all nearest neighbors within 5 m of the silverback.
- 5. Distance of recorder to silverback (to the nearest meter).

Distances were measured by eye, following an intensive training period to reduce potential inaccuracies and with regular interobserver reliability checks. For analysis, distances were categorized to control for the potential effects of visual binning as: (1) 1-5 m, (2) 6-10 m, (3) 11-15 m, (4) 16-20 m, and (5) 21+ m. The total number of observers (research teams and tourist groups) was used in the distance analyses.

In addition to scans, continuous records of all auditory signals were made for Makumba and gorillas in his presence (within human earshot). Auditory signals were categorized by age-sex class and defined as any sound made by a gorilla, either orally or via other signals (ground slapping, tree breaking, chest beating, displaying, and hand clapping). If an individual exhibited a repeat of an auditory signal less than 5 sec after the earlier one, this was counted as one bout.

Aggressive auditory signals directed toward humans (bark, soft bark, charge, display, scream) are the focus of the analyses here. As western lowland gorilla auditory communication (vocal or

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via other auditory signals) has not yet been classified, definitions were taken from published work on mountain gorilla vocalizations [Fossey, 1972; Harcourt & Stewart, 2001]. As younger or more fearful gorillas might also emit human-directed distress signals (i.e. scream, cry) rather than overt aggression, these were also included in the analyses. Immatures were considered as a single category in analysis.

Auditory data were analyzed by session to limit any effects of dependence. The median distance to the silverback was calculated per session from scan data. Median scores were used to control for the influence of tree heights affecting distance records where human-directed aggression was unlikely to occur. Mean team and tourist numbers were calculated for each session and corrected for the number of minutes that different team sizes were present. Aggression rates were calculated relative to the number of minutes of observation in each session, computed hourly, normalized using square root transformations, and analyzed using Analysis of Variance (type I models) to control for the potential influences of other factors. Analyses (apart from distance analyses which were based on total observer units) were separated into research team (trackers and researchers) and tourist groups for comparison.

Activity budgets and monitoring were analyzed using logistic regressions, where zero represents the activity occurring, and one represents the activity not occurring; results are based on the activity not occurring. All statistical analyses were conducted using the SPSS statistical package, Version 16, results are two-tailed, and considered significant when $P < 0.05$.

This research complied with ethical protocols approved by the University of Stirling, Ethics Committee, and the Bai Hokou study site code of conduct, as well as adhered to the legal requirements for research within the Central African Republic and the ASP ethical guidelines for the treatment of nonhuman primates.

RESULTS

Tourist and Research Team Presence

Data were recorded during 258 sessions throughout the study period. Tourists were present in 63 of these sessions (24.4%) and in 320 of the 1,885 silverback scans. A total of 135 tourists visited the group during these recording sessions, with mean tourist numbers per visit of 2.14 ± 0.981 (range: 1–4). Mean total group size when tourists were present was 6.22 ± 1.325 (range: 4–9). Mean research team size over the study period was 3.95 ± 0.704 (range: 3–7). Total observer group size, encompassing both tourists and team members, stayed within the seven-person limit on all but seven occasions (35 scans); for

these, the total group size did not exceed nine and tourist numbers did not exceed four.

Tourist–Silverback Distance

Distance between human observers and the silverback was significantly lower when tourists were present compared with when only researchers and trackers were present. More time was spent at distance category 6–10 m from the silverback when tourists were present ($N = 63$), whereas more time was spent at 11–15 m when only researchers and trackers ($N = 191$) were following the silverback (Mann–Whitney: $U = 5104.5$, $P = 0.046$). To determine whether human distance to the silverback was affected by the number of tourists, distance categories were grouped at 1–10 m ($N = 40$) or 11–20 m ($N = 23$). The number of tourists present did not significantly affect mean human distance to the silverback (Mann–Whitney test: $U = 396.5$, $P = 0.396$).

Human Directed Aggression

Of the 22,343 auditory signals, 2,009 were aggressive in context. Furthermore, 23% (460) of all aggressive events were directed toward human observers. Because data were collected on the silverback and only those individuals in his presence (within human earshot), total group auditory signals will be underrepresented. The silverback was responsible for 593 of all aggressive events, and 39% (229) of those events were directed toward observers. However, low-level aggression (soft barks) was the most common form of aggression directed at humans by the silverback (Table I).

Effect of Human–Silverback Distance on Aggression Toward Observers

Rate of silverback aggression to observers was significantly related to human–silverback distance (controlling for time of day, season, silverback activity, and human group size) ($F = 5.339$, $P = 0.001$, $df = 4,249$, $r^2 = 0.077$). When observers were further from the silverback, his rates of aggression toward

TABLE I. Silverback Aggression Toward Observers

| Low Level | Medium | High |
|-------------|---|---|
| -Soft barks | -Barks only -Displays [ground and tree slaps/breaks, chest beats] | -Charges [with or without barking] -Contact -Scream |
| 148 | 57 | 24 |
| 65% | 25% | 10% |

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humans significantly decreased ($\alpha = 0.512$, $\beta = -0.011$, $F = 6.500$, $P = 0.011$, $df = 1,252$, $r^2 = 0.025$).

Observers spent 48.5% of their time within 6–10 m of the silverback (Fig. 1A). A cumulative rate of change plot shows a reduction in silverback aggression toward observers at 6–10 m (Fig. 1A), as seen by the breaks in the slope of the line [Slater, 1974]. Aggression continues, until it distinctly plateaus at 16–20 m. A cumulative rate of change

plot calculated for the median total session (un-grouped) distances (Fig. 1B) shows that aggression rates decreased most markedly at 10 m, but also at 6 and 15 m, ceasing after 18 m.

Effect of Group Type and Size on Aggression Toward Observers

Rates of aggression toward observers were not significantly affected by the presence or absence of

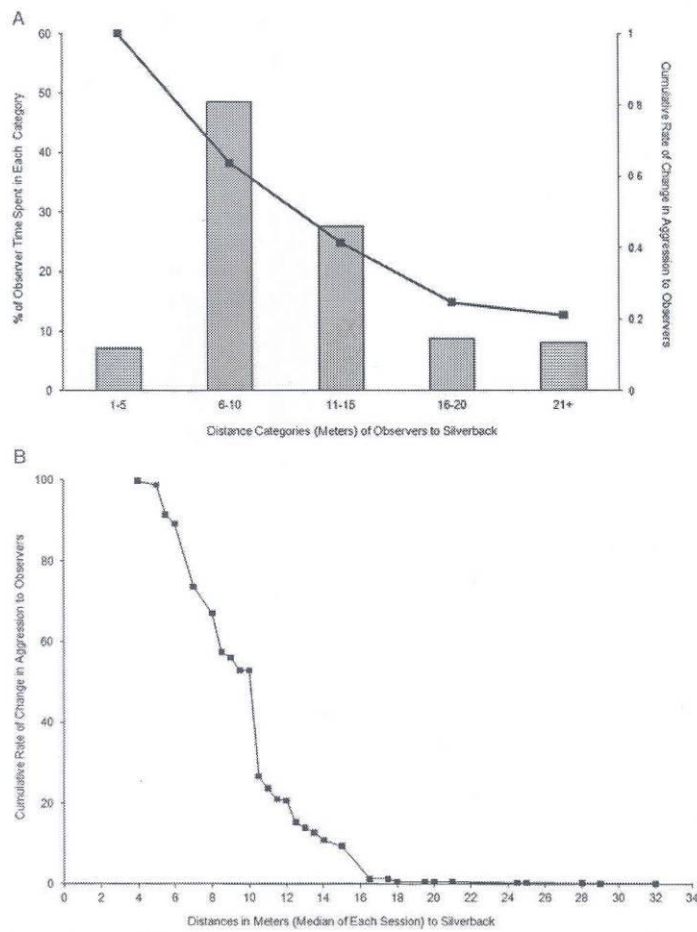


Fig. 1. (A) The bar graph represents the percentage of total scans spent within each distance category (meters) of the silverback ($N = 1,878$). The line graph represents the cumulative rate of change in silverback aggression toward humans as a function of observer–silverback distance (categorical meters, $N = 254$). (B) Cumulative rate of change in silverback aggression toward humans against observer–silverback absolute distance (meters) ($N = 254$).

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tourists (controlled for time of day, season, group activity and observer-gorilla distance (Supplementary Table I). This lack of effect was similar for all age-sex classes. Likewise, in all but one case, rates of aggression were not significantly affected by the number of people in either the research team or tourist groups (Supplementary Table I). When considering individual females, research team size had a significant effect on the rates of aggression toward humans from one female (Bombe) ($F = 3.097$, $P = 0.029$, $df = 3,236$, $r^2 = 0.041$). As researcher and tracker numbers increased, Bombe's rates of aggression toward people also significantly increased ($\alpha = -0.105$, $\beta = 0.081$, $F = 6.900$, $df = 1,239$, $P = 0.009$, $r^2 = 0.028$).

Of the 460 human-directed aggressive events, the silverback was responsible for 229 events, adult females for 185 (Bombe, 122; Malui, 61; Mopambe, 2), and immatures for 25. Although the silverback seemed to be responsible for the largest number of aggressive events directed toward humans, when correcting for the proportion of time other individuals were seen within 5 m of Makumba (since he was followed by humans 100% of the time), adult females were the most likely age-sex class to direct aggression toward observers (Fig. 2A). One female in particular, Bombe, was more likely to direct aggression to humans in comparison with any other gorilla within the group including Makumba (Fig. 2B).

Bombe's high rates of human-directed aggression may be the result of partial or delayed habituation [Doran-Sheehy et al., 2007]. However, if this was the chief cause of aggression toward observers, Bombe should be seen less than the other females and as the study (habituation) progressed, she should have spent more time with Makumba (and thus humans). Rates of aggression should, therefore, decrease over time as the level of habituation increases. Bombe spent similar proportions of time within 5 m of the silverback as did Mopambe, and even though Malui spent slightly more time next to Makumba, this difference was minimal (3%). Bombe did not differ significantly from the other females in time spent within 5 m of Makumba (Table II). In addition, Bombe's human-directed aggression did not change significantly as the year progressed ($\alpha = 0.141$, $\beta = 0.100$, $P = 0.095$, $F = 2,804$, $df = 1,239$, $r^2 = 0.012$) nor did her time spent with Makumba ($\alpha = 0.284$, $\beta = -0.011$, $F = 3.484$, $df = 1,252$, $P = 0.063$, $r^2 = 0.014$).

Effect of Human Group Type and Size on Activity Budget and Silverback Monitoring

Presence or absence of tourists did not significantly affect group or silverback activity budgets (logistic regression, controlling for time of day, distance, and season; Supplementary Table IIa). As team size increased, group feeding rates decreased ($\beta = 0.185$, $SE = 0.089$, $P = 0.037$, $r^2 = 0.003$) and mixed behaviors increased ($\beta = -0.284$, $SE = 0.100$,

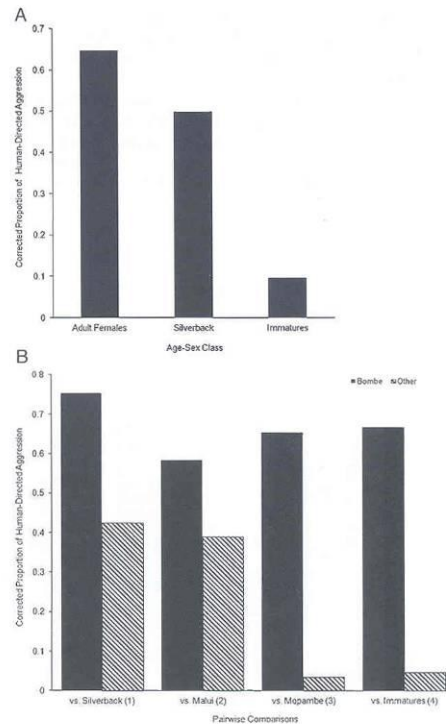


Fig. 2. (A) Corrected proportion of human-directed aggression by age-sex class; $\chi^2 = 52.024$, $df = 2$, $P < 0.001$ [expected values and proportions of aggression: adult females, 36 (0.12); silverback, 232 (0.78); immatures, 31 (0.10)]. (B) Corrected proportion pairwise comparisons of Bombe's (black bars) human-directed aggression with that of other individuals or age-sex classes (lined bars). (1) $\chi^2 = 189.721$, $df = 1$, $P < 0.001$, (2) $\chi^2 = 26.841$, $df = 1$, $P < 0.001$ (3) $\chi^2 = 104.879$, $df = 1$, $P < 0.001$ (4) $\chi^2 = 119.141$, $df = 1$, $P < 0.001$.

TABLE II. Bombe-Female Comparisons of Time Spent Within 5 m of Makumba

| Mopambe/Bombe | Bombe/Malui | Occasions within 5 m of SB (N = 1,090) |
|------------------|------------------|--|
| $\chi^2 = 0.035$ | $\chi^2 = 5.662$ | Mopambe 126 (0.116) |
| $df = 1$ | $df = 1$ | Bombe 129 (0.118) |
| $P = 0.835$ | $P = 0.018$ | Malui 162 (0.149) |

Bonferroni Correction $P < 0.017$.

$P = 0.005$, $r^2 = 0.008$), whereas silverback activity budget remained unaffected by team size. Tourist numbers did not have a significant effect on silverback or group activity budgets (Supplementary Table IIa).

Observer distance did have a predictive effect on silverback activity budgets (logistic regression controlling for time of day, season, group type, and size). As observer–silverback distance increased, Makumba spent more time feeding ($\beta = -0.595$, $SE = 0.053$, $P < 0.001$, $r^2 = 0.081$) and less time resting ($\beta = 0.605$, $SE = 0.058$, $P < 0.001$, $r^2 = 0.009$). Because monitoring was recorded separately from activity budgets (i.e. not included as an “activity”), it is possible that resting and monitoring behaviors might overlap. As silverback monitoring of observers (controlled for time of day, season, group type, and distance) increased, resting also increased ($\beta = -0.280$, $SE = 0.121$, $P = 0.021$, $r^2 = 0.006$) but feeding decreased ($\beta = 0.377$, $SE = 0.132$, $P = 0.004$, $r^2 = 0.006$). These results indicate that there is an overlap between the silverback’s resting and monitoring behaviors.

Furthermore, as observer–silverback distances increased, monitoring rates of humans decreased ($\beta = 0.291$, $SE = 0.068$, $P < 0.001$, $r^2 = 0.024$; logistic regression controlling for time of day, season, group type and activity budget). However, neither group type nor size was significantly associated with monitoring rates (Supplementary Table IIb).

DISCUSSION

Although habituation may be neatly described as the acceptance of humans as a neutral element in the environment [Tutin & Fernandez, 1991], it is not always clear when, if ever, this state is reached. The nature of observational studies means that it is not possible to compare gorilla behavior to what might be considered “normal,” as trackers and at least one researcher must always be present. What is possible, however, is to see if gorilla behavioral changes are associated with changes in human variables, such as the type and number of humans’ present as well as gorilla–human distance.

The maximum total observer group size limit of seven was generally adhered to, other than a few exceptional circumstances where tourist time constraints and safety measures necessitated a breach of this rule. Even so, numbers never reached the ten person maximum recommended for mountain gorillas [Homsy, 1999]. We clearly show that observers spent more time within 6–10 m of the silverback when tourists were present. Although this does not necessarily represent regular breaches in the 7 m rule, human–gorilla distance has certainly moved closer to this minimum recommended limit. This is made evident when compared with the Hodgkinson and Cipolletta [2009] study on the same group, where even though humans were found to stand closer when tourists were present, distances fell well outside the 7 m policy (averaging 17–18 m). This increasing closeness is most likely a result of moving from a semi-habituated state to a later stage in the habituation process.

Throughout the study period, 39% of silverback and 23% of total group aggressive events were directed at humans. Although these percentages represent a large effect, 65% of silverback and 47% of group human-directed aggression were low-level soft barks. Soft barks are warning signals that if ignored can escalate into high-level aggression, and as such should be considered an important indicator of human–gorilla tension.

Even though 48.5% of observation time was spent within 6–10 m of the silverback, there were distinct decreases in human-directed aggression at 10 m and then again at 15 m, to plateau at 18 m. The current 7 m limit, derived from mountain gorillas, is based predominantly on the risk of disease transmission and does not take into account the potential behavioral impact of close human presence. Although several studies recommend avoiding contact with unhabituated gorillas at distances <10 m [Ando, 2009; Blom et al., 2004], no study has explored this issue with gorillas in the later stages of habituation. Our results suggest that in order to eliminate aggression toward observers by the silverback, humans should maintain a distance of >18 m from Makumba. It is however, unrealistic to expect quality viewing at these distances when gorillas are on the ground. Yet, the clear drop in aggression at 10 m indicates further that human-directed aggression may be greatly reduced if humans avoided proximity within this distance. Again, given the dense habitats in which western lowland gorillas live, it is not always possible to optimally view them for the purpose of tourism or research at this distance. Blom et al. [2004] suggested that gorillas seem to be more comfortable with closer human approaches in dense habitats as opposed to open habitats. In more open habitats, viewing can easily be achieved when standing at >10 m away from the silverback. In denser habitats, this will not always be feasible and approaches to 7 m may be necessary.

The presence of tourists did not affect rates of aggression toward humans for any of the gorilla age–sex classes, nor did the number of people present in either research team or tourist groups. However, one female, Bombe, did show a significant increase in rates of aggression as research team numbers increased, although there was no additional effect of tourist numbers. Bombe was also responsible for more human-directed aggression than any other gorilla in the group, and adult females were the most likely age–sex class to aggress humans.

Sex-biased responses to habituation have been noted earlier [Ando, 2009; Cipolletta, 2003; Doran-Sheehy et al., 2007; Tutin & Fernandez, 1991]. Doran-Sheehy et al. [2007] found that females tend to stay away from humans until later in the habituation process and, as a result, move through the stages of habituation well after the silverback. This delay may present itself in the form of heightened aggression from females at a stage when

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the silverback is already tolerant of human presence. Individual gorilla personality may also play a role in their rates of human-directed aggression, with some great ape sites still experiencing high levels of female aggression up to 15 years after group habituation began [Bertolani & Boesch, 2008; Doran-Sheehy et al., 2007]. Although it is impossible to tease apart the possible causes of Bombe's aggression (since an individual is less likely to become habituated if her personality does not readily accept human presence), she spent a similar proportion of time within 5 m of the silverback as did other females, her aggression rates did not significantly change throughout the year, and the time she spent in Makumba's presence did not increase over the study period. Thus, habituation alone seems an unlikely explanation. This study suggests personality played a role in the aggression Bombe directed toward humans. In some circumstances, even when adhering to all ethical gorilla viewing guidelines, humans may receive aggression simply because certain individuals remain intolerant of their presence.

The presence and numbers of tourists did not significantly influence group or silverback activity budgets; however, as research team numbers increased, group feeding decreased while mixed behaviors increased. Research team size affected the gorillas resulting in alterations in their behavior. Silverback activity budget was unaffected by research team size, but as human-silverback distance decreased, Makumba fed less and monitored humans more at the cost of feeding time.

Research teams may have a more pronounced effect on the behavior of the Makumba group than do tourist groups. Although this difference may partly be owing to lower tourist pressure at this site compared with the highly visited mountain gorillas, management of the number of trackers and researchers visiting wild gorilla groups needs stricter consideration. It is also important to note that the factors analyzed in this article explain only approximately 1–10% of the overall variance in the data. Thus, on a biological scale, there are other important but as yet undetermined factors that affect the gorillas' behavior far more than simply human presence. Human-gorilla distance, however, explains much more of the variance in the data than does human group type or size, further suggesting the need to reexamine the current distance rule of 7 m.

Based on our results, we make the following recommendations:

1. Limit distance between observers and gorillas to >10 m where possible (i.e. in more open habitats where visibility can be easily achieved at distances >10 m).
2. Limit research team size to a maximum of five observers (two/three trackers and one/two researchers), but make efforts to reduce researcher

team size to three people as often as possible (two trackers and one researcher). Bai Hokou has decreased research team sizes as of 2008 (A. Todd, personal communication, 2009).

3. Limit total group size when tourists are present to a maximum of six observers (two trackers, one guide/researcher, three tourists). Bai Hokou has altered their policy to reflect this change as of 2008 (A. Todd, personal communication, 2009).
4. When larger team sizes cannot be avoided (i.e. tourists, training of assistants/volunteers/researchers), ensure that team size is kept to a three person maximum in the subsequent observation session(s). Bai Hokou makes every effort to minimize team sizes after larger group visits to the gorillas. (A. Todd, personal communication, 2009).
5. Limit tourist visits to one tourist group per day. Western lowland gorilla sites are often very remote and difficult to access. As a result, tourists often arrive in large groups with strict timelines, which makes adhering to the one visit per day recommendation challenging. Although in the past tourist and film crew visits remained low and intermittent, numbers at this site are on the rise. Compliance will be increasingly challenging as visitor numbers continue to grow, but with careful consideration of logistics before problems arise and an increase in the cost of gorilla visits (which is currently being implemented at Bai Hokou), this recommendation should be attainable.

Ecotourism, when conducted properly, should both conserve the environment and sustain the well being of local people [Muelhenbein & Ancrenaz, 2009]. Gorilla tourism programs have been found to contribute significantly to both local and national economies [Wilkie et al., 2001], improve the attitudes of local communities and governments toward gorillas and their conservation [Archabald & Naughton-Treves, 2001; Weber, 1995], and funded the management of the gorilla parks as well as other less-productive parks [Adams & Infield, 2003]. Although factors, such as high travel costs relative to other travel destinations in Africa, poor infrastructure, frequent political instability, and a deficit of other close tourist attractions, currently limit tourist numbers at western lowland gorilla sites, these programs may still benefit the gorillas, their habitat, and the local human communities. Over 40 BaAka trackers and 6 local assistants are employed at Bai Hokou, with many more local residents accessing tourism revenue through craft sales or accompanying tourists on cultural trips [Hodgkinson, 2009]. As a result, local communities surrounding the Dzanga-Sangha project are generally very supportive of the tourism program [Hodgkinson, 2009] and there is a high degree of pride amongst local residents working directly with the gorilla groups, particularly amongst the BaAka trackers. Furthermore, although

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unquantified, there is considerable evidence that the presence of researchers and tourists in a gorilla range can act as a significant deterrent to poachers, as well as allow anti-poaching units to be alerted if illegal activities are detected (personal observation).

This article does not purport to provide an overall analysis of the success or value of gorilla tourism, but a specific facet—that of exploring the impact of human observers on gorilla behaviour. This study forms part of a long-term program at Bai Hokou, designed to monitor human impact when following western lowland gorillas and identify potential negative triggers [Blom et al., 2004; Cipolletta, 2004; Hodgkinson & Cipolletta, 2009]. In doing so, we learn how best to minimize our level of disturbance when following habituated and semi-habituated western gorilla groups.

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